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# Inter-individual heterogeneity of demographic performance and personality in roe deer (*Capreolus capreolus*)

Chloé Monestier

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Université  
de Toulouse

# THÈSE

En vue de l'obtention du

**DOCTORAT DE L'UNIVERSITE DE TOULOUSE**

Délivré par : *l'Université Toulouse 3 Paul Sabatier (UT3 Paul Sabatier)*

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Présentée et soutenue le 11/03/2016 par :  
Chloé MONESTIER

**Inter-individual heterogeneity of demographic performance and  
personality in Roe deer (*Capreolus capreolus*)**

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## JURY

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Niels DINGEMANS	Directeur de Recherche	Rapporteur
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**Ecole doctorale et spécialité :** *SEVAB : Ecologie, Biodiversité, Evolution*

**Unité de Recherche :**

*Comportement et Ecologie de la Faune Sauvage (UR 0035), INRA Castanet Tolosan (31)*

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**“ You can't always get what you want, but if  
you try sometimes you might find  
you get what you need “**

M. Jagger, 1969





## **Avant propos**

Cette thèse de l'Ecole Doctorale SEVAB de l'Université Toulouse III a été réalisée au sein des laboratoires « Comportement et Ecologie de la Faune Sauvage » (CEFS, UR 0035 INRA) et « Laboratoire de Biométrie et Biologie Evolutive » (LBBE, UMR 5558 CNRS). Elle a été financée par une bourse du Ministère de l'Enseignement et de la Recherche.

Elle est constituée d'une introduction générale, d'un matériel et méthodes général, de quatre chapitres rédigés sous forme d'articles scientifiques et d'une discussion générale. Les sept chapitres sont écrits en anglais.



## Remerciements

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On se dit que c'est la partie « no souci » de la rédaction du manuscrit de thèse. Eh bien que nenni. On se retrouve face à cette habituelle feuille blanche devenue presque (j'ai bien dit presque) une copine et là, à ce moment présent, toutes ces années passées défilent devant nous. Ça sent le bilan. Un peu de nostalgie aussi (quoique si on repense à la rédaction du manuscrit...). On se dit que tout cela va nous manquer... M'enfin, trêve de blues, il reste encore pas mal de moments rock'n roll, sans parler de la soutenance de thèse. Je ne suis pas encore partie !

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La thèse, un réel cap à passer je crois. Une leçon de vie ou un condensé de vie qui ne relève pas juste du travail. Oh non, c'est ce que j'ai cru au début mais, je me suis bien trompée ! On se retrouve vite prise au jeu et tout se retrouve mêlé : le travail, les émotions, les relations ici et là. Bref, la vie mais, dans un microcosme. Un grand merci donc à toutes ces personnes qui ont partagé des bouts de thèse avec moi que ce soit de près ou de loin. Je ne serai pas en train de remplir ces pages sans vous.

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Sur ces belles paroles, j'arrête, il faut dire stop à un moment donné.

Bonne lecture à tous ceux qui auront le courage de lire cette thèse et à très vite !



Drawing by Georges Gonzalez

## A little story

### Absolutely not shy or naïve?

We are Wednesday, May 30th, 2012. Just another typical day of capture...but it did not. After 'meeting' Wagon, as usually, Nicolas laid it down somewhere in the cover a few meters away. Generally, fawns stay motionless in their hiding place or, in some rarer cases, go further. Nicolas and Bruno were putting the equipment away when Wagon came back trotting. It stayed there, close to Bruno for a while.

What an amazing day!! Well, bold or naïve?



Photo by N. Morellet

Wagon is dead almost one month later due to mowing...





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Gr. 90

Drawing by Georges Gonzalez



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# **Chapter I**

## **Introduction**

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## I. Individual heterogeneity and consequences for population dynamics and demography

### *1.1. Population dynamics: from the population level...*

An obvious observation when looking at nature is that species, but also populations of a given species, differ in their life-history strategies. Indeed, the evolution of life-history traits and their infinite number of combinations has led to a large variety of life-history strategies distributed along a continuum. At one end, species have a fast strategy characterized by a high fecundity and a short longevity, while at the other end, species have a slow strategy with a low fecundity but a long longevity (Stearns 1983). In mammals, for instance, a female house mouse (*Mus musculus*) reaches maturity at around 45 days of age, gives birth to six to twelve offspring five to six times a year and dies at two or three years of age. In contrast, a female blue whale (*Balaenoptera musculus*) reaches maturity at around five to seven years of age, gives birth to one young every three years and dies between forty to fifty years of age. Similarly, in birds, the blue tit (*Parus caeruleus*) has a life expectancy of about eight years, breeds at one year of age and lays ten to twenty eggs, whereas the wandering albatross (*Diomedea exulans*) does not breed before 10 years of age, lays generally one egg every two years and probably lives more than fifty years (Stearns 1976). From a general point of view, life-history traits are often linked to the body size of the species in mammals and birds. Thus, small species tend to have a fast strategy (Stearns 1983). However, this is only a general rule since the common ostrich (*Struthio camelus*) may lay ten times more eggs than the hummingbird (Trochilidae familia). There seems to exist some variability in these life-history strategies between species and populations (Newton 1998).

### *1.2. ...to the individual level*

At the individual level, there is also some variability in life-history traits which may, in turn, impact and shape individual fitness, forming the basis of life-history strategies. Individuals face multiple energy demands, mainly to meet reproductive-related activities (gamete production, searching for a partner, parental care etc.), or to ensure their maintenance in a broad sense (growth, predator avoidance, immune defense etc.). Resource acquisition is



consequently crucial for individuals. The ideal free distribution theory (Fretwell and Lucas 1970; Fretwell 1972) states that, in the absence of constraints on movement, individuals are expected to be distributed so that differences in local densities reflect differences in habitat quality. As a result, resources are equally shared among individuals and fitness is equal in all habitats (Fretwell and Lucas 1970; Fretwell 1972). However, the ideal free distribution theory generally is not representative of food acquisition in wild environments since often the number of individuals or competitors for each patch is not proportional to the resources availability in the patch. In addition, the optimal foraging theory (Charnov 1976) predicts that individuals should select feeding patches in a way that maximizes their energetic benefits (Cézilly and Benhamou 1996; Kie 1999). However, that depends on both the risk of predation (Lima and Dill 1990; Brown and Kotler 2004) and the resources availability which are generally limited in time and/or space (Williams 1966), so that individuals face a trade-off between resource acquisition and the potential risk of predation. Facing this trade-off, individuals are unable to acquire sufficient energy to offset all their energetic needs required for different activities which may have marked consequences for their fitness (S.C. Stearns 1992). Indeed, individuals are limited by trade-offs since the benefit obtained through a change in one trait is linked to a cost paid out through a change in another one (S.C. Stearns 1992). For example, individuals breeding earlier have a shorter lifespan.

A large number of trade-offs are readily defined between life-history traits. Two main trade-offs are current reproduction versus future reproduction and growth versus survival. The first one is widespread in both a large number of animal and plant species. For instance, in female red deer (*Cervus elaphus*), reproductive success in a given year has a negative impact on fecundity and survival the following year (Clutton-Brock et al. 1983). In birds, production of ornamental display is an important component of reproductive effort. To investigate trade-offs between current reproductive effort and the future expression of a sexually selected ornament, (Siefferman and Hill 2003) manipulated the parental effort of males by changing their brood sizes. The modification of parental effort had a significant effect on the relative plumage ornamentation of males in the subsequent year and had a direct effect on the timing of breeding in the following season. Thus, males with reduced broods significantly increased plumage brightness and mated with females that initiated egg laying earlier in the season. In plant species, there is a negative correlation between the

number of inflorescences produced in the first year and the number produced in the next year in annual meadow grass (*Poa annua*). Plants flowering heavily in their first year produced fewer inflorescences in their next year than plants with less flowers (Law 1979).

As regards to the second trade-off, we might expect organisms to grow as fast as they can since they would then get through the vulnerable stages and on to reproduction as fast as possible. However, adopting such a strategy has costs as regards to the current survival of individuals, but also their lifespan. A faster growth rate requires an increase in food intake which may expose the individual to a greater risk of being caught by a predator, either because of reduced vigilance or because a greater proportion of the time must be spent gathering food in an exposed site (Gotthard 2000). Individuals on a fast growth strategy are also more vulnerable to starvation during periods of food shortage (Blanckenhorn 2000). A potential explanation could be that their metabolism is adjusted to a high rate of nutrient supply and they cannot quickly down-regulate when conditions become unfavorable (Arendt 1997). Such effects may underlie the observed sex differences in vulnerability to poor environmental conditions in sexually dimorphic species (Clutton-Brock et al. 1985). In addition, there is also increasing evidence that a fast growth may cause a reduction in lifespan through long-term effects on the phenotype. For instance, mice and rats with more rapid juvenile growth tend to have reduced adult lifespans (Bartke et al. 2001; Rollo 2002).

Trade-offs can be more intense in poor environmental conditions characterized by high density or low resource availability which force individuals to make a choice between, for example, favoring their survival at the expense of their reproduction or vice versa. Thus, the way individuals deal with a given trade-off will have direct consequences for their life-history traits and so for their fitness.

Consequently, we can easily observe that species are not similar, adopting, for instance, a specific strategy along the 'slow-fast' continuum. However, at the population level, there are also inter-individual differences in life-history traits leading to trade-offs and, in turn, to within population heterogeneity. Indeed, some individuals of the population may prioritize a first trait (for example, the current reproduction) whereas other ones may prioritize a second trait (future reproduction). Thus, it appears clearly that populations are

heterogeneous meaning there is some individual heterogeneity in their overall life-history traits and that populations are not homogeneous as it was supposed to be in the past (Arnold and Wade 1984). Moreover, it seems obvious that all individuals differ in their phenotypic characteristics for example and that these differences influence the individual's strategy which, in turn, influence its fitness, but also population growth (i.e. the population demography). However, demographic patterns are generally studied at the population level and do not take into account the individual level even though it is known that there are consistent differences in individuals' strategies and that these differences can influence population dynamics (Łomnicki 1978). Thus, studying individual heterogeneity, their causes and consequences is of major interest to have a better estimation and understanding of population dynamics.

## **II. Sources of individual heterogeneity: state of the art**

We have previously seen that individual heterogeneity is marked in life-history traits and results, in the end, in heterogeneous populations. The heterogeneity sources are diverse. In population dynamics, we generally recognized and account for the environmental variability with resource availability being likely the main factor (Łomnicki 1978; van Noordwijk and de Jong 1986). But, individual characteristics such as individual's body mass are also recognized to affect fitness and population structure (Caswell 2001; Coulson et al. 2001). Therefore, patterns across different taxa are consistent in the way that a positive correlation exists between female body mass and fitness (in birds: (Newton 1989); in ungulates: (Clutton-Brock et al. 1988); in bats: (Ransome 1995); in feral horses: (Berger 1986); in wolves: (Stahler et al. 2013)). Moreover, body mass is generally a good indicator of an individual's condition (Toïgo et al. 2006) which is generally defined as the body mass of an individual for a given size (Jakob et al. 1996) and provides information about individual fat reserves. Body condition influences numerous individual's life-history traits such as dispersal and fitness components such as growth or reproduction (Linnell et al. 1998). Besides, studying for heterogeneity in individuals as a whole, it is clear that heterogeneity in life-history traits and fitness may appear at different stages of an individual's life: at birth, during its development, or later in its adult stage. Then, we could divide the sources of individual heterogeneity in

life-history and fitness into fixed heterogeneity specifically linked to early stages of individuals, and non-fixed heterogeneity occurring all life-long and impacting the individuals' fitness.

### ***II.1. Fixed heterogeneity***

Fixed heterogeneity is set up early in life during the development and first stage of life of individuals. Thus, genetic source for individual heterogeneity plays a main role; however, it is widely recognized that a large part of individual variability depends on genetic (Dobzhansky 1937) since most life-history traits are influenced by many genes. These genes code for proteins which may have several different functions and shape morphological, physiological and behavioral traits. For example, an obvious parameter which contributes to variation in demographic rates and which is under genetic influence is the sex of individuals (Gaillard et al. 2000). In polygynous species, for instance, males may mate with dozens of females whereas females mate only with one male (Clutton-Brock et al. 1982). Life expectancy is also lower in males than in females in polygynous and highly dimorphic species (Clutton-Brock et al. 1982). Growth could be sex-specific, for example, in (Biro et al. 2014)'s study where male freshwater crayfish (*Cherax destructor*) grew faster than females. Moreover, gene expression may be modulated or modified by mutations or alternative splicing or simply by genetic correlations (Roff 1992; Sinervo and Svensson 2002). For example, trade-offs are specified in quantitative genetics by a negative genetic covariance between traits, a covariance that could be caused by antagonistic pleiotropy or linkage disequilibrium. Hence, genetic variation among life history traits has been well studied (Roff 1992) and, based on a long history of evolutionary theory, it is known that genetic variation can be maintained by a variety of mechanisms, including a mutation/selection balance, migration/selection balance, frequency dependence, or over-dominance (Barton and Turelli 1989; Hedrick 2000; Burger and Gimelfarb 2002). That being said, at a larger scale, which is the one generally chosen to study individual heterogeneity: the phenotypic level, individual heterogeneity has an added dimension. Indeed, all traits are not under genetic influence meaning that individual heterogeneity is influenced by other factors (Roff 1992; Bonduriansky and Day 2009) with possible correlations between each others. For instance, interactions between genotype and environment (Comstock and Moll 1963; Pani and Lasley 1972; Gupta and Lewontin 1982) are

commonly observed in life-history traits (Gebhardt and Stearns 1988). This means that genotypes react differently to variable environments.

By the way, environmental conditions during early development may have important consequences for the whole life of individuals (McNamara 1998). High population density, adverse weather conditions or low resource availability may lower phenotypic quality (Albon et al. 1987; Saether 1997; Solberg et al. 2004), often in interaction with the genotype (Coulson et al. 1998). Individuals born during the same year experience globally similar environmental conditions thus, individual variability may arise from cohort effects (Lindstrom 1999; Gaillard et al. 2003). Hamel et al. (2009) found that these early-life conditions account for 35 to 55% of variation in individual quality. Thus, (Kruuk et al. 1999) found that lifetime reproductive success decreases with low temperatures at birth in female red deer. In addition, Łomnicki (1978) predicted that this individual heterogeneity due to cohort effects may increase when resources are scarce during the early development of individuals because of uneven access to resources among individuals of a given cohort. Therefore, the among-individual heterogeneity of life-history traits will increase for individuals born into poor cohorts.

Then, parental care actively acts on individual heterogeneity in life-history traits, but, in most polygynous mammals, only females contribute to parental care (Nowak et al. 2000). Consequently, the growth and survival of offspring are largely determined by maternal care which can be defined as the amount of resources invested in an offspring multiplied by the number of offspring (Andersen et al. 2000). Maternal care is a major component of demographic strategies in mammals, but could be highly variable among females which results in an increase in offspring heterogeneity (Nowak et al. 2000). Lactation is likely the most important caring behavior, providing the main source of energy for mammalian offspring early in development (Oftedal 1985). Nursing behaviors also directly influence offspring growth, and thus indirectly influence offspring survival since mass is an important determinant of offspring survival (Gaillard et al. 1997; Loison et al. 1999). Female experience may also shape the development of their young. Offspring cared for by older females may have a higher survival because older mothers are likely to provide greater allocation than younger mothers due to their increased reproductive experience or reduced reproductive value (Pianka and Parker 1975; Solberg et al. 2007; Meijer et al. 2011). The direct effects of

maternal experience on maternal care have been reported for a large range of mammals (in mice: (Nephew et al. 2009; Lopatina et al. 2011); in ungulates: (Haupt and Kusunose 2000; Dwyer 2008); in pigs: (Albers et al. 1999)). Comparatively, in birds there are fewer studies about the influence of maternal experience on the expression of care. However, in common terns (*Sterna hirundo*), chick provisioning was improved by experience, but this activity involved both parents (Limmer and Becker 2009). Finally, other maternal traits such as social rank and home range quality can indirectly enhance juvenile survival, notably through access to high quality forage and reduced vulnerability to predation (Van Moorter et al. 2009). Thus, in baboons (*Papio* species or subspecies other than hamadryas baboons of the horn of Africa), the sociality of adult females is positively associated with their infant's survival (Altmann and Alberts 2003). Females that spend more time with adult males increase their infant survival because males may protect them from harassment.

## ***II.2. Non-fixed heterogeneity***

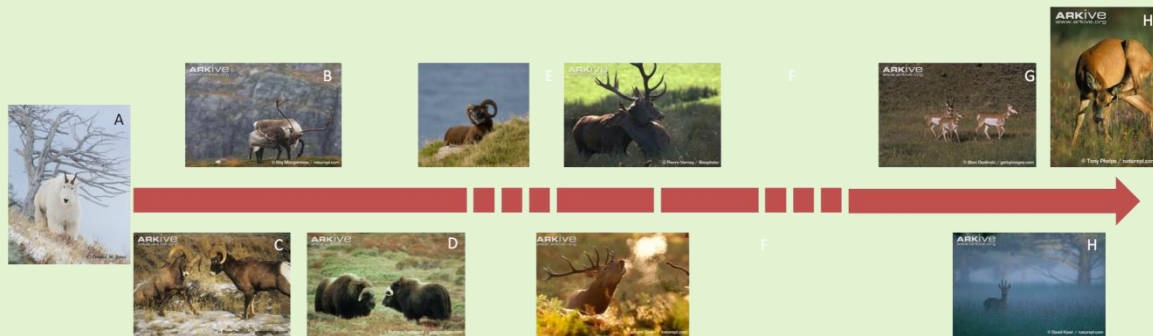
The acquisition of food resources is crucial for the condition and survival of individuals and has strong impacts on their fitness (McLoughlin et al. 2007; Panzacchi et al. 2010). However, generally, food resources are spatially and/or temporally variable. Hence, food is a major driver of reproductive success since the availability of energy is crucial to offset the reproduction costs. As regards to energy storage, a range of strategies are recognized among species, from pure income breeders at one extreme to pure capital breeders at the other extreme (Thomas 1988; Box 1). For capital breeders, compensatory feeding takes place in advance of breeding, so that reproduction may be financed from stored energetic capital, whereas for income breeders, reproduction is financed using current energetic income (Thomas 1988; Stearns 1992). Hence, synchronization between birth and the spring flush is crucial for income breeders (Andersen et al. 2000a). However, the spring flush or more generally, the resources availability, is determined by climatic conditions (such as temperature and precipitation) and seasonality. Hence, for example, for large herbivores

**Box 1. Capital vs. Income breeders**

There is a continuum from capital breeders to income breeders among many taxa and notably in ungulate species. Capital breeders use stored energy for reproduction whereas income breeders have to use energy acquired during the reproductive period (Thomas 1988; S.C. Stearns 1992; Jönsson 1997; Houston et al. 2007). A major disadvantage for a capital breeder is that storage is costly, while a major advantage is the spatial and temporal uncoupling between feeding and breeding. Indeed, the energetic needs for breeding and raising offspring are highly demanding, so that food acquisition is crucial. Thus, when food resources are poor at birth, for example, that may have strong effects on offspring survival and growth. But, the advantage of the capital breeding tactic is that females do not rely on current food resources but rather on their reserves so that they can feed their offspring irrespective of the current availability of resources. A capital breeder relies heavily on body reserves for raising their offspring. The quality of the summer range is thus important as females then build up their capital in terms of stored fat. Consequently, their body weight fluctuates strongly, both seasonally (Festa-Bianchet et al. 1996) and annually (Festa-Bianchet et al. 1998). On the contrary, small ungulates like roe deer seem to be closer to the income breeder end of the continuum (R Andersen et al. 1998). In income breeders, body weights only vary weakly among seasons (Hewison et al. 1996) and year (Andersen et al. 2000a). They stock few reserves (Hewison et al. 1996) and rely instead on current energy intake to offset the costs of reproduction (Andersen et al. 2000a). They face particularly acute trade-offs between foraging and offspring survival (Bongi et al. 2008) as they have to search for highly nutritious forage at the very same time that their offspring are most exposed to predation (Clutton-Brock et al. 1989; Linnell et al. 1995). Besides, in capital breeders body weight and reproductive success affect each other reciprocally (Festa-Bianchet et al. 1998). For instance, in Soay sheep (closer to the capital breeder end of the continuum), lambs are

### Box 1. Capital vs. Income breeders

born in April allowing ewes to regain body mass after June when lactation ceases and enter the winter with a body mass similar to non-reproductive females. Moreover, females that have successfully reared lambs the previous season were more likely to give birth again than non-reproductive females. In roe deer, on the contrary, previous reproductive success does not affect current reproductive success (Andersen et al. 2000a).



**Figure 1. Illustration of the income vs. capital breeding gradient among few ungulates.** A: mountain goat, B: reindeer, C: bighorn sheep, D: muskox, E: Soay sheep, F: red deer, G: pronghorn, H: roe deer.



living in temperate areas, cold and long winter decrease the early survival of newborns likely via a reduction in the quality and/or quantity of food resources acquired by the mother during late gestation (McCorquodale et al. 1988; Adams et al. 1995). On the contrary, high richness and availability of food resources during late gestation and early life of newborns large herbivores increase their early survival (Murphy and Coates 1966; Wilson and Hirst 1977; Rognum et al. 1983) likely via an increase in milk quality (Wilson and Hirst 1977). Consequently, climatic conditions indirectly shape the individual's early life stages and thus create some individual heterogeneity in life-history traits. Besides, the environment is often seasonal, including a period of variable length with higher resource availability that is suitable for the reproduction and growth of organisms, and a period during which reproduction and growth are not possible due to harsh weather and/or lack of food resources (Fretwell 1972). During this latter period, a large number of species migrate to better ranges whereas others go into hibernation or diapause. This period is important for individuals as it can influence their future reproduction (Fretwell 1972). Consequently, seasonality imposes strong constraints on the phenology of individuals and may shape individual heterogeneity in life-history traits and demographic components. Finally, more generally, irrespective of the strategy an individual adopts, food quantity and quality affect its diet (i.e. botanical composition) and nutrition (i.e. the relationship between the supply and the requirement of energy and nutrients, DelGiudice 1995) with a critical impact on reproduction (review in Parker 2003). Thus, all these factors shape and strongly impact the individual's reproduction and offspring survival, growth rate or condition.

In addition, another crucial factor influencing individual heterogeneity in life-history traits and fitness is predation. In its broadest sense, predation includes any interaction in which energy flows from one organism to another one (see Sih et al. 1985 for a review). With this definition, all animals and some plants are predators. In the prey-predator system, the type of predator is of major importance for individual heterogeneity in fitness, but the density of predators and prey, as well as their behavioral interactions (hunting strategies, anti-predators behaviors, distance to cover) are also fundamental (Sinclair 1989; Goldsmith 1990; Messier 1991). For instance, wherever ungulates coexist with large predators, predation accounts for most of the mortality in multi-predator systems (see Jedrzejewski et al. 2011 for a review). Thus, Eurasian lynx (*Lynx lynx*), when sympatric with roe deer,

randomly kill individuals (Jedrzejewski et al. 1993; Jobin et al. 2000; Odden et al. 2006; Andersen et al. 2007), whereas red foxes (*Vulpes vulpes*) specialize on fawns (Linnell et al. 1995; Jarnemo 2004; Panzacchi et al. 2008) which leads to individual heterogeneity in fitness. In addition, predation may also have indirect effects on individuals and their fitness. Predation can profoundly affect the morphology, physiology or behavior of prey via modifications of their foraging behavior or habitat use, for example (Sih et al. 1985). Hence, predators and predators' density greatly influence overall prey fitness and create among individual heterogeneity due their hunting strategies and relationship with prey.

Then, individual heterogeneity in fitness components may vary according to the degree of infestation of individuals by parasites (Beckage 1997). Their impact on hosts is generally negative because parasitism causes expensive behavioral and immune responses in terms of, for example, production of proteins and energy and it often causes a reduction in survival and fecundity (Hudson et al. 2002). In mammals for example, high parasite abundances lead to reduced fecundity in mountain hares (*Lepus timidus*, Newey and Thirgood 2004) and reindeer (*Rangifer tarandus*, Stien et al. 2002) and lowered growth rate and reproductive success in yellow bellied marmots (*Marmota flaviventris*, van Vuren 1966).

### **II.3. Conclusion**

Both fixed and non-fixed individual heterogeneity greatly shape life-history traits and so, fitness. That being said, thanks to the study of individuals' behavior, behavioral ecologists recently focused on how individuals differ in their behavioral responses for a given situation. Indeed, for a long time, researchers considered behaviors as highly plastic traits, with individuals capable of rapidly changing the expression of a behavior in response to changes in the surrounding environmental conditions (Sih et al. 2004). This implied that most of the individual heterogeneity observed in a behavioral trait could be explained by environmental factors or intrinsic state differences. However, animals often show limited behavioral plasticity (Sih et al. 2004a; Sih et al. 2004b) and commonly differ consistently in their reaction towards the same environmental stimuli (Clark and Ehlinger 1987; Wilson et al. 1994; Boissy 1995; Wilson 1998; Gosling 2001; Greenberg and Mettke-Hofmann 2001).

Hence, since the 2000s, the interest for the study of inter-individual variability in behavior has increased and contributes to individual heterogeneity in life-history traits and fitness.

### **III. Sources of individual heterogeneity: on the importance of personality**

#### ***III.1. Definitions and history***

Individual variability was once viewed for a long time as a statistical noise (Wilson 1998). However, recently, behavioral ecologists have recognized that consistent behavioral differences among individuals exist. Several terms are used to refer to individual behavioral differences: temperament (Réale et al. 2007), personality (Gosling 2001; Réale et al. 2007), behavioral profile (Groothuis and Carere 2005) or coping style (Koolhaas et al. 1999) (BOX 2). Coping styles are most of the time used in both ecology and neuroscience, while temperament and personality are used more in ecology and evolution. The distinction between the definitions of temperament and personality is vague and often based on arbitrary grounds; however, temperament generally has a more restrictive meaning than personality. It often describes differences in emotionality or describes traits that are demonstrated very early in life (Budaev 1997; Box 1999). In this manuscript, we will use the notion of personality, as the individual behavioral differences which are consistent over time and/or across situations (Gosling 2001).

From a general point of view, a huge number of traits exist which describe the individual's behavior. That being said, in the framework of the study of animal behavior, five behavioral dimensions are usually identified and form the 'Big Five' theory: shyness-boldness, exploration-avoidance, activity, aggressiveness and sociability (Gosling and John 1999a; Réale et al. 2007). The shyness-boldness dimension represents an individual's reaction to any risky situation (e.g. humans or animal predators), but not to a novel situation. Docility and fearfulness are specific cases of the shyness-boldness personality dimension occurring when individuals face humans (Boissy 1995; Grandin 1998; Boissy et al.

2005). When an individual deals with a novel situation, its reaction is seen through the exploration-avoidance personality dimension. Classical situations include the exploration of a new habitat, the search for novel food resources or an individual's reaction toward a novel object, notably for tests in captivity. The neophobia-neophilia dimension is included in the exploration-avoidance personality dimension. For Réale et al. (2007), neophobia and neophilia are component parts of exploration except that their study is more directed toward mechanisms responsible for individual variation in exploration. Others consider? exploration and neophobia behaviours as a whole in that neophobia is linked to exploration because individuals only explore if they are interested in a given object and the same is true for active avoidance (Day et al. 2003; Stöwe et al. 2006). Their relationship is influenced by the cost-benefits of the particular context (Stöwe et al. 2006). Indeed, neophobic responses can reduce exposure to predators, but they can also constrain exploration and thus opportunities for learning and innovating. Thus, the exploration-avoidance personality dimension may concern a risky situation, whereas the shyness-boldness dimension only includes risky situations, and so no novelty, according to Réale et al. (2007). For instance, a novel object could represent a potential predator in captivity (Moretti et al. 2015). This situation could be quite common for individuals living in the wild. Individuals may have to search for food in a novel environment which can be risky due to high predator density such as in highly urbanized environments (Sol et al. 2011). Activity corresponds to the general level of an individual's activity. This personality trait is supposed to be measured in non-risky and non-novel environments (Barnett and Cowan 1976; Renner 1990) in order to be independent of both the shyness-boldness and exploration-avoidance personality dimension. The aggressiveness is an individual's agonistic reaction towards conspecifics, whereas sociability concerns an individual's reaction to the presence or absence of conspecifics (excluding aggression). Both the latter two personality traits are expressed in a social environment.

These five personality traits are independent from each other so that there is no overlap between definitions (that is why studying neophobia in a risky context is possible, but the shyness-boldness is solely studied in non-novel situation to avoid any overlap or confusion between the personality traits). Moreover, correlations among the five personality dimensions are not expected in order to study the whole personality. Each personality trait

can be studied independently of the other ones. These definitions are deliberately simplified in order to encourage researchers to conduct studies within the personality framework and to make their study easier in captivity, but also in the wild where observations of wild animals may be difficult and to avoid too much confusion as regards personality studies carried out on Humans. That being said, correlations among personality traits are possible. When these individual differences in suites of correlated traits are consistent across either different situations or contexts we speak about behavioral syndromes (Sih et al. 2004b). One of the first demonstrations of a behavioral syndrome was Huntingford (1976)'s study. She worked on aggressiveness, exploratory behavior and anti-predator behavior in three-spined sticklebacks (*Gasterosteus aculeatus*). Thus, she showed that individual differences in aggressiveness were consistent across contexts and that boldness and aggressiveness were positively correlated to each other.

**Box 2. Personality and co.**

**Temperament:** Several definitions for temperament exist but in behavioral ecology, two definitions are generally known. Budaev (1997): Temperaments: integrated behavioral phenotypes and stable traits that are consistent over time and across situations; broad and consistent dimensions of individuality. Box (1999): The characteristic style of emotional and behavioral response of an individual in a variety of different situations that is often, but not invariably, demonstrated very early in life. It is the stance that an individual takes towards its environment across time and situations. It refers to styles of responsiveness and not to specific acts.

**Animal personality:** consistent differences between individuals in their behavior over time and across contexts (Gosling 2001); or, consistent differences between individuals in their behavior over time and/or across contexts (Réale et al. 2007). This implies that inter-individual correlations exist in behavior across time or contexts. The term 'animal personality' has recently been coined by behavioral ecologists to describe a particular type of individual variation and does not imply a link with human personality (Réale et al. 2007), which has traditionally been quantified in other ways.

**Behavioral syndrome:** a suite of correlated behaviors reflecting among-individual consistency in behavior across contexts or situations (Sih et al. 2004a,b). A context is a functional behavioral category (e.g. feeding, mating, predator avoidance etc.). A situation is a set of conditions at a particular time. Different situations could involve different levels along an environmental gradient (e.g. different levels of predation risk) or different conditions across time (e.g. breeding vs. non-breeding seasons). A population or species can exhibit a behavioral syndrome. Within the syndrome, individuals have a behavioral type (e.g. more aggressive versus less aggressive behavioral types). As in the personality framework, inter-individual differences in

## Box 2. Personality and co.

behavior are consistent meaning that a given individual will always have the same behavioral tendency, e.g. bolder than a shy individual irrespective of the context. Thus, within the behavioral syndrome framework, individuals differ in behavioral type, i.e. some individuals will have a bold or aggressive behavioral type whereas others will have a shy or less aggressive behavioral type. (e.g. more aggressive versus less aggressive behavioral types).

**Coping style:** the suite of behavioral and physiological responses of an individual that characterize its reactions to a range of stressful situations (Koolhaas et al. 1999). A coping style can be defined as a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals. Two extremes coping style types are recognized. Proactive individuals are fast explorers, novelty seekers, highly aggressive, impulsive in decision-making, take risks in the face of potential dangers. Physiologically, they predominantly display a sympathetic activation (the fight/flight response; Koolhaas et al. 1999). On the contrary, reactive individuals respond to the same challenge with immobility and lack of initiative. Physiologically, they predominantly show a parasympathetic/hypothalamic activation (the conservation/withdrawal response; Koolhaas et al. 1999). Thus, reactive individuals show higher hypothalamic-pituitary-adrenocortical (HPA) axis reactivity, and therefore a larger increase in plasma glucocorticoid levels in response to stress compared with proactive individuals.

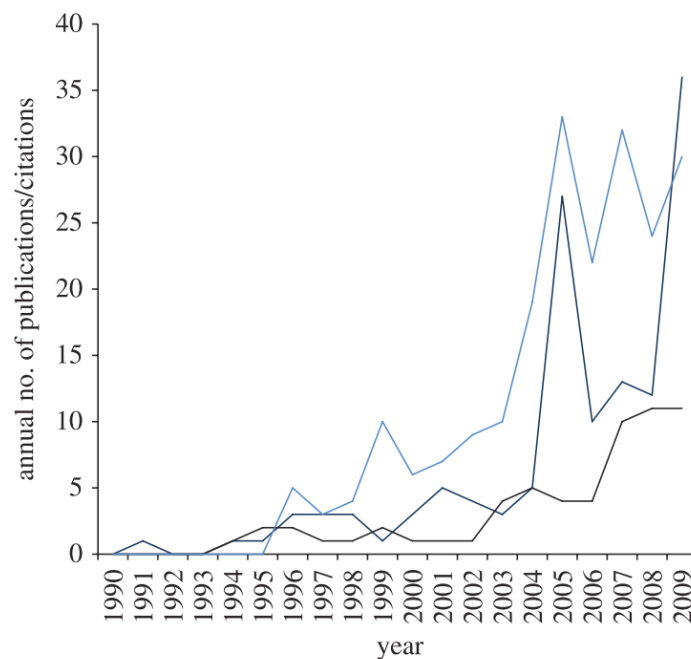
### **III.2. Personality: who and where?**

Consistent differences in behavior between individuals have long been studied first by psychologists, using both humans and other animals as subjects (Gosling 2001; Brosnan et al. 2009). Research on non-humans has typically occurred in the laboratory, using rodent models to extend knowledge of human personality and its effects on well-being and health. For example, there are many studies that have addressed addiction such as drug addiction principally studied in rats in laboratory (see Olmstead 2006 for a review) and anxiety and novelty-seeking (see Pawlak et al. 2008 for a review on mammals such as horses, hyenas, baboons, chickens and rodents). Besides, these consistent behavioral differences between individuals had also an interest for improvement in animal production and welfare (Price 1999). Tamelessness toward humans and associated ease of handling are among the more important aspects of the domestic phenotype. Tamelessness can minimize the negative effects of handling in animal agricultural enterprises (Barnett et al. 1994; Hemsworth et al. 1994) and when conducting scientific investigations (Gross and Siegel 1979). Popova et al. (1991) have demonstrated that the tamelessness of silver foxes in the presence of humans differed between individuals and was directly related to brain chemistry. Thus, tamer foxes have higher levels of serotonin and its metabolite 5-hydroxyindole acetic acid and greater tryptophan hydroxylase activity in the midbrain and hypothalamus than their less tame foxes.

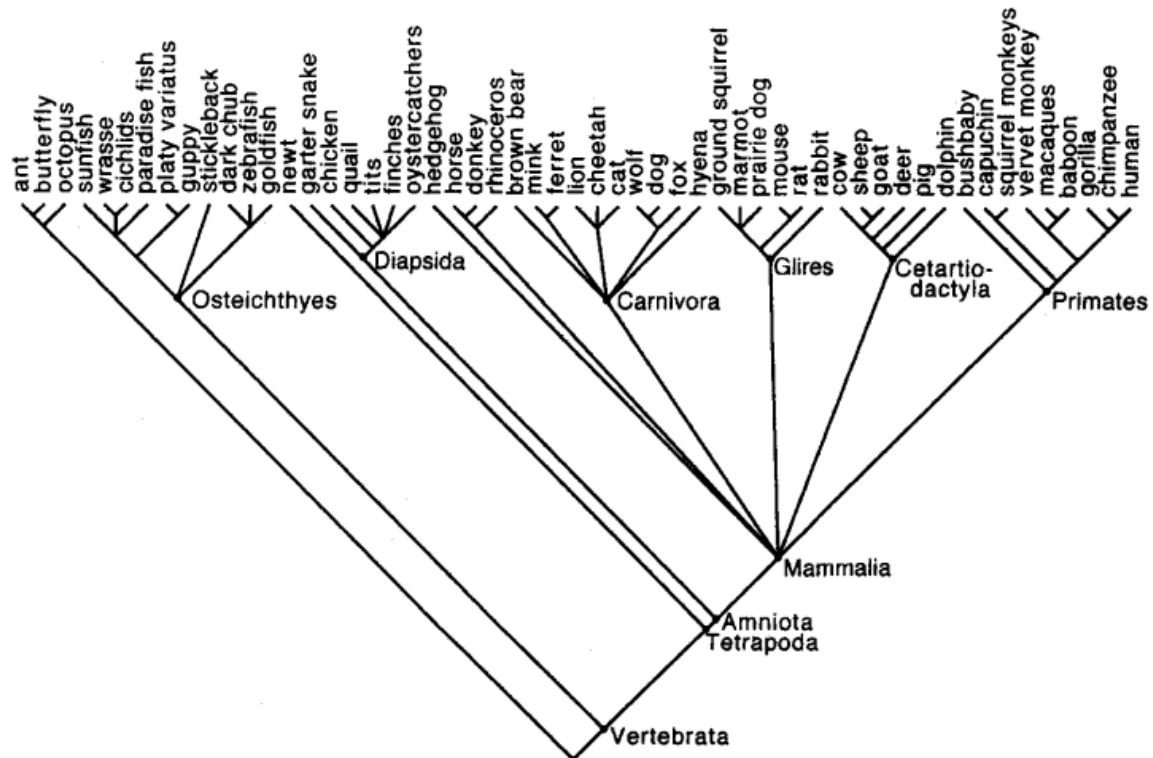
The interest for the study of inter-individual differences in behavior for behavioral and evolutionary ecologists has taken longer despite some pioneering studies such as the one of Huntingford (1976). However, during the 1990s, the number of studies on different taxa increased. For example, in birds, Verbeek et al. (1996) showed in the laboratory that wild great tits (*Parus major*) differed in their boldness and exploration and that the two traits were correlated. A large number of studies were also carried out in primatology. Thus, studies carried out in captivity or on semi-free ranging rhesus macaques (*Macaca mulatta*) found that males with a lower level of 5-HIAA (5-hydroxyindoleacetic acid which is a measure of serotonin activity) were more impulsive, took more risks, and had a lower level of sociability (Mehlman et al. 1995; Higley et al. 1996). This influence of serotonin on the level of aggressiveness has also been studied in many other vertebrates (Nelson and Chiavegatto 2001; Miczek et al. 2002).



Thus, the interest for the study of inter-individual differences in behavior in animals has increased since the 1990s-2000s (Fig. 2) so that in a review Gosling (2001) identified more than 180 studies dealing with inter-individual differences in behavior in more than 60 species (Fig. 3) from captivity to the semi-wild. Hence, inter-individual behavioral differences between individuals seem to be an inherent component of the individual, shaping its choices such as foraging or anti-predator behavior, and thus are present in a wide range of species. However, highlighting such inter-individual differences is not simple (questions about the studied traits, their definitions and measures, and their repeatability) and a large number of the studies have focused on vertebrates, and more specifically on mammals (Fig. 3). In addition, most of the studies have been carried out in captivity for technical and feasibility reasons, thus we lack empirical studies in the wild.



**Figure 2. Increase in the number of publications and citations on animal personality from 1999 to 2009 (from Réale et al. 2010).** Blue line is the number of citations of Wilson et al. (1994), the navy blue line represents citations from journals specialized in behavioral study, and the black line refers to publications from journals in ecology and evolution.

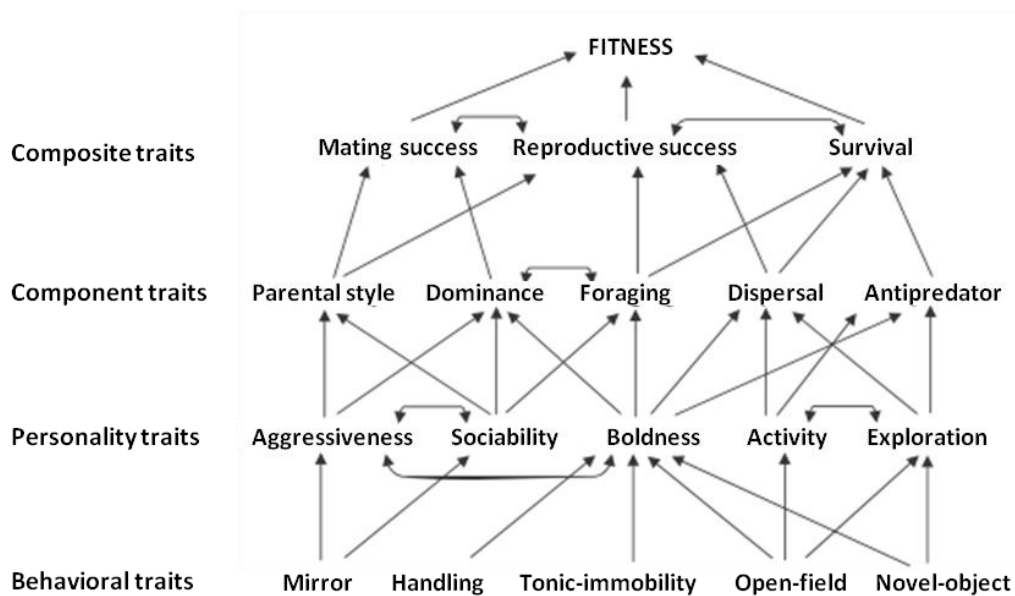


**Figure 3. Phylogenetic relationships among species studied in the ‘personality’ framework (from Gosling 2001).** Branch divergences represent speciation events, in which an ancestral species gives rise to two or more descendant species. Thus, relationships among species are depicted by the branches pattern of the tree.

### **III.3. Personality and life-history traits**

Although we cannot reduce personality simply to these five behavioral dimensions, they are expected to have important implications for ecology and evolution (Fig. 4, Wilson et al. 1994; Réale et al. 2007). Several studies have already shown that personality affects traits such as dominance (Dingemanse and de Goede 2004), stress response (Carere et al. 2001), parental care (Cleveland et al. 2004; Both et al. 2005), territory quality or size (Civantos 2000; Both et al. 2005) and natal dispersal (Dingemanse et al. 2003). The link between personality and dispersal is frequently studied and highlighted in a number of species (birds: Dingemanse et al. 2003; reptiles: Cote et al. 2007; non-human primates: Mehlman et al. 1995; mammals: Debeffe et al. 2014; fish: Fraser et al. 2001). For instance, boldness is positively correlated to the individuals’ propensity to migrate in roach (*Rutilus rutilus*, Chapman et al. 2011) or to dispersal distance in the Trinidad guppy (*Rivulus hartii*, Fraser et al. 2001). In the great tit, future dispersers are fast-exploring individuals (Dingemanse et al. 2003). Bank voles

(*Clethrionomys glareolus*) with a high capacity for colonization also have a high level of activity (Ebenhard 1987). Sociality is linked to the decision to disperse in the common lizard (*Lacerta vivipara*, Cote and Clobert 2007). More broadly, at the population level, personality contributes to determine species distribution with, for example, their tendency to be invasive (Cote et al. 2010) and their ability to adapt to environmental changes (Sih et al. 2004a). For instance, as regards invasions, a key issue seems to be personality-dependent dispersal (see Fraser et al. 2001; Dingemanse et al. 2003; Cote and Clobert 2007; Duckworth and Badyaev 2007). If the personality or behavioral syndrome type of the disperser enhances its colonization success (Cote and Clobert 2007; Duckworth and Badyaev 2007; Clobert et al. 2009; Duckworth and Kruuk 2009), then personality-dependent dispersal might play an important role in invasions. Thus, Duckworth and Badyaev (2007) showed a biased dispersal of highly aggressive western bluebirds (*Sialia mexicana*) to the invasion front, allowing this species to outcompete and displace less aggressive mountain bluebirds. The general hypothesis is that with personality-dependent dispersal, individuals leading an invasion front might often display behavioral characteristics that facilitate the colonization of new habitats and hasten the spread of an invasive species. Cote et al. (2010) confirmed that personality-dependent dispersal plays an important role in the species invasion in mosquitofish (*Gambusia affinis*).



**Figure 4. Flow diagram representing potential links among personality dimensions and their potential links with fitness components (from Réale et al. 2007).** The arrows do not represent all the possible links between variables.

### ***III.4. How and why personality exists?***

While more and more researchers have identified personality and/or behavioral syndromes in a large range of taxa, it is not clear why personality exists and what are the mechanisms maintaining these individual behavioral differences. Therefore, two main questions arise. Why do individuals of the same population differ in their behavioral reaction to the same situation? A classical illustration is linked to risk-taking while foraging. Shy individuals prefer to forage close to protective cover even if food resources are of lower quality or quantity, whereas bold individuals take more risks foraging away from cover but acquiring access to better resources. The second question is why individuals exhibit consistent behavior across different periods of time?

#### *III.4.1. Theoretical and evolutionary explanations: architecture of behavior*

Classical explanations for the maintenance of inter-individual differences in behavior assume that the behavior of each individual is fixed and genetically controlled. In this situation, phenotypic variation can be maintained by a number of processes including temporal or spatial variation in environmental conditions, with for example differences in food resources, predation risk among habitats or social conditions (Mangel 1991), frequency-dependent selection (Roff 1998) or a balance between mutation and weak selection (Santiago 1998). More recently, theoreticians have considered situations in which genes determine reaction norms such that genotypes differ with respect to the phenotypes they develop in response to environmental conditions encountered early in life. Technically, this approach considers that the phenotype of an individual can be expressed in different environments (or moments) as a line, described by an elevation (the individual's level of behavior on average) and a slope (the individual's plasticity over an environmental or temporal gradient). The environmental gradient could be represented by different habitats for example, but also other environmental contexts such as social or physiological contexts. For instance, offspring may differ in their phenotypes because their parents have different genotypes and because they may provide different parental care (Mendl and Paul 1991) or maternal effects (Groothuis et al. 2005). Furthermore, correlational selection (Brodie 1992;

Sinervo and Svensson 2002) on the link between different traits might provide a powerful adaptive mechanism for the existence of suites of correlated traits (Bell and Sih 2007). Correlational selection occurs when certain combinations of traits are favored over others, such that the fitness of one trait depends on the value of other traits (Lande and Arnold 1983; Brodie et al. 1995; Svensson et al. 2001). For example, correlational selection favors certain combinations of color patterns and escape behaviors in garter snakes (Brodie 1992). These explanations for the maintenance of genetic variance in quantitative traits can be applied to any type of trait (Roff 1997; Mousseau et al. 2000; Penke et al. 2007) and so may provide initial insight into why personality variation might persist.

Thus, behavioral correlations can often be understood in terms of the architecture of behavior, that is, the genetic but also the physiological, neurobiological and cognitive systems underlying behavior. This architecture gives rise to behavioral correlations whenever multiple traits are affected by a common underlying mechanism within this architecture such as hormones with a given hormone coding for several traits (Ketterson and Nolan 1999; Lessells 2008), or neurotransmitters (Bond 2001) affecting multiple traits at the same time.

#### *III.4.2. Adaptive explanations*

A recent assertion is that inter-individual differences and their consistency may be adaptive. For example, theoretical studies have suggested that when the environment is uncertain, or when there are social benefits associated with being predictable (Dall et al. 2004; McNamara et al. 2009), consistency is the best response (McElreath and Strimling 2006). Another hypothesis to explain individual consistency is that adaptive behavior is stabilized by a consistent trait called 'state-variable' meaning that individuals vary with respect to morphological, physiological or behavioral characteristics (Houston and McNamara 1999). Originally, the term 'state' was used by physiologists to refer to the psychological state of an individual such as its state of arousal or its motivational state, but in the context of life-history theory, the 'state' of an individual refers to all those features that are strategically relevant, meaning features that should be taken into consideration in behavioral decisions in order to increase fitness (McNamara and Houston 1996; Houston and McNamara 1999; Clark and Mangel 2000). For example, these features include the age, size

and morphology of an individual and its physiological condition, but also the information available to an individual and the type of environment where an individual finds itself.

States are important since they should give rise to state-dependent behavior (condition-dependent behavior, phenotypic plasticity). Hence, individual differences in state should be reflected in individual differences in behavior. Importantly, single states are often relevant for different types of behavior in different contexts. As a consequence, the behaviors in these contexts will tend to be correlated if they reflect the same underlying state. Hence, stable differences in states in combination with state-dependent behavior provide a powerful framework for explaining adaptive differences in suites of correlated behavioral traits that are stable over time. Thus, for example, if predation risk varies according to body size, individuals with different body sizes should consistently differ with respect to their tendency to take risk while foraging. As body size is supposed to be stable on a day-to-day basis, any behavioral pattern whose payoff depends on body size should also be quite stable over time (McElreath and Strimling 2006).

Some theoretical studies highlighted that life-history trade-offs could favor the evolution of personalities (Wolf et al. 2007; Biro and Stamps 2008). Wolf et al. (2007) suggest that personality may have an adaptive origin. Indeed, life history trade-offs could be the cause of inter-individual variations in terms of personality. The authors take the example of the trade-off between immediate and future reproduction which results in a polymorphic population. Thus, individuals investing immediately in reproduction and those investing in later reproduction do not have the same fitness. These differences in terms of fitness involve different risk-taking behaviors which are consistent between contexts and over time. Other studies promote the expression and maintenance of personality through life-history trade-offs. For instance, Stamps (2007) suggest that correlations between certain types of behavioral traits will depend on the effects of those traits on growth and mortality.

Another theory has been advanced to explain the maintenance of personality owing to feedback loops with variation in state. Luttbegg and Sih (2010) explained that behavioral consistency can be seen at two different levels: over the short- or the long-term. Very few studies have studied behavioral consistency over the long term due to the difficulty of observing animals throughout their lives. They explained that over the short-term, the protection of assets (for example, individuals having information for good quality habitat

that would enjoy high reproductive success later in life), or the search for food of good quality to avoid starvation could explain short-term behavioral consistency which was in agreement with Wolf et al. (2007)'s study suggesting that risk-taking differences generate consistent inter-individual differences in behavior. However, both asset protection and starvation avoidance cannot explain long-term behavioral consistency. On the contrary, by the end, individuals with initial differences in behavior would adopt a similar behavior meaning there will be convergence of behavior and no consistent behavioral differences between individuals anymore. In addition, they found another mechanism that would explain consistent inter-individual differences in behavior over the long-term. This is the state-dependent safety. Irrespective of predation pressure, individuals with a high state (large size, good physical condition) are and will remain bold individuals, whereas those with a small size are and will remain shy individuals and even more so when predation risk is high. Moreover, all these mechanisms (over short and long-term) depend highly on environmental conditions (i.e. resource availability and risk of predation). Thus, consistent inter-individual differences in behaviors would be favored under intermediate ecological conditions (e.g. similar risk and resource levels), whereas when environmental conditions are not similar (low risk, high resources or high risk, low resources) individuals would tend to adopt the same behavior (respectively bold or shy individuals).

Thus, an important but neglected aspect of personality is the timescale over which consistency of behavioral variation is considered. Although all short- and long-term forms of consistency can be ecologically important (Sih et al. 2003), their consequences at the ecological or evolutionary level differ substantially (see Luttbeg and Sih 2010; Wolf and Weissing 2010).

Besides, when speaking about consistency of a behavioral trait, it does not mean that its intensity is fixed. On the contrary, it can vary according to situations. An individual that is relatively more aggressive than a second one in a given situation (presence of predators) will also be more aggressive in a different situation (absence of predators), although his absolute level of aggressiveness varies according to context (Biro and Stamps 2008). Moreover, even though behavior can be highly plastic in principle, a given behavioral trait can be associated with a state variable (size, energy reserves, condition, morphology or reproductive value)

evolving very slowly so that behavior will evolve also slowly. This mechanism could explain the consistency of behavior across time and contexts.

### ***III.5. Fitness consequences of personality***

Even if we do not exactly know why personality exists and what the mechanisms are involved in maintaining inter-individual differences and consistency within individuals, one certainty is that personality has profound effects on life-history traits and on fitness. That being said, only a handful of studies are available regarding the link between personality and fitness. To really have a good understanding of the link between personality traits or behavioral syndromes and fitness components, we need to carry out studies in the wild (since behaviors may be misleading in captivity, particularly as regards the survival or reproductive success of individuals which are not exposed to predation or food starvation). However, it is challenging to obtain long-term data on individuals living in the wild (see Dingemanse and Réale 2005; Réale et al. 2007 for a study-case). Thus, the lack of knowledge of general links between personality traits and fitness across species has been implicated as one of the main reasons why personality has not been embraced by ecological theory and may explain why long-term studies on the effects of personality on fitness are relatively non-existent (Réale et al. 2007).

However, it seems that the survival and reproductive success of individuals vary according to the individuals' personality as has been shown in a few empirical studies. For instance, the survival and reproductive success of blue tits depend on the interaction between their exploration speed, sex and availability of resources (Dingemanse et al. 2004). Bold Canadian bighorn sheep (*Ovis canadensis*) are less likely to be killed by cougars than shy ones (Réale and Festa-Bianchet 2003), and they also have a better weaning success (Réale et al. 2000). Rhesus macaques with a high level of 5-hydroxyindoleacetic acid have a low level of aggressiveness, take few risks and are sociable, all of which increase weaning success of their infants (Mehlman et al. 1994; Mehlman et al. 1995).

That being said, personality is also associated with maternal care behavior. Thus, in birds, great tits that explore little are better parents because they respond more readily to



environmental change (Both et al. 2005). In mammals, female mice (*Mus domesticus*) that show high levels of aggression take care and better groom their pups than less aggressive mice (Benus and Röndigs 1996). However, they took longer to retrieve their pups in a behavioral trial (Gammie et al. 2006). The rhesus macaque females with a low level of 5-HIAA are highly protective of their infants (Cleveland et al. 2004). Boon et al. (2007) showed that aggressiveness and activity level of mothers have no effect on the date of birth or litter size at birth in the red squirrel (*Tamiasciurus hudsonicus*), but their level of activity is correlated with the growth rate of their offspring and their aggressiveness is correlated to their offspring's survival. A mother's personality may also have persistent effects on the stress responses of their offspring (Weaver et al. 2004).

In addition, most studies dealing with the fitness consequences of personality assumed that there was a linear relationships between personality traits and fitness (see Smith and Blumstein 2008 for a review). However, this finding does not win unanimous support and the relationship between personality and fitness seems rather more complex. In some studies, environmental variability also shapes the fitness consequences of personality. For instance, the survival of adult great tits varied according to their exploratory level and differed between sex and among years. Thus, adult females with a higher behavioral score survived better in years with poor beech crop, whereas the relationships was the opposite for males (Dingemanse et al. 2004). These authors also found that the number of offspring surviving to breeding was related to their parents' personalities, and that selection changed between years. Moreover, Boon et al. (2007) also showed that fitness consequences of personality varied over time. in particular, the mother's level of activity influenced her offspring's growth rate, while her aggressiveness impacted the survival of her offspring in red squirrel (*Tamiasciurus hudsonicus* Erxleben), but these effects varied across life-history stages and over time, possibly due to fluctuations in food availability.

Thus, we have seen that there is enormous within-population heterogeneity in life-history traits and this heterogeneity may have marked consequences for individual fitness and, in turn, population dynamics. The sources of this heterogeneity are numerous. However, there is a crucial lack of studies, notably empirical studies, on the effect of inter-individual

differences in what? on individual performance and, hence, on their consequences for population dynamics, especially for free-ranging populations (Smith and Blumstein 2008). We need additional morphological and environmental data to determine whether these general trends found across species are due to state variables, environmental variability, or individual differences in life-history trade-offs, or a combination of all these factors.

#### **IV. Aim of the PhD**

Therefore, the aim of this PhD was to explore the link between behavioral traits (personality or behavioral syndrome) and demographic traits such as survival, growth and reproductive success in roe deer. In other words, we wanted to evaluate and understand how inter-individual variability (behavioral, physiological, etc.) affects the way individuals solve life history trade-offs and the possible consequences for their fitness (Roff 1992; S.C. Stearns 1992). This subject has been treated relatively recently from a theoretical point of view (Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008; Réale, Dingemanse, et al. 2010), but as yet there are few empirical studies (Réale et al. 2000,2009).

Roe deer is a long-lived and iteroparous species. Studies were carried out in two different contexts: the first concerned a population living in a natural environment, and the second used deer living in captivity. Both situations have been intensively monitored for over 15 years allowing us to collect numerous and repeated data (spatial, morphological, physiological, behavioral ...) and so allowing us to test for the existence of personality dimensions and behavioral syndromes. Moreover, roe deer is a widespread ungulate and its biology and demography is well studied thanks to long and intensive monitoring. Thus, this is a great opportunity to test for the fitness consequences of inter-individual variability in behavior. The study is divided into four different parts:

In the first chapter, I attempted to identify personality or behavioral syndromes of roe deer in the wild. Personality and behavioral syndromes are known to play an important role in life-histories (Wilson et al. 1994; Réale et al. 2007). That being said, despite their

interest, personality studies remain particularly challenging to carry out in the wild. Thus, do inter-individual differences in behavior exist in a given species?, which are the behavioral traits of interest?, and how can we highlight these inter-individual differences?, with which parameters are crucial questions with few answers. We have a large data set with repeated values for wild roe deer; hence, our aim was to test for consistent inter-individual differences in wild roe deer in different contexts using physiological measures and several context-dependent behavioral measures, and then to test for potential correlation among parameters which would indicate a behavioral syndrome. Indeed, it is recognized that inter-individual differences do not concern a single personality trait, but rather several traits (i.e. a behavioral syndrome, Sih et al. 2004a,2004b).

The second chapter attempts to make the link between personality in captivity and personality in the wild. Indeed, my main goal was to study inter-individual differences in the wild. However, its study in the wild is quite hard so that a large number of studies have been carried out in captivity (Herborn et al. 2010). That is why my aim was to calibrate the measures taken in the wild thanks to similar measures collected in captivity. This chapter includes two sub-chapters. With the first one, I tested for inter-individual differences in behavior during an acute stress and I evaluated the repeatability of each parameter. Indeed, if we wish to consider some behavioral measures as true indicators of personality traits, then those behaviors should be consistent (Gosling 2001; Bell et al. 2009). Hence, I quantified the degree of repeatability of morphological and behavioral traits taken on the captive animals several times over a year. With the second chapter, I tested for the existence of neophobia in roe deer living in captivity. Then, I wanted to validate and calibrate our measure of docility (behavioral score of the individual during handling) taken in the wild using these animals in captivity. To do that, I tested for its consistency among individuals and then, I tested for its potential correlation with neophobia indices. I assumed that if a relationship existed between the neophobia index and the behavioral score, this means that behavioral score may also index neophobia or inter-individual differences in behavior in both captivity and the wild.

With the third chapter, I focused more specifically on two other behavioral traits: activity (as an indicator of foraging efficiency) and boldness (as an indicator of risk-taking behavior) to highlight and describe inter-individual differences in the 'risk avoidance –

resources acquisition' behavioral trade-off. For prey living in an agricultural and fragmented landscape where the risk of predation is high (hunting), the trade-off between resource acquisition and avoiding predation may be particularly acute. This is likely especially true for income breeders such as roe deer which do not constitute fat reserves so that they need to forage frequently in sufficient quantity irrespective of the level of risk. Moreover, we might expect to observe inter-individual differences in such behavioral trade-offs as theoretical studies suggest that trade-offs favor inter-individual differences in behavior (Stamps 2007; Wolf et al. 2007), although this has received little attention to date (Brown and Kotler 2004; Verdolin 2006; Favreau et al. 2014). To do that, I explored to what extent behaviors such as the individual's vigilance level could act as a mediator of these individual tactics.

The fourth and last chapter aimed to explore both the effect of the environment and the mothers' behavior on the early survival of her fawns. Environmental conditions during late gestation and early life of mammals, and more specifically of ungulates, are known to shape the survival of offspring (Gaillard et al. 2000). In addition, it is recognized that inter-individual differences in behavior may have strong impacts on fitness (Smith and Blumstein 2008). However, very few studies have demonstrated a link between individual behavior and fitness in the wild (but see Réale et al. 2000; Dingemanse and Réale 2005). Thus, my aim was to explore the importance of the mothers' behavior on offspring survival or growth.



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## **Chapter II**

### **Material and Methods**

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## I. The roe deer as a study model

### *I.1. Systematic and distribution*

The European roe deer (*Capreolus capreolus*) belongs to the *Artiodactyla* order and to the *Cervidae* family. The genus *Capreolus* includes two species: the Siberian deer (*Capreolus pygargus*, Pallas 1771) and the European roe deer (*Capreolus capreolus*, Linnaeus 1758). The European roe deer species is itself divided into several sub-species such as *Capreolus capreolus italicus* inhabiting the Italian peninsula or *Capreolus capreolus garganta* inhabiting the South of Spain (Fig. 1). The deer is a small-sized cervid (adults weigh about 20-30 kg, with a body length of 95-135 cm, Fig. 2) with low male-biased sexual size dimorphism (males are less than 10% heavier than females, Andersen et al. 1998) and strong territoriality of adult males (see Liberg et al. 1998). Most of the year, males carry antlers (25-30 cm) allowing us to distinguish them from females. These antlers grow from December to March and only fall the following fall (Danilkin and Hewison 1996).

During the last glaciation period, roe deer like numerous other species took shelter in the Mediterranean regions but with the warming episode, deer have largely increased their distribution. Hence, roe deer are present across all the European continent (except Ireland) with a high abundance in very different habitats (J. D. C. Linnell et al. 1998). Since the mid-XX<sup>th</sup> century, roe deer have colonized novel environments thanks to their high ecological and behavioral plasticity, the countryside desertion by humans and the decrease of its natural predators. Since then, roe deer is the most widely distributed and abundant large herbivore in Europe (around 15 million in Europe and more than 1.5 million in France; annual harvest x 6.1 over the last 30 years in France and since 2000 around 500 000 deer are killed every year; data ONCFS; see Fig. 3a,b) which ranks it as a species of 'least concern' by the IUCN (source: Red List of Threatened Species IUCN Version 2012.1). In France, it occupies woodland areas, but also highly fragmented environments where woodland habitat is fragmented (Hewison et al. 2001) as well as large agricultural plains without woodland patches (Cibien et al. 1989). Therefore, roe deer has been described as a successful species (R. Andersen et al. 1998).

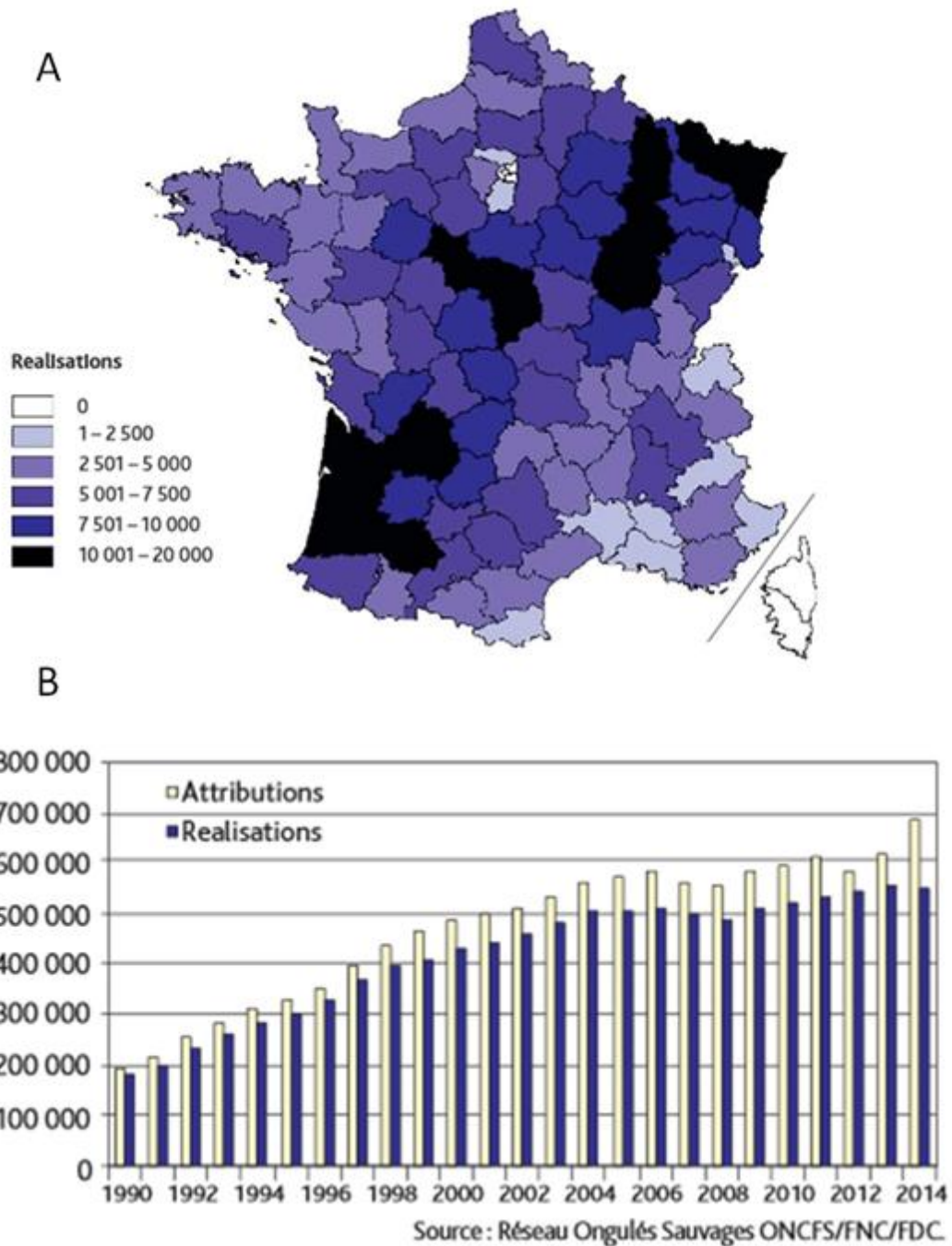




**Figure 1.** The present distribution of European roe deer in western Europe. Source: IUCN (International Union for Conservation of Nature) 2008.



**Figure 2.** Morphological differences between male and female roe deer.



**Figure 3. Variation of the number of roe deer shot in France until 2014.**

a. Number of roe deer shot by region, b. Variation of the number of roe deer allowed to be shot (in light) and actually shot (in dark) in France from 1990 to 2014 (excluding enclosures). Source: Réseau Ongulés Sauvages ONCFS/FNC/FDC.

## ***1.2. Biology and reproduction***

Roe deer is a generalist herbivore which feeds on a large number of plant species such as grasses, crop plants, conifers, deciduous trees and shrubs, mosses, ferns, fungi or lichens (R. Andersen et al. 1998). This species is weakly gregarious, living alone or in small groups in most environments (Hewison et al. 1998).

Through various aspects of its breeding behavior, roe deer is unique among ungulates. Females in roe deer are commonly considered as non-territorial. Females seem to range independently of males, so that female ranges often overlap several male territories (e.g. Bramley 1970). During summer, they live solitarily (alone or only with their fawns) in overlapping home ranges (Bramley 1970; Strandgaard 1972). During winter, they form small matriarchal groups consisting of one or a few adults, their dependent offspring and yearling daughters. These groups are often accompanied by one or two males (Kurt 1968; Hewison et al. 1998). The reproductive cycle of female roe deer, with embryonic implantation delayed by five months (Lambert 2002) and only one short ovulation each year, is unique among ungulates (Fig. 4). Despite being monestrous, up to 98% of females in a population are fertilized (Gaillard et al. 1992; Hewison 1996). Females are polytocous: they give birth to 1-4 neonates in May-June, with twins being most common and four being extremely rare. Fawn body mass at birth is about 1.6 kg on average, but highly variable (Gaillard et al. 1993). They grow rapidly the first year to reach 70% of adult body mass at eight months old (onset of first winter, Hewison et al. 2011). Fawns adopt a hider strategy in the first three to four weeks of life (Linnell 1994). Indeed, in ungulates, the mother-young behaviors are represented by the 'hiding-to-following' spectrum (Geist 1971; Lent 1974). The species of these groups are basically classified as 'hidiers' or 'followers' depending on whether the newborn lie concealed for their first few days or actively follow their mothers (Lent 1974; Ralls et al. 1986). When the pair has a 'follower' strategy, mothers remain in constant proximity with their offspring. 'Hider' offspring (Lent 1974), as roe deer fawns, lie hidden secluded from the mother for most of the time up to the age of 6-8 weeks (Espmark 1969; Linnell 1994). The mother visits the fawns three to seven times a day for care and changing of the bed site (Espmark 1969). Consequently, while 'following' has been viewed as a strategy for avoiding predators in open habitats and generally for group-living species, 'hiding' is thought to reduce predation risk in closed habitats or habitat with a protective

cover for more sedentary species (Lent 1974; Estes and Estes 1979). 'Hider' offspring have a short detection radius making the searching systematically of predators uneconomical (Byers and Byers 1983) but, the distance between the mother and her newborn is important for not giving cues about the fawn's location to predators. The mothers should maintain a minimum distance to the hidden offspring and should not look more in the direction of the newborn than in any other direction (Byers and Byers 1983; Fitzgibbon 1993). However, they should not stay too far away and thereby miss the chance to detect predators approaching the hiding place (Lent 1974; Litvaitis and Bartush 1980; Fitzgibbon 1993; Schwede et al. 1994). After weaning, they usually stay with their mother over their first winter before becoming independent when they reach approximately one year of age when most dispersal takes place (Wahlström and Liberg 1995; Debeffe et al. 2012). Both sexes disperse, females as one-year olds and males either as one-year olds or as two-year-olds. Females normally attain sexual maturity at 1.5 years of age, giving birth at 2 years old, but under favorable conditions they may become pregnant already as fawns (Hewison 1996) whereas under poor conditions first reproduction is often delayed one year until the age of 3 years old (Gaillard et al. 1992; Hewison 1996).

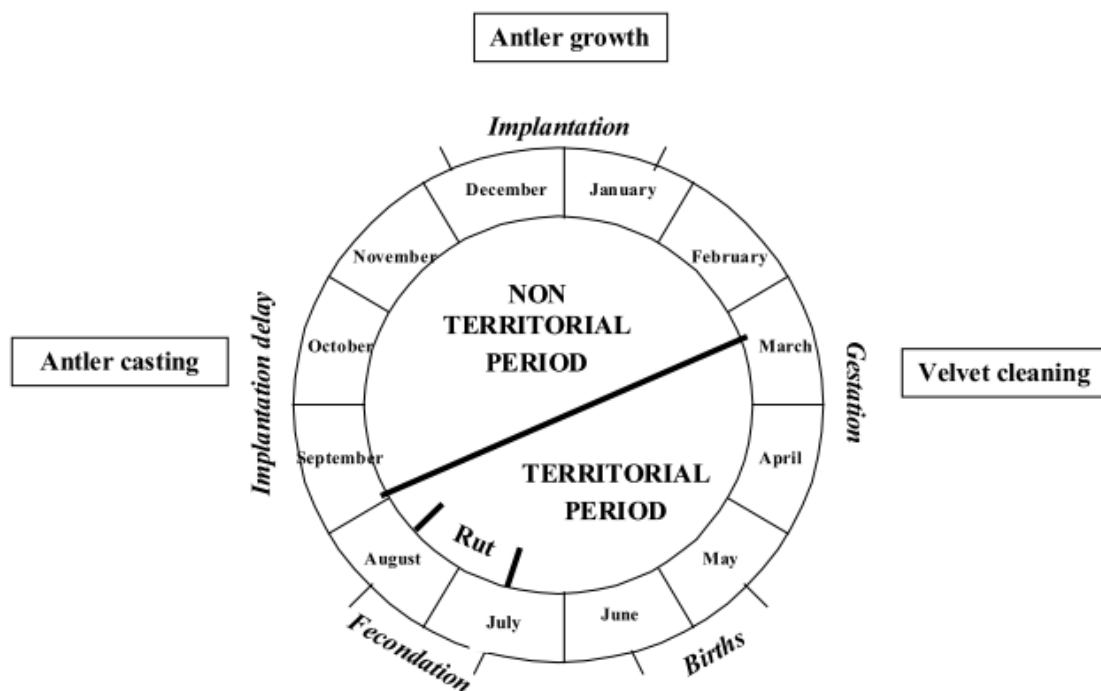


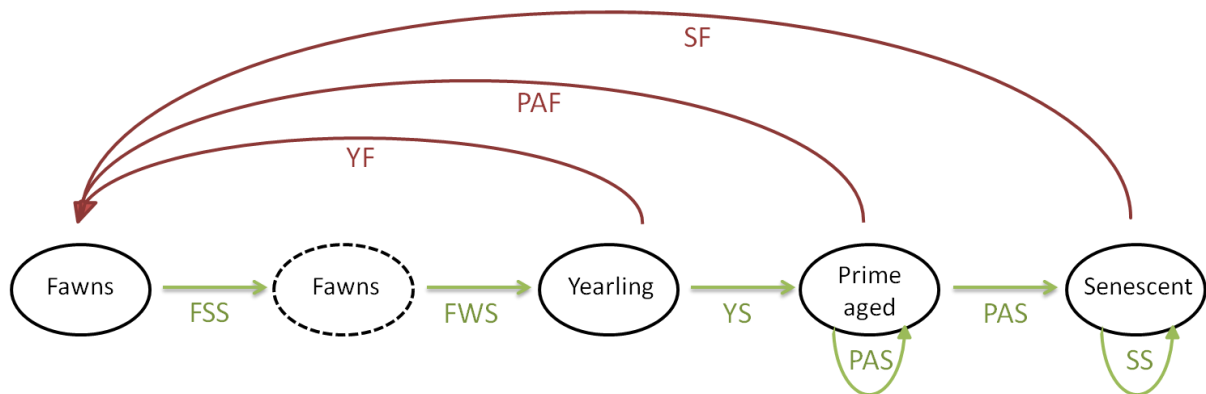
Figure 4. Reproductive cycle of male (not in italic) and female (in italic) roe deer.

Adult males in roe deer are considered strongly territorial (Bramley 1970; Strandgaard 1972). Territorial males are aggressive and intolerant towards intruder males (adults and sub-adults). Aggressive behaviors can take the form of threat, advertisement and fighting. It is often ritualized in displays (e.g. parallel walk, rubbing, scraping, barking), chases and retreats, more rarely actual combat (Bramley 1970; Danilkin and Hewison 1996). Dominance appears mainly site-specific with reciprocity of dominance among neighboring territory holders: territorial males are dominant within their own territory, but subordinate when exploring a neighboring territory (Danilkin and Hewison 1996). Male territoriality is seasonal (Fig. 4). Territories are established in early spring (March-April) and maintained until late August - early September (e.g. Bramley 1970; Strandgaard 1972). Rut occurs from mid-July to mid-August.

### ***1.3. Life cycle and demographic rates***

The demographic rates of roe deer are largely influenced by the age structure of the population (Fig. 5). Roe deer survival follows the typical pattern of survival of many populations of vertebrates (Caughley 1966). There are three specific stages. A juvenile stage characterized by a low survival from birth to one year of age, a prime-aged stage with a high and constant survival during prime-aged stage (from one to seven years old) and a senescent stage with a decreasing survival from 8 years of age to death. In large herbivores such as roe deer, adult survival is stable among populations (except under very harsh climatic conditions) and among years, whereas fawn survival may fluctuate highly among years (Gaillard et al. 1998a). Fawn survival is a major driver of roe deer population dynamics (Gaillard et al. 1998a). For instance, in two French populations, fawn survival accounted for about 50-75 % of the variability observed in growth rate of populations, while adult survival accounted for less than 20 %. When focusing on fawn survival, two different components can be defined: one from birth to the onset of winter, the summer survival, and one from the onset of winter to spring, the winter survival (Gaillard et al. 1998a). Summer mortality is mostly dependent on maternal care. Thus, the availability of quality resources is crucial to offset the costs of late gestation and early lactation where the energetic needs dramatically increase (Clutton-Brock et al. 1989). Thus, the availability of quality resources is a key

component of fawn summer survival and predation is another major cause of mortality in early-life (Linnell et al. 1995). Once the onset of winter is reached, most variation in fawn winter survival is care independent and depends on winter severity and density-dependent effects (Gaillard et al. 2000). Besides, demographic rates are also impacted by the sex structure of the population. Indeed, despite a low sexual size dimorphism, roe deer males



have lower survival rates than females as adults.

**Figure 5. Roe deer life cycle.** FSS: fawn summer survival, FWS: fawn winter survival, YS: Yearling survival, PAS: prime-aged survival, SS: senescent survival, YF: yearling fecundity, PAF: prime-aged fertility, SF: senescent fertility.

#### ***1.4. Roe deer as an important socio-economical species***

The European roe deer is an economically and socially important game species. It constitutes in Europe, with other wild ungulates, a resource of high economic (hunting, Fig. 3), cultural (photography and other recreational activities) and ecological value (as part of biodiversity) (Cederlund et al. 1998).

With its impressive demographic explosion, roe deer has thus increased the number of damages (Putman and Moore 1998). Contrary to wild boar, deer cause little damage on field crops since the majority of agricultural damages are focused on nurseries and vineyards. But the most significant damages caused by deer are on forestry. Indeed, it consumes the young shoots of trees and males spoil trees by rubbing their antlers on bark. In France, compensation for these damages amounts to more than 0.69 million euro per year since 2000 (Carnis and Facchini 2012). Finally, deer causes more than 20 000 accidents



in France with vehicles per year with both economic (over 15 million euro/year in France) and human (several deaths per year) damages.

## II. The study

### II.1. Study sites

#### II.1.1. Aurignac

The study was carried out in a 7500 ha agricultural area of south-western France, about 60 km south-west of Toulouse (Fig. 6a). This area is a designated LTSER (long-term socio-economic and ecological research) site. It is a hilly region (maximum 380 m a.s.l.) which has undergone substantial modification over the last century due to intensification of agricultural practice, with a loss of woodlands and hedges, the planting of new crop types (corn, sorghum) and an increase in average field size. The climate is mild oceanic with an average annual temperature of 11–12°C and an average precipitation of 800 mm, mainly in the form of rain. The human population is present throughout the site, in small villages and farms distributed along the extensive road network which covers the study site. It is a mixed and fragmented landscape of open fields with hedges and small woodland patches which vary in number among sectors, plus two main forests. Three sectors based on the degree of woodland fragmentation are distinguishable: a closed sector corresponding to the two forests, an intermediate partially wooded sector and an open agricultural sector with highly fragmented woodland (Fig. 6a). The Lilhac-Fabas forest covers 672 ha and mainly consists of Douglas pine (*Pseudotsuga menziesii*), other pines (*Pinus spp.*), oak (*Quercus spp.*) and common hornbeam (*Carpinus betulus*). The Mauboussin forest is the second largest forest (515 ha) constituted of oak (*Quercus spp.*) and common hornbeam (*Carpinus betulus*). The agricultural plain contains more than 1 300 small woodland patches with an average size of  $1.7 \pm 4.0$  ha. The wooded area covers 20% of the area whereas the rest of the site is made up of 36% of meadows, 33% of crops and 4% of hedges. Crops are dominated by wheat

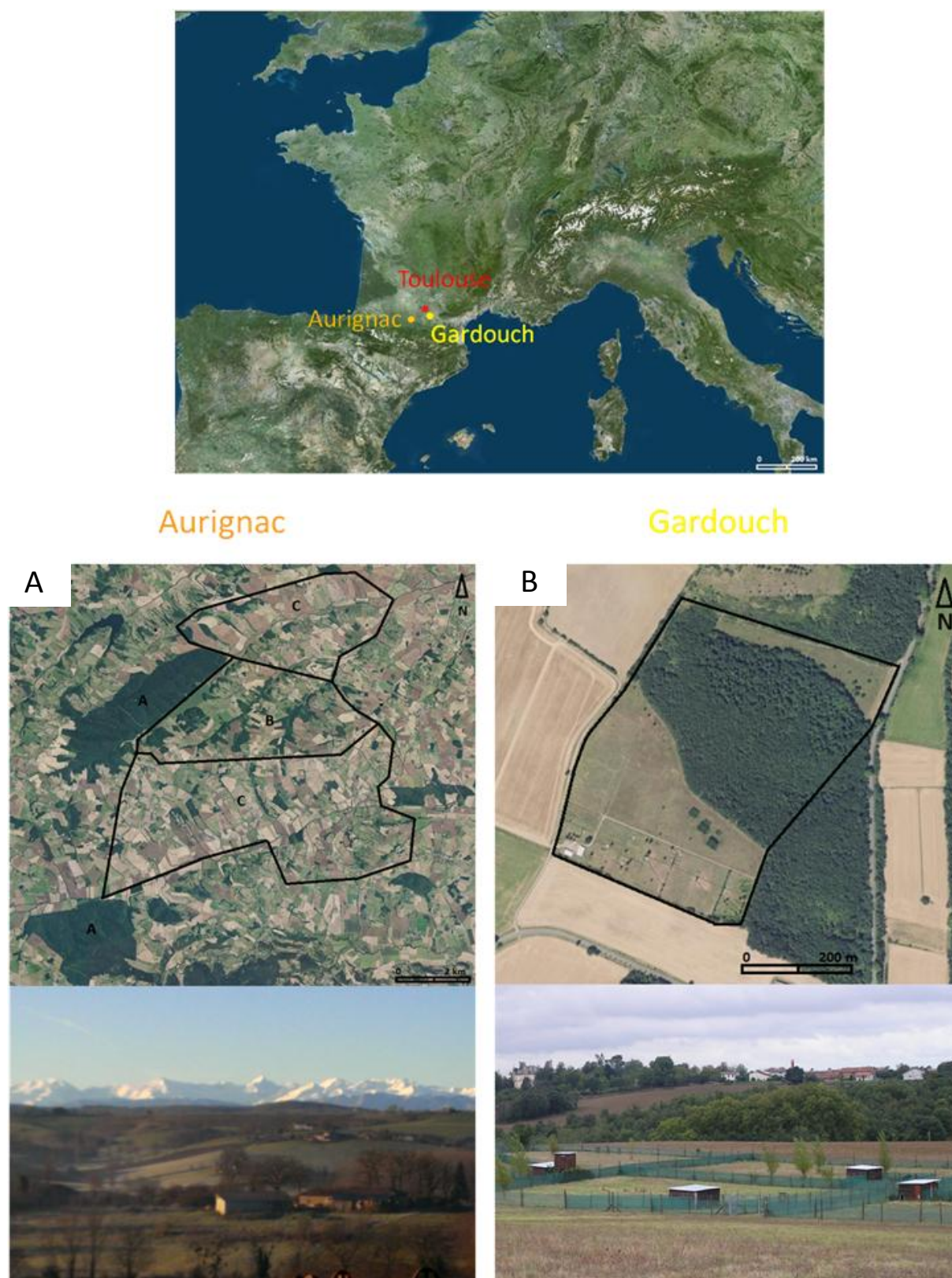
(*Triticum sp.*, 51%), sunflower (*Helianthus annuus*, 15%), maize (*Zea mays*, 10%), soya (*Glycine max*, 5%), sorghum (*Sorghum bicolor*, 8%) and rapeseed (*Brassica napus*, 4%).

### II.1.2. Gardouch

The research station is located in south-western France, about 30 km south-east of Toulouse and about 100 km north of the foothills of the Pyrénées mountains (Fig. 6b). The landscape is hilly and mostly cultivated, with patches of woods. The station is located on the slopes of a hill, around 230 meters above sea level. The climate is of the 'aquitain' Atlantic type, although subject to a strong Mediterranean influence, especially in summer.

The station is a 14 ha enclosure owned and managed by the French Institute for Agricultural Research (Institut de la Recherche Agronomique), INRA. The station is mostly devoted to research on the behavioral ecology of roe deer, and on the study of roe deer - vegetation interactions. Some captive roe deer (some of them are tame), are kept in small enclosures of 5000 m<sup>2</sup>, and are used for research on behavior, including cafeteria-type experiments. In addition, a small population of about 10 roe deer freely roams in the large enclosure (9 ha).





**Figure 6. Situation and view of the two study sites: Aurignac and Gardouch.** Three main sectors are present in Aurignac: A = closed sector corresponding to forests, B = intermediate partially wooded sector, and C = open agricultural sector with highly fragmented woodland. Sources: Géoportail, and photos by C. Monestier

## ***II.2. Study populations***

### *II.2.1. Aurignac*

The population has been long-term monitored for almost 20 years. The first capture events took place in 1996 and 1997 and then each winter since 2001. Animals were initially equipped with a VHF (Very High Frequency) collar and then from 2003 onwards with a GPS (Global Position System) collar. VHF collars coupled with a receptor allow the location of the focal individual thanks to repeated fixes obtained via a radio signal emitted by the collar. GPS collars record the position of individuals thanks to the use of several satellites. Most collars are also equipped with an activity sensor.

Deer density is estimated using radio-tracking data and direct observation (Hewison et al. 2007) to an average of  $9.3 \pm 1.32$  individuals per 100 hectares in the open and intermediate sectors. In both forests, density is two to three times higher than in the surrounding landscape, although estimates are approximate. Car circuits are also carried out each year since 1992 to estimate a kilometric index of abundance (IKA). Two circuits (one in the north and another one in the south of the site) are realized and repeated 7 to 10 times per year. The car driver and another person write down the number of deer seen during the circuit. The kilometric index of abundance is calculated as the ratio between the total number of observed deer and the total covered distance. Hence, notably thanks to this index of abundance, we observe that the population seems stable since 2005 (Fig. 7) and the analyses presented here were mainly carried out on individuals caught after this year (more than 400 individuals).

Because all individuals also have a unique numbered ear tags, we could identify each dead individual (hunted or found in the field) and its cause of mortality when possible. Individuals are on the whole in good condition from an epidemiological point of view; parasite prevalence and abundance is low but highly variable among years. Since 1996, 198 dead deer have been inventoried. 64.0 % of deaths were from anthropogenic causes (winter hunting, summer shooting, poaching, collisions with vehicles or capture consequences), 15.0 % were natural deaths (disease, predation by dogs, complications during calving or following fighting between males during the rut) and 21.0 % are of unknown cause. Therefore, the human pressure (direct lethal effects with hunting, collisions, etc. or indirect lethal effects

with recreational activities, presence of domestic animals, etc.) has a major impact on the population.

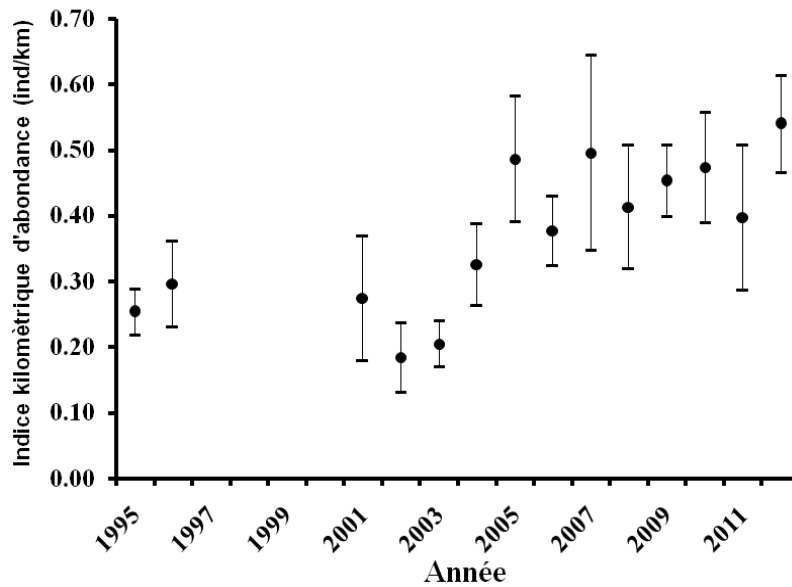


Figure 7. Variation in the kilometric index of abundance from 1995 to 2013. Source: A.J.M. Hewison, unpublished data

### II.2.2. Gardouch

For this study, we used individuals living in the small experimental enclosures. Most of these individuals were born and raised in the Gardouch station. Originally, roe deer came from Chizé Centre for Biological Studies (INEE, CNRS). Since their first reproduction in 2001, female fawns (and only few males) have been raised by technicians and researchers of the laboratory rather than by their own mother. This allows us to carry out behavioral experimentation with individuals that are not wary of humans due to a lower level of fear or stress. However, almost each year new individuals are imported to Gardouch following accident, injury etc. That being said, at the start of the PhD, solely 8 individuals on 26 were not raised by humans. Currently, there are 19 individuals, all raised by humans. Individuals can feed pellets almost *ad libitum* in their cabin, and grass and lives of shrubs in their enclosure. The cabin acts as a foraging site but also as a shelter in relation to weather conditions, and perceived perturbations due to human activities for exemple. In addition,

individuals are caught every winter for routine monitoring purposes (same protocols as those used in Aurignac, see next section).

### III. Data collection

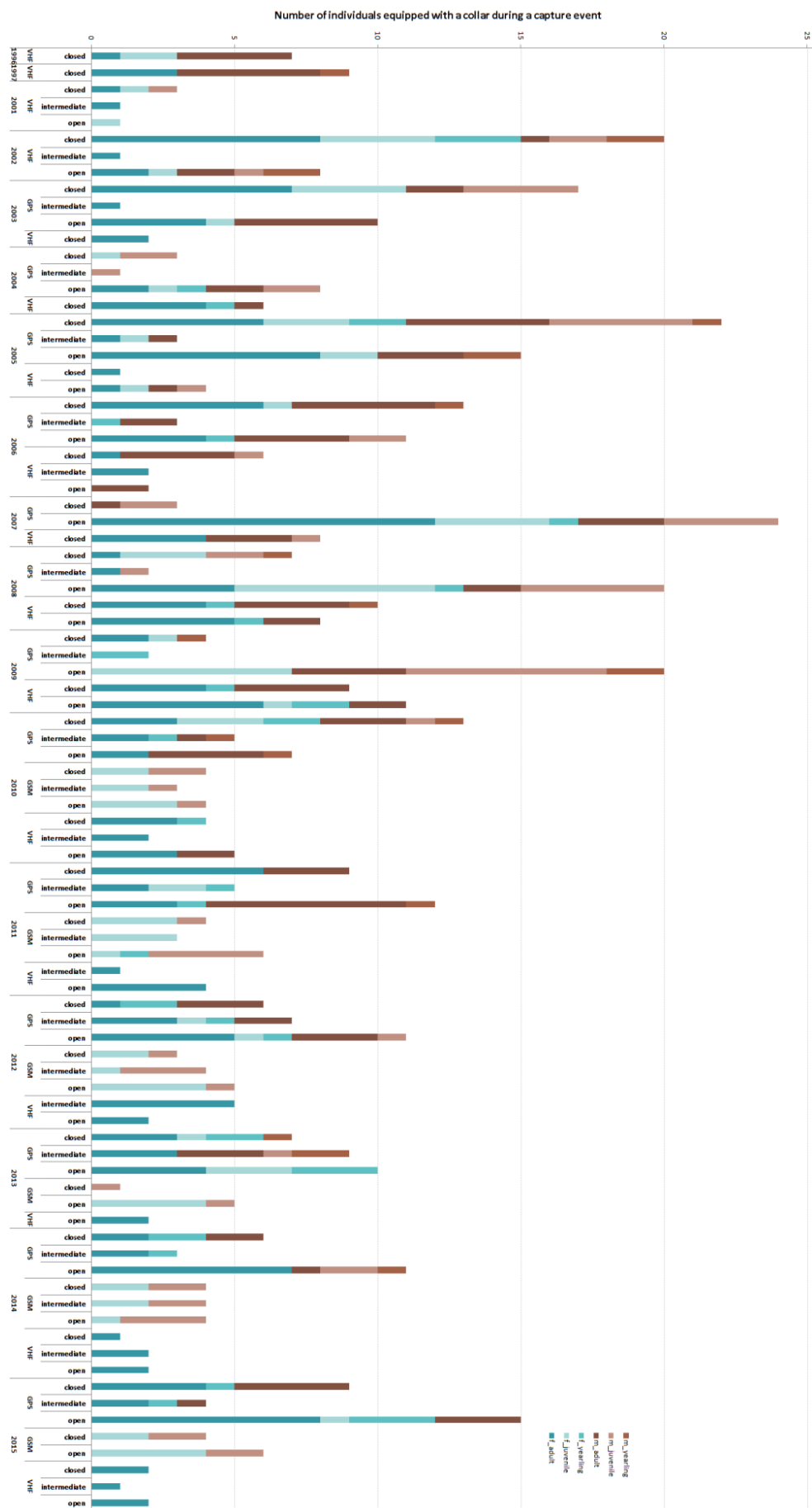
#### *III.1. Capture and behavioral data*

Every winter since 2001 (plus two other winters in 1996 and 1997) roe deer in the Aurignac population are caught from November to March (Fig. 8). About six to eight captures are carried out on eleven sites chosen throughout the study site to cover the whole gradient of landscape structure. A U-shaped device is set up using 4 km of nets. A hundred people push animals towards the nets and once a deer is caught in a net, we tranquillize it with an intramuscular injection of acepromazine (Calmivet 3cc). Then, we transferred the animal to a small wooden retaining box designed to minimize risk of injury and to limit stress until its handling for marking.

During marking, for each animal, we recorded its body mass to the nearest 0.1 kg and its sex, and we attributed an age class before fitting it with a collar, 2 plastic ear tags and releasing it on site. Fawns (less than 1 year old) are distinguishable from older deer by the presence of a tri-cuspid third pre-molar milk tooth and the presence of cartilage (Ratcliffe and Mayle 1992). Adults were divided in different age-classes (0.5, 1.5, 2.5, 3.5, 4.5-5.5,  $\geq 6.5$  years old or more than 6 years old) in relation to tooth wear. Adults are equipped with a VHF or GPS collar (Lotek 3300 GPS) and juveniles with a GPS or a GSM (Lotek Small WildCell GSM) collar (Table 1).

From 2009, physiological and behavioral data have been collected to index the individual's reactivity to the capture event, and so the inter-individual differences in the response to a stressful situation for the animal (Réale et al. 2000). We measured the rectal temperature (using a Digitemp Color thermometer with a precision of 0.1 C). Following Montané et al. (2003)'s study showing that body temperature of roe deer decreases over time from capture to 45 min after capture before stabilizing, we recorded temperature more than 1 h after the capture event in all cases. We recorded the temperature of each individual

Table 1. Graphical representation for the number of individuals equipped with a collar (GPS, GSM, VHF) during a capture event according to their sex, age and their site of capture.





at the beginning and at the end of the marking procedure, and used the mean of these 2 values. We also collected blood samples and feces to check for the state of health and parasite exposure of each individual.

Individual behaviors are recorded throughout the capture process. Thus, the arrival in the net (running or walking, panicked or calm), the struggle and panting levels in the net and on the marking table, cries and the running type at release (panic or calm, falls, attempts to remove its collar) are recorded and transformed into a behavioral score.



**Figure 8. A capture event in Aurignac.** Roe deer are caught using nets (A, by C. Monestier), then, they are transferred in a retaining box (B, by C. Monestier). During handling (C, by a student), we collect behavioral and physiological data and, most of the time, we equip them with a collar before releasing them in their natural environment (D, by O. Couriot).

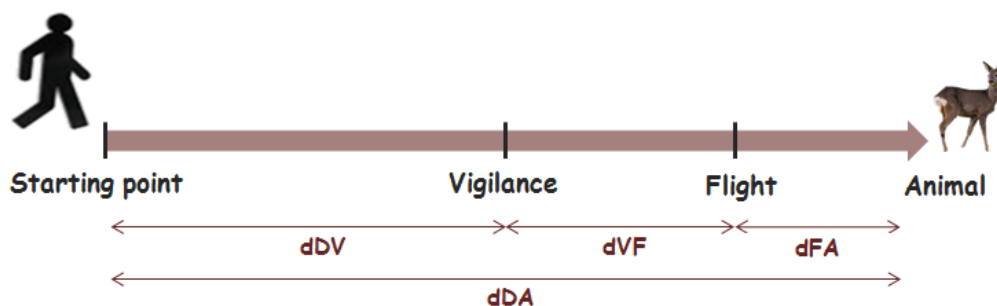
In addition, since 2010, behavioral observation campaigns have been carried out every year. These campaigns occur during two months (end of February to April), at least 2 weeks after capture and release. In 2010 and 2011, two other campaigns took place in autumn. These observations allow us to monitor the vigilance and flight behavior of individually marked undisturbed foraging roe deer to study variation among individuals in behavioral profile in relation to the baseline level of predation risk and/or disturbance. Observations were carried out during peak activity of roe deer activity (Jeppesen 1989), at dawn and dusk, at an average distance of 260 m. First, we located and identified the focal individual by manual radio tracking. Then, we carried out a focal observation with binoculars (10x42) during foraging activity by recording the behavioral sequences on a numeric recorder for 9 min on average (min=5 min, max=15 min). We recorded 6 exclusive behaviors: vigilance (head above shoulder level while scanning surroundings), feeding (collecting food, or searching for food with head at ground level), head raised (head above shoulder level but without scanning), moving (walking or trotting, head above shoulder level), grooming, and 'others' (Fig. 9). We stopped the focal observation after approximately 10 min of observation or when the individual laid down or was no longer visible. No individual was observed more than once a day. To calculate the proportion of time spent on each behavior during each behavioral sequence, we used behavioral observation transcription software (EthoLog 2.2; Ottoni 2000). To date, 527 observations have been carried out on 101 individuals with an average 5 repeated values (min=2, max=10) per year.

After the focal sampling, if the individual was still visible and if the landscape topography was suitable, we performed a flight initiation distance experiment (FID). That is, we measured the distance between the individual and a source or risk or a potential predator when the individual took flight (Ydenberg and Dill 1986; Stankowich 2008). These observations allow us to study variation among individuals in their behavioral response to a stressful event. To carry out a FID, two people are needed: one walking toward the roe deer at normal walking pace and a second observing and noting the animal's behavior. The two people use walkie-talkies to communicate with each other. Therefore, when the roe deer i/ became vigilant and ii/ when it took flight the walker pushed flags into the ground. Then, using a rangefinder, we measured distance between the walker and the animal when it took flight (Fig. 10). As far as possible, we tried to standardize conditions during these

observations by initiating the approach when the focal animal was side-on and engaged in a feeding phase, with its head above shoulder level, and at a lower altitude than the initial position of the observer. We ensured that the total distance between the observer and the initial position of the focal individual was never inferior to 100 m. To date, 324 observations have been carried out on 79 individuals with an average 4 repeated values (min=2, max=7).



**Figure 9. Observation of a male during a focal sampling.** We recorded the behavior of the individual for 9 min on average based on 6 exclusive behaviors such as here: foraging (A and D), head raised (B) or vigilance (C, by B. Lourtet).



**Figure 10. Schematization of a flight initiation distance realized on a focal individual.** During the flight initiation distance, we noted behavior and we measured four distances: the total distance between the initial position of the walker and the individual (dDA, at least 100 m), the distance before detection (dDV), the tolerance distance (dVF), and the flight distance (dFID).



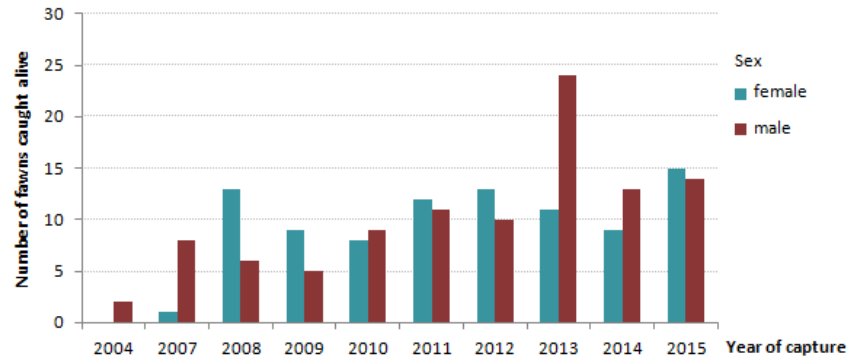
### ***III.2. Fawn capture***

Since 2004, newborn fawns (97 % less than 20 days old, average age at capture = 6.3 days) have been caught by hand each year between the end of April and the middle of June, but more intensively since 2009 (Table 2), mostly by observing the behavior of the mother. Note that roe deer females generally give birth to two fawns per litter (Hewison and Gaillard 2001), but even when we located both fawns of a single litter, we manipulated and marked only one of the siblings as the fate of litter mates is highly inter-dependent, especially in poor cohorts (Gaillard et al. 1998b). We marked fawns only once the mother had fed it and moved away when possible. We first weighed (with a precision of 50 g), sexed and aged fawns using age-classes (1-2, 2-3, 3-5, 5-7, 7-10, 10-15, 15-20, 20-25, 25-30 days old) marked them with two metallic ear tags and an expandable VHF radio collar (Biotrack, Fig. 11). The age of fawns was established in relation to daily monitoring of the mother's appearance (size of her belly, presence/absence of udders) and behavior (reaction to a whistle mimicking the call of a fawn), which provided information on the approximate date of birth, and in relation to the fawn's behavior (Jullien et al. 1992).

In addition, we recorded their behaviors at four different stages of the capture process. At the first stage, we characterized the fawn's behavior before the capture event. We noted if the mother was close to the fawn, if the fawn was lying with the mother or not, and its activity (motionless, moving, following its mother). At the second stage, we noted the fawn's behavior when it was with the observers but before handling. We described the initial position of the fawn at the capture event (lying or standing), the behavior (motionless, moving, fleeing), if it cried (none, a little, a lot), if the capture was easy or not and the number of attempts before catching the fawn. At the third stage, we collected the fawn's behavior during handling. The level of agitation was noted (none, a little, a lot) and as previously, we noted if the fawn cried or not and if he tried to flee. At the last stage, we characterized the fawn's behavior at release. Thus, we measured the latency before the fawn moved, we noted if he came near or close to the observers or if he fled. Moreover, around 15 days after birth, we tried to re-catch all fawns to record both their behavior and body mass to index early stage growth.

We also recorded the characteristics of the site where fawns were found in terms of habitat type (woodland, crops, natural meadows, or artificial meadows such as ray grass,

*Lolium perenne*). Subsequently, fawns were located each day from marking to the end of the summer (1.5 locations per day per individual on average) by radio-telemetry and triangulation. The radio-collars were equipped with a mortality sensor, providing us with information about the current fate of each fawn. When a mortality signal was detected, we immediately recovered the dead animal and, where possible, ascertained the cause of its death.



**Table 2. Number of fawns males and females caught every year since 2004.**



**Figure 11. Fawn's capture.** Photos of the fawn's bed site (A-B, by B. Cargnelutti), its weighing (C, by C. Monestier) and release with an expendable collar (D, by C. Monestier).

### ***III.3. Spatial data***

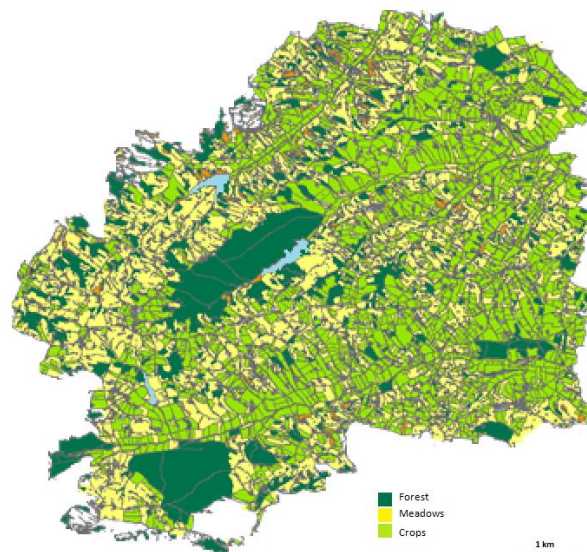
Two types of GPS collars are used to monitor space use of deer: GPS collars (Lotek 3300) and GSM-GPS (Lotek Small WildCell). With GSM, we are able to periodically download the locations of individuals via SMS when the network coverage is good which ensures a better monitoring of animals especially during the dispersal period. For collars without GSM capacity, GPS data are only recovered at the end of a year's monitoring when the collar falls thanks to a pyrotechnic system called "drop-off". The collars are programmed to collect GPS locations at different rates for key life history events. The basic rate is one fix every 4 hours location (between 2002 and 2004) or 6 hours (after 2004) for 11 months. Since 2005, around 13 intensive monitoring periods (range: 5 to 17 per individual) of one location every 10 min for a period of 24 h spaced across the year are included. There is also one fix taken every hour during the natal dispersal period (March-May) for juveniles and during the breeding season (July-August) for adults since 2009.

The error of location associated with each data fix depends on the landscape topography and openness and on the satellite number (Cargnelutti et al. 2007). Thus, locations are more accurate in open areas than in forest, with a median error from 7.0 m to 22.8 m respectively (Cargnelutti et al. 2007). Overall, the collected data have a high resolution. Thus, in relation to their true position, 50% of fix locations were within a 14 m radius. Moreover, for each fix we obtain other information such as the date, time, altitude, time taken by satellites to do the fix, number of satellites and the quality of satellite configuration (PDOP), and the fix status (index of its quality). Once GPS data are downloaded, we performed differential correction to improve their fix accuracy (Adrados et al. 2002).

### ***III.4. Cartography***

The study site has been fully mapped using GIS software (Geographic Information System), ArcView GIS 3.2a, in order to identify the different habitats making up the mosaic landscape. Each habitat patch has been digitalized manually from aerial photographs and then identified in the field (Fig. 12). Each year, field surveys are carried out to update these data

because of crop rotation for example. Data are represented as a layer of geographic information of patch use including different categories, as follows: water, woods, hedgerows, natural grasslands, crops (cereal, corn, sunflower, sorghum, rapeseed ...) and infrastructures (roads, homes, outbuildings, gardens ...). More precisely, the woodland category gathered forests and copses together. The hedgerow are defined as narrow linear separating two parcels and with a small area (average area of 0.09 ha) contrary to copses which are densely wooded (average area of 1.68 ha).



**Figure 12. Study site cartography.** Solely the forests, meadows and crops are represented on this map, but each habitat is known so that we can create different types of map according to our needs.

### III.5. Statistical analyses

All analyzes were performed using the R software versions 2.15.1 and 3.1.0 (R Development Core Team 2013). R is a free software with a GNU license <http://cran.r-project.org>. It compiles and runs on a wide variety of UNIX platforms and similar systems (including FreeBSD and Linux), Windows and MacOS. R contains many extensions through "packages" or libraries developed independently and downloadable on CRAN (Comprehensive R Archive Network) enabling a wide variety of modern statistics. The software, commonly used in biology research, is a powerful tool for matrix calculation, statistical analyzes and composition of graphics and is also a simple and powerful programming language (related to C).



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## **Chapter III**

### **Into the wild...personality**

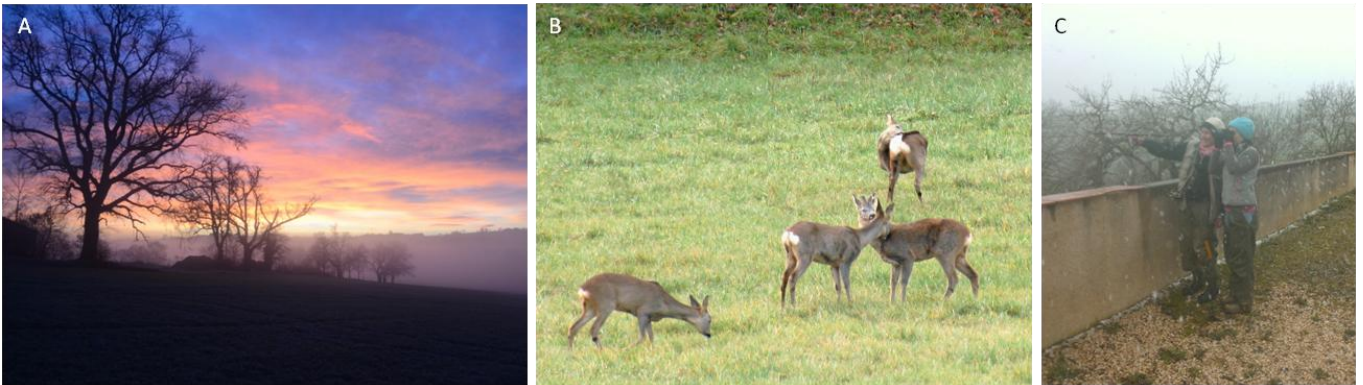
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## Inter-individual variability in behavior in a wild population, the case of roe deer

*'Observations were carried out during peak activity of roe deer , at dawn and dusk (A)[...]. After identification of the focal individual, we carried out a focal observation with binoculars (C) during foraging activity by recording the behavioral sequences (B) on a numeric recorder [...].'*



Photos: A by O. Couriot, B by B. Lourtet, and C by S. Rubiero





## RESUME

Il est maintenant reconnu que les individus d'une espèce ou d'une population diffèrent dans leur comportement. Cette variabilité interindividuelle, appelée communément personnalité, est d'ailleurs présente au sein d'un très grand nombre de taxons. Depuis les années 2000, l'attrait pour l'étude de la personnalité n'a cessé d'augmenter. Il apparaît d'ailleurs intéressant d'étudier la personnalité au sein de populations sauvages afin de mieux appréhender les mécanismes permettant le maintien de ces différences comportementales. Cependant, mener de telles études en milieu naturel se révèle être particulièrement ardu surtout pour obtenir des mesures répétées. C'est dans ce contexte que se place notre étude dont l'objectif principal était de mettre en évidence de la variabilité interindividuelle comportementale et physiologique chez le chevreuil dans différents contextes que nous supposons pouvoir refléter certains traits de personnalité (la timidité-témérité dans une situation stressante mais également dans une situation sans risque particulier puis, l'activité). Ainsi, nous avons d'abord testé la cohérence des paramètres comportementaux et physiologiques en estimant leur répétabilité dans un contexte donné. Ensuite, nous nous sommes intéressés aux corrélations possibles entre ces différents paramètres au sein d'un contexte ou entre contextes. Nous avons trouvé que certains paramètres étaient bien cohérents dans le temps ce qui prône pour l'existence de traits de personnalité au moins dans un contexte donné. Nous avons également trouvé que les paramètres comportementaux et physiologiques étaient corrélés dans un contexte donné ce qui suggère l'existence d'une multi-dimensionnalité à l'échelle de l'individu. Enfin, les paramètres étaient aussi corrélés entre contextes ce qui suggère l'existence de syndromes comportementaux. Par conséquent, cette étude exploratoire nous aura permis de mettre en évidence de la variabilité interindividuelle comportementale chez le chevreuil vivant dans des milieux naturels et semble donc être une première étape prometteuse dans ce domaine d'étude.

**Mots clés :** syndrome comportemental, multi-dimensionnalité, ongulés sauvages, comportement, physiologie

## **ABSTRACT**

Recently behavioral ecologists have recognized that individual variability in behavior exist in a wide range of taxa. Hence, the attractiveness for the study of personality has increased since the 2000s, but its study in natural environments is particularly challenging because of the difficulty of obtaining high quality repeat observations. The general aim of this study was to test for consistent inter-individuals differences in behavioral and physiological parameters in wild roe deer in different contexts which we assumed to reflect different personality traits or proxies of personality traits (shyness-boldness in a risky situation, shyness-boldness in a baseline risk context, and activity). Thus, we first tested for the temporal consistency of behaviors expressed in a given context and then, we tested for their potential covariations within and between contexts. We found that certain behaviors were consistent over time, suggesting that they characterize some personality traits in specific contexts. Then, we found correlations among behavioral parameters and temperature within a given context, suggesting a multi-dimensionality in the inter-individual variability of behavior as well as correlations among parameters in different contexts suggesting the existence of a behavioral syndrome. Consequently, this exploratory study seems a particularly promising approach for understanding the evolution of personality and behavioral syndromes in wild large mammals.

**Key words:** behavioral syndrome, multi-dimensionality, wild ungulates, behavior, temperature

## INTRODUCTION

Individual variability has been viewed and treated as a noise for a long time (Wilson 1998). However, recently behavioral ecologists have recognized that individual variability in life-history traits could be partly explained by differences in individuals' behavior. In general, inter-individual heterogeneity in life-history traits is often associated with phenotypic attributes such as sex (Kruuk et al. 1999), body mass (Hewison and Gaillard 2001), age (Yoccoz et al. 2002), social status (Altmann and Alberts 2003) or more commonly with plasticity. Thus, behavior flexibility is often seen as immediate, reversible and not very limited. However, individuals often show limited plasticity and differ in their response to the same environmental stimulus (Dingemanse and Réale 2005). When these behavioral differences among individuals are consistent over time and across situations (Gosling 2001; Réale et al. 2007), they may make up an overall personality trait (Gosling 2001). Five behavioral dimensions ("Big Five" theory: Gosling and John 1999; Réale et al. 2007) are commonly used in behavioral ecology to describe personality: shyness-boldness, exploration-avoidance, activity, sociability and aggressiveness. Besides, these personality traits have important evolutionary and ecological implications (Wilson et al. 1994; Réale et al. 2007). Thus, a growing number of studies have shown that personality traits affect life-history traits such as dominance (Dingemanse and de Goede 2004), natal dispersal (Dingemanse et al. 2003), the stress response (Carere et al. 2001), reproductive performance, or other fitness components of individuals (Both et al. 2005). More broadly, at a population level, personality influences species' distribution (Clobert et al. 2009), explaining for example their tendency to be invasive (Cote et al. 2010) and their ability to adapt to rapid environmental changes (Sih, Bell, and Johnson 2004; Sih et al. 2011).

The attractiveness for the study of personality has increased since the 2000s, but how personality traits are maintained and what exactly are the effects of environmental factors on these personality traits is still not clear, especially in wild populations. However, several explanations have been proposed to explain why natural selection has not resulted in the selection of a single type of personality with the highest fitness, but rather has favored the maintenance of contrasting types of personality with, ultimately, an equal fitness (see the trade-off theory for an exemple, Wolf and Weissing 2010). For instance, one mechanism promoting maintenance of behavioral variation which assumes fitness equality involves

spatial variation (i.e. for example, variability in food resources or predators) in combination with limits to phenotype-environment matching (Pearish et al. 2013). Indeed, there is some evidence that specific behavioral profiles occur more frequently in certain environments (Dingemanse et al. 2010; J. Stamps and Groothuis 2010; Pearish et al. 2013). In this scenario, the favored behavioral type in one habitat differs from the one in another habitat. For example, shy individuals would be more likely to occur in relatively safe habitats where predation risk is lower. Thus, the optimal strategy for individuals is to adjust their behavior so that it is best suited to a particular habitat (Wolf and Weissing 2010).

The study of personality in natural environments is particularly interesting to highlight personality traits and to better understand the mechanisms maintaining them. However, its study is also challenging because of the difficulty of obtaining high quality repeat observations. Indeed, a crucial point when studying personality is to test for the consistency of the individual's behavior through time or across contexts (Campbell et al. 2009). Indeed, repeatability can be used as a first estimate of individual consistency in a behavioral trait (Boake 1989), but this requires repeat observations to measure repeatability which is complicated in the wild (Campbell et al. 2009). Consequently, much research on personality to date has measured behavior in captivity (Bell 2005; Herborn et al. 2010). However, studying personality only in captivity may be misleading because personality is often highly context-specific (Réale et al. 2007). Isolation from the appropriate context may suppress or subvert personality traits in captivity. For example, numerous studies suggest individuals modify their risk-taking behavior in relation to the presence and identity of conspecifics meaning that social isolation in captivity may modify an individual's responses and behavior (van Oers et al. 2005; Apfelbeck and Raess 2008; Pike et al. 2008). Another context-specific example refers to territorial species where results may differ between captivity and the wild. For example, Verbeek et al. (1999) found a negative relationship between dominance and exploratory tendency in artificially constructed groups of great tits (*Parus major*), whereas Dingemanse and de Goede (2004) found the opposite in wild groups of the same species. So the absence of a territorial context in captivity may limit our ability to predict the ecological significance of personality traits expressed in captivity.

In addition, it is recognized that inter-individual differences in behavior are often not solely involved in one personality trait, but rather in several traits, resulting in a behavioral

syndrome (Sih, Bell, and Johnson 2004). A behavioral syndrome is a suite of correlated behaviors expressed either within a given behavioral context, across different contexts or situations (Sih, Bell, and Johnson 2004). For instance, Bell and Sih (2007) found that aggression and risk taking were correlated only after exposure to a predator in a predator-naïve population of sticklebacks (*Gasterosteus aculeatus*), suggesting that the absence of the predator-prey context affects personality trait estimates in captivity. Thus, the relationship between different behavioral traits is generally context dependent, which reinforces the interest of studying personality in the wild. Moreover, personality seems particularly interesting from an evolutionary point of view. For example, what an individual does in one context is linked to what it does in other contexts. Thus, bolder individuals will be always bolder than shyer individuals whatever the context. Consequently, this behavior will be appropriate in some situations, such as searching for food or growth, but unsuitable in situations where caution or care is more appropriate, such as in the presence of predators Biro et al. (2004, 2006). This results in a trade-off between different contexts or situations with behaviors fitting well or poorly depending on the context which could explain the maintenance of individual variation in behavior (Sih, Bell, and Johnson 2004).

In addition to the fact that behavioral traits may be correlated to each other, a multi-dimensionality may also exist as regards to the origin of the expression of a given behavior. Indeed, personality involves correlations among parameters at different levels including, for example, correlations between behavioral, physiological and biochemical parameters. For instance, Koolhaas et al. (1999) defined inter-individual differences in the stress response as “a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals”. Links between the behavioral level and the neuro-physiological level have been described in a few species, suggesting the necessity and relevance to include parameters from different scales within the organism (in mice and rats: Koolhaas et al. 1999; birds: Carere et al. 2003; fish: Overli et al. 2005). Thus, a multi-trait multi-method design is needed to understand these dimensions and their relationship with each other (Campbell and Fiske 1959).

The general aim of this study was to test for consistent inter-individuals differences in behavior in wild roe deer (*Capreolus capreolus*) in different contexts which we assumed to reflect different personality traits or proxies of personality traits (i/ shyness-boldness in a

risky situation, ii/ shyness-boldness in a baseline risk context, iii/ activity). To do that, we collected behavioral (behavioral scores) and physiological (temperature) data in a stressful situation (at handling during capture events and during flight initiation distance) potentially reflecting the i/ shyness-boldness gradient (Réale et al. 2000, 2007). In addition, we also recorded behaviors during observation (without any contact with individuals) supposed to reflect ii/ the shyness-boldness during routine activities such as the search for food acquisition without perceived risk (i.e. in a baseline risk context). Then, we measured the mobility (with GPS data) and activity (with activity sensors on GPS collar) of individuals to index iii/ their activity level. Thus, we first tested for the temporal consistency of behaviors expressed in a given context and then, we tested for their potential covariations within and between contexts. Indeed, rather than focus on a particular personality trait, the aim was to be able to describe the inclusive personality, including its multi-dimensionality and correlations among personality traits across different contexts or situations (behavioral syndrome) and the multi-dimensionality with the use of different levels of the organism (behavioral and physiological levels).

## **MATERIAL AND METHODS**

### ***Study site***

The study was carried out at Aurignac (7500 ha) in the south-west of France (43°13'N, 0°52'E). The climate is oceanic with Mediterranean tendencies, with an average annual temperature of 11-12 °C and total precipitation of 800 mm. This hilly region is a mixed landscape mostly covered by open habitats interspersed with small woodland patches (mean  $\pm$  SD: 2.9  $\pm$  7.6 ha) and two main forests (672 ha and 515 ha). Meadows and cultivated fields occupy 31.9 and 36.2 %, respectively, of the total surface area of the study site. Woodland covers 19.3 % of the total study site and is dominated by oak (*Quercus spp.*) (see Hewison et al. 2009 for further details).

## ***Data collection for the response to a stressful and/or risky situation***

### *Capture and handling*

Roe deer were caught from 2002 to 2015 during winter (from November to March) using drive netting. Since 2009, we recorded the behavior at capture, during handling and at release for 190 adults (i.e. older than 1 year at first winter capture). We attributed a score of 1 (occurrence) or 0 (absence) for each of the following behaviors: 1) the individual struggled in the net (see also Réale et al. 2000), 2) it turned upside down in the box, 3) it attempted to remove its collar at release, and 4) it fell (i.e., stumbled and fell to the ground) at release. In addition, we attributed a score of 1 if 5) the individual struggled and panted on the table during marking, or a score of 0.5 if it struggled only (otherwise 0), and a score of 1 (high speed running), 0.5 (moderate running), or 0 (trotting) in relation to 6) its flight behavior at release. Indeed, flight speed at release is commonly used for the assessment of temperament in cattle (Müller and von Keyserlingk 2006). An index of reaction to this stressful event was then calculated as the mean of the scores for these 6 behavioral items describing a stress profile gradient ranging from 0 to 1, with 1 indicating a priori an individual with a high response to a stressful situation.

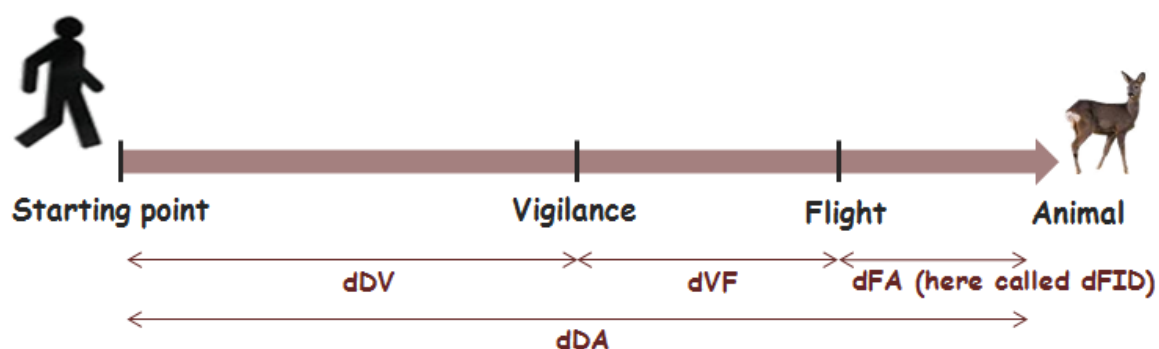
We also measured the rectal temperature of 187 adults (using a Digitemp Color thermometer with a precision of 0.1 °C, potentially taking 36 different values, over the recorded range). Following Montané et al. (2003)'s study showing that body temperature of roe deer decreases over time from capture to 45 min after capture before stabilizing, we recorded temperature more than 1 h after the capture event in all cases. We recorded the temperature of each individual at the beginning and at the end of the marking procedure, and used the mean of these 2 values to index the adult's stress-induced hyperthermia (Korhonen et al. 2000; Carere and van Oers 2004a). We removed three individuals from the dataset with a very low mean temperature (<36.9 °C) because they were clearly suffering from hypothermia (compared with the average rectal temperature of  $38.8 \pm 0.04$ ).

### *Flight initiation distance*

Since 2010, behavioral campaigns have been carried out every year from the end of February to the end of April where we measured flight initiation distance (i.e. the distance



between the predator/observer and the target individual when it takes flight; Ydenberg and Dill 1986; Stankowich 2008). To measure a FID two people are needed: after the identification of a focal individual, one walks toward the roe deer at normal walking pace, while a second observer notes the individual's behavior. Both people transmit information to each other by walkie-talkie. When i/ the deer became vigilant and ii/ when it took flight, the walker pushes a flag into the ground. Then, using a rangefinder or a tape measure, we subsequently measure: i/ the total distance between the initial position of the individual and the initial position of the observer, ii/ the tolerance distance, that is, the distance between the locations when the individual became vigilant and when it took flight, and iii/ the flight distance, that is, the distance between the walker's location and the location of the animal when it took flight (Fig. 1). We ensured that the total distance between the initial location of the observer and the initial location of the focal individual was never inferior to 100 m (see the general Material and Methods for more details). We obtained observations for 49 adult individuals.

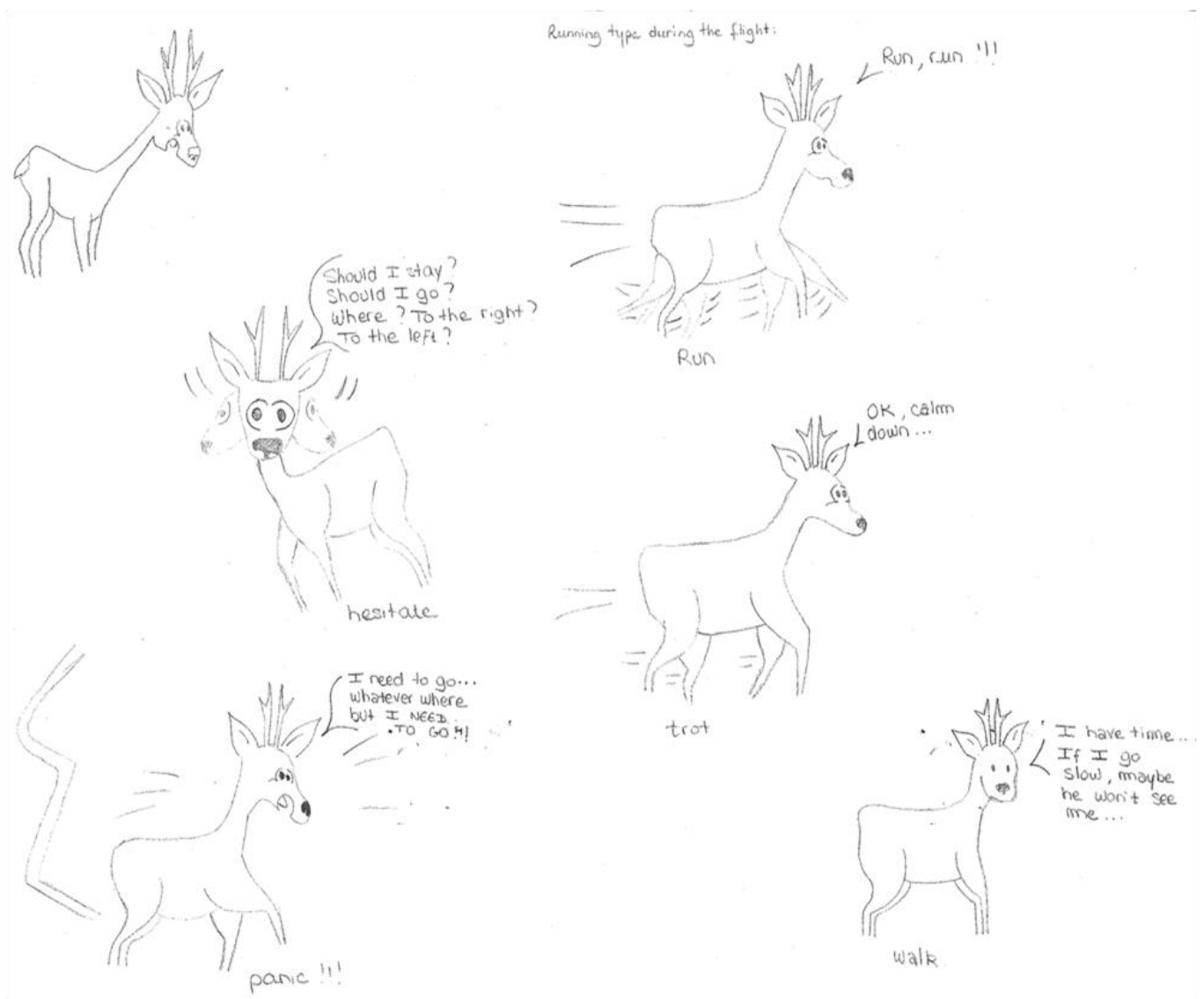


**Figure 1. Schematization of a flight initiation distance realized on a focal individual.** The distance between the walker and the individual is at least of 100 m. During the flight initiation distance, we noted when the individual becomes vigilant and when it flees. Then, we measure four distances: the total distance between the initial position of the walker and the individual (dDA), the distance before detection (dDV), the tolerance distance (dVF), and the flight distance (dFID).

### *Flight score*

During flight initiation distance measures, we also recorded the flight behavior of individuals from which we generated a flight score. We attributed a score of 1 (absence) or 0 (occurrence) for each of the following behaviors: 1) the individual appears to hesitate to leave its foraging site, 2) it stops during its flight meaning it was totally immobile at least two seconds before starting again its run, and 3) it turns towards the walker meaning after it

stopped, we note whether it turns the head in the direction of the walker and looked at him. We also attributed a score of 1 if 4) it panics so that, irrespectively of the landscape, it zigzags (otherwise 0, i.e. straight trajectory). Finally, we characterize its flight behavior once the walker was detected and the individual decided to flee the habitat (Fig. 2). Thus, we attributed a score of 1 if the individual had a high speed running, 0.5 for a moderate running, and 0 for trotting. An index of reaction to the observer's approach was then calculated as the mean of the scores for these 5 behavioral items, ranging from 0 to 1, with 1 indicating a priori highly reactive individuals to the observer.



**Figure 2.** Illustration of behaviors expressed by the focal individual during a flight initiation distance. From top to bottom, left to right: the hesitation, panic and running type of the individual (by O. Couriot).

### ***Data collection for behaviors expressed during a baseline risk context***

In addition, from the end of February to the end of April, and before carrying out a FID measure, we monitored the individual's behavior during an undisturbed foraging phase to index variation among individuals in behavioral profile in a context of baseline level of predation risk and/or disturbance. Observations were carried out during peak activity of roe deer (Jeppesen 1989), at dawn and dusk, at an average distance of 260 m. After identification of the focal individual, we carried out a focal observation with binoculars (10x42) during foraging activity by recording the behavioral sequences on a numeric recorder for 9 min on average (min=5 min, max=15 min). We recorded 6 exclusive behaviors: vigilance (head above shoulder level while scanning surroundings), feeding (collecting food, or searching for food with head at ground level), head raised (head above shoulder level but without scanning), walking (head above shoulder level), grooming, and 'others' (accounting for less than 10 % of the focal duration and so not taken into account in the analyses). To calculate the proportion of time spent on each behavior for each observation, we used a transcription software (EthoLog 2.2; Ottoni 2000; see the general Material and Methods for more details). We obtained these behavioral sequences for 72 individuals.

### ***Data collection for estimating individual activity***

#### *Mobility*

During capture events, we equipped most of the adults with a GPS collar giving us detailed information on the spatial behavior of the individual for the current year. To describe the behavior of the individual at a fine temporal scale, since 2005 we programmed around 12 intensive monitoring periods of one location every 10 min for a period of 24 h spaced across the year. We performed differential correction to improve fix accuracy (Adrados et al. 2002).

From these data, we calculated mean average speed (m/s) for each individual as the distance between two successive locations divided by the 600 s fix interval. We also used a feature of the movement trajectory: the mean turning angle between two successive segments and its standard error, to provide an index of path sinuosity, with low values corresponding to a more linear path. Both measures were obtained using the adehabitatLT

package (Calenge 2015). We obtained data on individual mobility for 165 individuals with an average of 13 periods/individual.

#### *Activity sensors*

GPS collars also provided information on activity through two head position sensors (Gottardi et al. 2010). To estimate variation in the level of activity for each intensive monitoring period, we used the recorded activity sensor data. These sensors provide the sum of the number of horizontal and vertical head movements every 5 min. Hence, we described inter-individual variability in the mean daily activity for i/ vertical, and ii/ horizontal movements, and iii/ combined mean activity for the vertical and horizontal movements. High values indicated adults with high variation in their head movements, i.e. individuals with more strongly contrasted phases of behavior. We obtained the individual's activity thanks to activity sensors for 152 individuals.

### ***Statistical analyses***

#### *Within individual repeatability of the behavioral measures*

We assessed the within-individual consistency of the i/ response to a stressful and/or risky situation, ii/ behaviors expressed during a context of baseline level of predation risk, iii/ activity. The repeatability was calculated with at least two repetitions of each parameter per individual (i.e. 31 adults were sampled at least twice during capture events: behavioral score = mean of 2.43 measures/individuals; temperature = mean of 2.50; 41 adults had at least two flight initiation distance observations: tolerance distance = mean of 4.52; flight distance = mean of 4.52; flight score = mean of 4.52; 60 adult individuals had at least two focal sampling observations: vigilance level = mean of 5.00; 161 adults had at least two periods of intensive monitoring: turning angle = mean of 13.20; speed = mean of 13.20; 149 individuals had at least two days of activity sensors: X activity = mean of 13.19; Y activity = mean of 13.19; mean activity = mean of 13.19). Repeatability coefficients were calculated using the most commonly used method in behavioral ecology: the Lessells and Boag (1987) method which corresponds to an *F* table of an ANOVA with individual identity treated as a factorial

predictor. To do that, we used the “rpt.aov” function of the “rptR” package (Schielzeth and Nakagawa 2011) in R version 3.1.0 software (R Development Core Team 2013). We log-transformed mobility and activity data prior to the estimation of repeatability to achieve normality. We also used an arcsinus squared root transformation for the time spent vigilant which was expressed as a proportion. Moreover, as the tolerance distance and the flight distance depend on the total distance between the observer and the focal individual, we controlled for that effect using the residuals of the simple linear regression between the total distance and the tolerance distance or the flight distance, respectively. Note also that repeatability estimates were calculated within a year for all parameters except for the capture data (i.e. behavioral score and temperature) as individuals are only caught once per year. We choose to estimate repeatability within a year since we have a sufficient number of repetitions for a given individual per year. Moreover, the probability to obtain repetitions another year is always lower than the one within a given year in our study site. Hence, repeatability estimates were measured between years for the capture data and within a year for the other parameters.

#### *Data descriptions and correlations among behaviors*

As we used several behaviors expressed each time in a given context, the aim of the first analyses was to explore the degree of autocorrelation among parameters using a Principal Component Analysis (PCA). For these analyses, we used the mean value of each behavior per individual. Indeed, in addition to the fact that performing PCA with repeated data where the number of repetitions differs among individuals is not appropriate, within the context of personality, inter-individual variability in individual behavior is supposed to be consistent across contexts and/or over time (Réale et al. 2007). Therefore, we included individuals with only one observation. Thus, we performed three different PCA: one for the behaviors expressed during flight initiation distance (i.e. a stressful and risky context; 49 individuals); one for the behaviors expressed during a baseline risk context (72 individuals); and a last one combining the behaviors retained in the two previous PCA plus the behaviors collected during capture events (behavioral score and temperature) and the behaviors measuring the individual’s activity. Indeed, contrary to the behaviors expressed during flight initiation distance and a baseline risk context where we collected numerous behaviors, we collected

only few behaviors during capture events and for the activity. Hence, we did not need to summarize the information, and so perform a PCA was useless. We also quantified the degree of correlation among these selected behaviors using a Pearson correlation using both the “cor” and “rcorr” functions in the “Hmisc” package (Harrell 2015) to obtain the correlation matrix (see Results) with their associated p-value.

## RESULTS

### *Within individual repeatability of the behavioral measures*

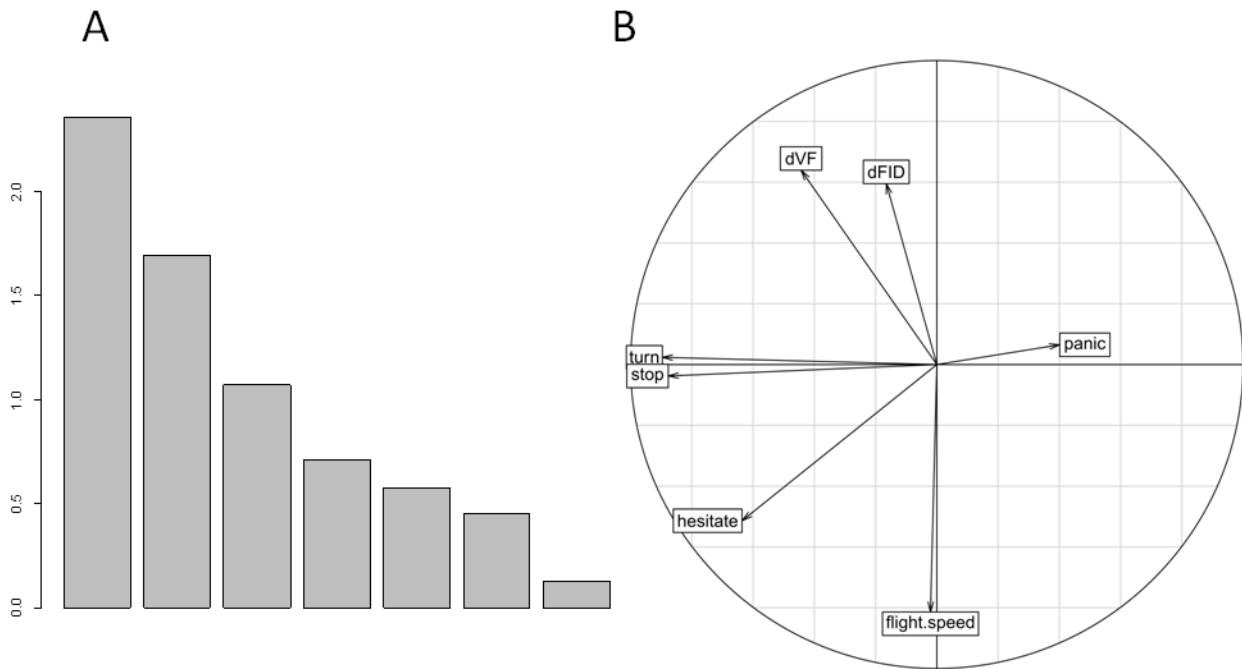
The activity in x, y together with the combined mean activity, speed and temperature were all highly repeatable (Table 1). The behavioral score during capture and vigilance level were moderately repeatable. The flight distance was repeatable, but with quite low values, whereas the tolerance distance, the flight score and the turning angle were not repeatable.

**Table 1. Repeatability estimates (r) of the behaviors in a population of wild roe deer.** The behavioral score and temperature were measured during capture events. The tolerance distance, flight distance and flight score were measured during observations of flight initiation distance. Thus, these five behaviors were measured in stressful and risky situations. The vigilance level was measured during a context of baseline risk. The turning angle and the speed of individuals were measured thanks to intensive monitoring periods obtained from GPS locations and characterized the individuals’ mobility. Finally, the activity level of individuals was characterized using activity sensors in x and y or using the mean activity from both sensors.

Trait	r	CI
Behavioral score	0.214	[0.000, 0.209]
Temperature	0.463	[0.075, 0.652]
Tolerance distance	0.010	[-0.137, 0.165]
Flight distance	0.150	[0.000, 0.319]
Flight score	0.050	[-0.110, 0.214]
Vigilance level	0.221	[0.088, 0.351]
Turning angle	0.025	[0.001, 0.049]
Speed	0.364	[0.208, 0.319]
Activity in x	0.823	[0.787, 0.859]
Activity in y	0.682	[0.628, 0.736]
Mean activity	0.728	[0.679, 0.777]

***Data descriptions and correlations among behaviors***

As regards the PCA for the flight initiation distance observations, the two first components of the PCA captured 58 % the total inertia (33.70 % for PC1 and 24.30 for PC2; Fig. 3a). All behaviors correlated negatively with PC1 except panic behavior (Fig. 3b). More precisely, the three behaviors: 'stop', 'turn' and 'hesitate' were highly and significantly correlated to each other (Table 2), but 'flight speed' behavior was poorly correlated with these three behaviors as it was more correlated with PC2. Indeed, it was negatively correlated to PC2 whereas the flight distance (dFID) and the tolerance distance (dVF) were positively correlated to PC2. Thus, we supposed that PC1 reflected an individual's decisiveness to risk, with negative values indicating that individuals were not really decided to leave the site so that they can interrupt their run whereas positive values indicate more that the individual really want to escape to the perceived risk (i.e. they are decided to leave the foraging site). We supposed that PC2 reflected risk tolerance of individuals, with positive values for individuals leaving the foraging site earlier when disturbed (longer distance of tolerance and flight), i.e. individuals with a lower level of risk acceptance. On the contrary, negative values indicate individuals that had high tolerance distance and flight distance (i.e. short distance between them and the source of disturbance) and so, adopted a fast running type to leave the foraging site. Hence, due to behavioral correlations and the fact that most of the total inertia was explained by the two first components analysis, we retained one behavior on each principal component to summarize the information: the "stop" variable for PC1, and the flight distance for PC2. Hence, we used these two behaviors in the third and final PCA.



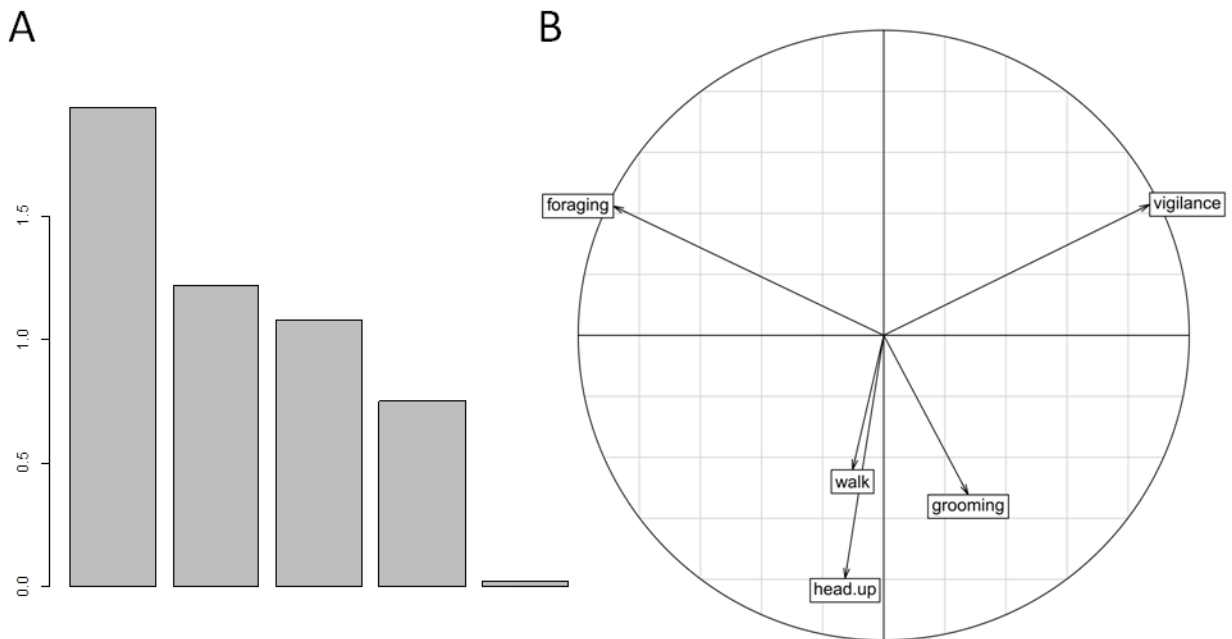
**Figure 3. Behaviors expressed during flight initiation distance observations (i.e. risky situation) in a wild population of roe deer.** Principal Component Analysis for 7 behaviors: the tolerance distance (dVF), flight distance (dFID), flight behavior including flight speed, hesitate, stop, panic, and turn. A: decomposition of variance among principal components; B: correlation circle showing the projection of all the behaviors on principal components (x-axis = PC1; y-axis = PC2).

**Table 2. Matrix of the Pearson correlation coefficients among 7 behaviors measured during flight initiation distance observations (tolerance distance (dVF), flight distance (dFID), flight behavior including flight speed, turn, stop, panic, hesitate).** Stars (\*) indicate significant correlation coefficients (p-value > 0.05).

	dVF	dFID	flight.speed	turn	stop	panic	hesitate
dVF	1						
dFID	0.27 .	1					
flight.speed	-0.35 *	-0.26	1				
turn	0.29 .	0.1	-0.06	1			
stop	0.32 *	0.01	0.07	0.83 *	1		
panic	-0.07	-0.14	0	-0.14	-0.17	1	
hesitate	-0.01	-0.07	0.35 *	0.46 *	0.37 *	-0.34 *	1



As regards the PCA for the behaviors expressed during a context of baseline risk, the first component of the PCA (PC1) captured 38.75 % of the total inertia and was much more informative than all subsequent axes (Fig. 4a). ‘Foraging’ and ‘vigilance’ were projected on PC1 and negatively correlated to each other (Fig. 4b). Moreover, their negative correlation was significant (Table 3). However, the three other behaviors were correlated with PC2 (explaining 24.30 % of the total inertia). That being said, if we focused solely on PC1, we found that ‘walk’, ‘head up’ and ‘foraging’ were positively correlated to each other with significant correlations between foraging and the two other behaviors and negatively correlated to ‘grooming’ and ‘vigilance’. Knowing that PC1 explained a great part of the total inertia and that foraging and vigilance level were negatively correlated, we only kept the vigilance level for the third PCA.

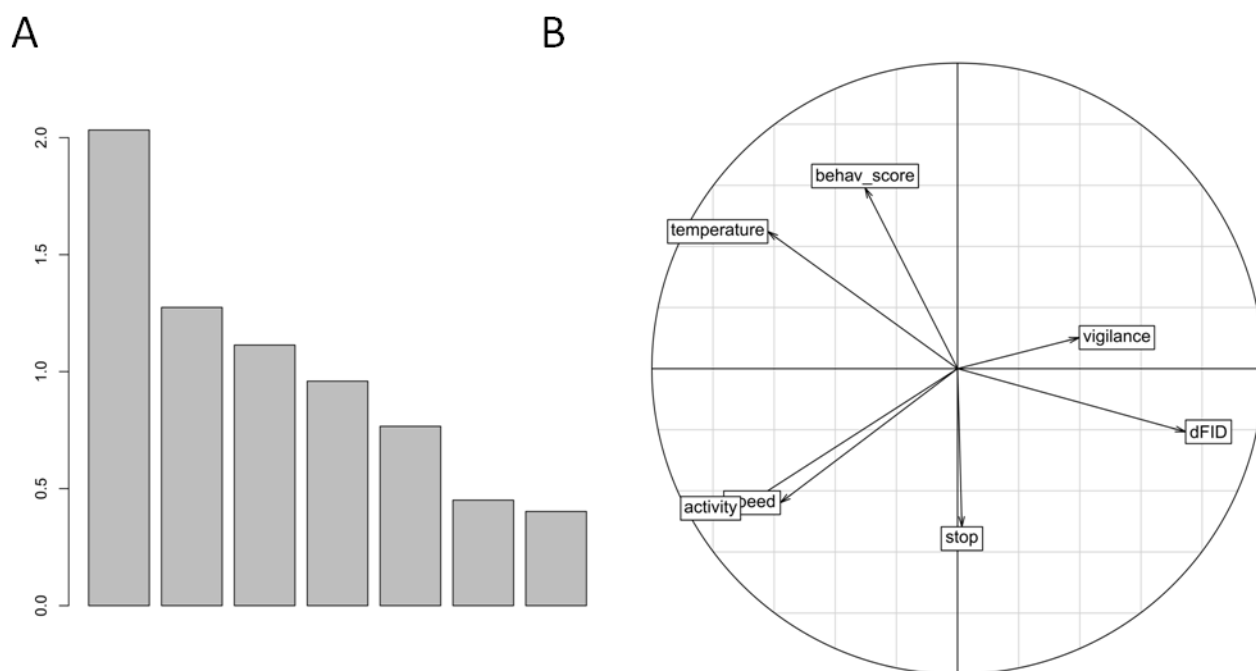


**Figure 4. Behaviors expressed during a context of baseline risk in a wild population of roe deer.** Principal Component Analysis for 5 behaviors: the time spent foraging, vigilant, grooming, walking or having the head raised (head above shoulder level but without scanning). A: decomposition of variance among principal components; B: correlation circle showing the projection of all the behaviors on principal components (x-axis = PC1; y-axis = PC2).

**Table 3. Matrix of the Pearson correlation coefficients among 5 behaviors measured during a context of baseline risk (vigilance, head up, walk, grooming, and foraging).** Stars (\*) indicate significant correlation coefficients (p-value > 0.05).

	vigilance	head up	walk	grooming	foraging
vigilance	1				
head up	-0.34 *	1			
walk	-0.24 *	0.13	1		
grooming	-0.15	0.16	-0.21 .	1	
foraging	-0.6 *	-0.21 .	-0.25 *	-0.35 *	1

Finally, the last PCA explored the correlations between 7 behaviors within and across contexts: whether the individual stops during its run (i.e. the decisiveness in the first PCA), the vigilance level (second PCA), and the behavioral score and rectal temperature measured during capture events, and the speed and combined mean activity. The first component of the PCA (PC1) captured 30.04 % of the total inertia and was much more informative than all subsequent axes (Fig. 5a). The mean behavioral score, mean temperature, mean speed and mean activity were correlated to each other and negatively correlated with PC1 whereas the mean flight distance and mean level of vigilance were positively correlated to this axis (Fig. 5b) but the decisiveness (represented by the fact that individuals stop during their run) was not projected on PC1. Moreover, 'speed' and 'activity' behaviors were significantly correlated according to the Pearson correlation matrix (Table 4).



**Figure 5. Correlations within and between contexts among seven parameters.** Principal Component Analysis for 7 behaviors: the flight distance (dFID), decisiveness (stop), vigilance, behavioral score (behav\_score), temperature, speed and mean activity (activity). The flight distance and decisiveness (retained in the PCA for the behaviors expressed during flight initiation distance), and temperature and behavioral score are supposed to reflect the shyness-boldness in a stressful and risky situation. The vigilance level (retained in the PCA for the behaviors expressed during a baseline risk context) is supposed to index the shyness-boldness in a baseline risk context. The speed and the combined mean activity are assumed to index activity. A: decomposition of variance among principal components; B: correlation circle showing the projection of all the behaviors on principal components (x-axis = PC1; y-axis = PC2).

**Table 4. Matrix of the Pearson correlation coefficients among 7 behaviors within and between contexts (speed, behavioral score, temperature, mean activity, vigilance, flight distance (dFID), and decisiveness).** Stars (\*) indicate significant correlation coefficients (p-value > 0.05).

	speed	behav_score	temperature	activity	vigilance	dFID	decisiveness
speed	1						
behav_score	0.07	1					
temperature	0.00	0.24	1				
activity	0.40 *	-0.10	0.27	1			
vigilance	-0.05	-0.04	-0.20	-0.32	1		
dFID	-0.37	-0.24	-0.40 *	-0.32	0.03	1	
decisiveness	0.10	0.00	-0.09	0.10	0.04	0.09	1

## DISCUSSION

Our first aim was to test for consistent inter-individual differences in behavior in wild roe deer in different contexts, assuming that these behaviors reflect different personality traits or proxies of personality traits. We found that certain behaviors were consistent over time, suggesting that they characterize some personality traits in specific contexts. In a meta-analysis, Bell et al. (2009) found an average repeatability of behavioral traits of 0.37, providing a baseline level with which to compare our estimations of repeatability. Using this as a standard, activity for x and y positions and combined mean activity were highly repeatable ( $r = 0.823$ ,  $r = 0.682$ ,  $r = 0.728$  respectively), as was individual speed ( $r = 0.364$ ) which is consistent with more detailed results reported later (Chapter V). Body temperature was also highly repeatable ( $r = 0.463$ ). Behavioral score at capture and vigilance level were moderately repeatable ( $r = 0.214$ ,  $r = 0.221$  respectively). In contrast, the flight distance was only weakly repeatable ( $r = 0.150$ ). We previously found similar results as regards to the behavioral score and temperature (Bonnot et al. 2014; Monestier et al. 2015; Chapter V). We suggest that these measures index the reactivity-proactivity gradient of individuals, with proactive individuals having higher behavioral score and temperature (Monestier et al. 2015). However, we expected to find higher repeatability estimates for vigilance level and flight distance as they are generally considered as important components of animal personality or behavioral syndromes, particularly in ungulates and birds (Bergvall et al. 2011; Couchoux and Cresswell 2012; Chapter V). Given that repeatability estimates vary greatly between different classes of behavior (Bell et al. 2009), we suggest that vigilance level and flight distance are more sensitive to environmental context (Couchoux and Cresswell 2012) and, hence, are somewhat more variable for a given individual. An idea could be to study personality in the context of reaction norms of behavior (Dingemanse et al. 2010). However, we would need more data and that for different types of habitat; however we only measure vigilance level and flight distance in open habitat since in the individuals' observation in closed habitats is highly challenging.

Our second aim was to be able to describe the personality using a multi-dimensional approach across personality traits and across different contexts or situations (behavioral syndrome) and using information across different levels of the organism (behavioral and

physiological levels). As regards to the study of behaviors expressed during a controlled disturbance (flight initiation distances), we found correlations among behaviors allowing us to determine individual behavioral types along two gradients. The first continuum distinguished individuals that expressed a higher level of panic from those who hesitated to leave the foraging site, stopping their flight and turning towards the foraging site and the walker more often. We supposed that this continuum probably reflected the individuals' decisiveness toward a risk with positive values indicating individuals favoring their food intake and positive values indicating individuals preferring leaving the site due to the perceived risk. The second continuum seemed to reflect risk acceptance of individuals with positive values reflecting individuals leaving earlier the foraging site so individuals with a lower risk acceptance. Thus, individuals with higher flight distance or tolerance distance had a slower escape speed. In contrast, individuals which expressed shorter distances with respect to the source of risk before leaving the foraging site, seemed to be risk-tolerant. Therefore, they left the site later, but ran faster when they did so to escape to the potential predator. With this second continuum, we observed a trade-off between food acquisition and risk avoidance. Individuals favoring their food intake must have a higher tolerance to the perceived risk but have to leave the foraging site with a fast run to escape predation risk meaning they pay a cost in terms of energetic expenditure. On the contrary, individuals favoring their security, leave the site earlier meaning with higher flight distance so that they can have a slower running type since the risk is far away from them, but they pay a cost stopping acquiring energy via their food intake.

In addition, from the exploration of co-variation among behaviors expressed during a context of baseline risk, we found strong negative auto-correlation between foraging level and vigilance level which were also the principal behaviors expressed during observations. Other behaviors were much less frequently observed and were not correlated to either the foraging or vigilance level. Foraging and vigilance levels of individuals were negatively correlated which is consistent with other studies. Indeed, individuals generally face the trade-off between 'resource acquisition-risk avoidance' since continually avoid predator and/or hunting areas is often incompatible with some key activities like foraging (Dill 1990). In such conditions, prey has to tolerate a higher level of predation risk in order to meet their energy budget (Brown and Kotler 2004). Therefore, they must increase their vigilance in

order to limit predation risks so as to increase the detection of predators (Hopewell et al. 2005), allowing them to escape more efficiently. Furthermore, vigilance is often considered as mutually exclusive with foraging (Underwood 1982), reducing food intake by taking time away from food processing (Lima and Dill 1990). Indeed, this negative relationship had been reported in many species (Fritz et al. 2002; Cowlshaw et al. 2004; Blanchard and Fritz 2007). As a result, if the individual wants to satisfy its energy requirements, it must stay longer on the feeding site to compensate for time spent in vigilance. That being said, vigilance may be free cost which is less well known (Illius and Fitzgibbon 1994; Cowlshaw et al. 2004; Blanchard and Fritz 2007). Indeed, during chewing, herbivores often look for the next bite they will eat without being able to do so. Therefore, this 'free-time' can be allocated to vigilance (Illius and Fitzgibbon 1994; Cowlshaw et al. 2004). This vigilance is defined as a 'routine vigilance' which means that the individual scans the surroundings without any real risk of predation (Blanchard and Fritz 2007).

Finally, we found relationships between behaviors expressed in the three different contexts which was in line with the behavioral syndrome definition (Sih, Bell, and Johnson 2004). Thus, we observed a gradient with at one extreme side, more mobile and active individuals having also a higher temperature and behavioral score but lower vigilance level and flight distance whereas, at the other extreme side, individuals had higher vigilance level and flight distance but lower behavioral score and temperature and were less mobile and active. These results are similar to those of Bonnot et al. (2014) studying behavioral inter-individual variability linked to habitat use. Indeed, they found that individuals with a high temperature and behavioral score during a highly stressful event (capture event) used open habitat less, especially during daytime, when anthropogenic disturbance is highest. Moreover, individuals expressing higher levels of vigilance and longer flight distance used open habitat more during daytime than individuals with lower vigilance level and flight distance. One possible explanation for these results could be that individuals that live in, or use more frequently, open and risky habitats are adapted to express appropriate behaviors. Indeed, increased anti-predator behaviors would allow individuals to spend more time in risky habitats and to detect potential risk earlier than individuals which are not familiar with risk or disturbance. In contrast, individuals that are highly reactive when confronted with an unusually stressful event would be unable to deal with habitual sources of disturbance and,

therefore, mostly confine their space use to closed protective habitats during the day when such disturbance events are common.

To conclude, we found that our behavioral measures collected in different contexts were consistent within individuals for most of them. Thus, these measures may index personality traits for a given context. We also found correlations among these behavioral parameters and temperature within a given context, suggesting a multi-dimensionality in the inter-individual variability of behavior (Koolhaas et al. 1999) as well as correlations among parameters in different contexts suggesting the existence of a behavioral syndrome (Sih, Bell, and Johnson 2004). Consequently, this exploratory study seems a particularly promising approach for understanding the evolution of personality and behavioral syndromes in wild large mammals. That being said, this study was only a first description and we need more data to strengthen the present results. As personality in captivity appears to be similar to personality in the wild (Herborn et al. 2010), a perspective would be to study inter-individual variability of behavior in captivity to offset environmental variability. Hence, we could identify in an easier way which parameters index personality and what could be the relationship between parameters across contexts, but also over time, and the link between behavioral, physiological and biochemical parameters. These parameters could then be also measured in wild populations and their link with fitness components explored.

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**Figure 6.** Before the capture day, we have to prepare the device with nets and retaining boxes. Photo by J.M. Angibault

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## **Chapter IV**

# **Personality in captivity and its link with personality in the wild**

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## Synthesis

Study and highlight inter-individual variability is of main interest in behavioral ecology for few years but still remain challenging in its determination and comprehension with, for instance, implications at different levels (behavioral, physiological, hematological and biochemical; Koolhaas et al. 1999; Réale et al. 2007; Koolhaas et al. 2010). Its study especially for wild animals is also challenging because of the difficulty to make long and good observations and obtain repetitions is even more complicated. In addition, another difficulty is that conditions are uncontrolled in the wild and other factors may influence the behavior of a given individual, and so its observation. Consequently, most of the time, researchers measure the behavior in captivity (Bell 2005; Herborn et al. 2010).

In all cases, we lack of empirical studies whether it be in captivity or in the wild particularly in large mammals. As Herborn et al. (2010) showed that personality in captivity reflects personality in the wild, an idea could be to study some aspects of inter-individual variability such as their correlations or the mechanisms involved in captivity, and to use these indicators of inter-individual variability in the wild to highlight behavioral syndrome. Thus, our aims here were to highlight and study inter-individual variability in captivity in two different contexts: in a risky situation to study the individual's response to stress and with a novel object to study their neophobia. Then, we tried to test correlations between different traits (leading to a behavioral syndrome) and index the differences in a gradient of coping styles or neophobia. Finally, we looked at their potential link with life-history traits. Here, we choose to focus on the body mass which is recognized to be a reliable indicator of body condition and of phenotypic quality (Toïgo et al. 2006).

With both studies, we found that highly energetic individuals during capture had a high behavioral score, temperature and micro-hematocrit and had a higher body mass too. We supposed these individuals were proactive. Then, in the second study, we found a general trend to decrease both, the feeding efficiency and the probability to feed for a second time in the presence of a novel object. Moreover, we found consistent inter-individual differences in these two measures. We indexed the neophobia levels using two indices: the differences in the feeding efficiency and the differences in the latency to feed for a second time at a rate of 25 %. Indices were correlated to each other but they were also

correlated to behavioral and physiological parameters collected in a stressful context. Thus, these results indicated the existence of a behavioral syndrome with more neophilic individuals being more proactive.

Finally, both studies seemed consistent. Indeed, individuals with a higher body mass would have more energy than lighter individuals allowing them to respond faster and with a higher intensity to a risky and stressful situation but also in other situation as a novel situation. Consequently, this proactivity may allow individuals to cope with a potential danger in a faster and more intensively. In addition, as personality in captivity reflects personality in the wild (Herborn et al. 2010), and knowing that we collect exactly the same parameters using the same protocol in the wild, we assumed that indexes and parameters involving consistent inter-individual differences in roe deer living in captivity can be used as good estimator of inter-individual differences in wild roe deer.

Hence, we show experimentally that inter-individual variability exist in roe deer and that these differences are consistent across situations and over time. Moreover, we found that involved parameters are numerous and of different natures leading to complex set as suggesting by Koolhaas et al. (1999).

## Part 1

# Consistent individual's behavioral response during an acute stress in a large ungulate

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*'During each capture event, individuals were weighed with an electronic balance, [...] we measured their rectal temperature during handling [...], we recorded behavior during handling and calculated a behavioral score describing a stress profile gradient. [...]. We also took blood samples from each individual [...]. Four tubes (4 mL) were collected and then agitated lightly a dozen times to avoid blood clotting and stored in an ice box.'*



Photos: A by H. Dupuy and a student

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## RESUME

Les activités humaines et les perturbations engendrées par l'Homme sont assimilables à un risque de prédation perçu par les animaux sauvages. En effet, ces perturbations sont connues pour affecter la survie des populations mais également le comportement des animaux. Il paraît donc capital lorsque l'on étudie les réponses de populations sauvages aux changements environnementaux induits par l'Homme de tenir compte de ces différences de comportement entre individus. Lorsque les différences comportementales sont exprimées dans une situation stressante caractérisée, par exemple, par un environnement au risque changeant, celles-ci entrent dans le cadre d'étude du « coping style ». Ce concept est généralement vu comme un continuum avec des individus réactifs ou proactifs à chacune de ses extrémités. Les individus plutôt « proactifs » sont des individus téméraires, prenant des risques, plus actifs et agressifs et réagissant rapidement et fortement à une situation stressante. A l'inverse, les individus plutôt « réactifs » sont plus timides et ont tendance à plus adopter un comportement d'immobilisation face à un risque. Sachant qu'il est particulièrement difficile de mettre en évidence des différences interindividuelles en milieu naturel, nous avons réalisé cette étude en captivité. Notre objectif était de tester cette variabilité interindividuelle chez le chevreuil dans le cadre du « coping style » soit d'une situation stressante pour les individus au moyen de paramètres comportementaux, physiologiques et hématologiques. Ces paramètres ont été mesurés six fois au cours d'une année de manière à tester leur cohérence au cours du temps. Nous nous sommes ensuite intéressés aux corrélations possibles entre ces différents paramètres de manière à déceler un syndrome comportemental. Enfin, le dernier objectif était de tester la relation entre les paramètres (comportementaux, physiologiques et hématologiques) et la masse corporelle des individus. En effet, la masse corporelle chez le chevreuil est un bon indicateur de leur condition corporelle et de leur qualité phénotypique. Nous avons trouvé que les paramètres étaient cohérents dans le temps et qu'ils étaient corrélés entre eux ce qui nous permet de valider le fait que ces paramètres indexent le « coping style » des individus avec aux extrémités du gradient des individus plus « proactifs » ou plus « réactifs ». Ainsi, la variabilité interindividuelle en réponse à un stress donné ne dépend pas seulement du comportement de l'individu mais, plutôt de plusieurs mécanismes ou paramètres agissant à différentes échelles. Enfin, nous avons mis en évidence un lien entre la réponse des individus vis-à-vis



d'une situation stressante et leur masse corporelle à savoir que des individus plutôt « proactifs » auraient une masse corporelle plus importante en captivité que des individus « réactifs ». Nous supposons que cela pourrait être dû à la stratégie comportementale des individus ou alors à leur métabolisme basal qui agirait sur l'acquisition des ressources. Une compréhension approfondie de ces mécanismes ainsi que de leurs conséquences sur les traits d'histoire de vie et la valeur sélective pourrait avoir d'importantes conséquences.

**Mots clés :** chevreuil, répétabilité, « coping style », masse corporelle

**ABSTRACT**

Human activities and disturbances are recognized to represent a form of predation risk for wild animals. These disturbances impact the survival of population but also the behavior of individuals. Thus, it is of particular importance to account for these behavioral differences when studying the responses of wild populations to human-induced rapid environmental change. When these behavioral differences are manifested in stressful situations characterized by risky or challenging environments, they are generally interpreted within the “coping style” framework. As studying inter-individual variability in behavior is particularly challenging in the wild, we performed the study in captivity. Our aim was to test for individual’s consistency in its response to an acute stress using behavioral, physiological and haematological parameters measured six times across a year. Then, we tested for correlations between these parameters. Our last aim was to test for the inter-individual relationship between the behavioral, physiological and haematological parameters with body mass which constitutes a reliable indicator of an individual’s body condition and phenotypic quality in roe deer. We found that behavioral, physiological and haematological parameters were all highly repeatable across seasons, so that the stress response of each individual appears to be consistent over the year. Moreover, we found that proactive individuals had higher body mass under captive and controlled conditions and we suppose that could be due to the behavioral strategy of individuals or their metabolism via their food acquisition. A better understanding of these mechanisms and their consequences for life-history traits and fitness components may have great implications.

**Key words:** roe deer, repeatability, coping styles, body mass



## INTRODUCTION

Consistent individual differences in behavior are now widely considered to be ubiquitous in nature (Sih et al. 2004), most notably in terms of individual behavioral differences in response to environmental perturbations (Koolhaas et al. 1999; Sih, Bell, and Johnson 2004; Réale et al. 2007). It is of particular importance to account for these behavioral differences when studying the responses of wild populations to human-induced rapid environmental change (Sih et al. 2011). Indeed, over recent decades, all across Europe, agricultural practices have changed leading to a general reduction and fragmentation of natural habitats, such as broadleaf woodland, a loss of hedgerows and an increase in field size and landscape openness (Sotherton 1998). In addition, urbanization, hunting, eco-tourism, and off-road recreation have increased too (Stankowich 2008). These processes have led to a decrease in the availability of refuge habitats and an increase in disturbance due to the higher proximity of human activities to wildlife (Cole et al. 1997; Liu et al. 1999; Munns 2006; Markovchick-Nicholls et al. 2008). Moreover, human activities and disturbances impact the survival of population but also the behavior of individuals (Boyle and Samson 1985; Stankowich and Blumstein 2005; Knight and Gutzwiller 2013). For instance, human disturbances cause a modification of habitat and space use (Manor and Saltz 2005), or again modifications of the diet composition (Jayakody et al. 2008). All these disturbances and stress sources may result in an increase in heart rate (Ward and Cupal 1979; MacArthur et al. 1982) or flight initiation distance (Stankowich and Blumstein 2005) which are recognized to indexed the fear of animals (Dwyer 2004; Miller et al. 2015). Thus, disturbance due to human activities can be assimilated to a form of predation risk (Frid and Dill 2002).

Recently, Sih et al. (2011) explained that species but also individuals of a species facing human disturbance and human-induced rapid environmental change (HIREC) could exhibit different behavioral responses or behavioral syndrome. For instance, some individuals may be bolder, and generally also more aggressive, notably spending more time in open habitat to obtain higher quantity and/or quality of forage, despite potentially higher risk (Bonnot et al. 2015), whereas others may be less risk-prone for the same situation or context (Koolhaas et al. 1999; Réale et al. 2007). Thus, bold and/or individuals with a high level of exploration would cope with environmental changes in a better way whereas others would be more vulnerable to these changes as they are supposed to experience more their

environment and to learn more rapidly than shyer ones (Sih et al. 2004). This might result in inter-individual variations within a species which could better adapt to a wider number of environmental changes (Fogarty et al. 2011).

When these behavioral differences are manifested in stressful situations characterized by risky or challenging environments, they are generally interpreted within the “coping style” framework (Koolhaas et al. 1999). Koolhaas et al. (1999) defined a coping style as “a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals.” Two different strategies are well recognized: the proactive and the reactive types (Koolhaas et al. 1999; Groothuis and Carere 2005). Compared to reactive individuals, proactive individuals are fast explorers, highly aggressive, impulsive in decision-making, novelty seekers and take risks in the face of potential dangers (Koolhaas et al. 1999; Koolhaas et al. 2010). They are thus assumed to cope actively with the source of stress through a “flight-or-fight” response, whereas reactive individuals tend to react to challenges by freezing (Korte et al. 2005). Links between the expression of coping styles at the behavioral level and the neuro-physiological level have been described in a few species (in mice and rats: Koolhaas et al. 1999; birds: Carere et al. 2003; fish: Overli et al. 2005). Proactive individuals (i.e. bold, active and aggressive animals) are assumed to show high sympathetic reactivity and low parasympathetic reactivity contrary to reactive individuals which are more characterized by a high hypothalamus-pituitary-adrenal (HPA) axis activity and reactivity (Koolhaas et al. 1999; Ellis et al. 2006). Hence, generally speaking this means that proactive individuals are assumed to have a higher levels of catecholamines concentration in the blood leading to higher levels of red blood cells in the blood (Stockham and Scott 2013; Weiss and Wardrop 2011) or again a high but consistent heart rate under an acute stress (Koolhaas et al. 1999; Ellis et al. 2006) contrary to more reactive ones.

In addition, inter-individual differences in behavior notably in stress responses may affect life-history traits and individual’s fitness (Smith and Blumstein 2008). Hence, the set of behavioral and physiological but also metabolic parameters may be linked to individuals’ fitness or performance. Few studies are available as regard the individual’s performance or productivity. However, some theoretical (Wolf et al. 2007) or empirical (Stamps 2007; Biro and Stamps 2008; Careau et al. 2008) studies found correlations between inter-individual

differences in behavior and the productivity viewed generally as growth rate or fecundity. Stamps (2007) and Biro and Stamps (2008) predicted a positive relationship between boldness, activity or aggressiveness and the individual's growth rate. They also reviewed empirical studies including a positive correlation between (among other factors) adult body size and activity. Moreover, it seems that inter-individual differences in behavior such as stress response and resting metabolic rate are tightly correlated notably because they are both mainly controlled by the hypothalamic-pituitary-adrenal (HPA) axis (Veenema et al. 2003; Jacobson 2005). For example, Lantova et al. (2011) explained that proactive individuals should expend energy at a higher rate. Then, resting metabolic rate and body mass are positively correlated (Szafranska et al. 2007; Careau et al. 2008; Lantova et al. 2011). Thus, it seems that stress response, resting metabolic rate and individual's performance or productivity be linked but very few studies are available on this topic.

A full description of the relationships between neuro-physiological and behavioral parameters would allow us to gain a better understanding of inter-individual differences in behavioral strategies within a given population and their consequences for life history evolution (Bell et al. 2007; Smith and Blumstein 2008; Del Giudice et al. 2011). However, it is particularly complicated to study such differences among individuals in the wild where repeated observations of identifiable individuals across a range of environmental contexts and in response to a variety of stressors are difficult. In particular, obtaining enough repeat observations to explore inter-individual consistency is challenging, particularly as the multiple uncontrolled and/or unidentified stressors in the wild may mask the underlying patterns of association among traits (Campbell et al. 2009). Thus, even though documenting coping styles in the wild and understanding the underlying mechanisms seem particularly appropriate, most studies in this research domain have been carried out in captivity (Herborn et al. 2010). For example, Dingemanse et al. (2002) measured the exploratory behavior of wild great tits and its repeatability in laboratory before releasing them in their capture site.

The initial response of an individual to a stressor is generally manifested through its behavior (Reimoser 2012). For instance, during capture, which is recognized to be an acute stressor, animals may change their postural position, their level of aggression or docility, or may vocalize (Lay et al. 1992; Moberg and Mench 2000; Réale et al. 2000; Trevisi and Bertoni

2009). From a physiological point of view, changes in heart rate and temperature are considered reliable ways to evaluate the response of an animal to an acute stress (Moberg 1985; Zethof et al. 1994; Moe and Bakken 1997; Carere and van Oers 2004b). Indeed, a rise in heart rate resulting in tachycardia and an increase in body temperature too indicate a fever-like response and are recognized as typical components of an acute stress response in a wide range of species (Zethof et al. 1994; Moe and Bakken 1997; Cabanac and Aizawa 2000; Cabanac and Guillemette 2001). In species where the assessment of heart rate is particularly difficult especially for small birds, respiratory rate is more convenient to measure since it similarly responds to cardiovascular parameters to stressful or fearful events (Carere and van Oers 2004b). From a haematological point of view, the levels of hematocrit, hemoglobin concentration and red blood cells are commonly used in the study of stress (Montané et al. 2007; Mentaberre et al. 2010). The stress response causes a rapid contraction of the spleen capsule and results in a significant blood release from the spleen to the blood flow. Blood in the spleen is richer in red blood cells than the blood flow. Thus, an acute stress results in a higher concentration of red blood cells (hematocrit, hemoglobin) and we could easily test for it collecting blood samples on individuals (Stockham and Scott 2013). With regard to the immune response, the mechanisms seems a little more complex, but most studies indicated that stress provokes an increase in neutrophils and a decrease in lymphocytes (Montané et al. 2007; Casas-Diaz et al. 2010; Mentaberre et al. 2010; Munerato et al. 2010). More generally, when an individual faces an acute stress, the neutrophil / lymphocyte (N/L) ratio increases proportionally with the amount of secreted glucocorticoids and is used in many species to index physiological stress (Davis et al. 2008).

Despite these few studies, the link between behavioral, physiological and haematological parameters in response to stress remains few studied and poorly understood. Our first aim in the present study was to highlight inter-individual differences in stress response using behavioral, physiological and haematological parameters among adult roe deer living in captivity. Because Koolhaas et al. (1999) emphasized that coping should be consistent over time, we first explored individual repeatability in the behavioral, physiological and haematological measures. Then, we tested for correlations between these parameters as, following Koolhaas et al.'s study (1999), the stress response should be coherent across a set of behavioral and physiological parameters, describing a gradient

in coping style from proactivity at one end to reactivity at the other. Our last aim was to test for the inter-individual relationship between the behavioral, physiological and haematological parameters with body mass which constitutes a reliable indicator of an individual's body condition and phenotypic quality in roe deer (Toïgo et al. 2006).

## **MATERIAL AND METHODS**

### ***Study site and population***

The research station is located in south-western France, about 30 km south-east of Toulouse and about 100 km north of the foothills of the Pyrénées mountains. The landscape is hilly and mostly cultivated, with patches of woods. The station is located on the slopes of a hill, around 230 meters above sea level. The climate is of the 'Aquitain' Atlantic type, although subject to a strong Mediterranean influence, especially in summer.

Roe deer live in enclosures of about 0.5 ha containing between 1 to 4 individuals which are housed according to their status (raised by humans during their two first months of life or not for example) and sex. Each enclosure consists of a meadow and a hut where individuals can feed daily pellets (600 g per individual) and shelter. Most individuals are raised by technicians for their two first months of life and all have some awareness of humans. This ensures more security for both animals and humans during experiments and during routine activities such as for feeding animals. The current experiment was based on a total of 10 adult individuals: 4 males and 6 females from 4 to 10 years old which live alone except three individuals living in the same enclosure.

### ***Data collection***

#### ***Behavioral and physiological parameters***

For the experiment, each individual was caught 6 times, once every two months, from March 2013 to January 2014. During each capture event, individuals were weighed with an electronic balance. Then, we continuously measured their rectal temperature during



handling until it stabilized (using a Digitemp Color thermometer with a precision of 0.1 °C). We also recorded behavior at capture and during handling and calculated a behavioral score describing a stress profile gradient. We attributed a score of 1 if it vocalized on the table during marking or 0 if not, and we attributed a score of 1 if it struggled and panted on the table during marking, or a score of 0.5 if it struggled only (otherwise 0). An index of stress response was then calculated as the sum of the scores for these 3 behaviors, describing a stress profile gradient ranging from 0 to 3, with 3 indicating a priori proactive individuals (see Debeffe et al. 2014; Bonnot et al. 2015; Monestier et al. 2015 for a similar approach).

#### *Haematological parameters*

We took blood samples from each individual from the left jugular vein using manual compression. The equipment used consists of a holder associated with a needle of 20 Gauge (0.9 mm), with a length of 25 mm (Venoject, Terumo Europe NV, Leuven, Belgium). Four tubes (4 mL) were collected and then agitated lightly a dozen times to avoid blood clotting and stored in an ice box. The next morning, we used a manual reading of the blood sample to obtain the hematocrit (Ht). The slides were stained with RAL 555 kit according to the protocol provided by the manufacturer (RAL Reagents, Martillac, France). In addition, the proportion of each cell type was obtained by manual reading of blood smears. We used these values to calculate the N/L ratio.

### ***Statistical analyses***

#### *Repeatability of stress response parameters*

Consistency in the behavioral score, temperature and haematological parameters (hematocrit and the N/L ratio) was estimated by calculating individual repeatability with mixed models (Nakagawa and Schielzeth 2010). Repeatability coefficients for all the stress response parameters were calculated using the most commonly used method in behavioral ecology: the Lessells and Boag (1987)'s method which corresponds to an *F* table of an ANOVA with the individual identity treated as a factorial predictor. To do that, we used the

“rpt.aov” function of the “rptR” package (Schielzeth and Nakagawa 2011) in R version 3.1.0 software (R Development Core Team 2013). The N/L ratio was log-transformed in order to used the Lessells and Boag (1987)’s method to estimate repeatability. All parameters had at least two repetitions per individual (temperature: range = [2.0-6.0], mean = 4.0, and median = 3.5; behavioral score: range = [2.0-6.0], mean = 4.1, and median = 4.0; hematocrit: range = [2.0-6.0], mean = 3.7, and median = 3.5; N/L ratio: range = [2.0-6.0], mean = 3.7, and median = 3.5).

#### *Inter-individual variability in stress response parameters*

To investigate inter-individual variability in the behavioral score, rectal temperature, the hematocrit, and the N/L ratio we used linear models (LM) with each of the four stress response parameters as the dependent variable and individual identity as a fixed explanatory factor. For the N/L ratio, note that we previously log-transformed the N/L ratio to fit the Gaussian distribution. In addition, to control for possible seasonal variation of each of the four stress response parameters, we included the period at which the capture event occurred (categorical variable, 6 modalities: March, May, July, September, and November 2013, January 2014).

In addition, inter-individual differences may depend on the permanent (sex) or non-permanent (age) sources of among individuals differences at capture (Herborn et al. 2010). That being said, we assumed that there was no age-dependence in the variation of these parameters as all individuals were prime-aged. Besides, even if we supposed that there were no differences in the stress response parameters due to the sex as data were collected in captivity and out of the reproductive period, we tested for a potential relationship between the stress response parameters and the sex. For the four stress response parameters, we used linear models (LM) and we did not find any significant relationship between three stress response parameters and the sex (behavioral score:  $N = 39$ ,  $R^2 = 0.04$ ,  $p$ -value = 0.18; hematocrit:  $N = 37$ ,  $R^2 = 0.07$ ; N/L ratio:  $N = 37$ ,  $R^2 = 0.04$ ,  $p$ -value = 0.22) whereas we found a significant relationship between the rectal temperature and the sex with males having a higher rectal temperature (temperature:  $N = 38$ ,  $R^2 = 0.10$ ,  $p$ -value = 0.03). However, we could not include the sex with another explanatory variable because of lack of statistical power. Consequently, we did not take into account the sex in the analyses.

*Relationships among stress response parameters and the link with individual body mass*

To explore inter-individual differences in the stress response within the coping style framework, we assumed that the behavioral, physiological and haematological parameters should be inter-related at the individual level. Thus, we first explored these relationships using a simple correlation matrix on the individual means of the four parameters (“spearman.test” function in the “pspearman” package, Savicky 2014). Second, we performed a centered and scaled Principal Component Analysis (PCA) on the individual-specific means of these four stress response parameters to generate one or more synthetic variables (from the Principal Components) summarizing the individual’s overall stress response. Finally, we used linear models (LM) to test the relationship between the individual’s overall stress response (extracted from the PCA) and its mean body mass (adult body mass is generally stable over the prime-age stage in roe deer, Hewison et al. 2011) as the dependent variable.

All analyses were performed in R version 3.1.0 (R Development Core Team 2013). We selected the best model with the lowest Akaike’s information criterion (AIC) value (AICc, i.e. AIC corrected for small sample size), reflecting the best compromise between precision and complexity of the model (Burnham and Anderson 2002).  $\Delta$ AIC values exceeding 2 are considered indicative of substantial differences in support for the compared models, whereas models with a  $\Delta$ AIC within 2 of the model with the lowest AIC are equally likely to be the best model (Burnham and Anderson 2002). We also calculated AICc weights as a measure of the likelihood that a given model was the best among the set of fitted models.

## RESULTS

### *Repeatability of stress response parameters*

Rectal temperature was moderately repeatable for a given individual ( $r = 0.30$ , 95% confidence of interval = [0.035, 0.605]). The N/L ratio was quite strongly repeatable ( $r = 0.47$ , 95% confidence of interval = [0.121, 0.749]). Both the behavioral score ( $r = 0.64$ , 95%

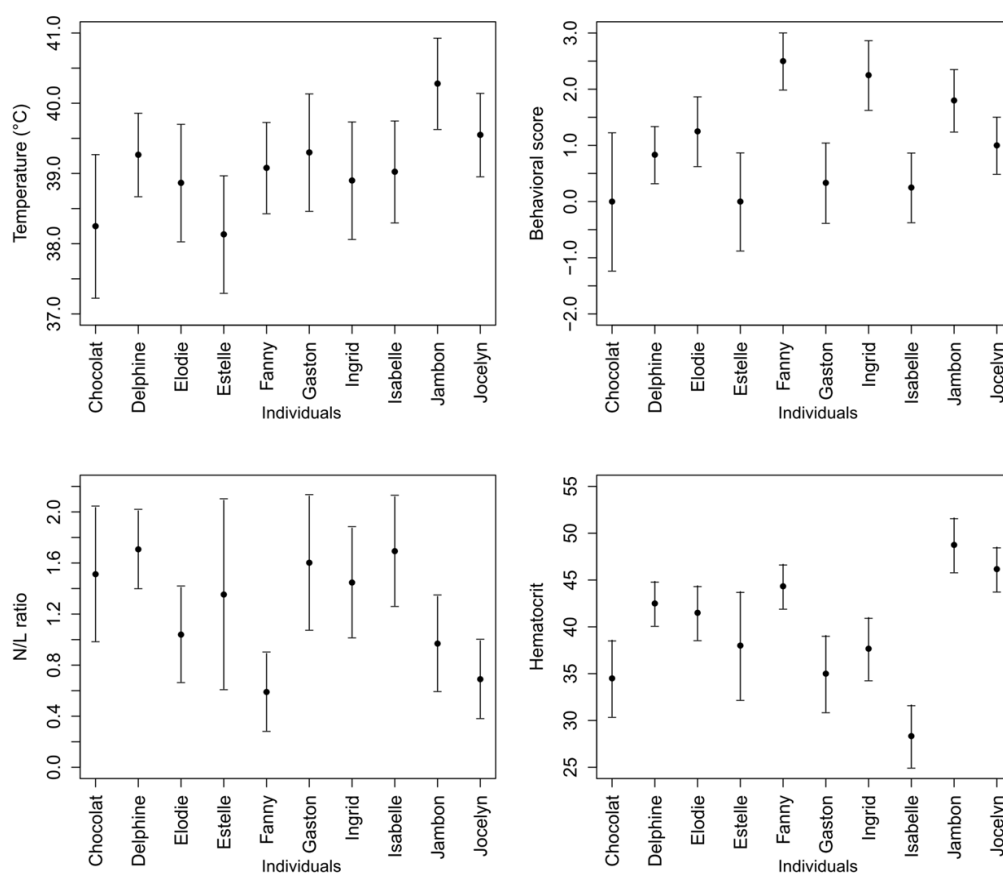
confidence of interval = [0.284, 0.796]) and the hematocrit ( $r = 0.81$ , 95% confidence of interval = [0.501, 0.92]) were highly repeatable within individuals.

*Inter-individual variability in stress response parameters*

For each of three of the four stress response parameters (behavioral score, hematocrit and N/L ratio), the model with the highest support contained individual identity alone as the sole explanatory variable whereas for the rectal temperature, the best model was the constant model (Table 1). These results indicate that, for each of the three parameters, there was no substantial seasonal variation across the year, but that these parameters varied markedly among individuals (Fig. 1).

**Table 1. Candidate linear models (rectal temperature, behavioral score, hematocrit) and generalized linear model (N/L ratio) fitted to investigate seasonal and individual variation in the four stress response parameters.** AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for  $\Delta$ AICc and on the Akaike weights.

Dependent variable	Models	K	AICc	$\Delta$ AICc	AICcWt
Temperature	constant model	2	104.52	0.00	0.85
	individual	11	108.37	3.85	0.12
	period	7	111.44	6.92	0.03
	individual + period	16	127.74	23.22	0.00
Behavioral score	individual	11	97.25	0.00	1.00
	individual + period	16	116.40	19.15	0.00
	constant model	2	119.20	21.95	0.00
	period	7	129.10	31.85	0.00
N/L ratio	individual	11	53.62	0.00	0.99
	constant model	2	64.07	10.45	0.01
	period	7	72.12	18.50	0.00
	individual + period	16	73.12	19.50	0.00
Hematocrit	individual	11	205.69	0.00	1.00
	individual + period	16	227.64	21.96	0.00
	constant model	2	243.45	37.76	0.00
	period	7	252.31	46.63	0.00



**Figure 1. Inter-individual variability in the four stress response parameters** (rectal temperature, behavioral score, N/L ratio, hematocrit level). The graph presents the predicted values for each individual from linear models of each of the parameters as the dependent variable and the individual identity (N = 10 individuals) as the explanatory variable.

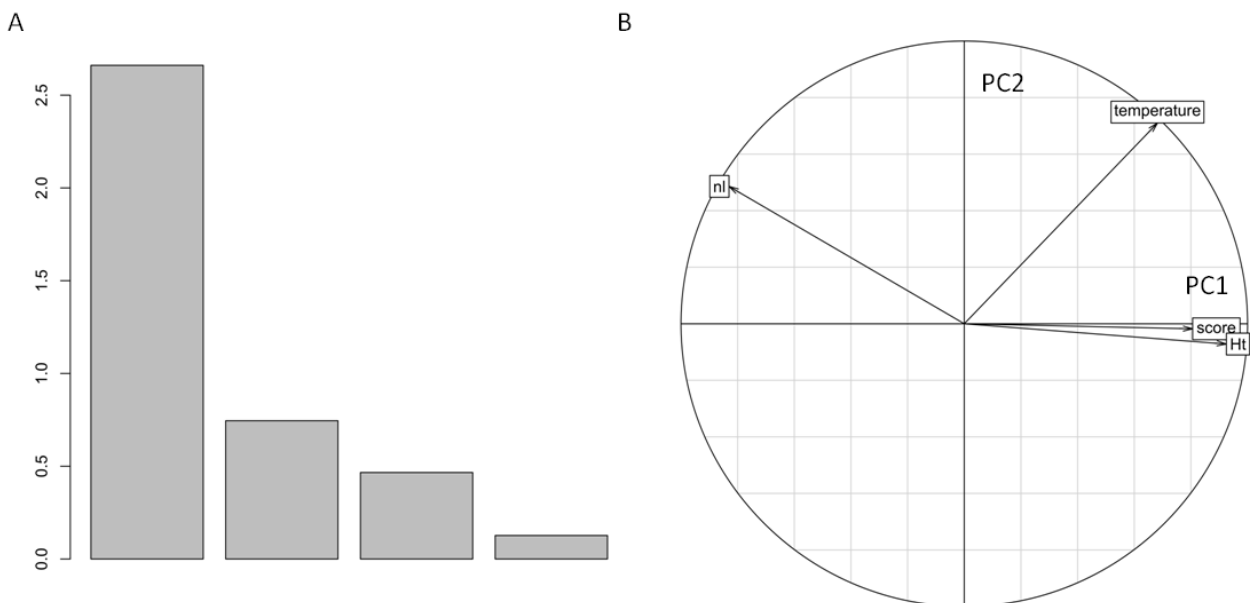
***Relationships among stress response parameters and the link with individual body mass***

The correlation matrix indicated that the four stress response parameters were inter-correlated (Table 2). The rectal temperature, behavioral score and hematocrit were positively correlated, whereas the N/L ratio was negatively correlated to the three other stress response parameters.

**Table 2. Matrix of the Spearman's rank correlation coefficients among the 4 stress response parameters (rectal temperature, behavioral score, hematocrit and N/L ratio).** Significant correlation coefficients (P values < 0.05) are indicated by stars (\*).

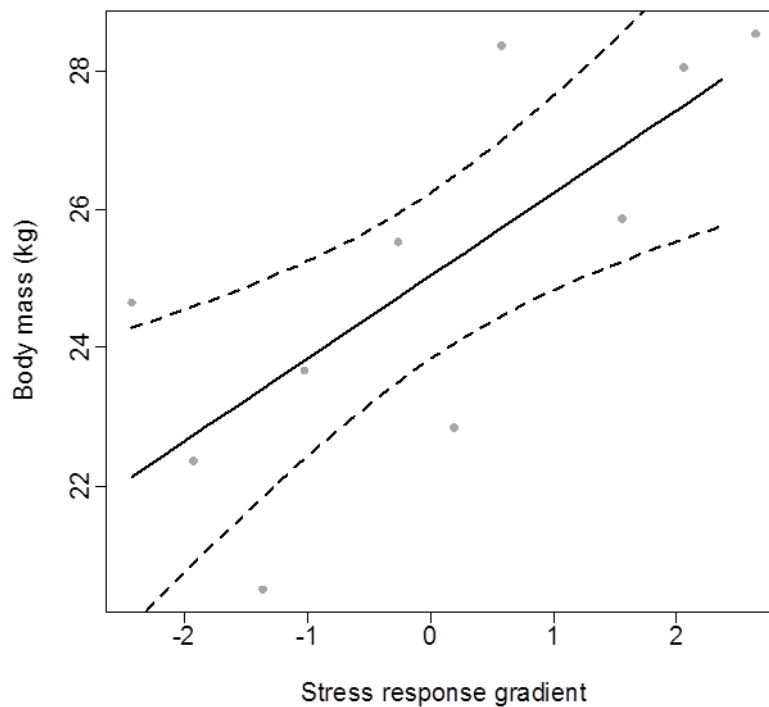
	Temperature	Behavioral score	Micro-hematocrit percentage	N/L ratio
Temperature	1.00			
Behavioral score	0.36	1.00		
Hematocrit	0.58 *	0.49	1.00	
N/L ratio	-0.27	-0.51	-0.79 *	1.00

In the PCA of the 4 stress response parameters, the first principal component (PC1) captured 66.5 % of the total inertia and was much more informative than all the subsequent axes (Fig. 2). Rectal temperature, behavioral score and hematocrit were all positively correlated to PC1, whereas the N/L ratio was negatively correlated with it. Thus, this axis represented a gradient of stress response, with positive values indicating a rapid and marked response to a stressful event (capture), and negative values indicating a low level of response.



**Figure 2. Covariation of the four stress response parameters.** Principal Component Analysis of individual mean values for rectal temperature, behavioral score, N/L ratio, hematocrit. A: decomposition of the variance among principal components; B: correlation circle showing the projection of all variables on principal components 1 (x axis) 2 (y axis).

To explore the link between body mass and the overall stress response at the individual level, from the above PCA, we retained the individuals' scores on the first Principal Component (PC1) as a descriptor of an individual's overall stress response. We found that the best model describing variation in individual body mass included the PC1 (AICc weight 0.83,  $\Delta$ AICc to constant model = 4.93). We observed that body mass increased with the positive values of the PC1. Thus, body mass increased with high value of temperature, behavioral score and hematocrit and low N/L ratio (Fig. 3).



**Figure 3. Relationship between individual mean body mass (dependent variable) and the stress response gradient (PC1).** Positive values for the stress response gradient indicate a high rectal temperature, a high behavioral score, a high hematocrit and a low value for the N/L ratio.

## DISCUSSION

Our overall aim was to highlight inter-individual variation in the stress response in captive roe deer and to link this variation to individual condition/quality. Firstly, we showed that the four stress response parameters we used, rectal temperature, behavioral score, hematocrit and N/L ratio, were all highly repeatable across seasons, so that the stress response of each individual appears to be consistent over the year. Bell et al. (2009) reported in a meta-analysis that behavioral traits are generally repeatable, with an average value of 0.37; hence, repeatability of our behavioral score was substantially higher ( $r = 0.64$ , 95% confidence of interval = [0.284, 0.796]). As regard the other stress parameters, the literature is increasingly scarce especially for their repeatability (Szafranska et al. 2007; Biro and Stamps 2010). For instance, although stress-induced rise in temperature has been extensively studied on model organisms under controlled environments (Cabanac 1975; Moe and Bakken 1997; Cabanac and Guillemette 2001; Carere and van Oers 2004b), consistency in this parameter was solely clearly found recently with the Careau et al. (2011)'s study in eastern chipmunks (*Tamias striatus*). Our temperature repeatability is lower but close to the Careau et al. (2011)'s temperature (0.30 vs. 0.40 respectively). Moreover, our temperature and behavioral score repeatability were in line with those of a previous study carried on a wild roe deer population where we found that both parameters were consistent (Monestier et al. 2015). For the haematological parameters, we did not find any repeatability study including the N/L ratio and we found solely a handful studies concerning the hematocrit repeatability. We found the same result as the other studies namely that the hematocrit parameter is highly repeatable across taxa (Hatch and Smith 2010; Escribano et al. 2013). Consequently, the present study provided more knowledge about the consistency of stress response parameters especially for large ungulates for which we did not find repeatability for stress response parameters across a year. Second, as we hypothesized, we found strong evidence for substantial variation among individuals in this stress response. This suggests, in the coping styles context, that a gradient from reactive to proactive individuals exist with, for example, most proactive ones having a higher hematocrit. Indeed, proactivity seems principally to depend on the sympathetic axis (Koolhaas et al. 1999, 2010) and a fast increase of hematocrit in the blood during an acute stress is also due to the sympathetic axis



(Stockham and Scott 2013). Catecholamines act on the splenic capsule and then increase the blood richness in red blood cells (Weiss and Wardrop 2011).

In addition, we found that the behavioral, physiological and haematological parameters that we measured were inter-correlated. This finding is in agreement with the Koolhaas et al.'s (1999) definition explaining that a coping style is “a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals.” More precisely, we found a positive correlation between rectal temperature, behavioral score and hematocrit, whereas the N/L ratio was negatively correlated with these three parameters. The fact we found a positive correlation between the temperature and the behavioral score was in line with another study carried on wild roe deer where Monestier et al. (2015) interpreted high behavioral score and rectal temperature as proactivity and low behavioral score and rectal temperature as reactivity. Then, the positive correlation between behavioral score and hematocrit seemed consistent to knowledge available in the literature. Indeed, as explained above, a fast increase in hematocrit during an acute stress may characterize proactive individuals. Together, these results indicate that individuals with a more proactive profile may have a higher rectal temperature, behavioral score and hematocrit, but a lower N/L ratio. The N/L ratio depends on both the sympathetic and the HPA axis. After an acute stress, the number of neutrophils and lymphocytes increases, but rapidly the activity of the sympathetic axis tends to decrease while the HPA axis activity increases the number of neutrophils but decrease the one of lymphocytes in the blood (Davis et al. 2008; Weiss and Wardrop 2011). Consequently, depending on the latency between the capture and the collect of blood sample, the N/L ratio was neither completely influence in the same way nor by the same axis. That being said, it seemed that the understanding of the N/L ratio is quite complicate. Moreover, another explanation could be that we did not measure the individual's stress response but rather its basal state before reaction. Indeed, the latency between the individual's capture and the blood sample was quite short (in average 36 min) meaning that the time was quite short to see the inflammatory response of the individual. In this case, this means that an individual with a high basal N/L ratio expressed a low behavioral response to an acute stress; but, we have to interpret this result with cautious because we did not find any similar result in the literature. However, we found correlations between the four stress

parameters and they are typical of the proactive-reactive syndrome (Koolhaas et al. 1999; Sih et al. 2004).

Finally, we found evidence for a link between the stress response of an individual and its body condition such that body mass increased as our score of overall stress response increased. That is, heavy individuals had a higher rectal temperature, behavioral score and hematocrit and a lower N/L ratio. We interpret this to show that proactive individuals had higher body mass under captive and controlled conditions (e.g. equal access to feeding resources) and we suppose that could be due to the behavioral strategy of individuals or their metabolism via their food acquisition.

It is generally recognized that proactive individuals are more aggressive and bolder than reactive animals (Koolhaas et al. 1999; Koolhaas et al. 2010; Réale, Garant, et al. 2010). Consequently, they take more risk notably to feed in areas of better quality but pay a cost in term of survival for example (Smith and Blumstein 2008). In agricultural landscape, the quality of food resources for roe deer is far better in open habitats (Hewison et al. 2009; Abbas et al. 2011) even if the risk of mortality is more important than in more closed habitats such as forest (Myserud et al. 1999a, 1999b). Hence, Hewison et al. (2009) found that deer taking more risk living in open habitats had a higher body mass than individuals living in more closed and secured habitats. As personality expressed in captivity reflects personality in the wild (Herborn et al. 2010), we supposed to have the same phenomenon in captivity except the fact that individuals in captivity do not pay a cost in term of survival as there is no predation risk. Individuals living in captivity have exactly the same quality and quantity of food every day contrary to individuals living in the wild. However, differences may appear in their frequency and time of feeding. A recent experiment showed that more neophilic roe deer (so, more proactive) had a higher feeding efficiency even if in the presence of a disturbance and that the latency to feed for a second time was shorter than the one of more neophobic individuals (Monestier et al. 2015, Chapter IV). Hence, differences in the behavioral strategy and behavioral trait of individuals appeared and may explain that more proactive individuals have a higher body mass than more reactive ones via their decision taking to feed.

The second explanation explaining the link between body mass and our score of overall stress response referred to the link between personality traits, basal metabolic rate

and productivity which is gaining attention. A first observation is that consistent individual differences in energy metabolism might promote consistent individual differences in behavioral traits (Biro and Stamps 2008; Careau et al. 2008). Thus, individuals with a high basal metabolic rate seem to be more aggressive, active, dominant or bold (see Biro and Stamps 2010 for a review). Moreover, it is recognized that metabolic rate and body mass are positively and closely correlated (Schmidt-Nielsen 1990; Konarzewski and Diamond 1995; Labocha et al. 2004). In addition, consistent individual differences in metabolism seem link the behavior of individuals but also to their productivity (Biro and Stamps 2008). Hence, individuals with a higher resting metabolic rate should be more active, aggressive and bold in contexts related to food acquisition but also fast-growing (i.e. larger size, mass) and highly fecund (Biro and Stamps 2008). Thus, our study seems in line with the previous findings linking personality, metabolic rate and thus body condition of individuals which attest that inter-individual differences in stress responses may affect life-history traits and individual's fitness (Smith and Blumstein 2008). Indeed, the expression of life history traits depends partly on individual condition which is one of the oldest and best established concepts in evolutionary ecology (Darwin 1871; Fisher 1930; Roff 1992; S. Stearns 1992) and we found that body condition depends on several parameters as the metabolic rate, the behavior or the haematological parameters which also index some individual condition or well-being but at different levels (Schluter and Gustafsson 1993; Hatch and Smith 2010).

To conclude, with this study we highlighted that some behavioral, physiological and haematological parameters indexing the stress response were repeatable, inter-correlated and varied substantially among individuals in captive roe deer, describing a reactivity-proactivity gradient. As predicted by the Koolhaas et al. (1999)'s study, we found with that inter-individual variability in response to a given trait not solely depends on behavior but rather depends on several mechanisms or parameters acting at different levels. A better understanding of these mechanisms and their consequences for life-history traits and fitness components may have great implications.

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## Part 2

# To go or not to go: food neophobia is related to behavioral and haematological parameters in captive roe deer

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*'We measured neophobia as the ratio between the total number of visits to the cabin and the number of visits that resulted in a successful feeding bout [...]. We also measured neophobia as the time-related probability that a given individual fed a second time following a first successful feeding visit [...].'*



In preparation



## RESUME

L'exploration et la néophobie sont des comportements très importants pour les animaux. L'exploration permet aux individus d'acquérir des informations en ce qui concerne leur environnement comme la distribution et l'abondance des ressources, la présence de prédateurs et de zones refuges ou encore de potentiels partenaires de reproduction. La néophobie, quand à elle, permet de réduire les risques d'exposition à un danger. Ainsi, des individus plutôt néophobes mettront du temps à approcher un nouvel objet par exemple puis, à l'explorer. L'exploration et la néophobie sont étroitement liées. En effet, un individu n'explorera que s'il est intéressé par un objet et vice-versa. De plus, ces traits de personnalité ont été étudiés au sein d'un grand nombre de taxons montrant qu'ils affectent plusieurs traits d'histoire de vie comme la dispersion par exemple. Ainsi, notre premier objectif était d'inférer l'existence de différences comportementales dans le niveau de néophobie des individus. Ensuite, le second objectif visait à valider notre approche pour décrire les différences comportementales entre individus en milieu naturel. Pour cela, nous avons testé le lien entre le niveau de néophobie des individus et leur réponse à un stress aigu mesurée au moyen de paramètres comportementaux et physiologiques lors d'une situation stressante (les protocoles de collecte des paramètres étant identique en milieu naturel et en captivité). D'une manière générale, nous avons trouvé que les individus sont moins efficaces dans leur prise alimentaire et que la probabilité qu'ils viennent s'alimenter une seconde fois diminuent en présence d'un objet nouveau. Cependant, nous avons également trouvé de la variabilité interindividuelle dans ces deux dernières mesures de néophobie ce qui revient à mettre en évidence l'existence d'un gradient de néophobie avec à ses extrêmes des individus plus néophobes ou néophiles. Ensuite, pour tester les liens possibles entre le niveau de néophobie et les paramètres mesurés lors d'une situation stressante, nous avons défini deux indices de néophobie à savoir : la différence dans l'efficacité alimentaire avec et sans objet nouveau et la latence pour s'alimenter une seconde fois à hauteur de 25 % avec et sans objet nouveau. Nous avons trouvé que ces deux indices sont corrélés entre eux et qu'ils sont également corrélés dans une certaine mesure aux paramètres collectés dans une situation stressante. Ces résultats indiquent donc que nous sommes en présence d'un syndrome comportemental avec des individus plus néophiles qui seraient plutôt « proactifs » contrairement à des individus plus néophobes et



donc plus « réactifs ». Par conséquent, cette étude semble valider le fait que les mesures faites en milieu naturel lors d'une situation stressante peuvent être interprétées en termes de différences comportementales entre individus.

**Mots clés :** chevreuil, néophobie, syndrome comportemental, captivité

**ABSTRACT**

Both exploration and neophobia behaviors are important for animals. Exploration allows individuals to gather information about their environment and neophobic responses reduce exposure to danger. Hence, these closely related behaviors are known to affect life-history traits. Here, we investigated the existence of consistent inter-individual variation in the level of neophobia in captive roe deer. Then, we wanted to validate our approach to describe inter-individual behavioral differences in the wild by establishing a link between neophobia and behavioral and biochemical parameters collected during a stressful situation with the same protocol both, in captivity and wild. Globally, we found that the feeding efficiency and the probability to feed a second time decreased in the presence of a novel object. Moreover, we found inter-individual differences in these two measures. Then, to index neophobia and link this trait to behavioral and physiological parameters, we used two neophobia indices: the differences in the feeding efficiency and the differences in the latency to feed for a second time at a rate of 25%. We found that both neophobia indices were correlated to each other and some weak evidence for correlations between the individual's neophobia and its responses to a stressful situation. More precisely, the more neophobic individuals (high differences in feeding efficiency and latency to feed for a second time) seemed to have a lower behavioral reaction in a stressful situation. Results indicated the existence of a behavioral syndrome with more neophilic individuals being more proactive. We suggest that behavioral traits and physiological parameters measurable in wild roe deer can be reliably interpreted in terms of established behavioral gradients by validating this approach in captivity.

**Key words:** roe deer, neophobia, behavioral syndrome, captivity



## INTRODUCTION

Differences in behavior are often observed among individuals within a population when they are confronted with the same environmental context or stimuli, whether it be in the wild or in captivity (Gosling 2001; Sih, Bell, Johnson, et al. 2004). Recently, understanding how personality emerges, as well as its causes and consequences, has become of prime interest in behavioral and evolutionary biology (Wolf et al. 2007). Overall, in behavioral ecology, five major personality dimensions have been identified (so-called the 'Big Five'; Réale et al. 2007). Of these five dimension, the exploration-neophobia gradient is certainly one of the most studied traits (Réale et al. 2007) and has been investigated in a wide variety of taxa, from reptiles to mammals, and particularly in birds (Verbeek et al. 1994; Greenberg and Mettke-Hofmann 2001; Dingemanse et al. 2002; Dingemanse and de Goede 2004). Overall, exploration and neophobia are closely link which has been viewed across a wide range of taxa (birds: Greenberg 1983; Sol et al. 2002; rodents: Reader and Laland 2003; monkeys: Day et al. 2003 but not in parrots Mettke-Hofmann et al. 2002), while Réale et al. (2007) consider that neophobia is a component of exploration. Neophobia is the avoidance or novel stimuli in the environment solely because those stimuli never been encountered previously and because they are dissimilar from stimuli that have been experienced in the individual's past. This concept is thus associated with fear and the physiological and behavioral correlates of fear responses (Greenberg and Mettke-Hofmann 2001).

In this context, several empirical studies have recently shown that neophobia can impact other behaviors such as feeding (Richard et al. 2008; Herborn et al. 2010; King et al. 2015). Indeed, neophobia is often considered as part of a behavioral syndrome (i.e neophobia is correlated with other personality traits) (Sih, Bell, Johnson, et al. 2004). For instance, in domestic mammals, aggressive individuals were found to be fast and superficial explorers, while non-aggressive individuals were slow and thorough explorers (Benus et al. 1987, 1990; Hessing et al. 1994). Based on complementary experiments, both Benus et al. (1988) and Hessing et al. (1994) concluded that these individual differences represent different behavioral strategies that become particularly expressed in stressful situations such as novel environments, during fights, and in response to inescapable shocks. More generally, two strategies to cope with stress have been described: proactive individuals (which handle the situation and manifest aggression or escape) are usually more active, explorative,

neophilic, bold and aggressive than reactive individuals (which are motionless or passive; Koolhaas et al. 1999; Groothuis and Carere 2005). For example, in great tits (*Parus major*), fast explorers approached a novel object faster than slower and shyer individuals (Verbeek et al. 1994) and returned sooner to a feeding table than slow explorers (Oers et al. 2004a, 2004b). Indeed, Verbeek et al. (1996) identified a behavioral syndrome defined by exploration behavior, aggressiveness and social rank in this same species.

It is increasingly apparent that personality traits have strong impacts on life-history traits and, ultimately, fitness evolving through both natural (Quinn et al. 2009) and sexual (Schuett et al. 2010) selection. However, linking personality traits and/or behavioral syndromes with life histories is particularly hard in the wild (Smith and Blumstein 2008). Among the handful of available studies, a link between neophobia, or a behavioral syndrome including neophobia, and dispersal appears to be potentially widespread. For instance, Fraser et al. (2001) showed that the dispersal distance of Trinidad killifish (*Rivulus hartii*) in natural streams was positively related to the individual's score for exploration in unfamiliar habitat. It has also been demonstrated that exploration has the potential to influence certain features of the dispersal movement. For example, exploration distance and direction seem to determine, at least in part, the subsequent direction and distance of the dispersal movement in North American red squirrels (*Tamiasciurus hudsonicus*, Haughland and Larsen 2004).

From a general point of view, personality is particularly difficult to study in the wild given the difficulty of obtaining repeated measures of individual behavior under standardized conditions (Campbell et al. 2009). Consequently, much work on the description of personalities has been carried out in captivity (see Herborn et al. 2010), while to investigate the ecological significance of personality, researchers have generally measured behavior in captivity and compared the distribution or fitness of individuals in the wild thereafter (Dingemanse et al. 2004b; Bell 2005). For example, neophobia is commonly assessed by manipulating the feeding environment using novel food, containers or objects placed near food. Neophobia is generally measured in terms of the time the individual takes to approach and manipulate the object, or the duration and frequency of investigation (Greenberg 1983; Oers, Drent, et al. 2004, 2005), but physiological measures such as heart rate are also sometimes taken into account (Greenberg and Mettke-Hofmann 2001). Studies

in captivity are thus an interesting first step towards understanding the link between personality and life histories in wild populations. Indeed, Herborn et al. (2010) found that an individual's exploratory tendency and level of neophobia measured in captivity successfully predicted the analogous traits measured in the wild.

Consequently, the first aim of the present study was to investigate the existence of consistent inter-individual variation in the level of neophobia in captive roe deer. Indeed, inter-individual differences in behavior linked to several life history traits have been previously demonstrated in a wild population of this species (Debeffe et al. 2014; Monestier et al. 2015; Bonnot et al. 2015). In particular, Debeffe et al. (2014) suggested that future dispersers were less neophobic (indexed by their exploration behavior) than future philopatric individuals. Hence, we hypothesized that we should be able to detect consistent inter-individual variability in behavior linked to neophobia with a standardized experimental protocol of the type commonly employed for other taxa (Greenberg 1983; Oers, Drent, et al. 2004, 2005). Our second aim was to validate our approach to describe inter-individual variation in behavior of this species in the wild. To that end, we used our experimental set up to explore the link between neophobia and both the behavioral and biochemical measures that are routinely recorded during capture of individuals in both the wild and captivity. Indeed, behavioral syndromes can be indexed by physiological parameters and behavioral traits (Koolhaas et al. 1999), with the link between behavior and the hypothalamus-pituitary-adrenal axis particularly promising (Koolhaas et al. 1999, 2010). For instance, following handling in birds, there is a rapid rise in glucocorticoids (Silverin 1998) and both body temperature and heart rate, particularly in shy individuals compared to bold ones (Carere and van Oers 2004b) which is linked to the 'emotional' stress response. Thus, by establishing a link between neophobia and other behavioral and biochemical responses to stress in captivity, and given that personality in captivity should reflect personality in the wild (Herborn et al. 2010), we should be able to reliably interpret inter-individual behavioral differences measured in the wild in terms of a behavioral syndrome.

## **MATERIAL AND METHODS**

### ***Study site and population***

The research station is located in south-western France, about 30 km south-east of Toulouse and about 100 km north of the foothills of the Pyrénées mountains. The station is located on the slopes of a hill, around 230 meters above sea level. The climate is of the 'Aquitaine' Atlantic type, although subject to a strong Mediterranean influence, especially in summer.

Captive roe deer live in enclosures of 5000 m<sup>2</sup>. There are 9 permanently occupied enclosures by individuals which are housed according to their status (tame or wild) and sex. In each enclosure, there is a cabin where individuals can also shelter and feed daily pellets (600 g per individual) in a feeder put on the ground. For this experiment, we only used individuals which are habituated to humans. Indeed, these individuals are born in the research station and were raised by technicians for their 2 first months of life. They quickly lost their proximity to humans and are considered as wild individuals since they have the same behaviors same but they have some awareness of humans. This ensures more security for both animals and humans during experiments and during routine activities such as for feeding animals. Thus, experiment was carried out on 14 different individuals: 5 males (2 juveniles and 3 adults) and 9 females (1 juvenile, 3 yearlings and 5 adults), comprising 13 individuals for the first field session and 11 for the second one (see below). Indeed, three individuals died between the two sessions and were replaced by a new individual for the second session. Individuals were divided among 7 enclosures with group sizes ranging from 1 to 3.

### ***Experimental design***

The neophobia experiment occurred across two different field sessions: one in February 2014 and one in November of the same year so as to avoid the reproductive period or late gestation for females. For each session, the neophobia trial comprised two phases: a control phase with no disturbance, and a novel object phase. During this second phase, a novel object (a geometric shape made of polystyrene) was placed on alternate days above the feeder, more specifically slightly off the feeder so that individuals are not annoyed to feed. The shape of the novel object was varied so as to avoid habituation since roe deer seem more sensitive to shapes and contrasts rather than colors. In total, a field session consisted

of 10 consecutive days of testing for 7 hours per day: 5 days with no disturbance and 5 with disturbance novel object.

For each test, a few hours before, the feeder was removed to ensure that the deer would attempt to feed once the test started. Then, at the start of the test, we replaced the feeder with the same nutrient as usually together with the novel object next to the feeder and we triggered a camera trap (Reconyx, HyperFire). Each camera was fixed to the corner opposite to the feeder to see the feeder and the novel object and the cabin trapdoor to see the individual entering and going out the cabin. The cameras were placed into the cabin one week before the beginning of the test so that individuals were not disturbed by the cameras during the tests. The cameras were set on high sensitivity, 10 picks per trigger, a rapidfire picture interval and no quiet period. Thus, they are motion sensitive meaning that filming began as soon as an animal entered the cabin, and ceased only when the animal left the cabin.

For this study, we indexed an individual's level of neophobia in two different ways. First, we measured neophobia as the ratio between the total number of visits to the cabin (denominator) and the number of visits that resulted in a successful feeding bout (numerator) (subsequently, we refer to this as feeding efficiency). This supposes that more neophobic individuals will be less inclined to feed during a given visit when there is a novel object potentially present. Second, we measured neophobia as the time-related probability that a given individual fed a second time following a first successful feeding visit (subsequently, we refer to this as 2<sup>nd</sup> feeding bout probability). This supposes that more neophobic individuals will be less inclined to return to the cabin to feed during the novel object experiment.

### ***Behavioral and biochemical data collected during capture events***

Every winter, individuals are caught for routine monitoring purposes. All individuals were weighed with an electronic balance to the nearest 0.1 kg before being released back into their enclosure. Since 2011, we have continuously measured the rectal temperature during the handling process until it stabilized (using a Digitemp Color thermometer with a precision



of 0.1 °C). We also took blood samples to analyze some biochemical parameters related to stress in particular, micro hematocrit percentage or the ratio between neutrophils and lymphocytes. **Indeed, hematological parameters as the micro-hematocrit** are commonly used in the study of stress (Montané et al. 2007; Mentaberre et al. 2010). As regard the immunological parameters, Davis et al. (2008) showed that high ratios of heterophils or neutrophils to lymphocytes reliably indicate high glucocorticoid levels which are known to play an important role in stress responses and may be directly related to stress hormone levels. In addition, since 2013, we recorded the behavior at capture and during handling for each individual and calculated a behavioral score to describe the individual's stress profile in response to this stressful event (see also (Debeffe et al. 2014; Monestier et al. 2015; Bonnot et al. 2015). That is, we attributed a score of 1 (occurrence) or 0 (absence) for the three following behaviors: 1) the individual struggled, 2) it panted, 3) it vocalized on the table during marking. A behavioral score was then calculated as the sum of the scores for these 3 behavioral items describing a stress profile gradient ranging from 0 to 3, with 3 indicating a priori individuals with a high response to stress.

### ***Statistical methods***

#### *Inter-individual variation in neophobia*

To analyze inter-individual variation in neophobia when measured as the ratio between the total number of visits and the number of visits that resulted in a successful feeding bout (feeding efficiency) for a given individual, we used a logistic regression with this proportion as the dependent variable and the disturbance regime (presence/absence of the novel object), the season (February vs. November, to account for potential seasonal variation in food intake) and the individual's identity as fixed factors. We did not code the individual as a random factor because our aim was to explicitly test for among individuals differences in behavior. Because the propensity to feed may be impacted by the disturbance regime in a context-specific manner (i.e. between seasons), we also tested for the effects of the two 2-way interactions between the disturbance regime and season, and between season and individual identity. In all cases, models that included an interaction term also included the main effects of the variables involved in that interaction.

To analyze inter-individual variation in neophobia when measured as the time-related probability that a given individual fed a second time following a first successful feeding visit (2<sup>nd</sup> feeding bout probability), we used Cox proportional hazard models which are generally used in multivariate analyses of survival, but have broader potential application (Cox 1972; Therneau and Grambsch 2000). More generally, Cox models are used to study the probability that a specific event occurs at different instants for an individual based on its characteristics. The model is written as:  $h(t) = \exp(\beta_1 X_1 + \dots + \beta_p X_p) h_0(t)$

where  $h(t)$  is the hazard function at time  $t$  and here measures the probability that a given individual fed for a second time at a given time,  $X_p$  are the covariates influencing food intake (i.e., disturbance regime, season and individual's identity, plus certain 2-way interactions in the most complex model),  $\beta_p$  are the regression coefficients of these respective covariates, and  $h_0(t)$  is the baseline hazard function. We carried out the analyses on the period covering a maximum of 25200 seconds of the experiment (i.e. equal to the 7h of a given day's test which occurred when an individual fed immediately at the beginning of the test, but then did not feed again for the duration of that test). We checked the assumption of proportional hazards which is critical to Cox proportional models through an analysis of residuals (Grambsch and Therneau 1994). We used model diagnostics based on scaled Schoenfeld residuals and checked the hypothesis of log-linearity and identified the most influential observations. As above, we tested for the effects of the disturbance regime, the season and the individual's identity on the 2<sup>nd</sup> feeding bout probability of an individual.

Model selection was based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002) and Akaike weights to identify the model that best described the data. All analyses were performed in R version 2.15.1 (R Development Core Team 2013) using the lme4 package (Bates et al. 2015) and the survival package (Therneau 2014).

### *Consistency of traits*

We evaluated the within-individual consistency in neophobia measured as the ratio between the total number of visits and the number of visits that resulted in a successful feeding bout over the 14 individuals by calculating the repeatability of this measure with mixed models (Nakagawa and Schielzeth 2010). We also evaluated consistency in both the

number of successful feeding bouts and the total number of visits separately, since the above proportion depends on both variables. Repeatability coefficients (that is, intra-class correlation coefficients) were calculated using the “`rpt.binomGLMM.multi`” function of the “`rptR`” package for the feeding ratio and the “`rpt.poisGLMM.multi`” for both the number of successful feeding bouts and the total number of visits which had Poisson distributions (Schielzeth and Nakagawa 2011) in R version 2.15.1 software (R Development Core Team 2013). Repeatability is estimated as the ratio of between-individual variance to total variance with linear mixed-effects models (with individual identity as a random factor).

### *Correlations among traits*

Our second objective was to explore the link between neophobia measured in captivity using our experimental set-up with the behavioral and biochemical measures that are routinely recorded to index stress responsiveness during capture in the wild. For this, we described inter-individual variation in neophobia as the difference in feeding efficiency (number of feeding bouts/total number of visits) between days with no novel object and days with a novel object for each animal. We used the predicted values for each individual derived from the best model retained in the previous analysis. Similarly, we calculated the difference between the time taken to reach a probability of 25% (i.e. first quartile of data) that a given individual fed for a second time when there was no novel object and the equivalent time when the novel object was present (subsequently, we refer to this measure of inter-individual variation in neophobia as differences in latency to fed for a second time). Again, we used the predicted values for each individual extracted from the best Cox proportional hazard model retained in the previous analysis.

To explore the degree of inter-correlation between these measures of neophobia and the behavioral and biochemical measures taken during capture, we constructed two sets of linear models with each of the two measures of neophobia as the dependent variable and the behavioral and biochemical measures as explanatory variables.

## RESULTS

### *Consistency of traits*

Both the number of visits to the cabin ( $r = 0.608$ , 95% confidence of interval = [0.229, 0.717]) and the number of successful feeding bouts ( $r = 0.542$ , 95% confidence of interval = [0.247, 0.698]) were highly repeatable. As a result, the ratio between the number of visits and the number of successful feeding bouts was also repeatable, although to a somewhat lower extent ( $r = 0.418$ , 95% confidence of interval = [0.07, 0.351]).

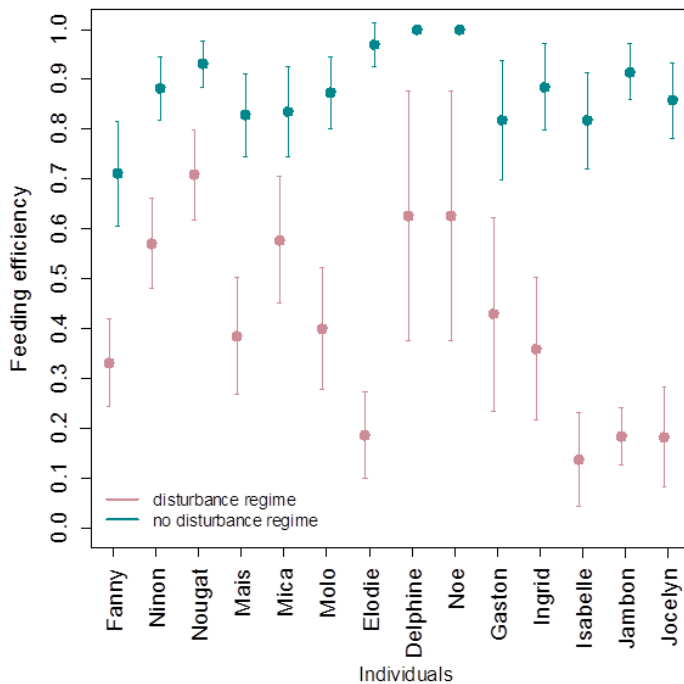
### *Inter-individual variation in neophobia*

The model with the highest support describing variation in the feeding efficiency contained the two two-way interactions between disturbance regime and individual's identity, and between disturbance regime and season (AICc weight 0.95,  $\Delta$ AICc to the second best model = 7.03,  $\Delta$ AICc to constant model = 171.27; Table 1).

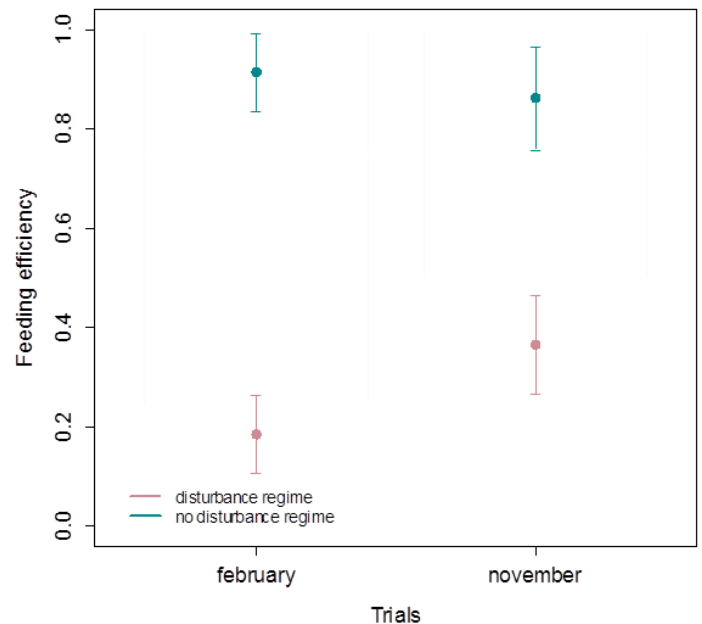
**Table 1. Candidate generalized linear models (GLM) fitted to investigate variation in the ratio between the number of visits and the number of successful feeding bouts (dependent variable).** AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for  $\Delta$ AICc and on the Akaike weights. Only models with an AICc lower than that of the baseline model are presented.

Models	K	AICc	$\Delta$ AICc	AICcWt
disturbance regime * individuals + disturbance regime * trails	30	583.05	0.00	0.95
disturbance regime * trails + individuals	17	590.08	7.03	0.03
disturbance regime * individuals + disturbance regime * trails + individuals * trails	39	591.24	8.19	0.02
disturbance regime * trails + individuals * trails	26	596.57	13.52	0.00
disturbance regime * individuals * trails	48	597.49	14.44	0.00
disturbance regime * individuals + trails	29	599.13	16.09	0.00
disturbance regime + individuals + trails	16	602.21	19.16	0.00
disturbance regime * individuals	28	604.50	21.45	0.00
disturbance regime + individuals	15	606.76	23.72	0.00
disturbance regime * individuals + individuals * trails	38	609.91	26.86	0.00
disturbance regime * trails	4	639.66	56.61	0.00
disturbance regime + trails	3	651.51	68.46	0.00
disturbance regime	2	651.55	68.50	0.00
individuals	14	715.92	132.87	0.00
trails	2	753.80	170.75	0.00
constant model	1	754.32	171.27	0.00

This model thus supports the hypothesis that feeding efficiency is affected by the introduction of a novel object inside the cabin, but that this effect varies in intensity among individuals and between the two seasons. Indeed, while most individuals had a high successful feeding ratio when there was no novel object (mean = 0.85, ranging between 0.69 for one individual and 1.0 for two individuals), it was consistently lower, but to a varying degree among individuals, when a novel object was present (ranging from 0.15 to 0.82, mean = 0.49; Fig. 1). In addition, the drop in feeding efficiency when a novel object was introduced was somewhat higher in February than in November (Fig. 2).



**Figure 1. Individual variation in the feeding efficiency with (red) and without (blue) the presence of a novel object.** This representation was obtained from the best model that included two 2-way interactions between the disturbance regime and individual's identity and between the disturbance regime and season.

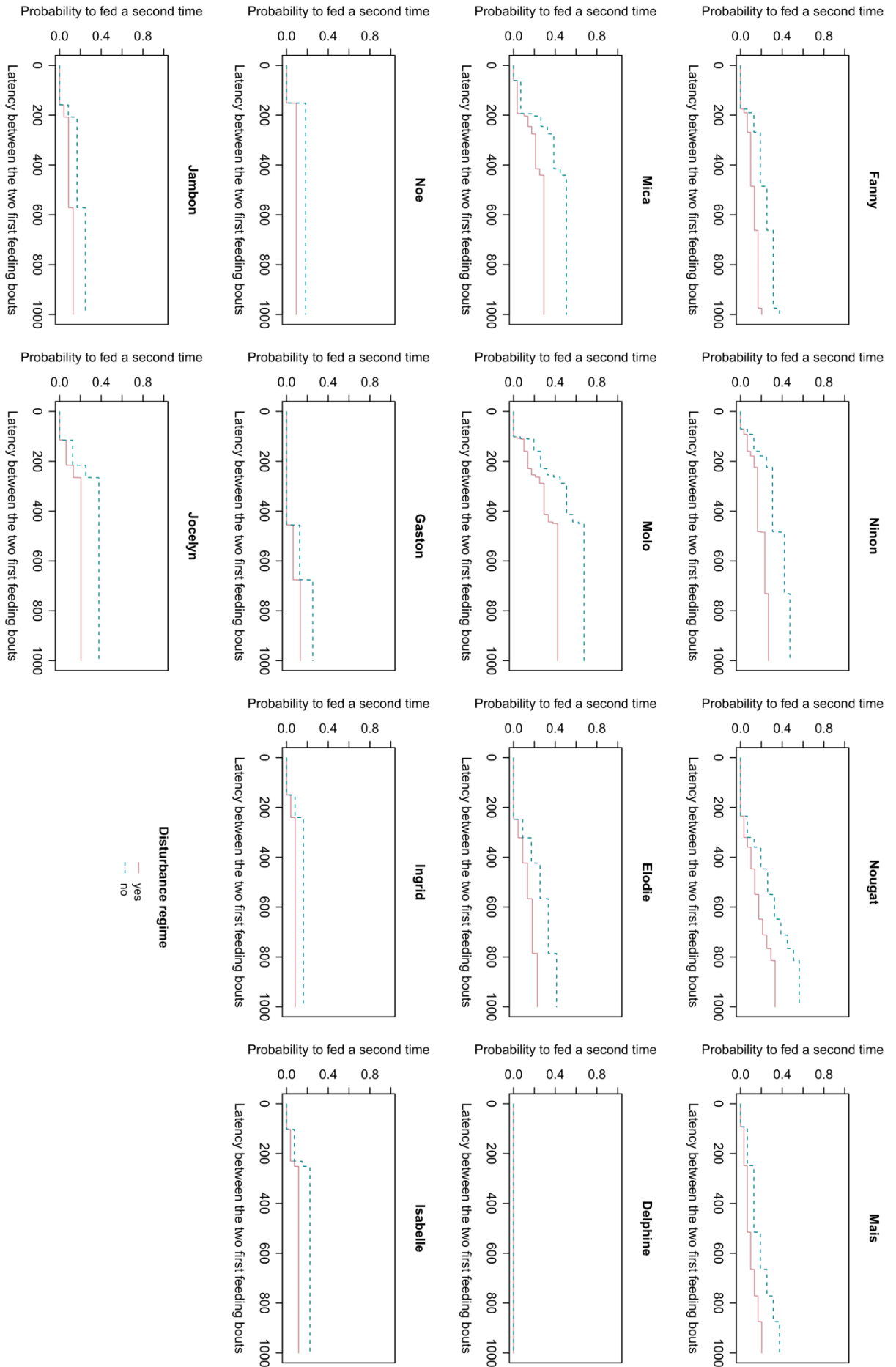


**Figure 2. Seasonal variation in the feeding efficiency with (red) and without (blue) the presence of a novel object.** This representation was obtained from the best model that included two 2-way interactions between the disturbance regime and individual's identity and between the disturbance regime and season.

The model with the highest support describing variation in the 2<sup>nd</sup> feeding bout probability of an individual contained the disturbance regime and individual's identity as fixed effects (AICc weight 0.99,  $\Delta$ AICc to the second best model = 8.65,  $\Delta$ AICc to constant model = 1031.70; Table 2). Thus, the 2<sup>nd</sup> feeding bout probability varied among individuals whether it be with or without novel object and decreased in the presence of a novel object (ranging from 0 to 44.0 %, mean = 20.6% for a latency of 1000 s between the two first feeding bouts with a disturbance regime; Fig. 3).

**Table 2. Candidate Cox proportional hazard models fitted to describe variation in 2<sup>nd</sup> feeding bout probability (i.e. time-related probability that the individual feed for a second time).** AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for  $\Delta$ AICc and on the Akaike weights. Only models with an AICc lower than that of the baseline model are presented.

Models	K	AICc	Delta_AICc	AICcWt
perturbation+strata(animal)	1	737.09	0	0.98
perturbation*strata(animal)	14	744.49	7.41	0.02
strata(animal)	0	754.49	17.4	0
perturbation	1	1615.35	878.26	0
constant model	0	1631.9	894.81	0



**Figure 3. Variation in the 2<sup>nd</sup> feeding bout probability (i.e. time-related probability that the individual feed for a second time) among the 14 individuals.** This representation was obtained from the best model that included the disturbance regime and individual's identity as fixed effects. We restricted the graphical representation to a maximum time elapsed between the two first feeding bouts of 1000 seconds to illustrate the immediate response of individuals to the novel object.

### ***Correlations among traits***

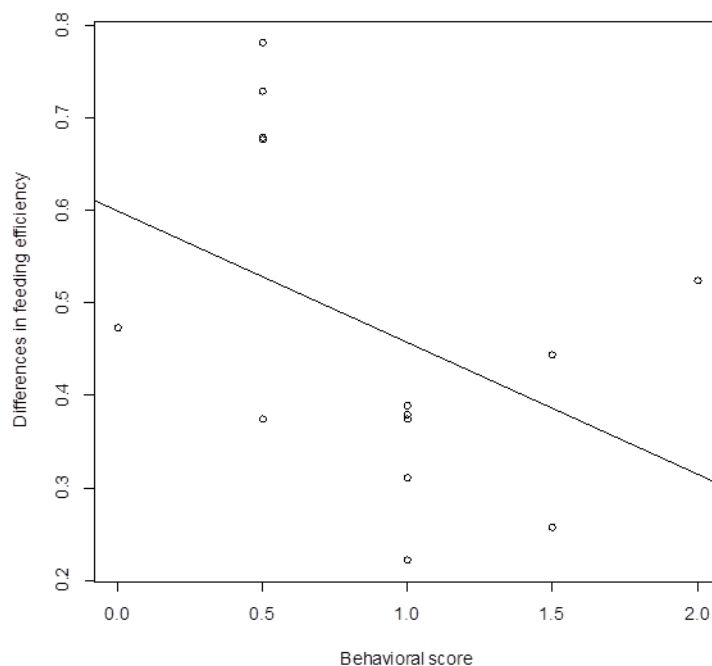
The model with the highest support describing inter-individual variation in the differences of feeding efficiency between days with no novel object and days with a novel object was the constant model (AICc weight 0.44,  $\Delta$ AICc to second best model = 1.80,  $\Delta$ AICc to constant model = 0.00; Table 3). However, there was some support for the model including the behavioral score at capture, (AICc weight 0.18,  $\Delta$ AICc to best model = 1.80,  $\Delta$ AICc to constant model = 1.80; Fig. 4). Thus, when individuals had a high difference in feeding efficiency that suggests they had a strong decrease in their feeding efficiency when a novel object was introduced in the cabin and had a less pronounced reaction to the capture event ( $R^2 = 0.18$ ).

The model with the highest support describing inter-individual variation in the differences of latency (difference between the time taken to reach a probability of 25% that a given individual fed for a second time with and without novel object) was the model including the micro-hematocrit percentage (AICc weight 0.48,  $\Delta$ AICc to second best model = 0.76,  $\Delta$ AICc to constant model = 0.76; Table 4). Thus, when individuals had a low difference in latency that suggests they took few time to reach the probability of 25% to fed for a second time when a novel object was introduced in the cabin and had a higher percentage of micro-hematocrit whereas individuals having a higher latency took more time to reach the probability of 25% to fed for a second time and had a lower percentage of micro-hematocrit ( $R^2 = 0.35$ ; Fig. 5).

**Table 3. Candidate linear models to describe inter-individual variation in the differences of feeding efficiency (differences in the ratio between the number of visits and the number of successful feeding bouts with and without novel object) (dependent variable) in relation to the behavioral score and the biochemical parameters collected during capture (explanatory variables).** AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for  $\Delta$ AICc and on the Akaike weights.

Models	K	AICc	$\Delta$ AICc	AICcWt
constant model	2	-2.46	0.00	0.50
behavioral score	3	-0.66	1.80	0.20
temperature	3	0.12	2.58	0.14
N/L ratio	3	0.95	3.40	0.09
micro-hematocrit	3	1.37	3.83	0.07

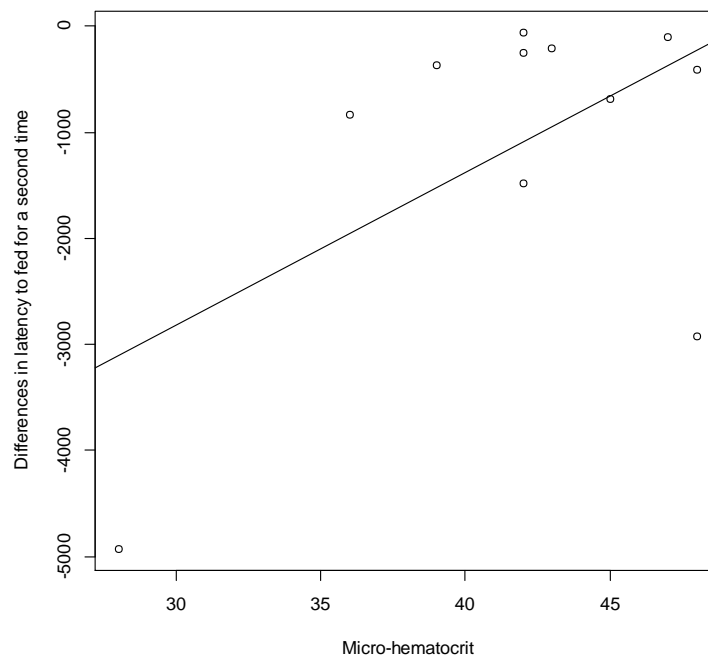




**Figure 4. Relationship between inter-individual variation in the differences of feeding efficiency between days with novel object and days without a novel object and it's behavioral score at capture.** Behavioral score ranging from 0 to 3, with 3 indicating a priori individuals with a high stress response.

**Table 4. Candidate linear models to describe inter-individual variation in the differences of latency (difference between the time taken to reach a probability of 25% that a given individual fed for a second time with and without novel object) (dependent variable) in relation to the individual's behavioral score and biochemical parameters at capture (explanatory variables).** AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for  $\Delta AICc$  and on the Akaike weights.

Models	K	AICc	$\Delta AICc$	AICcWt
micro-hematocrite	3	202.03	0.00	0.48
constant model	2	202.80	0.76	0.33
behavioral score	3	206.00	3.97	0.07
temperature	3	206.08	4.05	0.06
N/Lratio	3	206.18	4.15	0.06



**Figure 5. Relationship between the differences of latency between days with novel object and days without a novel object and its micro-hematocrit level.** The delta corresponded to the difference between the time spent by the individual to reach the probability that it feed itself at a rate of 25% without disturbance regime and the time spent by the individual to reach the probability to feed itself at a rate of 25 % with a disturbance regime. These predicted values were extracted from the predictions of the model (logistic regression and Cox proportional hazard model). The level of micro-hematocrit was measured in blood samples collected during capture event.

## DISCUSSION

Our first aim was to investigate the existence of consistent inter-individual variation in the level of neophobia using an experimental set-up on captive roe deer. In this study, we observed inter-individual differences in both, the feeding efficiency and the 2<sup>nd</sup> feeding bout probability. Thus, we found that globally, individuals decreased both their feeding efficiency and their probability to feed for a second time in the presence of a novel object. These results are consistent with others studies carried out in the neophobia context. For example, Herborn et al. (2010) found that the latency to feed in the presence of a novel object

increased, indicating neophobia in blue tits (*Cyanistes caeruleus*). Mettke-Hofmann et al. (2002) showed in parrots species (*Psittacidae*) that objects placed near the feeding dish resulted in significantly longer latencies until first food intake than in the controls. Parrots approached the dish and withdrew from it several times before they commenced feeding. In addition, we found that the feeding efficiency (reflecting the neophobia gradient) was consistent over time ( $r = 0.418$ , 95% confidence of interval = [0.07, 0.351]). This result was in line with others studies on neophobia or exploration. For instance, Dingemanse et al. (2002) measured the exploratory behavior of wild great tits in laboratory and found that it was repeatable. Repeatabilities ranged from 0.27 to 0.48 depending on the sexes and on the field of capture with no significant differences between the sexes, and age. Moreover, we found that the consistency of the feeding efficiency was quite high. Bell et al. (2009) reported in a meta-analysis that among-individual repeatability of behavioral traits (excluding physiological traits such as body temperature) averaged 0.37 across taxa.

Besides, we also identify that the feeding efficiency differed according to the test period. Indeed, the decrease in feeding efficiency when a novel object was introduced was slightly more marked during February than during November. This could indicate that the deer had become habituated to the experimental set-up during the second field session in November, as 10 of the 14 individuals were tested in both sessions. To check for this hypothesis, we performed a linear model with the feeding efficiency as the dependent variable and the repetitions as the explanatory variable. It seemed that the feeding efficiency increased slightly over time ( $p$ -value = 0.047, Appendix 1) which prone for a weak habituation of individuals to the trial. Alternatively, another hypothesis explaining this result may be due to the lower energetic needs of deer during the winter when their metabolic rate and appetite are lower than during autumn (Moen 1978). This seasonal fluctuation in energy requirements potentially shifts the tipping point in the trade-off between resource acquisition and risk, so that individuals should appear to be more risk averse during periods when their metabolic requirements are lower.

Moreover, to index neophobia and link this trait to behavioral, physiological and hematological parameters, we used two neophobia indices: the differences in the feeding efficiency and the differences in the latency to fed for a second time at a rate of 25%. These indicators of neophobia seemed complementary and slightly correlated each other ( $R^2 =$

0.22,  $p$ -value = 0.09; Appendix 2). Thus, individuals with a low difference in their feeding efficiency tend to have a lower latency and are assumed in this study to be less neophobic. Despite this general rule, it seemed that some inter-individual differences exist. For instance, some individuals which clearly seemed neophobic when looking at its feeding efficiency had a quite high probability to feed for a second time rapidly which was not consistent with the neophobia definition. We could suggest that some neophobic individuals (from the feeding efficiency test) would choose to feed a second time soon after the first feeding bout in order not to come again during the test period and so avoid any novelty situation and stress. It may be another alternative allowing individuals to trade-off between their food consumption and the 'fear' of novelty. That being said, this was only an assumption as our sample size was weak and we did not find similar results in literature.

Our second aim was to validate our approach to describe inter-individual variation in behavior of this species by exploring the relationship between our gradient of neophobia measured in captivity and the behavioral and biochemical parameters collected during capture carried out both in the wild and in captivity for indexing behavioral syndromes in the wild (Debeffe et al. 2014; Monestier et al. 2015; Bonnot et al. 2015). We found some weak evidence for an inverse correlation between the individual-specific decrease in feeding efficiency in the novel object experiment and the individual's behavioral score at capture. This suggests that the more neophobic individuals had a lower behavioral reaction to the stress induced by physical restraint. In a previous study on a wild roe deer population, individuals with a high behavioral score at capture were interpreted to be proactive (Monestier et al. 2015), hence our present results suggest that proactive individuals are less neophobic. This result is in line with previous studies (Koolhaas et al. 1999; Koolhaas et al. 2010) where proactive individuals were found to be fast explorers and so neophilic, highly aggressive, impulsive in decision-making, novelty seekers which take risks in the face of potential danger. Proactive individuals are thus assumed to cope actively with the source of stress through a "flight-or-fight" response whereas reactive individuals show the opposite physiological patterns and tend to react to challenges by freezing. However, our sample size was weak and even though we found some support for an effect of the behavioral score on the feeding efficiency of individuals, we have to keep in mind that the best retained model was the constant model.

We also found a some consistency for a correlation between the differences in the latency to feed a second time and the percentage of micro-hematocrit in individual's blood. Thus, the latency decreased with an increase in micro-hematocrit percentage suggesting that neophilia increased with an increase in hematocrit percentage. **Haematological parameters as the micro-hematocrit** are commonly used in the study of stress (Montané et al. 2007; Mentaberre et al. 2010) and are known to increase during an acute stress thanks to the sympathetic axis (also called orthosympathetic axis; Davis et al. 2008; Weiss and Wardrop 2011). Moreover, variations in haematological and biochemical variables have been described in the past in ungulates and indicated that these animals could experience a degree of chronic stress (Franzmann and Thorne 1970; Franzmann 1971; Del Giudice et al. 1987; Hattingh et al. 1990). Once again, results tend to indicate that neophilic individuals (individuals with a low latency and a high percentage of hematocrit) were proactive sensu the Koolhaas et al.'s (1999) definition.

Finally, we did not take into account neither the sex nor the age of individuals because of lack of statistical power. That being said, we did not expect for sex differences in roe deer living in captivity since sexual dimorphism is low in this species and the trials were carried out in non reproductive season where behaviors between sexes differed. This hypothesis would be in line with others studies carried out in captivity (Verbeek et al. 1994; Verbeek et al. 1996; Dingemanse et al. 2002; Herborn et al. 2010; King et al. 2015). As regard the age, even if these studies did not find an effect of age too, others studies showed that exploration differed at specific life stages with for example juveniles which are more investigative of novel items (Japanese macaque (*Macaca fuscata*): Menzel 1966; Australian magpies (*Cracticus tibicen*): Pellis 1981 vervet monkey, (*Cercopithecus aethiops sabaues*): Mcguire et al. 1994), which may reflect greater playfulness (Greenberg and Mettke-Hofmann 2001). We seemed to notice the same effect but our sample size was too weak to be statistically tested.

To conclude, we found that inter-individual variability exist in neophobia in captive roe deer. Moreover, we found that neophobia was linked with some support to the behavioral score of individual measured during capture (so, a stressful event) and to their percentage of hematocrit. Thanks to these correlations, it seems we found a behavioral syndrome. Indeed, Sih et al. (2004) defined behavioral syndrome as 'In evolutionary ecology,

suites of correlated characters are commonly referred to as syndromes (e.g., life-history syndromes, dispersal syndromes), thus we refer to suites of correlated behaviors as behavioral syndromes' and it is recognized that personality trait set behavioral syndrome may have strong effect on life-history traits and on fitness (Sih, Bell, Johnson, et al. 2004; Réale et al. 2007; Smith and Blumstein 2008). As Herborn et al. (2010) found that personality in captivity reflect personality in the wild, we suggest that this study in a first step to show that behavioral traits and physiological parameters which are measurable in wild roe deer can be reliably interpreted in terms of established behavioral gradients by validating this approach in captivity. Consequently, a next step could be to link it to life-history traits or demographic performance of roe deer in the wild which could open the gate of new perspectives as the personality pace-of-life. However, our results must be interpreted with caution as we need to build on this pilot study, notably by increasing sample sizes.

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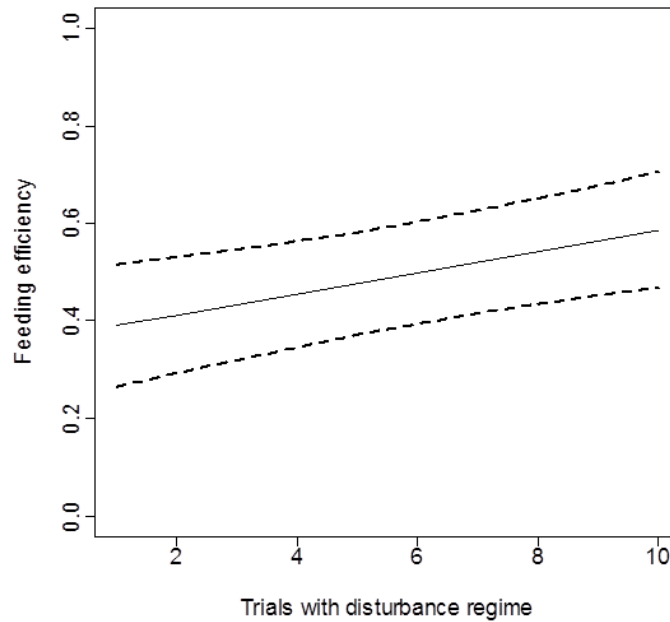
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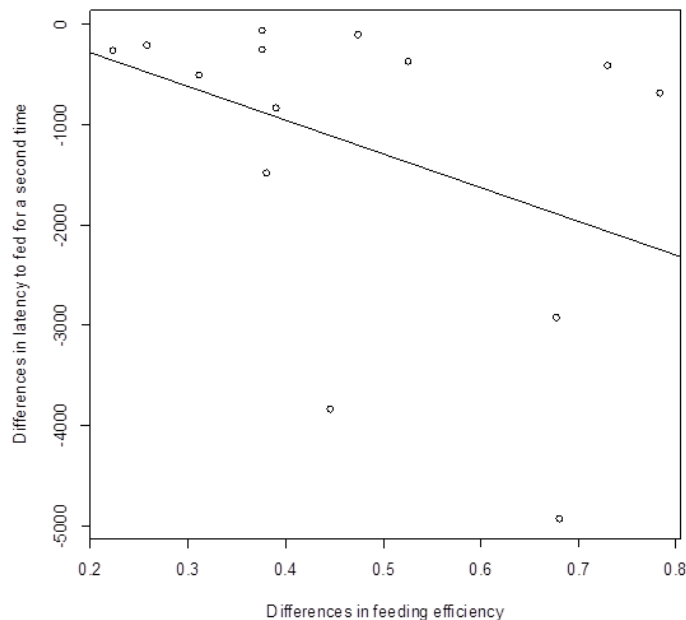
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**APPENDICES**



**Appendix 1. Evolution of the individuals’ feeding efficiency across the ten tests realized with a disturbance regime.** Here are represented the mean feeding efficiency for all the individuals and their 95 % confidence intervals.



**Appendix 2. Relationship between the differences in feeding efficiency and in the latency to feed a second time.** We described inter-individual variation in neophobia as two different indexes. The first one was the difference in feeding efficiency (number of feeding bouts/total number of visits) between days with no novel object and days with a novel object for each animal. The second one corresponded to the difference between the time taken to reach a probability of 25% that a given individual fed for a second time when there was no novel object and the equivalent time when the novel object was present.

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## **Chapter V**

# **Behavioral trade-off between two dimensions of a behavioral syndrome**

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# To eat but not be eaten: the risk avoidance resource acquisition trade-off is mediated by individual differences in vigilance behavior in a large herbivore

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*'Human activity generally leads to habitat fragmentation that may decrease the availability and quality of foraging and/or refuge habitats. As a result, to acquire food of better quality and/or quantity, animals often have to use risky habitats [...].'*



Photos: by B. Lourtet, J.M. Angibault, and N. Cebe from left to right

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## RESUME

Les compromis d'histoire de vie sont connus pour affecter la diversité des stratégies d'histoire de vie. Ceci étant, les compromis comportementaux sont beaucoup moins étudiés et donc à un état de connaissance moins avancé. Le compromis comportemental le plus connu est sûrement le compromis entre l'acquisition des ressources et le risque de prédation. Celui-ci a des conséquences importantes en termes de valeur sélective individuelle qui plus est lorsque les individus vivent dans des milieux fortement anthropisés et/ou façonnés par l'Homme. Par ailleurs, malgré une réponse générale au niveau d'une population, il est reconnu que les individus d'une même population peuvent répondre différemment aux contraintes imposées par le compromis. Ceci revient donc à avoir de la variabilité interindividuelle au sein de la population et donc à avoir une population polymorphique. Même si l'attrait de l'étude des compromis lié au concept de personnalité est important, cela reste encore nouveau et très peu d'études permettent de mettre en évidence et de quantifier de telles relations d'autant plus en milieu sauvage où il est particulièrement difficile d'observer les individus et de collecter des données à plusieurs reprises. Notre but était donc i/ de tester l'existence du compromis entre acquisition des ressources et risque de prédation au sein d'une population sauvage de chevreuils (*Capreolus capreolus*) à l'échelle individuelle puis, ii/ de quantifier les différences interindividuelles observées dans le compromis en termes de choix vis-à-vis du compromis mais également en termes d'intensité du compromis de manière à pouvoir identifier des stratégies individuelles. Enfin, le dernier objectif était iii/ de voir quelle part jouait la vigilance des individus dans la variabilité interindividuelle du compromis. Nous avons supposés que les individus enclins à prendre des risques favoriseraient leur efficacité alimentaire en s'alimentant dans des habitats riches d'un point de vue nutritif mais également plus risqués, c'est-à-dire avec un risque de prédation plus élevé. Ils seraient, cependant, plus vigilants de manière à compenser la prise de risque alors que des individus plus timides préféreraient assurer leur sécurité au détriment d'une efficacité alimentaire forte et seraient donc moins vigilants. Nous avons ainsi trouvé que le compromis entre acquisition des ressources et risque de prédation existe bien chez le chevreuil et qu'il est plus marqué pour les femelles au printemps. De plus, il existe de la variabilité interindividuelle dans ce compromis qui peut être expliqué, en partie, par le niveau de vigilance des individus. En effet, la probabilité de

faire un compromis mais également l'intensité de ce compromis, lorsque celui-ci a lieu, augmente avec le niveau de vigilance des individus. Ainsi, les femelles faisant un compromis et ayant une forte intensité de compromis, c'est-à-dire ayant une forte efficacité alimentaire dans des habitats riches mais risqués et donc une faible efficacité alimentaire dans des habitats plus sûrs, sont des femelles avec un fort niveau de vigilance. A l'inverse, les femelles ne faisant pas de compromis ou alors avec une faible intensité sont des individus avec un faible niveau de vigilance. A l'aide de ces résultats nous supposons et proposons que le niveau de vigilance des individus soit le résultat d'une adaptation dépendante de leur lieu et condition de vie.

**Mots clé:** herbivores, compromis, variabilité interindividuelle, comportement anti-prédateur

**ABSTRACT**

While trade-offs among life history traits have been shown to shape the diversity of life history strategies, behavioral trade-offs are poorly documented. The best known trade-off is likely the resource acquisition-risk avoidance trade-off which has strong impact on individual fitness especially in modern man-altered landscapes but it is particularly to highlight it in wild populations. Moreover, individuals may respond differently to the constraint imposed by trade-offs, although such among-individual differences have received little attention to date. With this study, we aim to i/ investigate this behavioral trade-off in a free-ranging population of roe deer (*Capreolus capreolus*) at the individual level; ii/ quantify individual differences in the shape and intensity of the trade-off to identify different behavioral tactics; and iii/ explore to what extent vigilance could mediate the diversity of these individual tactics. We hypothesize that risk-prone individuals should prioritize feeding efficiency by exploiting rich but risky habitats and should be more vigilant, whereas risk-averse individuals should be more inclined to feed in secure refuge habitats and pay the resulting cost of limited access to high quality resources. We found clear evidence for a trade-off between food acquisition and risk avoidance especially in spring among females. We also demonstrated that both the probability of facing a trade-off and its strength tended to increase with the vigilance level meaning that females facing a more important trade-off are more vigilant. We supposed that inter-individual differences in the behavioral trade-off mediated by the vigilance level are the result of an adaptation of vigilance to specific contexts.

**Key words:** herbivores, trade-off, inter-individual variability, anti-predator behavior





## INTRODUCTION

Trade-offs play a central role in shaping the diversity of life history strategies, both within and among species (S.C. Stearns 1992). Trade-offs among life history traits such as age and size at maturity, number of offspring and longevity determine among-species variation in the pace of life. This can be described in terms of a continuum, ranging from slow developing, long-lived and low fecundity organisms to rapidly developing, short-lived, and high fecundity organisms (Stearns 1983, Gaillard et al. 2015). Trade-offs can be measured using different currencies such as energy or time (Roff 1992; Stearns 1992). According to the principle of energy allocation (Cody 1966), maximum individual fitness is limited by trade-offs that occur among fitness components during its lifetime (Williams 1966). Individuals must thus allocate limited time or energy to competing activities, which should generate trade-offs.

While energy-based trade-offs among life history traits have been shown to shape the diversity of life history strategies (Roff 1992; Stearns 1992), behavioral trade-offs are, to date, poorly documented (but see Lima and Dill 1990; Houston et al. 1993; Brown 1999). The trade-off between resource acquisition and risk of predation or, more precisely, security has, however, been the object of some interest (Verdolin 2006). Thus, the constant search for food often forces prey to forage in areas of high predation risk and/or limits the ability of prey to detect a predator, e.g. through vigilance (Lima and Dill 1990). Indeed, vigilance is often considered as mutually exclusive to foraging (Underwood 1982). In this situation, animals face a behavioral conflict between increasing their exposure to potential predation and sacrificing high quality foraging opportunities.

The resource acquisition-risk avoidance trade-off likely has a strong impact on individual fitness of large herbivores and may be more pronounced in modern man-altered landscapes. Indeed, across much of Europe, the intensification of agricultural practices has modified natural habitats (Sotherton 1998; Robinson and Sutherland 2002), resulting in marked spatio-temporal heterogeneity in both resource distribution and risk. Even though agricultural practices may improve habitat quality locally, leading to a higher food quality for herbivorous species (Hewison et al. 2009; Torres et al. 2011), human activity generally leads to habitat fragmentation that may decrease the availability and quality of foraging and/or refuge habitats (Forman et al. 2002). As a result, to acquire food of better quality and/or

quantity, animals often have to use risky habitats (Mysterud et al. 1999a, 1999b). Indeed, cohabitation of wildlife with humans increases both potential direct lethal impacts (hunting, predation by dogs and collisions), as well as the non-lethal impacts (recreational activities and presence of domestic species) (Jayakody et al. 2008; Stankowich 2008; Webb et al. 2011). Hence, from a general point of view, humans and disturbance created by human activities generate disturbance similar to predation risk (Frid and Dill 2002).

Individuals may respond differently to the constraint imposed by the risk avoidance-resource acquisition trade-off, although such among-individual differences have received little attention to date (Favreau et al. 2014). However, exposure to predators might depend on personality or behavioral syndromes as has been shown experimentally and empirically for sticklebacks (Bell and Sih 2007; Dingemanse et al. 2009) and via game-theoretical modelling (Dall et al. 2004) because of differential susceptibility to risk taking among personality types (Sih et al. 2003; Quinn and Cresswell 2005). Moreover, it has also been shown theoretically that personality traits could be favored and maintained as a result of life-history tradeoffs that involve personality traits (Wolf et al. 2007; Biro and Stamps 2008). For example, Wolf et al. (2007) found that trade-offs between early and late fecundity might encourage the maintenance of individual differences in exploratory behavior, aggressiveness and boldness, while Stamps (2007) showed that trade-offs between growth and mortality might encourage the maintenance of variation in boldness or aggressiveness. In addition, more recently, researchers have investigated the link between personality traits, metabolism and hormones (Careau et al. 2008) and between personality traits and life-history differences (theoretical studies: Stamps (2007); Wolf et al. (2007); empirical studies: Boon et al. (2007); Réale et al. (2009); Monestier et al. (2015)). Hence, consistent inter-individual differences in behavior may covary with physiological and life-history traits at the inter-population level, but also within populations, leading to a personality pace-of-life syndrome (see (Réale, Garant, et al. 2010) for a review). This new concept clearly links personality traits or behavioral syndromes (Sih, Bell, and Johnson 2004; Réale et al. 2007) to inter-individual variation in life-history tactics.

Here, we aim to i/ investigate the behavioral trade-off between resource acquisition and risk avoidance in a free-ranging population of roe deer (*Capreolus capreolus*) at the individual level; ii/ quantify individual differences in the shape and intensity of the risk

avoidance-resource acquisition trade-off to identify different behavioral tactics; indeed, there is no unique optimal solution to a given trade-off so that we might expect individuals faced with the choice of maximizing foraging opportunities or minimizing exposure to predators to adopt alternative tactics according to their personality-driven pace of life (Dammhahn and Almeling 2012); and iii/ explore to what extent vigilance could mediate the diversity of these individual tactics. Vigilance is a crucial anti-predator behavior that reduces the risk of being predated (Lima and Dill 1990), but impairs an individual's feeding efficiency (Lima and Dill 1990), so that the interplay between feeding rate, use of risky habitat (Bonnot et al. 2015) and vigilance reflects the trade-off between food acquisition and risk avoidance (Lima and Dill 1990; Quenette 1990; Fritz et al. 2002; Cowlshaw et al. 2004; Blanchard and Fritz 2007). To what extent individuals differ in their resource acquisition-risk avoidance tactic and how this relates to the individual's behavioral profile remains largely unexplored (Brown and Kotler 2004; Verdolin 2006). We hypothesize that risk-prone individuals should prioritize feeding efficiency by exploiting rich but risky habitats, whereas risk-averse individuals should be more inclined to feed in secure refuge habitats and pay the resulting cost of limited access to high quality resources. We, therefore, expect risk-prone individuals to be inherently more vigilant in order to compensate for their higher exposure to risky situations.

## **MATERIAL AND METHODS**

### ***Study model and site***

The study site is an agricultural landscape mostly covered by open habitats interspersed with small woodland patches and two main forests. During annual roe deer capture events, we equipped individuals with a GPS collar (149 individuals in the present study) providing detailed data on spatial behavior including habitat use and movement speed (see *SI Materials and Methods* for details on data acquisition).

### ***Indexing resource acquisition: feeding efficiency***

Large herbivores spend most of their active time engaged in the search for and consumption of food (Georgii 1981; Owen-Smith 1998). The roe deer is characterized by a relatively small rumen relative to its overall body size (Duncan et al. 1998) so that feeding efficiency is limited by the time necessary to achieve rumen-fill (Holand et al. 1998). Hence, individuals feeding in rich open habitats such as meadows and cultivated fields (Hewison et al. 2009), where resources are spatially clumped, should cover less distance during feeding bouts and, hence, exhibit lower average movement speeds than in poorer habitats where resources are more widely dispersed. Indeed, in our study site, deer movement rate and activity level are both lower in the richer more open habitats (unpubl. data).

We thus indexed feeding efficiency for each individual as its mean average speed (m/s) based on GPS location data during each of the intensive monitoring periods (location interval = 10 min) of 24 hours distributed across the year (an average of 13 periods/individual, see *SI Materials and Methods* for details). This assumes that movement speed indexes energetic expenditure linked to locomotion (Nilssen et al. 1984; Fancy and White 1987) so that speed should be inversely correlated with individual fitness. We thus used the negative value of average speed as a measure of feeding efficiency so that high values of this measure (i.e. low average speed) were taken to indicate high feeding efficiency.

### ***Indexing risk avoidance: the use of refuge habitat***

Wild herbivores clearly perceive open habitats as risky (Frid and Dill 2002; Stankowich 2008), whereas wooded habitats provide protective cover (Myysterud et al. 1999b; Myysterud and Ostbye 1999). Hence, we considered that an individual's propensity to use open habitat indexed its risk taking behavior (see Bonnot et al. 2015). We thus defined risk avoidance as the probability that an individual used the closed refuge habitats provided by woodland. As a result, we took the proportion of GPS locations during each of the same intensive monitoring periods that occurred in wooded habitat as our index of risk avoidance for a given individual, so that high values indicate marked avoidance of risky open habitat.

## ***Indexing inter-individual variation in anti-predator behavioral tactics: vigilance***

Vigilance is a pervasive anti-predator behavior used by large herbivores to avoid risk (Lima and Dill 1990). We thus focused on vigilance behavior to investigate among-individual variation in behavioral tactics influencing the resource allocation - risk avoidance trade-off. For this, we performed focal observations on individually identifiable GPS marked roe deer in the field (in open habitat, either meadows or crop fields) at dawn and dusk (during peak activity; Jeppesen (1989). From repeated observations lasting approximately 10 min (average of 4 observations/individual, range = 2 to 7), we calculated the mean proportion of time spent vigilant over all observations for each individual (head above shoulder level while scanning surroundings; *SI Materials and Methods*). High values of this measure thus indicate individuals that must compensate for their risk-prone spatial behavior by being more vigilant.

### ***Statistical analyses***

#### *Within individual repeatability of the behavioral measures*

We assessed the within-individual consistency of i/ feeding efficiency (N = 13 intensive monitoring periods in average on 149 different individuals), ii/ the use of refuge habitat (N = 13 intensive monitoring periods in average on 149 different individuals) and iii/ vigilance behavior (N = 4 observations in average on 35 different individuals) by calculating their repeatability (Nakagawa and Schielzeth 2010; Schielzeth and Nakagawa 2011) (see *SI Materials and Methods* for details)

#### *Assessing the trade-off between resource acquisition and risk avoidance*

To investigate the trade-off between resource acquisition and risk avoidance, we used generalized linear mixed models (GLMM) to analyze variation in feeding efficiency (i.e. resource acquisition) as a function of refuge habitat use (i.e. risk avoidance), including the individual's identity as a random effect on either the intercept and/or the slope of this relationship to account for repeat observations per individual. We also accounted for

possible confounding effects on feeding and spatial behavior: sex, season (Gaillard et al. 2000; Abbas et al. 2011) and sector (Hewison et al. 2009; Morellet et al. 2011). Hence, we defined 3 seasons reflecting variation in resource availability and risk, primarily from hunting: autumn, winter, and spring. We also defined three landscape sectors in relation to the proportion of wooded habitat in the local landscape: open (agricultural area with highly fragmented woodland), intermediate (partially wooded area) and closed (forest block; see Hewison et al. 2009; Morellet et al. 2011 and *SI Materials and Methods* for more details). We incorporated these four co-variables as fixed effects and tested for 2-way interactions between certain explanatory variables in relation to a priori hypotheses (*SI Materials and Methods*).

*Vigilance as a mediator of individual variation in behavioral tactics for the trade-off between resource acquisition and risk avoidance*

We investigated the relationship between individual tactics for resolving the risk avoidance - resource acquisition trade-off with individual differences in the propensity to be vigilant. In a first step, to describe the shape and strength of the trade-off at the individual level, we extracted the individual-specific slope from the best model describing variation in feeding efficiency in relation to the use of refuge habitat but only for the spring season. Indeed, we chose to focus more specifically on this season as the trade-off was more intensive in spring (see Results) with significant differences between sex. Moreover, from a biological point of view, spring is the most interesting season as resources are more attractive in open habitats leading individuals to face more the risk avoidance - resource acquisition trade-off. Besides, males become territorial (Bramley 1970) and females have high energetic demands to offset the cost of late gestation (Clutton-Brock et al. 1989). Then, we used logistic regression (Bates et al. 2015) to test whether the probability that an individual expressed a risk avoidance - resource acquisition trade-off (i.e. a negative slope) was related to the habitual level of vigilance expressed by that individual. As our analyses indicated sex-specific differences in the risk avoidance - resource acquisition trade-off (see Results), we performed separate analyses for males and females.

Subsequently, focusing solely on those individuals that expressed a risk avoidance - resource acquisition trade-off, we investigated how the strength of the trade-off and its

components (feeding efficiency, use of refuge habitat) were related to an individual's habitual level of vigilance using linear models (LM).

All model selection was based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002). All analyses were performed in R version 2.15.1 (R Development Core Team 2013).

## RESULTS

### *Within individual repeatability of the behavioral measures*

Both feeding efficiency ( $r = 0.637$ , 95% confidence of interval = [0.189, 0.213]) and the use of refuge habitat ( $r = 0.483$ , 95% confidence of interval = [0.283, 0.399]) were highly repeatable behaviors at the individual level, especially in spring (feeding efficiency:  $r = 0.824$ , 95% confidence of interval = [0.35, 0.533]; use of refuge habitat:  $r = 0.490$ , 95% confidence of interval = [0.335, 0.572]). The proportion of time spent vigilant (observations in spring only) was moderately repeatable ( $r = 0.348$ , 95% confidence of interval = [0.133, 0.518]) at the individual level.

### *Assessing the trade-off between resource acquisition and risk avoidance*

The model with the highest support describing variation in feeding efficiency in relation to the use of refuge habitat (Table 1) included the three two-way interactions between the use of refuge habitat and sex, the use of refuge habitat and season, and sex and season (AICc weight of 0.54,  $\Delta$ AICc to constant model of 356.97). In addition, the model included the individual's identity as a random effect on both the intercept and the slope of the relationship between feeding efficiency and the use of refuge habitat.

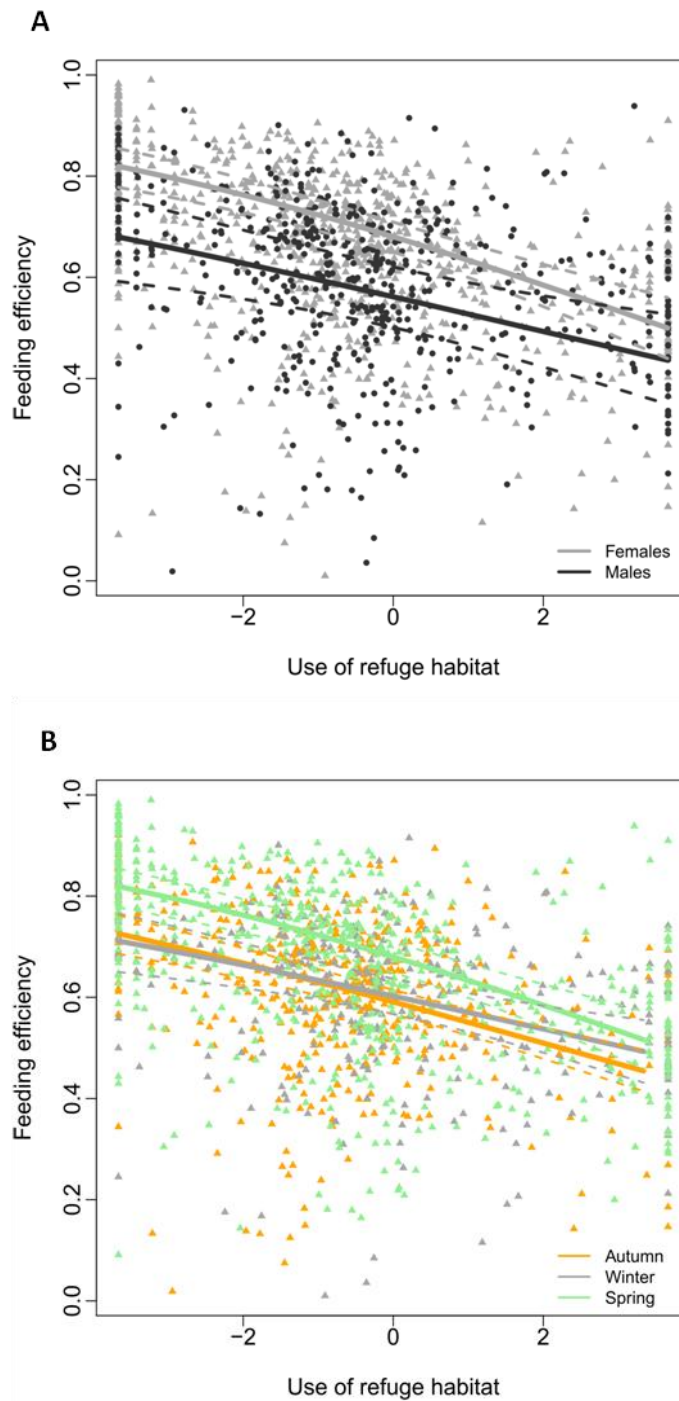
Overall, feeding efficiency decreased with increasing use of refuge habitat, but the rapidity of this decrease was higher for females than for males (Fig. 1a). Specifically, across the range of observed values for the use of refuge habitat, feeding efficiency decreased by 32 % for females and by 24 % for males. However, despite this, females had a consistently higher



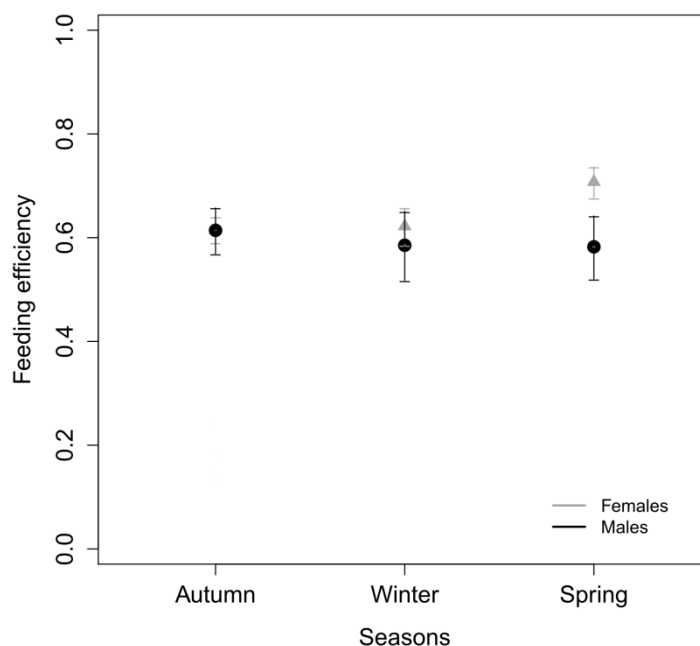
feeding efficiency than males for a given level of refuge habitat use. Second, the decrease in feeding efficiency with increasing use of refuge habitat also varied among seasons (Fig. 1b). While for a given level of refuge habitat use, feeding efficiency was consistently higher during spring, its decrease was more pronounced than during the other two seasons. Specifically, across the range of observed values for the use of refuge habitat, feeding efficiency decreased by 26% in autumn, 21% in winter and 30% in spring. Average feeding efficiency was higher in females than in males during spring, but not clearly so during the two other seasons (Fig. 2). Finally, in addition to these population-level effects, the marked effect of individual identity on the slope of the relationship between feeding efficiency and the use of refuge habitat indicated that the trade-off between resource acquisition and risk avoidance varied substantially among individuals (Fig. 3).

**Table 1. Candidate generalized linear mixed models (GLMM) fitted to investigate variation in feeding efficiency (dependent variable) as a function of refuge habitat use (explanatory variable).** These models included the use of refuge habitat (RHU), sex, season and sector as fixed effects and the individual's identity as a random effect on the intercept (1|Ind) or on both the slope and the intercept (RHU|Ind) of the relationship between feeding efficiency and the use of refuge habitat. AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in AICc values for and Akaike weights. Only models with an AICc lower than that of the constant model are presented.

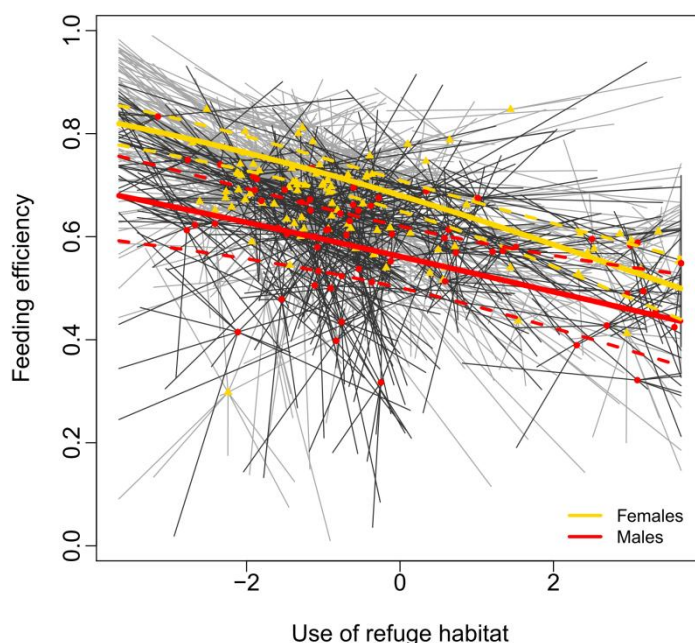
Models	K	AICc	ΔAICc	AICcWt
season*RHU + sex*RHU + season*sex + (RHU Ind)	13	-1668.50	0.00	0.54
season*sex*RHU + (RHU Ind)	15	-1667.00	1.54	0.25
sector*RHU + sex*RHU + season*RHU + sex*season + (RHU Ind)	17	-1665.30	3.20	0.11
sector*RHU + sex*season*RHU + (RHU Ind)	19	-1663.60	4.95	0.05
season*RHU + sex*RHU + season*sex + (1 Ind)	12	-1662.20	6.33	0.02
season*sex*RHU + (1 Ind)	14	-1660.20	8.33	0.02
sector*RHU + sex*RHU + season*RHU + sex*season + (1 Ind)	16	-1659.00	9.48	0.01
sector*RHU + sex*season*RHU + (1 Ind)	18	-1656.80	11.69	0.00
sex*RHU + season*RHU + (RHU Ind)	11	-1614.20	54.34	0.00
RHU*sector + sex*RHU + season*RHU + (RHU Ind)	15	-1611.00	57.48	0.00
sex*RHU + season*RHU + (1 Ind)	10	-1606.20	62.26	0.00
RHU*sector + sex*RHU + season*RHU + (1 Ind)	14	-1603.30	65.22	0.00
season*RHU + (RHU Ind)	9	-1595.60	72.92	0.00
season*RHU + (1 Ind)	8	-1583.90	84.59	0.00
sex*RHU + (RHU Ind)	7	-1573.60	94.86	0.00
sex*RHU + (1 Ind)	6	-1562.80	105.68	0.00
sector*RHU + (RHU Ind)	9	-1553.60	114.85	0.00
sector*RHU + (1 Ind)	8	-1539.00	129.53	0.00
constant model + (RHU Ind)	4	-1467.40	201.13	0.00
constant model + (1 Ind)	3	-1311.50	356.97	0.00



**Figure 1. Sex-specific (a) and season-specific (b) trade-offs between feeding efficiency and the use of refuge habitat.** The trade-offs were estimated from the best model describing the relationship between feeding efficiency and the use of refuge habitat that included the three two-way interactions (between the use of refuge habitat and sex, the use of refuge habitat and season, and sex and season) with individual identity (as a random effect on both the intercept and the slope). Feeding efficiency was measured as the negative value of average movement speed such that low values corresponded to high feeding efficiency. The use of refuge habitat was estimated as the proportion of GPS locations for each individual that occurred in wooded habitat. Thus, high values corresponded to high levels of risk avoidance.



**Figure 2. Variation in feeding efficiency in relation to season and sex.** The parameter estimates were obtained from the best model describing the relationship between feeding efficiency and the use of refuge habitat that included the three two-way interactions (between the use of refuge habitat and sex, the use of refuge habitat and season, and sex and season) with individual identity (as a random effect on both the intercept and the slope). Feeding efficiency was measured as the negative value of average movement speed such that low values corresponded to high feeding efficiency.



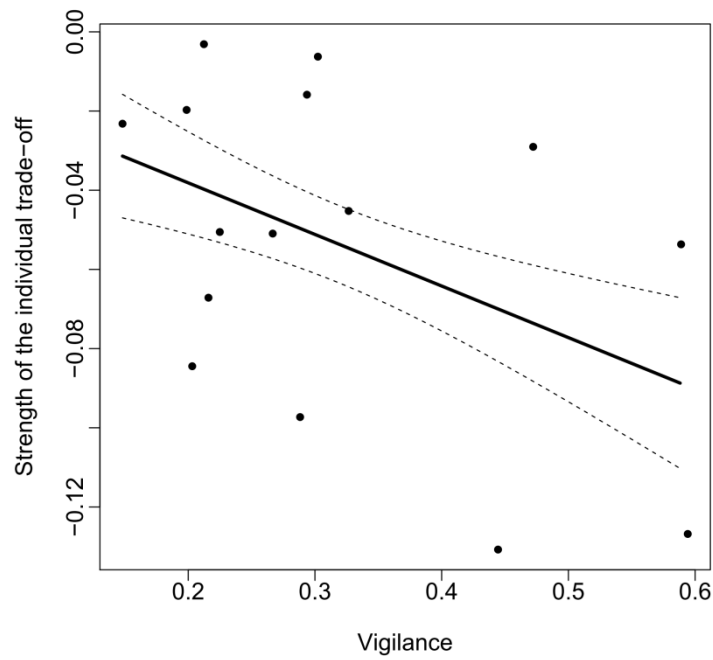
**Figure 3. Individual-level trade-offs between feeding efficiency and the use of refuge habitat** (see Fig. 1 for explanation of the measures and the model). Each point (red for males, yellow for females) indicates the centre of gravity for the use of refuge habitat for a single individual. Each segment links this centre of gravity to an observed use of refuge habitat during a given 24-hour monitoring period for that individual, resulting in a star representation of the observed use of refuge habitat with the centre of gravity at its heart.

***Vigilance as a mediator of individual variation in behavioral tactics for the trade-off between resource acquisition and risk avoidance***

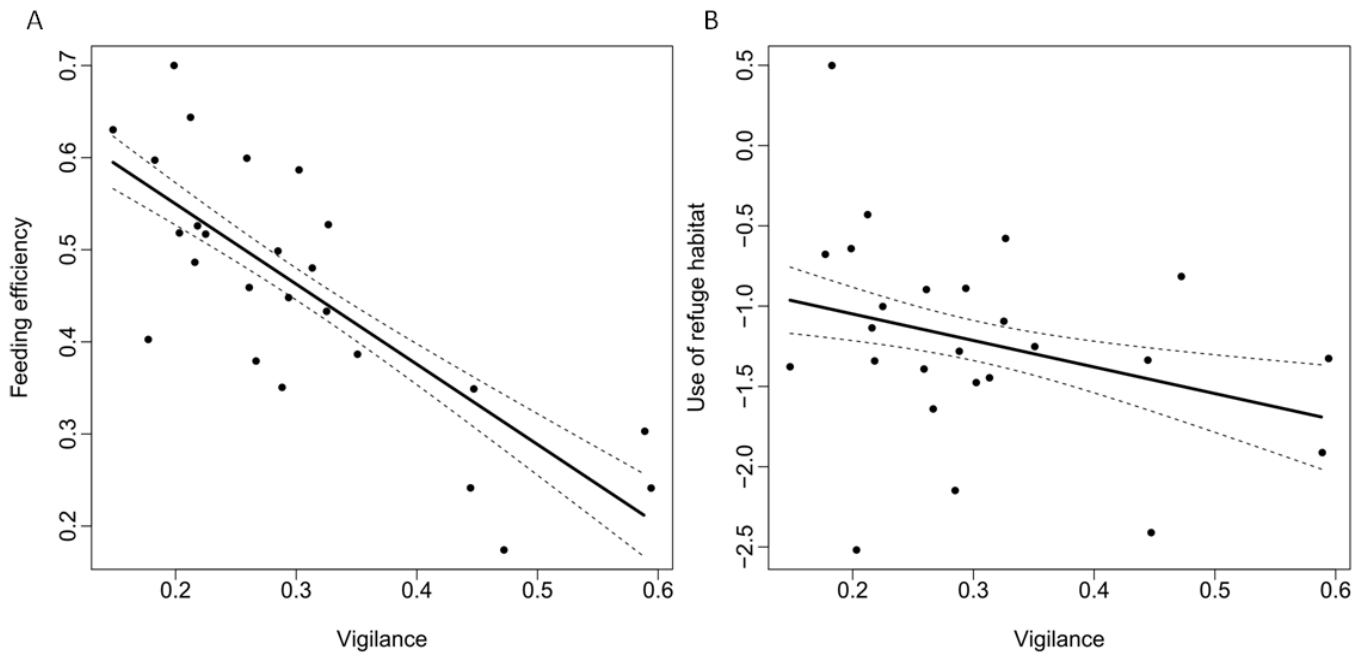
The best model describing the probability that an individual expressed a behavioral trade-off between feeding efficiency and the use of refuge habitat (i.e. a negative slope) in relation to its level of vigilance was the constant model for both sexes (females: AICc = 35.82, AICc weight = 0.71; males: AICc = 16.36, AICc weight = 0.81).

Subsequently, we focused solely on individuals that expressed a risk avoidance - resource acquisition trade-off (i.e. with a negative slope between feeding efficiency and the use of refuge habitat). For females, the best model indicated that the strength of the individual trade-off increased with increasing levels of habitual vigilance (slope =  $-0.13 \pm 0.07$ ; AICc = -49.66, AICc weight = 0.53, Fig. 4) although the constant model was the most parsimonious. For males, the constant model best described the data (AICc = -13.33, AICc weight = 1).

Individual feeding efficiency decreased with increasing levels of habitual vigilance in females (slope =  $-0.87 \pm 0.14$ ; AICc = -46.58, AICc weight = 1; Fig. 5a), but not in males (slope =  $-0.34 \pm 0.45$ ; AICc = -1.86, AICc weight = 0.14). Likewise, the use of refuge habitat by a given individual decreased with its level of vigilance in females (slope =  $-1.65 \pm 1.05$ ; AICc = 49.41, AICc weight = 0.61; Fig. 5b) but not in males (slope =  $-1.79 \pm 2.15$ ; AICc = 29.28, AICc weight = 0.15).



**Figure 4. Relationship between the level of habitual vigilance and the strength of the resource acquisition – risk avoidance trade-off (i.e. the slope of the relationship between feeding efficiency and use of refuge habitat for a given individual) during spring.** Vigilance behavior was measured as the mean proportion of time spent vigilant over all observations for a given individual.



**Figure 5. Relationship between the level of of habitual vigilance and the components of the resource acquisition – risk avoidance trade-off: a. feeding efficiency, b. the use of refuge habitat during spring.** For each individual, we used the centre of gravity of the observations describing a. feeding efficiency and b. use of refuge habitat across the 24-hour intensive monitoring periods as the dependent variables and the habitual level of vigilance (measured as the mean proportion of time spent vigilant over all observations) as the explanatory variable.

## DISCUSSION

We have provided clear evidence of a behavioral trade-off between food acquisition and risk avoidance in a wild large herbivore, the roe deer whatever the gender of individuals and the season. However, the intensity of this trade-off was particularly marked in spring i.e. after the end of the winter when the resources remaining in forest habitat are scarce (Abbas et al. 2011) and when open habitats become attractive thanks to higher quality and quantity of feeding resources available in meadows and crops (Abbas et al. 2011). Moreover, this trade-off is more marked among females than in males especially in spring. Indeed, they face conflicts between their high energetic demands to offset the cost of the late-gestation and lactation to provide high quality milk for newborns foraging in richest habitats (Clutton-Brock et al. 1989; Panzacchi et al. 2010) and the avoidance of predators notably to protect their offspring which are highly vulnerable during their first month of life Guinness et al. (1978).

Moreover, we demonstrated strong individual differences in this trade-off, partly mediated by variation in an individual's habitual level of vigilance. While food intake and vigilance are not recognized as personality traits per se, vigilance behavior is often index risk-taking behavior within the context of personalities or behavioral syndromes (Bergvall et al. 2011; Couchoux and Cresswell 2012). In the present study, we found that both the probability of facing a trade-off and its strength tended to increase with the vigilance level meaning that females facing a more important trade-off are more vigilant individuals. Thus, individuals with a higher level of vigilance would be able to obtain a high feeding efficiency when they are in open habitats. Always avoid predator detection, human and hunting areas is often incompatible with some key activity like foraging (Dill 1990) especially in man-altered landscape. When environmental conditions make the cost of predator avoidance too high, preys like roe deer must tolerate a higher level of predation risk in order to meet their energy budget (Brown and Kotler 2004). Therefore, they must increase their vigilance in order to limit predation risks by increasing the detection of predators (Hopewell et al. 2005) that allows them to escape more efficiently. These findings are consistent with one of our results linking individuals' vigilance level to the use of secure habitat (one of the two trade-off components). Indeed, we showed that the vigilance level increased with the use of non-secured habitat meaning that individuals foraging actively in open habitats have to acquire

anti-predator behaviors allowing them to forage in habitats of good quality and quantity of food resources while being aware of predation risk. What was interesting is to note that individuals with a higher vigilance level had a high feeding efficiency in open habitats but a significant lower feeding efficiency when they foraged in secure habitats. A potential explanation would be that these individuals were still vigilant (as we have seen this trait was consistent) in secure habitats where risk is lower. Consequently, they would lose time being vigilant instead of being foraging. The result linking the individuals' vigilance level to their feeding efficiency was in line with this hypothesis as feeding efficiency decreased with an increase in vigilance level. Most of the time, this anti-predator behavior occurs during feeding phases (Lung and Childress 2007) and is often considered as mutually exclusive to foraging (Underwood 1982). Vigilance has been assumed to reduce food intake by taking away time from food processing leading ultimately to a potential trade-off between foraging and vigilance (Lima and Dill 1990). This negative relationship had been reported in many species (Fritz et al. 2002; Cowlshaw et al. 2004; Blanchard and Fritz 2007). Consequently, more vigilant individuals seem to pay a cost losing time being vigilant while risk is low when they forage in secure habitat. Hence, we supposed that vigilance is not highly plastic but we rather supposed that the individuals' vigilance level result from an adaptation. This result seems in line with the Bonnot et al. (2015)'s study showing that individuals using open habitats during day time had higher level of vigilance. We also found that individuals with a low probability to face a trade-off and expressing a weak trade-off strength had lower vigilance level. This means that whatever their foraging habitat, their feeding efficiency seemed quite stable. They did not really take advantage of foraging in open habitat while they are richer (Hewison et al. 2009). The idea weights, once again, in favor of a vigilance adaptation. Indeed, open habitats are riskier so that individuals need to increase their anti-predator behaviors as vigilance to be able to escape sufficiently early (Hopewell et al. 2005). However, their vigilance level was too low to stay for a long time in such habitats which result in a lower feeding efficiency since they could not totally achieve rumen-fill.

Consequently, vigilant individuals pay a cost foraging in secure habitats whereas individuals with a lower vigilance level pay a cost using open habitats to feed. Vigilance level seems to be mal-adaptative in some contexts which prone for an adaptation of this anti-predator behavior and, in the end, for inter-individual differences. Indeed, our results

support theoretical work (Stamps 2007; Wolf et al. 2007) showing that variability in the way individuals solve the 'resource acquisition - risk avoidance' trade-off is linked to the individual's level of habitual vigilance, describing a gradient in behavioral tactics for risk-management. For example, Wolf et al. (2007) showed that the current vs. future reproduction life-history trade-off resulted in polymorphic populations where individuals with high future prospects tend to be more risk-averse, and so consistently less aggressive and shyer, than individuals with lower future expectations. Thus, personality may have a central role in governing life-history strategies (Wolf et al. 2007; Biro and Stamps 2008) and inter-individual differences in behavior and life-history trade-off seem tightly link. These findings are in line with a new concept: the personality pace-of-life syndrome implying that physiological, hormonal and behavioral traits are linked to demographic traits and variation in life-history tactics within a general life-history framework (Réale et al. 2010). Hence, future study should investigate how individual behavioral tactics are linked to physiological and life-history traits and, ultimately, to individual fitness to better understand the evolution of pace of life syndromes.



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## SUPPORTING INFORMATION

### SI MATERIALS AND METHODS

#### ***Study site***

The study was carried out in Aurignac (7500 ha) in the south-west of France (43°13'N, 0°52'E). This hilly region is a mixed landscape mostly covered by open habitats interspersed with small woodland patches (mean  $\pm$  SD: 2.9  $\pm$  7.6 ha) and two large forests (672 ha and 515 ha). Meadows and cultivated fields occupy 31.9% and 36.2%, respectively, of the total area. Woodland covers 19.3 % and is dominated by oak (*Quercus* spp) (see Hewison et al. 2009 for further details).

Human activity is omnipresent throughout the study site, whether through agricultural activity or housing. Moreover, the hunting pressure is high, as roe deer are hunted from September to February, most of the time using dogs, while males are also hunted for trophies in summer.

#### ***Capture and monitoring***

Each winter since 2003, roe deer were caught from November to March using drive netting. All individuals were weighed with an electronic balance, sexed, aged (we only analysed adults in the present study) according to tooth eruption, marked with two plastic ear tags, equipped with a GPS collar (Lotek 3300 GPS) and released on site. Monitoring lasted between 41 and 51 weeks over the subsequent calendar year. Since 2005, we could obtain one location every 10 min for a period of 24 h spaced across the year. We focused on this intensive monitoring which result in 13 intensive monitoring periods in average (range: 5 to 17 per individual). We performed differential correction to improve fix accuracy (Adrados et al. 2002). Roe deer capture and marking procedures were performed according to French law for animal welfare and approved by the French administration.

### ***Indexing resource acquisition: feeding efficiency***

Roe deer are income breeders (sensu (Jönsson 1997; Andersen et al. 2000b) because they store only little fat (Hewison 1996) and rely instead on current food intake to offset the increased energy expenditure during reproduction. Thus, a deer is active most of the time to search for and consume food (Georgii 1981; Owen-Smith 1998). In addition, roe deer are medium-sized herbivores with rather small rumens relative to their overall body size (Duncan et al. 1998). As a result, their feeding efficiency is limited by the time necessary to achieve rumen-fill (Holand et al. 1998). Hence, individuals feeding in rich open habitats such as meadows and cultivated fields (Hewison et al. 2009), where resources are spatially clumped, should cover less distance during feeding bouts and, hence, exhibit lower average speeds than in poorer habitats where resources are more widely dispersed. In addition, Gottardi et al. (unpublished data) found that movement rates and activity levels decreased with the openness (i.e. the richness) of habitats during daytime. We thus calculated mean average speed (m/s) based on GPS location data for each period of intensive monitoring and for each individual as the distance between two successive locations divided by the 10 min fix interval using the `adehabitatLT` package (Calenge 2015). Speed and more generally locomotion correspond to energetic expenditures (Nilssen et al. 1984; Fancy and White 1987) and is expected to decrease fitness, so that the opposite of the speed should be positively correlated with individual fitness and provides a proxy for food acquisition. We then used the opposite of the average speed as a measure of feeding efficiency so that high values of this index (i.e. low average speed) represent high feeding efficiency.

### ***Indexing risk avoidance: the use of refuge habitat***

Wild herbivores clearly perceive open habitats as risky (Frid and Dill 2002; Stankowich 2008), and wooded habitats as a protective cover (Myrsterud, Lian, et al. 1999; Myrsterud and Ostbye 1999). Hence, we considered that an individual's propensity to use open habitat measured its risk taking behavior. We defined risk avoidance as the probability that an individual use the closed cover habitats provided by woodland. As a result, we took the proportion of GPS locations for each period of intensive monitoring and for each individual that fell in wooded habitat as our index of risk avoidance, with high values indicating

individuals that avoided using risky open habitats. For the analyses, we log-transformed the risk avoidance variable to fit the Gaussian distribution.

### ***Indexing inter-individual variation in anti-predator behavioral tactics: vigilance***

Vigilance is a pervasive anti-predator behavior used by large herbivores to avoid risk (Lima and Dill 1990). Individual differences in the time spent vigilant correspond to individual differences in the propensity to take risk (Bonnot et al. 2015). We thus used individual differences in time spent vigilant to quantify how individuals cope with risk and how this may affect the way they trade risk for feeding efficiency.

From 2010 onwards, we observed individually identifiable GPS marked roe deer in the field (in open habitat, either meadows or crop fields) between February and April, at least 2 weeks after capture and release. Observations were carried out during peak activity of roe deer (Jeppesen 1989), at dawn and dusk. We recorded exclusive behaviors among which vigilance (head above shoulder level while scanning surroundings) for approximately 10 min of observation (see Bonnot et al. 2015 for more details). We calculated the time spent on vigilance during each behavioral sequence with a transcription software (EthoLog 2.2; Ottoni 2000; Bonnot et al. 2015 for more details). When a given individual was repeatedly observed (min=2, max=8, mean=4), we calculated the mean proportion of time spent vigilant (min=0.06, max=0.60, median=0.25, mean=0.27) over all observations for that individual. We assumed that variation in predation risk and resource quality across observations was minimal and random with respect to the identity of the individual observed.

### ***Statistical analyses***

#### *Within individual repeatability of the behavioral measures*

We assessed the within-individual consistency of the i/ feeding efficiency, ii/ use of secure habitat and iii/ vigilance. For feeding efficiency and the use of secure habitat, we used 149

individuals equipped with a GPS collar while for vigilance we used a subsample including 35 individuals that were observed at least twice since 2010 (8 observed twice, 4 observed 3 times, 6 observed 4 times, 8 observed 5 times, 5 observed 6 times and 4 observed 7 times). The repeatability was calculated with mixed models (Nakagawa and Schielzeth 2010). Repeatability coefficient for feeding efficiency, that is, intraclass correlation coefficients, was calculated using the “rpt.remlLMM” function of the “rptR” package (Schielzeth and Nakagawa 2011; see Debeffe et al. 2015 for a recent application to roe deer behavior) in R version 2.15.1 software (R Development Core Team 2013), which estimates repeatability as the ratio of between-individual variance to total variance with linear mixed-effects models (with individual identity as a random factor) using the restricted maximum likelihood (REML) method. Because the use of secure habitat and vigilance were proportion data, we calculated repeatability coefficients the “rpt. binomGLMM.multi” function of the “rptR” package using a generalized linear mixed-effects models with a logit-link (Schielzeth and Nakagawa 2011).

#### *Assessing the trade-off between resource acquisition and risk avoidance*

To investigate the trade-off between resource acquisition and risk avoidance, we assessed the relationship between feeding efficiency and the use of secure habitat (see above for the construction of these variables). We used generalized linear mixed models (GLMM) to analyze the variation in feeding efficiency (dependent variable) as a function of secure habitat use (explanatory variable) in the ‘glmmADMB’ package (Bolker et al. 2012). We used the ‘scales’ package (Wickham 2015) to rescale the explained variable. For this analysis, we had GPS monitoring data for 149 individuals (60 males and 87 females).

Resource availability and risk for large herbivores vary in both time and space, in relation to the phenology of vegetation, human activities or landscape structure (Gaillard et al. 2000; Rettie and Messier 2000). Therefore, we accounted for the possible confounding effects of season and local landscape structure on the relationship between feeding efficiency and the use of secure habitat. We defined 3 seasons based on variation in resource availability in open and closed habitats and risk, primarily from hunting: autumn (September-November) when risk is high due to regular hunting and resource quality is likely higher in woodland than in open habitats due to the availability of acorns (*Quercus* sp.), ivy

(*Hedera helix*) and brambles (*Rubus* sp.) (Abbas et al. 2011); winter (December-February) when hunting continues but resource quality is likely lower in both open and closed habitats; and spring (March to June) when risk is low as there is no hunting but resource quality is higher, particularly in open meadow and crop habitats (Abbas et al. 2011). We excluded data from summer (July and August) because the rut occurs during this period and markedly influences the behavior of both sexes (Liberg et al. 1998). We also defined three landscape sectors in relation to the proportion of wooded habitat in the local landscape: open (agricultural area with highly fragmented woodland), intermediate (partially wooded area) and closed (forest block); see Hewison et al. 2009; Morellet et al. 2011 for more details). Finally, although roe deer are not markedly size dimorphic (R Andersen et al. 1998), the risk-resource trade-off is expected to differ between males and females in relation to sex differences in reproductive allocation. Hence, we controlled for these confounding effects on the trade-off by including season (3 modalities), sector (3 modalities) and sex (2 modalities) as fixed effects in the 2-way interactions between security and season, between security and sector, and between security and sex. We also tested for an interaction between sex and season. Indeed, sex-specific energetic needs differ with a peak in summer for males (rutting period) and in spring for females (late gestation and early lactation). As we had repeated values (24-hour intensive GPS monitoring sessions) for all individuals, we included the individual's identity as a random effect on either the intercept and/or the slope of the relationship between feeding efficiency and the use of secure habitat. Model selection was based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002). We retained the model with the lowest AICc value, reflecting the best compromise between precision and accuracy (Burnham and Anderson 1998). We also calculated AICc weights as a measure of the likelihood that a given model was the best among the set of fitted models.

*Vigilance as a mediator of individual variation in behavioral tactics for the trade-off between resource acquisition and risk avoidance*

We investigated the relationship between individual tactics in the risk-resource acquisition trade-off and individual differences in the propensity to be vigilant using a sub-sample of 35 individuals for which we had both GPS and focal observation data. In a first step, from the

best model describing variation in feeding efficiency in relation to the use of secure habitat, to describe each individual's trade-off, we extracted the individual-level slope of this relationship. A negative slope indicates that a trade-off occurs for that individual, whereas a positive slope indicates that there is no trade-off (Hamel et al. 2014). Then, we used logistic regression ('lme4' package; Bates et al. 2015) to test whether the presence (negative slope) vs. absence (positive slope) of a risk-resource acquisition trade-off in an individual was related to the level of vigilance expressed by that individual. As our analyses indicated sex-specific and seasons differences in the risk-resource acquisition trade-off (see Results), we performed separate analyses for males (N = 10) and females (N = 25). We also found differences in the trade-off according to the seasons with more pronounced differences in spring (see Results). This season seemed more interesting as regard the trade-off because of the higher availability of food resources in open habitats (Abbas et al. 2011) and higher energetic needs especially for the late-gestation of females (Clutton-Brock et al. 1989; Panzacchi et al. 2010). Hence, we focused the next analyses on the slope of the trade-off expressed in spring for males and females.

Subsequently, we eliminated all individuals with positive slopes for the relationship between feeding efficiency and use of secure habitats to focus solely on individuals that expressed a risk-resource acquisition trade-off. We then performed three separate analyses using linear models (LM) with the individual's level of vigilance as the explanatory variable. In the first, we tested whether the strength of the risk-resource acquisition trade-off expressed by an individual was related to its level of vigilance. This analysis assumes that individuals with a more negative slope (dependent variable) express a more pronounced trade-off than individuals with a less steep slope, i.e. their feeding efficiency is more strongly affected by the perceived level of risk and that their vigilance behavior is linked to this sensitivity. Then, we explored how feeding efficiency was related to vigilance at the individual level. We used the centre of gravity describing feeding efficiency across the 24-hour intensive monitoring periods for each individual as the dependent variable. Lastly, we explored how the second component of the trade-off (i.e. the use of secure habitat) varied in relation to vigilance at the individual level. In an analogous way, we used the centre of gravity describing the use of secure habitat across the 24-hour intensive monitoring periods for each individual as the dependent variable.



All models selection were based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002). All analyses were performed in R version 2.15.1 (R Development Core Team 2013).



Photo by B. Lourtet

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## **Chapter VI**

**Does it exist a link between  
mother's behavior and  
fawn's survival?**

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## Synthesis

Individuals exhibit consistent behavioral differences which may affect their life-history traits (Civantos 2000; Dingemanse and de Goede 2004; Both et al. 2005; Réale et al. 2007) but also their fitness (Smith and Blumstein 2008). However, only a handful of studies have focus on the effect of behavioral traits on fitness (see Réale et al. 2000; Biro et al. 2003,2004; Réale and Festa-Bianchet 2003; Dingemanse and Réale 2005) and there is a real lack of empirical studies. Hence, the effects of personality on fitness stay unclear, especially in wild population (Dingemanse and Réale 2005; Smith and Blumstein 2008). Indeed, personality is most of the time studied in captivity, and although it seems that personality in captivity reflects the personality in the wild (Herborn et al. 2010), some behaviors such as foraging or predation avoidance are only completely expressed in the wild. Consequently, our main aim was to study the link between behavioral traits of mothers roe deer and their reproductive success in the wild and more precisely the juvenile survival and growth of their offspring. It should be noted that spatial and temporal variation in juvenile survival is a key component of the population demography of large herbivores in the wild (see Gaillard et al. 1998,2000 for a review), and that factors affecting the juvenile survival in wild ungulates are fairly well known which allow us to focus more precisely on the females' behavior.

The roe deer species is interesting because individuals have to satisfy their high energetic needs during late gestation and early life of their fawns by foraging in highly nutritious areas while minimizing the risk of predation of their offspring (Clutton-Brock 1989; Linnell 1994,1995). As matter of fact, predation is the most important mortality factor for fawns coexisting with large predators in temperate regions (Linnell et al. 1995; Jedrzejewski et al. 2011). Thus, fawning females roe deer seemed to modify their space use (Tufto et al. 1996; Bongi et al. 2008) and to adapt their distance to their fawns according to the habitat (Panzacchi et al. 2010) but, very little is known about the impact of their behavioral traits on their reproductive success. Moreover, we imagine that the presence of offspring, their condition and behavior may also influence their mothers' behavior.

Thus, we carried out two different and complementary studies. With the first one, our aim was to test for the link between the coping style of the mother and her reproductive success by investigating the impact of individual differences in coping styles of female roe

deer on the early survival of their fawns. We found that fawn's survival was highly dependent on the interaction between habitat use and the coping style of the mother. Compared to more reactive mothers, mothers with a more proactive coping style were more likely to wean a fawn in open meadows, but less likely to do so in forest or crops. Our findings therefore demonstrate that inter-individual differences in the coping style of mothers have a habitat-specific influence on offspring survival, and hence on female fitness, in wild populations of mammals. We suggest that spatial heterogeneity may potentially contribute to the maintenance of behavioral variation in wild populations. Then, our second study focused on the effects of the fawns' presence and growth on their mother's trade-off tactic between risk avoidance and resource acquisition. Indeed, we previously found that the trade-off between resource acquisition and risk avoidance exists in roe deer and is more pronounced during spring especially for females (Chapter V) which corresponds to late gestation and early life of fawns. We supposed that females would have different behavior according to notably the presence or not of their fawns. We found that females with fawns and fawns in good condition (i.e. higher growth) favored their resources acquisition rather than their security likely to offset their high energetic demands and those of their fawns. Consequently, the links between behavior and fitness does not happen only in one direction. On the contrary, consistent behaviors and fitness seems to influence each other.

**Part 1****Is a proactive mum a good mum? A mother's coping style influences early fawn survival in roe deer**

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*'The neonatal period is a critical phase for juvenile survival in most mammals and depends heavily on the nature and quality of the interactions between the mother and her offspring. In some species, mothers or other members of the group may actively defend the young, sometimes directly attacking a predator and/or attempting to disrupt its chase...'*



Photos: by D. Mason, B. Cargnelutti, and C. Salin from left to right

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## RESUME

Les différences comportementales entre individus peuvent influencer de manière conséquente les trajectoires d'histoire de vie. Cependant, peu d'études à l'heure actuelle se sont intéressées au lien potentiel entre traits comportementaux et valeur sélective et ce d'autant plus dans des populations sauvages. C'est pourquoi, nous avons notre étude dans ce contexte. Ainsi, nous avons cherché à mesurer et quantifier l'impact du comportement de chevrettes (*Capreolus capreolus*) sur les premiers mois de vie de leurs faons. Dans cette optique, nous avons émis deux hypothèses. La première était que le comportement de la mère devrait influencer la survie de sa progéniture. En effet, sous l'hypothèse de différences de comportements entre mères, nous avons supposé que les faons de mères plus « proactives » devraient avoir une meilleure survie notamment de part le fait que leur mère aurait un meilleur accès à des ressources de qualité et pourraient également mieux les protéger et les défendre des prédateurs que des mères « réactives ». La deuxième hypothèse était plus centrée sur le comportement « mère-faon » à savoir que le comportement spatial de la mère devrait impacter le choix du faon quant au choix de son site de repos et donc, *in fine*, sa survie puisque cette dernière dépend fortement des caractéristiques du site de repos du faon (van Moorter et al. 2009). A titre d'exemple, nous avons pensé que les mères utilisant préférentiellement des habitats fermés augmenteraient les chances de survie de leurs faons puisque ceux-ci choisiraient forcément un site de repos dans un de ces habitats fermés c'est-à-dire dans un habitat plus sûr vis-à-vis des risques de prédation. Enfin, sachant qu'une récente étude a montré que l'effet du comportement des mères sur la survie de leur progéniture pouvait fluctuer dans le temps, c'est-à-dire qu'il y a une hétérogénéité spatiale dans les effets du comportement, nous avons émis l'hypothèse que cette hétérogénéité pourrait également avoir une origine spatiale. D'un point de vue statistique, nous avons tenu compte d'autres facteurs connus pour influencer la survie des ongulés liés, par exemple, à l'hétérogénéité de l'habitat et des conditions climatiques. Nous avons trouvé que la survie des faons dépendait du comportement de la mère mais également de l'habitat dans lequel vit principalement le faon lors de son premier mois de vie. Ainsi, les faons ayant une mère plus « proactives » survivront mieux dans les habitats ouverts telles que les prairies naturelles alors que les faons de mères « réactives » survivront mieux dans des habitats fermés telles que les forêts et cultures qui sont hautes l'été. Par



conséquent, avec cette étude nous avons pu montrer de manière claire qu'il existe un continuum dans le comportement des chevrettes et que celui-ci influence fortement la survie de leur faon, en tenant compte de l'habitat dans lequel vit principalement le faon, et donc leur valeur sélective. Par ailleurs, cette étude est la première à notre connaissance à montrer qu'il peut exister une hétérogénéité spatiale dans les conséquences des différences comportementales entre individus. Cela offre la possibilité de suggérer que cette hétérogénéité soit un mécanisme permettant la maintenance de ces différences comportementales interindividuelles.

**Mots clés :** différences individuelles, survie juvénile, soins maternels, température corporelle, utilisation d'habitat

**ABSTRACT**

Individual differences in behavior may strongly shape life history trajectories. However, few empirical studies to date have investigated the link between behavioral traits and fitness, especially in wild populations. We measured the impact of coping style in female roe deer (*Capreolus capreolus*) on early survival of their offspring. Specifically, we expected offspring of proactive mothers, which should be more mobile and aggressive, to survive better than those of reactive females, which should be more passive and react less in stressful contexts. To test this prediction, we accounted for confounding effects of variation in early survival linked to habitat heterogeneity, as we also expected bed-site selection to impact fawn survival. Fawn survival was highly dependent on the interaction between habitat use and the coping style of the mother. As expected, fawns of proactive mothers survived better in open habitats. However, unexpectedly, fawns of reactive mothers had the highest survival in closed habitats. Our findings provide clear evidence that inter-individual differences in the coping style of the mother can markedly impact early offspring survival and, thereby, female fitness, in wild populations of mammals. Moreover, we provide evidence that fitness consequences of coping styles are habitat-dependent, providing a possible mechanism for the maintenance of within-population variation in behavior.

**Key words:** individual differences, juvenile survival, maternal care, body temperature, habitat use



## INTRODUCTION

It is increasingly recognized that, within populations, individuals exhibit consistent behavioral differences over their lifetime, and that these differences may have important ecological and evolutionary implications (Wilson et al. 1994; Réale et al. 2007). When these behavioral differences are manifested in stressful situations characterized by risky or challenging environments, they are generally interpreted within the ‘coping style’ framework (Koolhaas et al. 1999). Koolhaas et al. (1999) defined a coping style as “a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals”. Two distinct coping styles are generally identified, although these stress responses are more likely best described by a continuum. Proactive individuals are fast explorers, highly aggressive, impulsive in decision-making, novelty seekers and take risks in the face of potential dangers (Koolhaas et al. 1999, 2010). They are thus assumed to cope actively with the source of stress through a ‘flight-or-fight’ response. In contrast, reactive individuals show the opposite physiological patterns and tend to react to challenges by freezing. From a physiological viewpoint, proactive individuals show a high sympathetic reactivity and a low hypothalamus-pituitary-adrenal (HPA) axis responsiveness compared to reactive individuals (Koolhaas et al. 1999). However, the associations between physiological traits and behavioral traits are still poorly documented. Fast explorers may have a lower HPA (Montiglio et al. 2012), which is associated with increased frequency and variation in heart rate (Visser et al. 2002). Similarly, Groenink et al. (1994) showed that a high rectal temperature reliably indicates stress-induced hyperthermia (SIH), which has been repeatedly associated with personality. For instance, in great tits (*Parus major*), bold individuals (assumed to be proactive, Schjolden et al. 2005) had lower body temperature and respiration rate during handling than shy individuals (Carere and van Oers 2004). It is widely recognized that coping styles relate the level of boldness and aggression to the magnitude of the physiological response to stress (Koolhaas et al. 1999; Frost et al. 2013). Consequently, proactive individuals are also assumed to be bold and aggressive, while reactive individuals should be shy and less aggressive.

Most work on characterizing coping styles has been carried out under controlled laboratory conditions (Koolhaas et al. 1999; Overli et al. 2005), while evidence from field tests are much scarcer and have so far been conducted on semi-captive populations (e.g.

Rödel et al. 2006; Hoffman et al. 2011). Furthermore, there is a crucial lack of empirical studies on the effect of coping styles on individual performance and, hence, on their consequences for population dynamics. From a meta-analysis of studies performed on domestic, captive and wild animals, Smith and Blumstein (2008) concluded that bolder and more aggressive individuals generally have higher reproductive success than shyer or less aggressive individuals. For example, in bighorn sheep (*Ovis canadensis*), boldness is positively related to both weaning rate (Réale et al. 2000) and survival (Réale and Festa-Bianchet 2003). Hence, coping styles are likely to be associated with inter-individual differences in reproductive success, as reported in the Ural owl (*Strix uralensis*) in which proactive and aggressive females produced more recruits (Kontiainen et al. 2009).

Large herbivores are widespread in most temperate ecosystems and are the subject of a number of detailed long-term monitoring studies of behavior and population dynamics (e.g. Gaillard et al. 2013 on roe deer, Hallett et al. 2004 on Soay sheep *Ovis aries*, Coulson et al. 2004 on red deer *Cervus elaphus*, Garel et al. 2007 on mouflon *Ovis gmelini*, Toïgo et al. 2007 on ibex *Capra ibex*, Servanty et al. 2011 on wild boar *Sus scrofa*). These studies have shown that spatial and temporal variation in juvenile survival is a key component of the population demography of large herbivores in the wild (see Gaillard et al. 2000 for a review). Environmental factors such as predation and population density during the pre-weaning stage are critical for shaping variation in juvenile survival. Likewise, climatic conditions during late gestation and early lactation also influence juvenile survival through their effects on plant biomass and quality and, thereby, the availability of food for the mother (Gaillard et al. 2000). In addition, maternal physiological and morphological traits such as size, age, and previous reproductive success strongly impact juvenile survival, generating marked individual differences in female reproductive success (Gaillard et al. 2000). However, whether a mother's coping style influences juvenile survival in wild large herbivores remains virtually unknown (Smith and Blumstein 2008).

We aim here to fill this gap in our knowledge of the link between the coping style of the mother and her reproductive success by investigating the impact of individual differences in coping styles of female roe deer on the early survival of their fawns in an intensively studied roe deer population. Roe deer females are income breeders (sensu Jönsson 1997) such that females do not store fat reserves, relying instead on current energy

intake to offset the costs of reproduction (Andersen et al. 2000). For income breeders, the trade-off between foraging and risk of predation should be particularly acute (Bongi et al. 2008) because females have to forage intensively while simultaneously minimizing the risk of predation of their offspring (Linnell et al. 1995). Hence, females with newborns generally isolate themselves from conspecifics. This behavior is associated with lower disturbance by conspecifics and reduced risk of predation (Schwede et al. 1993). Females also often range less widely during the first months following parturition (Saïd et al. 2009). Moreover, roe deer are hidiers (*sensu* Lent 1974) where, apart from short visits for suckling (3-7 times/day), the fawns lie hidden, secluded from the mother for most of the time up to the age of 6-8 weeks (Espmark 1969). Thus, high female aggressiveness and short mother-fawn distance are associated with increased offspring survival during the hiding phase in open habitats (Panzacchi et al. 2010). Bongi et al. (2008) found that females tend to select denser habitats with high cover and concealment, which may contribute to increase offspring survival. However, the extremely high energetic needs of roe deer females during lactation are expected to constrain them to use habitats where predation risk for fawns is high (Panzacchi et al. 2010). Hence, during the hider phase, a fawn's survival mostly depends on its mother's ranging behavior (van Moorter et al. 2009) and care (Andersen et al. 2000; Gaillard et al. 2000). Maternal care behavior is likely highly variable among individuals (Nowak et al. 2000) but, to our knowledge, although some information is available for birds (Kontianen et al. 2009; Ringsby et al. 2009; Westneat et al. 2011; Betini and Norris 2012), no study has yet investigated how variation in coping styles among mothers impacts the survival of their offspring in any large mammal in the wild.

When faced with a challenge, proactive individuals are risk-takers that respond with high levels of general activity and aggression and low attack latency, whereas reactive individuals show high attack latency and a lack of initiative (Koolhaas et al. 1999, 2010). Ungulate females aggressively defend and protect their fawns (Truett 1979; Ozoga and Verme 1986; Lingle et al. 2005), and this is also the case in roe deer during attack by foxes (Jarnemo 2004). Consequently, we first hypothesized that the coping style of the mother should influence the survival of her fawns. In the absence of direct observations of maternal roe deer behavior in response to predation in our study area, we assumed that reactive mothers would not defend their fawns as strongly as proactive mothers against predators.

Second, we hypothesized that the spatial behavior of the mother should impact the choice of bed-site by the fawn and thus affect its early survival, which is highly dependent on bed-site characteristics (van Moorter et al. 2009). Hence, fawns of females that mostly used habitats with protective cover should have access to the most secure bed-sites and should thereby have higher early survival. Finally, Boon et al. (2007) showed that the aggressiveness of the mother impacted the survival of her offspring in red squirrel (*Tamiasciurus hudsonicus* Erxleben), but that these effects varied across life history stages and over time (i.e. temporal heterogeneity in the influence of behavior on individual performance). Furthermore, there is also some evidence that specific behavioral profiles occur more frequently in some environments than in others (Stamps and Groothuis 2010; Pearish et al. 2013). Consequently, we hypothesized that fawn survival should be impacted by the coping style of the mother in a context-specific manner (i.e. spatial heterogeneity in the influence of behavior on individual performance), although we had no clear prediction as to the form of this relationship.

## **MATERIAL AND METHODS**

### ***Study site***

The study was carried out at Aurignac (7500 ha) in the south-west of France (43°13'N, 0°52'E). The climate is oceanic with Mediterranean tendencies, with an average annual temperature of 11-12 °C and total precipitation of 800 mm. This hilly region is a mixed landscape mostly covered by open habitats interspersed with small woodland patches (mean  $\pm$  SD: 2.9  $\pm$  7.6 ha) and two main forests (672 ha and 515 ha). Meadows and cultivated fields occupy 31.9 and 36.2 %, respectively, of the total surface area of the study site. Woodland covers 19.3 % of the total study site and is dominated by oak (*Quercus spp.*) (see Hewison et al. 2009 for further details).

### ***Data collection for roe deer mothers***

Each winter between 2003 and 2013, roe deer were caught from November to March (i.e. at least six weeks before parturition, Gaillard et al. 1993) using drive netting. Roe deer capture and marking procedures were performed according to French laws for animal welfare and approved by the French administration. Once the deer was caught in the net, it was tranquilized with an intra-muscular injection of acepromazine (Calmivet 3cc). Then, we transferred the animal to a small wooden retaining box designed to minimize risk of injury and to limit stress. At the end of the capture event, each individual was weighed with an electronic balance, sexed, aged according to tooth eruption, marked with two plastic ear tags and equipped with a GPS collar (Lotek 3300 GPS).

Between 2009 and 2013, we recorded the behavior at capture, during handling and at release for 121 females. Of these, 86 were adults (i.e. older than 1 year at first winter capture), which generally give birth every year (Hewison 1996; Andersen et al. 1998). We attributed a score of 1 (occurrence) or 0 (absence) for each of the following behaviors: i/ the individual struggled in the net (see also Réale et al. 2000), ii/ it turned upside down in the box, iii/ it attempted to remove its collar at release, and iv/ it fell (i.e., stumbled and fell to the ground) at release. In addition, we attributed a score of 1 if v/ the individual struggled and panted on the table during marking, or a score of 0.5 if it struggled only (otherwise 0), and a score of 1 (high speed running), 0.5 (moderate running), or 0 (trotting) in relation to vi/ its flight behavior at release. Indeed, flight speed at release is commonly used for the assessment of temperament in cattle (Müller and von Keyserlingk 2006). An index of proactivity was then calculated as the sum of the scores for these six behavioral items describing a stress profile gradient ranging from 0 to 6, potentially taking 13 different values (9 over the recorded range), with 6 indicating a priori highly proactive individuals. We also measured the rectal temperature for each female (using a Digitemp Color thermometer with a precision of 0.1°C, potentially taking 36 different values, over the recorded range). Following Montané et al. (2003)'s study showing that body temperature of roe deer decreases over time from capture to 45 minutes after capture before stabilizing, we recorded temperature more than one hour after the capture event in all cases. We recorded the temperature of each individual at the beginning and at the end of the marking procedure, and used the mean of these two values (difference: range = [-0.4-0.7], mean =



0.1, median = 0.0) to index the female's stress response based on the existence of a positive correlation between the HPA axis and stress-induced hypothermia (SIH) (Moe and Bakken 1997; Korhonen et al. 2000). Thus, we assumed that a high index of proactivity and a low rectal temperature indicated more proactive individuals, while a low index of proactivity and a high rectal temperature typified more reactive individuals.

### ***Data collection for roe deer fawns***

Between 2004 and 2013, newborn fawns (97 % less than 20 days old, average age at capture = 6.3 days) were caught by hand each year between the end of April and the middle of June, but more intensively since 2009 (30 fawns caught between 2004 and 2008, with none in 2005 and 2006, and then 114 fawns caught since 2009), mostly by observing the behavior of the mother. We marked fawns only once the mother had fed it and moved away. We first weighed (with a precision of 50 g), sexed and aged fawns using three age-classes (<3, 3-5, ≥6 days old) and then marked them with two metallic ear tags and an expandable VHF radio collar (Biotrack). The age of fawns was established in relation to daily monitoring of the mother's appearance (size of her belly, presence/absence of udders) and behavior (reaction to a whistle mimicking the call of a fawn), which provided information on the approximate date of birth, and in relation to the fawn's behavior (Jullien et al. 1992). Roe deer females generally give birth to two fawns per litter (Hewison and Gaillard 2001), but even when we located both fawns of a single litter, we manipulated and marked only one of the siblings as the fate of litter mates is highly inter-dependent, especially in poor cohorts (Gaillard et al. 1998). We also recorded the characteristics of the site where fawns were found in terms of habitat type (woodland, crops, natural meadows, or artificial meadows such as ray grass, *Lolium perenne*). Subsequently, fawns were located each day from marking to the end of the summer (1.5 locations per day per individual on average) by radio-telemetry and triangulation. The radio-collars were equipped with a mortality sensor, providing us with information about the current fate of each fawn. When a mortality signal was detected, we immediately recovered the dead animal and, where possible, ascertained the cause of its death.

## ***Statistical analyses***

### *Proactivity index and rectal temperature of the mother: repeatability and inter-correlation*

Of the 39 mothers, we assessed the within-individual consistency of the proactivity index and of rectal temperature based on a sub-sample including only the 18 mothers that were caught at least twice between 2009 and 2013 (ten caught twice, seven caught three times, and one caught four times) by calculating their repeatability with mixed models (Nakagawa and Schielseth 2010). Bell et al. (2009) reported in a meta-analysis that repeatability of behavioral traits (excluding physiological traits such as body temperature) has an average value of 0.37. Repeatability coefficients, i.e. intra-class correlation coefficients, were calculated using the 'rpt.remlMM' function of the 'rptR' package (Schielseth and Nakagawa 2011) in R version 2.15.1 software (R Development Core Team 2013), which estimates repeatability as the ratio of between-individual variance to total variance with linear mixed-effects models (with individual identity as a random factor) using the restricted maximum likelihood (REML) method. Because it is widely employed in behavioral ecology, for comparative purposes we also used the Lessells and Boag (1987)'s method to estimate repeatability. Finally, since we had no a priori idea of the expected relationship between temperature and coping style, except for small mammals (Moe and Bakken 1997; Korhonen et al. 2000), we also tested this correlation in our sample of female roe deer.

### *Early survival of fawns*

To assess the influence of the mother's coping style on early fawn survival, we excluded fawns with unknown mothers and fawns of mothers with missing data for either rectal temperature or the proactivity index. Analyses were thus based on 57 fawns that were monitored over their first spring-summer during eight different years, belonging to 39 different females. To investigate the relationship between early fawn survival and habitat use, we used the broad scale habitat type in which the fawn was found. We checked that the habitat type where fawns were found reliably described the habitat used during their first month of life using the VHF locations (between 7 and 37) of fawns collected during that period. On average, 75 % of these locations fell within the habitat recorded at marking. In

addition, we accounted for possible confounding effects of age, body development at capture, cohort effects and spring weather conditions, all of which have been reported to influence markedly early survival of roe deer fawns (Gaillard et al. 1997; da Silva et al. 2009). Body development was calculated from the residuals of the simple linear regression between age and body mass at capture (see Gaillard et al. 1993 for further details). We tested for cohort effects by including the year of birth of the 57 fawns. To assess annual spring weather conditions, we used the number of degree-days higher than 7 °C from February to April as a proxy of the precocity of spring which has recently been shown to affect strongly roe deer population dynamics (Gaillard et al. 2013), and especially early fawn survival (Plard et al. 2014).

We estimated early fawn survival by fitting Cox proportional hazard models, which are the most widely used in multivariate analyses of survival (Cox 1972; Therneau and Grambsch 2000). The model was written as:

$$h(t)=\exp(\beta_1X_1 + \dots + \beta_pX_p)h_0(t) \quad (1)$$

where  $h(t)$  is the hazard function at time  $t$  and measures the risk that a fawn dies at a given time,  $X_p$  are the covariates influencing early fawn survival (i.e. age, early body development and number of degree-days in the baseline model, plus rectal temperature and proactivity index of the mother, plus certain two-way interactions in the most complex model),  $\beta_p$  are the regression coefficients of these respective covariates, and  $h_0(t)$  is the baseline hazard function. We carried out the analyses on the first 105 days of the fawns' life, which roughly corresponds to the period from the median date of parturition to weaning. We added the age at capture of each fawn to the total number of days of monitoring, allowing us to start the analyses from the birth date of each fawn.

The baseline model included the fawn's age at capture (discrete variable, three modalities), its index of body development (continuous variable, range = [-718.0 - 490.1], mean = 0.00, median = 6.097) and the number of degree-days higher than 7 °C in the spring of capture (continuous variable, range = [55 - 64], mean and median = 59.5). Then, we investigated the potential effect of the mother's coping style on the survival of her offspring by adding the mother's proactivity index (continuous variable, range = [0.0 - 4.0], mean = 2.07, median = 2.00) and the mother's rectal temperature (continuous variable, range =

[37.0 - 40.5°C], mean = 38.75°C, median = 38.80°C) to the baseline model. In addition, we tested for the potential effect of habitat use on early survival by adding the habitat type recorded at fawn capture to the baseline model (discrete variable, four modalities: woodland, crops, natural meadows, artificial meadows). Finally, because early fawn survival may be impacted by the coping style of the mother in a context-specific manner, either across space or through time (Smith and Blumstein 2008), we also tested for the effects of the four two-way interactions between the mother's proactivity index with both habitat type and cohort, and between the mother's rectal temperature with both habitat type and cohort on early fawn survival. In all cases, models that included an interaction also included the main effects of the variables involved in that interaction.

We checked the assumption of proportional hazards that is critical to Cox proportional models through an analysis of residuals (Grambsch and Therneau 1994). We used model diagnostics based on scaled Schoenfeld residuals and checked the hypothesis of log-linearity and identified the most influential observations. Model selection was based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002) and Akaike weights to identify the model that best described the data. All analyses were performed in R version 2.15.1 (R Development Core Team 2013) using the survival package (Therneau 2014).

## RESULTS

### ***Proactivity index and rectal temperature of the mother: repeatability and inter-correlation***

The proactivity index did not deviate from a Gaussian distribution on a statistical basis ( $W = 0.960$ ,  $p\text{-value} = 0.086$ ), ranging between 0.0 and 4.0, with a median value of 2.0 and a mean of 2.1. The rectal temperature was also normally distributed ( $W = 0.980$ ,  $p\text{-value} = 0.474$ ), ranging between 37.0 and 40.5°C, with both a median and a mean of 38.8°C. There was suggestive evidence for consistent individual differences in the proactivity index (rpt.remlMM method:  $r = 0.201$ , 95% confidence interval = [0, 0.592]; Lessells and Boag method:  $r = 0.193$ , 95% confidence interval = [0.027, 0.636]). In contrast, rectal temperature

was highly repeatable (rpt.remlMM method:  $r = 0.704$ , 95% confidence intervals = [0.185, 0.909]). Rectal temperature and the proactivity index were weakly, but significantly from a statistical viewpoint, positively correlated across mothers ( $p$ -value = 0.037,  $r = 0.26$ , Appendix 1).

### ***Early fawn survival***

Overall, 25 out of 57 (43.9%) fawns survived to 105 days. Of the 32 fawns which died, 10 died from predation, 4 died due to poor maternal care (abandonment, malnutrition), 7 died from human activity causes (5 from mowing and 2 from vehicle collisions), 3 died due to health problems (disease, cachexia), 2 died from accidents (falling into a ditch) and 6 died from unknown causes. There was no statistically significant variation in the proactivity index of the mother among these 6 categories of mortality causes ( $F_{5-26} = 2.05$ ,  $p$ -value = 0.10). However, mothers whose fawns were predated tended to have a lower proactivity index than those whose fawns died of other causes ( $F_{1-30} = 2.93$ ,  $p$ -value=0.10). There was also no statistically significant relationship between the proactivity index of the mother and the age of the fawn at capture ( $F_{2-54} = 0.87$ ,  $p$ -value = 0.43), indicating that there was no age-related sampling bias with respect to maternal coping style that might explain any link between fawn survival and the proactivity index. Similarly, there was no evidence of any habitat-related sampling bias because fawns were distributed more or less randomly across habitat types with respect to the proactivity index of their mother (see Appendix 2).

In addition to the baseline factors (number of degree-days > 7 °C, age at capture, early body development) that all influenced early fawn survival, the Cox proportional hazard model of early fawn survival with the highest support included the two-way interaction between habitat type and proactivity index of the mother, plus an additive effect of mother's rectal temperature (AICc = 217.10,  $\Delta$ AICc = 2.16, AICc weight = 0.55, Table 1).

As expected, early survival decreased with time, with the sharpest decrease in survival occurring during the first 20 days of the fawns' life (Appendices 3, 4, 5). All things being equal, fawns that were older ( $\geq 6$  days old) at capture survived better than younger (<6 days old) fawns (93% of fawns vs. 53% of fawns reached 105 days of life, Appendix 3). As

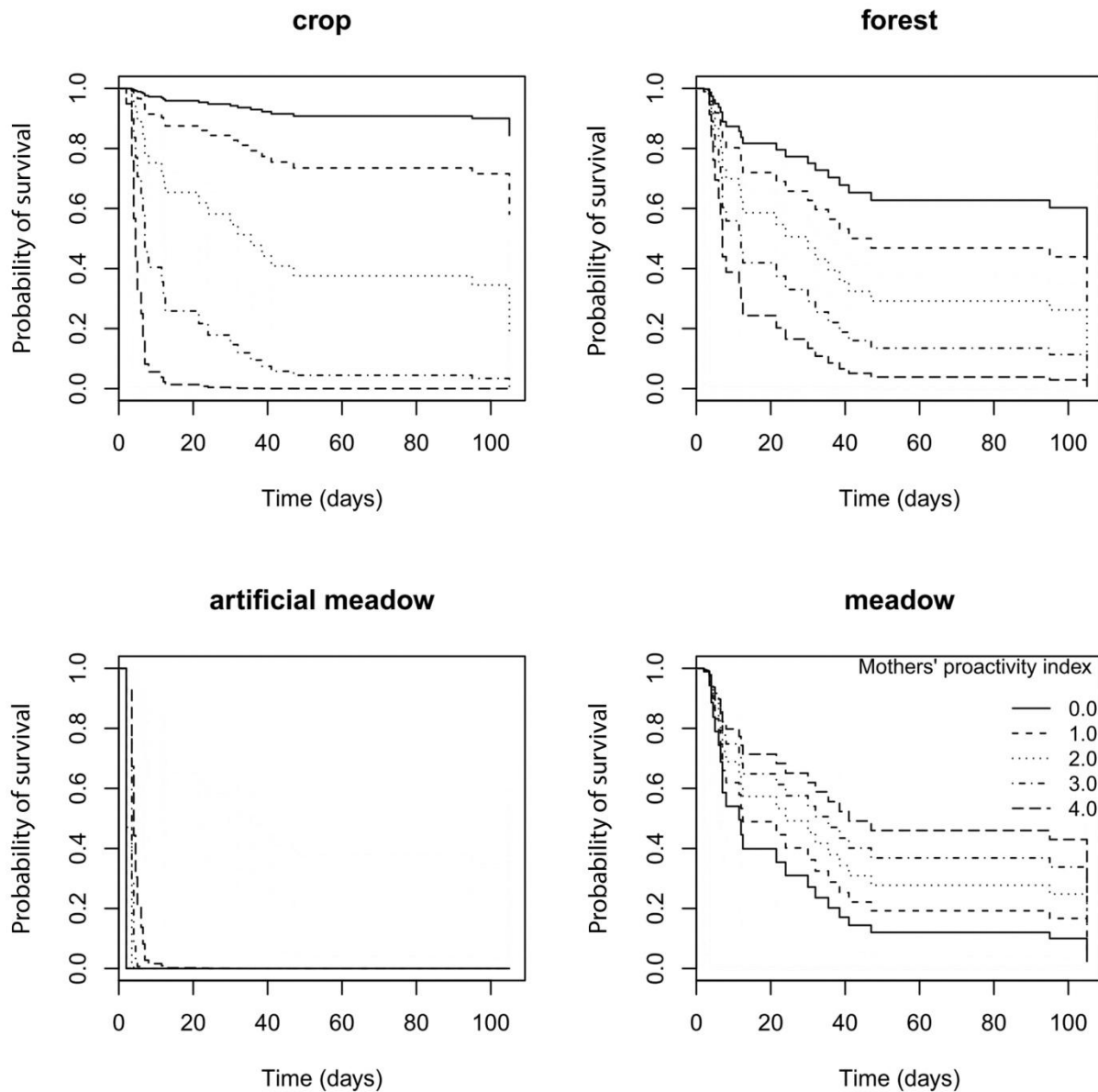
expected, fawns with a fast body development survived better than fawns with slow body development (68% of fawns for the heaviest fawns vs. 1% of fawns for the lightest fawns reached 105 days of life, Appendix 4). Likewise, as expected, early survival of fawns decreased with increasing number of degree-days (7% of fawns at 64 degree-days vs. 94% of fawns at 47 degree-days reached 105 days of life, Appendix 5).

**Table 1. Candidate Cox proportional hazard models fitted to investigate variation in the probability of fawns surviving to 105 days of age.** The baseline model includes the number of degree-days, early body development, and the fawn's age at capture. To this baseline model, we then added the cohort effect (cohort), the proactivity index of the mother (PI) and the rectal temperature (T) of the mother, as well as the habitat type where the fawn was caught (habitat). AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for  $\Delta AICc$  and on the Akaike weights. Only models with an AICc lower than that of the baseline model are presented.

Models	k	AICc	$\Delta AICc$	AICcWt
baseline model + habitat * PI + T	12	217.10	0.00	0.55
baseline model + habitat + PI + T	9	219.26	2.16	0.32
baseline model + cohort + habitat *				
PI + T	16	220.29	3.20	0.09
baseline model + cohort	8	223.93	6.83	0.01
baseline model + habitat * PI +				
habitat * T	15	224.64	7.54	0.01
baseline model + PI + habitat * T	12	224.82	7.73	0.01
baseline model + cohort + habitat +				
PI + T	13	226.81	9.71	0.01
baseline model	4	228.70	11.60	0

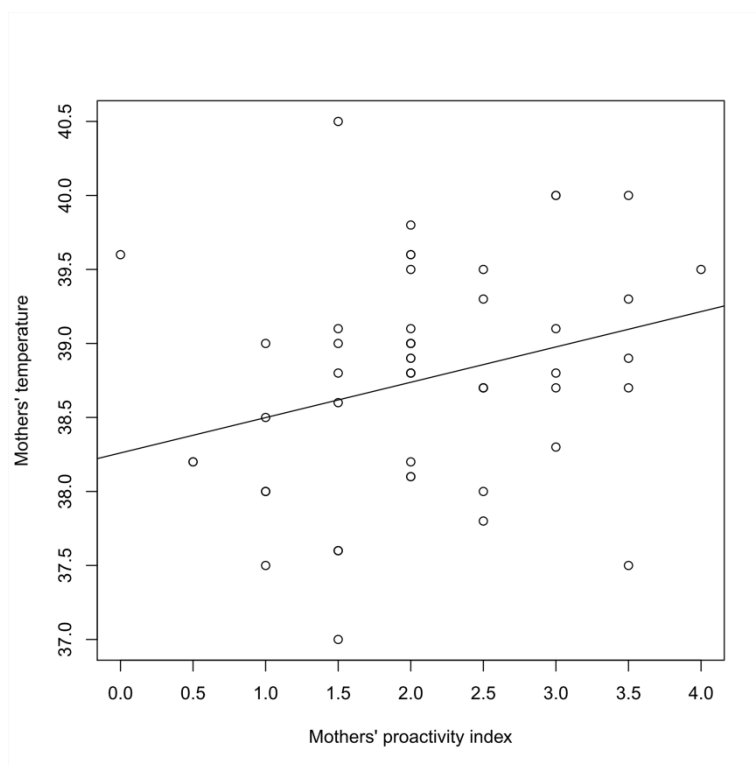
In addition to this support for the variables in our baseline model, we found that habitat type and proactivity index of the mother both shaped early fawn survival. Fawns born to mothers with a high proactivity index survived much better than fawns born to mothers with a low proactivity index when they principally used natural meadows (44 % of fawns for mothers with a proactivity index of 4.0 vs. 10% of fawns for mothers with a proactivity index of 0.0 reached 105 days of age, Fig. 1). In contrast, early survival was lower for fawns born to mothers with a high proactivity index than for fawns born to mothers with a low proactivity index when they principally used either forest (4 % of fawns for mothers

with a proactivity index of 4.0 vs. 61 % of fawns for mothers with a proactivity index of 0.0 reached 105 days of age) or crops (0 % of fawns for mothers with a proactivity index of 4.0 vs. 90 % of fawns for mothers with a proactivity index of 0.0 reached 105 days of age). No fawns born to mothers that principally used artificial meadows survived beyond 12 days of age (N=6), irrespective of the proactivity index of their mother. In addition, fawns born to mothers with a low rectal temperature survived slightly less well (33 % of fawns for mothers with a rectal temperature of 37.0 reached 105 days of age) than fawns born to mothers with a high rectal temperature (37 % of fawns for mothers with a rectal temperature of 40.0 reached 105 days of age, Fig. 2). Finally, contrary to our expectation, we found no evidence for a cohort effect on early survival, and no temporal variation in the influence of the mother's proactivity index or rectal temperature on early survival.



**Figure 1.** Probability of a roe deer fawn surviving to 105 days of life in relation to the proactivity index of its mother and to the habitat type (four modalities: crops, forest, artificial meadows, natural meadows) in which the fawn was found. The proactivity index potentially varies between 0 and 6, but the highest observed value was 4. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, fawn age at capture), the interaction between habitat type and the proactivity index of the mother, plus an additive effect of the mother's rectal temperature.





**Figure 2. Probability of a roe deer fawn surviving to 105 days of life in relation to the rectal temperature of its mother.** We used a Cox proportional hazard model with temperature as an explanatory variable with values ranging between 37 and 40 °C. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, fawn age at capture), the interaction between habitat type and the proactivity index, plus an additive effect of the mother’s rectal temperature.

## DISCUSSION

### *Overview*

The central aim of our study was to investigate how variation in the mother’s coping style and space use impact the early survival of her offspring. We detected consistent individual differences in both behavioral and physiological components of coping style, with roe deer mothers ranking along a continuum of the proactive-reactive response to stress. As expected, we found that the coping style of the mother affected early survival of her fawns. However, the pattern of variation in early fawn survival in relation to the coping style of their mother was context-specific. Compared to more reactive mothers, mothers with a more proactive coping style were more likely to wean a fawn in open meadows, but less likely to

do so in forest or crops. Our findings therefore demonstrate that inter-individual differences in the coping style of mothers have a habitat-specific influence on offspring survival, and hence on female fitness, in wild populations of mammals. Boon et al. (2007) found that maternal personality impacted both survival and growth rate of offspring in red squirrels, but that these effects varied across life history stages and among years, i.e. temporal heterogeneity in the influence of personality on individual performance. Here, we detected spatial heterogeneity in the influence of the coping style of mothers on an important fitness component, early offspring survival, in roe deer. We suggest that both these forms of heterogeneity may potentially contribute to the maintenance of behavioral variation in wild populations.

### ***Proactivity index and rectal temperature of the mother: repeatability and inter-correlation***

In a meta-analysis, Bell et al. (2009) reported that behavioral traits are generally repeatable with an average value of 0.37. In comparison, relative to this average value for repeatability, we found that the level of proactivity was only a moderately repeatable trait ( $r = 0.201$ ,  $CI = [0, 0.592]$ ), while rectal temperature was highly repeatable ( $r = 0.70704$ ,  $CI = [0.185, 0.909]$ ). In addition, in our study, these two maternal traits co-varied positively, although the relationship was weak. The fact that the correlation between rectal temperature and the proactivity index was positive was unexpected based on previous studies on small mammals (Moe and Bakken 1997, Korhonen et al. 2000), but there has been no equivalent study to date on ungulates. This unexpected result could be due to the fact that body temperature at capture reflects the combination of two physiological components: in a non-stressed situation, body temperature is a proxy of individual metabolic rate (Biro and Stamps 2008), while in a situation of stress, body temperature rises and indicates ‘stress-induced hyperthermia’ (Bakken et al. 1999; Korhonen et al. 2000). Hence, temperature at capture might reflect the effects of among-individual differences in metabolic rate modulated by the stress response (see Debeffe et al. 2014).

Phenotypic correlations among such traits are typical of the proactive-reactive syndrome (Koolhaas et al. 1999; Sih et al. 2004). We thus identified a gradient of coping

style, varying from mothers with a marked behavioral (i.e. a high proactivity index) and physiological (i.e. a high rectal temperature) response to capture (i.e. the most proactive) to those with a low level of response (i.e. the most reactive). We have recently shown elsewhere that both this proactivity index and rectal temperature contribute to shape a dispersal syndrome among juvenile roe deer (Debeffe et al. 2014) and a risk management syndrome among adults (Bonnot et al. 2015), suggesting that they reliably index consistent inter-individual variation in behavior. However, further work on a larger sample size will be necessary to obtain reliable estimates of repeatability for these traits so as to better apprehend how well they index a behavioral syndrome in roe deer more generally.

### ***Early fawn survival in relation to age, body development and spring conditions***

The results from our baseline model support previous studies that reported effects of age, body development and spring conditions on early survival in populations of large herbivores (see Gaillard et al. 2000 for a review). Older fawns at capture survived better than younger ones. In large herbivores, most mortality occurs within the first few weeks of life (e.g. Guinness et al. 1978). Within this critical period, the mortality risk is especially high during the first few days of life, when newborns are subject to thermoregulation problems, abandonment by the mother, disease, and, in some hider species, predation because newborns are immobile and isolated from the mother for most of the time. High quality and quantity of food resources is key for early survival in most large herbivores (Gaillard et al. 2000), which grow very fast from birth to weaning (Pontier et al. 1989). Using the number of degree-days as a proxy of plant phenology (Plard et al. 2014), we found that fawn survival decreased with increasing number of degree-days. Energetic needs of mammalian mothers peak during late pregnancy and early lactation (Clutton-Brock et al. 1989) so that the match between maternal energy requirements and the peak of resource availability is crucial to offspring survival. As roe deer birth timing is highly repeatable (Plard et al. 2013) and quite constrained (Gaillard et al. 2013), early vegetation flush leads to an increase in early fawn mortality (Plard et al. 2014) and, thereby, to lower population growth rate (Gaillard et al. 2013). These negative effects of early springs were reported for forest roe deer, but our

study indicates that this relationship holds even for populations living in more open landscapes. Likewise, our results also support previous observations of a positive influence of fast early body development on early survival of roe deer fawns in forest populations (da Silva et al. 2009).

### ***Early fawn survival in relation to the mother's coping style and habitat type***

The neonatal period is a critical phase for juvenile survival in most mammals and depends heavily on the nature and quality of the interactions between the mother and her offspring (Nowak 1996). In some species, mothers or other members of the group may actively defend the young (Leuthold 1977), sometimes directly attacking a predator and/or attempting to disrupt its chase (Jarnemo 2004; Lingle et al. 2005). These anti-predator behaviors vary in relation to the hunting tactic of the predator (ambush vs. coursing), predator abundance and diversity, and habitat type. For example, Panzacchi et al. (2010) concluded that meadows are an especially risky habitat for roe deer fawns because the density of small rodents is generally high. Because of this, meadows are hunting hot spots for red foxes (*Vulpes vulpes*), so that predation risk of fawns is likely to be higher in this habitat. Our findings support this hypothesis, as fawns born to more proactive mothers survived better than those born to more reactive mothers when in open meadow habitat (natural meadows). We suggest that this is because, when attacked by fox, proactive mothers are more mobile and aggressive, and so successfully defend their fawn, compared to reactive mothers who are more passive and display a high attack latency. However, none of the six fawns monitored in artificial meadows survived beyond 12 days of age, irrespective of the mother's coping style. This presumably occurred because fawns in this habitat type were killed by mowing, the second most important mortality factor for roe deer fawns in agricultural landscapes (Jarnemo 2002). In contrast, in closed habitats (i.e. forest and crops), fawns born to more proactive mothers survived less well than those born to more reactive mothers.

The marked influence of habitat type on the success of a given mother's coping style that we describe above is likely related to habitat-specific differences in the trade-off between resource acquisition and predation risk (Bongi et al. 2008; Boon et al. 2008). The requirement for high quality forage is particularly acute for income breeders like roe deer

(Bongi et al. 2008), so that risky tactics (e.g. in terms of exposure to fawn predation risk) may potentially be the most rewarding in terms of fitness. The quality of food resources for roe deer is far better in open habitats (Hewison et al. 2009; Abbas et al. 2011), so that females should preferentially select meadows. However, the risk of predation is also highest in open habitats (Panzacchi et al. 2010). As a result, females raising their fawns in meadows play a high risk-high benefit tactic, where the pay-off is greater if females actively defend their fawns. Our results indicate that this is the case for more proactive mothers who are better able to raise their fawns successfully in high risk open meadows, presumably because they respond more actively to the attack of a predator by actively defending their fawns (Jarnemo 2004), but also possibly because they are more attentive in general, thus also minimizing mortality due to other causes. In forest habitats, food resources are less plentiful and predation risk is much lower than in open habitats because alternative prey such as rodents are less abundant. Furthermore, closed habitats provide visual obstruction so that anti-predator behaviors such as vigilance may be less efficient and active defence of the fawn may be more difficult and/or inefficient. In this context, the best anti-predator tactic for the mother may be to range further away from the fawn's bed site during feeding, so as not to provide cues of the fawn's location to predators (Fitzgibbon 1993). Because food resources are of lower quality in closed habitats (Hewison et al. 2009), females have to spend more time on food acquisition, especially during the energetically demanding early lactation period. In this case, the pay-off associated with the low risk-low benefit tactic adopted by the more reactive mothers is maximized in closed habitat. While the above interpretation of our results is coherent with expectations, we did not have any direct observations of maternal behavior during attempted predation to confirm that this was the behavioral mechanism underlying the observed relationship between coping style and fawn survival. Future work should focus on how maternal care tactics, and specifically anti-predation behaviors, vary between habitats and among individuals in relation to variation in coping styles.

### ***Coping styles, fitness and the maintenance of behavioral variation***

Only a few studies to date have provided empirical evidence of an influence of inter-individual variation in behavior on fitness in the wild (Smith and Blumstein 2008), and only one has reported that a given behavioral phenotype is favored in some ecological conditions, but not in others, governed by life history trade-offs (Boon et al. 2007). These authors found that both the direction and magnitude of the influence of maternal aggressiveness on offspring survival differed among years in North American red squirrel, likely in response to marked yearly variation in food availability. Our findings that the direction and magnitude of the influence of the mother's coping style on offspring survival differ across the landscape provide clear evidence of spatially dynamic associations between behavioral phenotype and fitness components. These combined results imply that both temporal and spatial variation in resource acquisition and allocation contribute to ensure that no given behavioral phenotype is consistently associated with the highest fitness. The exact mechanisms by which variation among individuals in behavioral traits is maintained in the wild are largely unknown. Potential explanation for differences in fawn survival we reported in relation to their mother's behavior could involve genetic factors. Indeed, the aggressiveness of mothers towards their offspring, the responsiveness of mothers towards signals from their offspring or the nursing behavior of mothers can be under genetic control (Grandinson 2005). However, our findings directly suggest that spatial habitat heterogeneity could be involved. Indeed, recent theoretical models have demonstrated that, under variable food conditions, the involvement of behavioral traits in life-history trade-offs may lead to the maintenance of individual differences in behavioral phenotype (Stamps 2007; Wolf et al. 2007).

Depending on the strength of spatial variation in the fitness advantages associated with a given level of proactivity, one may hypothesize that certain behavioral phenotypes should predominate in a given habitat (see Dingemans et al. 2004; Bergmüller and Taborsky 2010). For example, in chipmunks (*Tamias striatus*), the most exploratory and docile individuals established their home ranges in those areas that were most frequented by humans (Martin and Réale 2008). Further studies investigating correlations between behavior and environment are needed so as to better understand their ecological and evolutionary implications in terms of the maintenance of inter-individual behavioral variation (Ravigné et al. 2003). In particular, we lack empirical case studies that directly link

inter-individual variation in behavioral phenotype with fitness components across variable environments. Our work provides evidence that spatial heterogeneity in fitness pay-offs for different coping styles may promote the maintenance of behavioral variation in wild populations.

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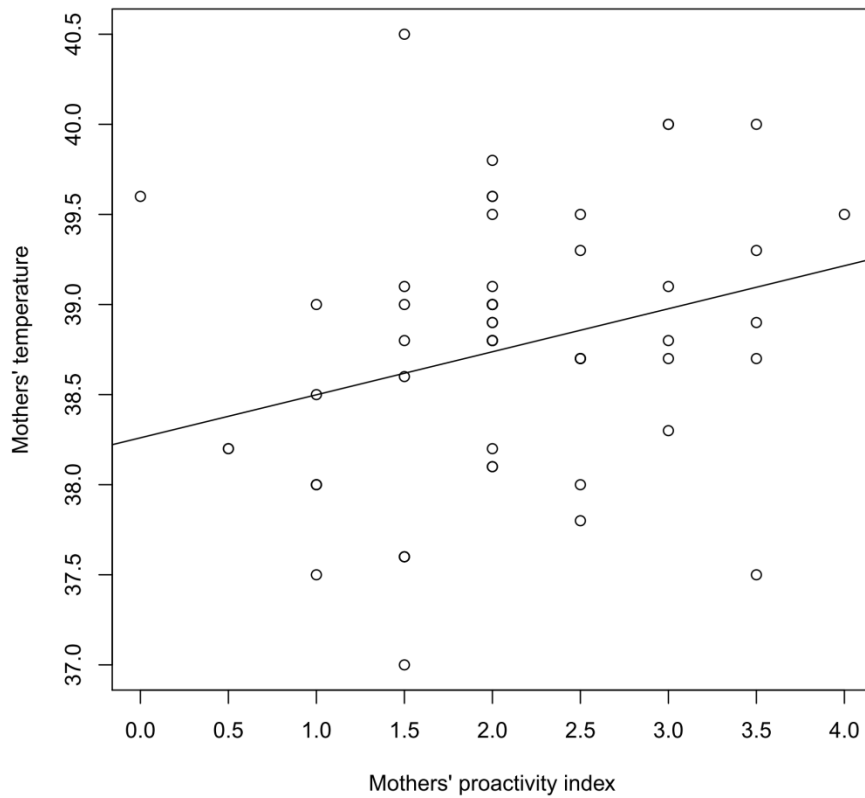
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## APPENDICES

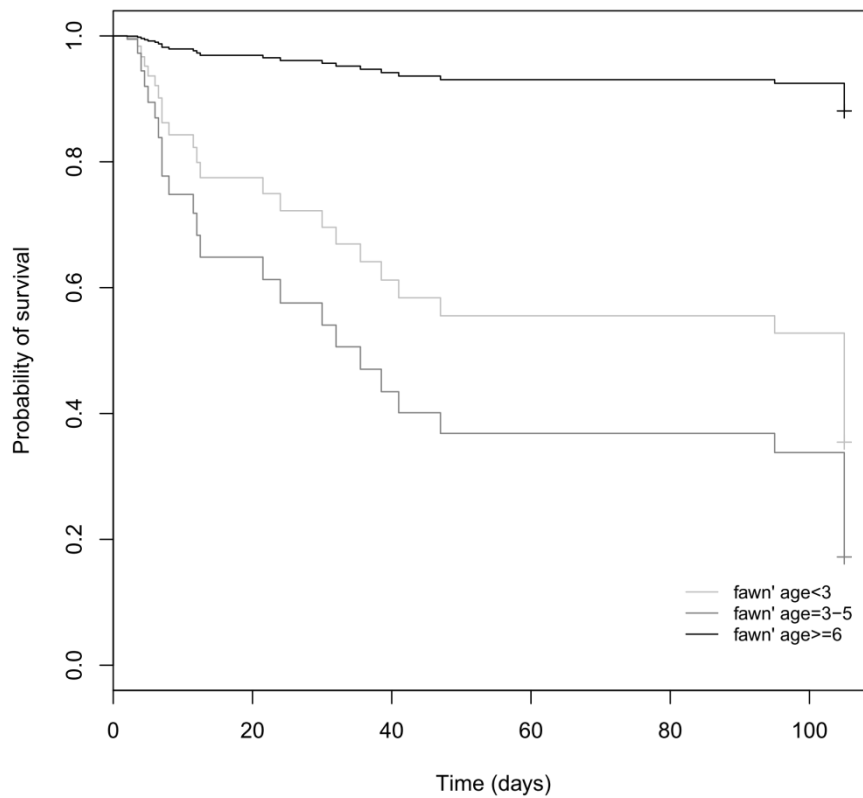


**Appendix 1. Relationship between the rectal temperature of a mother and her proactivity index (linear regression: p-value = 0.037,  $r = 0.26$ , N = 39 females).** The proactivity index potentially varies between 0 and 6, but the highest observed value was 4.

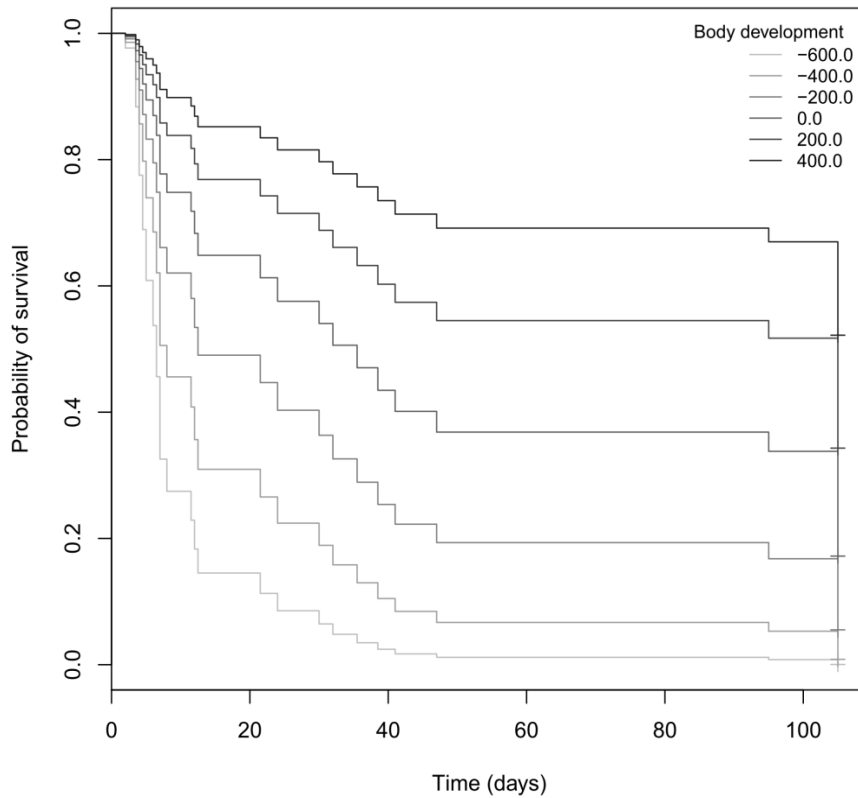
Habitat		Mothers' proactivity index								
		0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
Crop	Number of fawns dead	0	1	2	0	3	3	0	1	0
	Number of fawns alive	0	1	3	1	4	1	0	0	0
Forest	Number of fawns dead	0	0	1	1	1	1	1	0	1
	Number of fawns alive	1	0	0	3	1	0	1	0	0
Artificial meadow	Number of fawns dead	0	0	0	0	3	1	2	0	0
	Number of fawns alive	0	0	0	0	0	0	0	0	0
Natural meadow	Number of fawns dead	0	0	0	1	5	1	1	2	0
	Number of fawns alive	0	0	0	3	2	1	1	2	0

**Appendix 2. The distribution of fawns across the landscape in relation to their mother's proactivity index.**

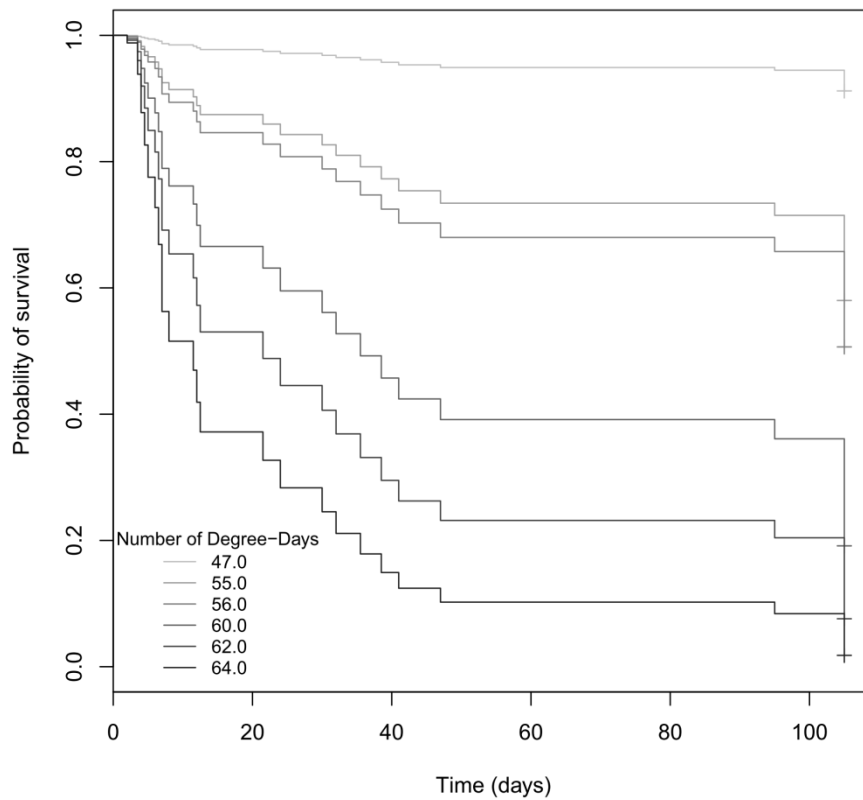




**Appendix 3. Probability of a roe deer fawn surviving to 105 days of life in relation to its age at capture.** We used a Cox proportional hazard model with age at capture as an explanatory variable in three categories (1: two days old or less, 2: between three and five days old, 3: older than 6 days). This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, fawn age at capture), the interaction between habitat type and the proactivity index of the mother, plus an additive effect of the rectal temperature of the mother.



**Appendix 4. Probability of a roe deer fawn surviving to 105 days of life in relation to its early body development.** We used a Cox proportional hazard model with this trait as an explanatory variable. Progressively higher body development is represented by increasingly darker lines. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, fawn age at capture), the interaction between habitat type and the proactivity index of the mother, plus an additive effect of the rectal temperature of the mother.



**Appendix 5. Probability of a roe deer fawn surviving to 105 days of life in relation to spring weather conditions.** We used a Cox proportional hazard model with the number of degree-days as an explanatory variable. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, fawn age at capture), the interaction between habitat type and the proactivity index of the mother, plus an additive effect of the rectal temperature of the mother.



Photos: by F. Renaud



## Part 2

# When inter-individual variability in a trade-off shapes the fitness: take risk and/or raise its offspring?

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*'Roe deer females are income breeders such that females do not store fat reserves, relying instead on current energy intake to offset the costs of reproduction. For income breeders, the trade-off between foraging and risk of predation should be particularly acute because females have to forage intensively while simultaneously minimizing the risk of predation of their offspring.'*



Photos: by N. Cebe, B. Cargnelutti, and C. Salin from left to right



## RESUME

Chez les ongulés, la survie précoce des faons dépend en premier lieu des soins maternels et du comportement de la mère. Dans ce contexte, il a récemment été démontré que la survie et la croissance des jeunes seraient influencées par le style maternel. Ainsi, les différences comportementales entre individus, et donc entre femelles, sont supposées avoir des conséquences en termes de valeur sélective. Par ailleurs, le lien entre la personnalité des individus et leur valeur sélective comme celui du comportement des femelles et la survie de leurs faons peut être bilatéral. En effet, on s'intéresse généralement plus à l'influence du comportement des parents sur la survie de leur progéniture mais, la présence des jeunes et le fait qu'ils soient en plus en moins bonne condition pourrait également impacter le comportement des parents. Notre objectif était donc d'étudier les liens possibles entre la présence du faon et sa croissance et le comportement spatial des mères vu à travers le compromis entre évitement du risque et acquisition des ressources. Nous avons supposé que les femelles suitées (cad les femelles avec leurs faons) feraient un compromis et passeraient plus de temps en milieu ouvert, c'est-à-dire dans des habitats plus risqués mais également plus riches d'un point de vue qualité nutritive, ce qui permettrait de répondre correctement aux besoins énergétiques des faons et leur assurerait une meilleure survie (hors risque de prédation) et croissance. Nous avons trouvé un certain support en ce qui concerne l'influence de la présence et de la croissance des faons sur le comportement de leur mère avec un effet plus marqué de la présence des faons. Les femelles avec leurs faons et des faons en bonne condition (plus forte croissance) favoriseraient leur prise alimentaire en milieu ouvert bien que le risque de mortalité soit plus élevé. Nous supposons qu'en ayant une prise alimentaire de meilleure qualité, les femelles pourraient mieux répondre à leurs besoins énergétiques ainsi qu'à ceux de leurs faons. Cependant, le risque de prédation est plus important dans les milieux ouverts mais, nous avons précédemment montré que les femelles faisant un compromis en favorisant leur prise alimentaire dans des milieux plus risqués avaient un niveau de vigilance plus élevé ce qui leur permettrait de détecter un risque suffisamment tôt pour peut-être mieux protéger leurs faons.

**Mots clés :** différences individuelles, faons, survie précoce, croissance, utilisation d'habitats



## **ABSTRACT**

In ungulates, the fawn's early survival mostly depends on its mother's ranging behavior and care. In this context, maternal style was recognized recently to influence the growth and survival of the offspring. Thus, inter-individual differences in females' behavior may influence their fitness. But, the fawns' presence may also modify their mothers' behavior. For example, mothers may modify their spatial behavior to provide them a better survival via their protection and/or feeding behavior. Therefore, in this study, we wanted to test the potential link existing between the fawns' presence and their growth and the spatial behavior of their mothers focusing on their 'resource acquisition – risk avoidance' trade-off tactics. We supposed that females having a fawn would express a trade-off, meaning they would spend more time foraging in open habitats to provide food of good quality to improve their fawns' survival and growth. We found some support for a link between the mothers' trade-off tactic and their fawns' growth and a more pronounced link as regards their fawns' survival. As we supposed it, when fawns are alive and in good condition, females expressed a trade-off favoring their resource acquisition in rich habitats. Consequently, foraging in open habitats may allow females to respond to their needs and to produce milk in sufficient quantity or quality to feed their fawns. Moreover, as regards the higher risk of fawns' predation in richer habitat for resource acquisition, we supposed that the higher vigilance level of females expressing a trade-off allow them to detect risk early enough to protect their fawns.

**Key words:** individual differences, juvenile survival, growth rate, habitat use

## INTRODUCTION

Parental care plays an important role in the juvenile survival of their offspring. In ungulates, males contribute no parental care. Thus, the size, growth and, *in fine*, the juvenile survival is solely determined by the maternal care meaning the energy allocated by the mother. Maternal care is a major component of demographic tactics in mammals (Andersen et al. 2000a). Thus, maternal attributes such as size, age, and previous reproductive success strongly impact juvenile survival, generating marked individual differences in female reproductive success (Gaillard et al. 2000). Previous rearing experiences (i.e. the maternal experience) may decrease the juvenile vulnerability towards predators (Ozoga and Verme 1986).

More recently, it has been showed that individuals vary consistently in their behavioral responses to environmental perturbations (Wilson 1998; Koolhaas et al. 1999; Gosling 2001; Sih, Bell, Johnson, et al. 2004; Réale et al. 2007). In this context, maternal style influences the growth and survival of the offspring (Pittet et al. 2014). Maternal styles can be defined only when mothers' behavioral traits are consistent over a number of breeding periods (Albers et al. 1999b; Dwyer and Lawrence 2000) which is not always easy to study especially in wild populations. But, it is recognized that mothers' personality influence maternal styles (Fairbanks 1996; Plush et al. 2011). Thus, some studies found a link between personality and individual fitness especially in birds (Hakkarainen and Korpimäki 1994; Moore et al. 1997; Rytönen 2002; Dingemans et al. 2004a; Kontiainen et al. 2009; Westneat et al. 2011). In this context, we highlighted that the mother's behavior influence the early survival of their offspring in a context-specific manner (Monestier et al. 2015). Proactive females improved their juvenile survival in open habitats whereas reactive females increased the survival of their offspring in closed habitats. Consequently, personality of parents plays an important role in their offspring survival.

However, speaking about the link between personality and fitness, we could also focus on the effect of offspring on the behavior of their parents. Maybe it seems not obvious but, parents may modify their behavior as their spatial behavior via habitat selection for example due to their offspring presence. In ungulates, for instance, the presence of fawns may influence the social organization and spatial behavior of females with offspring

(Schwede et al. 1993; Tufto et al. 1996; Bongi et al. 2008). It may induce anti-predator strategies in mothers such as their isolation from other individuals of the same species (Clutton-Brock and Guinness 1975; Clutton-Brock et al. 1982; Schwede et al. 1993; Ciuti et al. 2006; Bongi et al. 2008). Indeed, this behavior is associated with lower disturbance by conspecifics and reduced risk of predation (Schwede et al. 1993). Females also often range less widely during the first months after parturition (Saïd et al. 2009). Moreover, we previously highlighted that a trade-off between food acquisition and risk avoidance exists in roe deer (Monestier et al. Chapter V) and this trade-off would be particularly pronounced for females with offspring. Indeed, roe deer is an income breeder (sensu Jönsson 1997) such that females do not store fat reserves, relying instead on current energy intake to offset the costs of reproduction (Andersen et al. 2000a), and lactation is generally recognized to be the most energetically costly component of reproduction in mammals. Many studies have examined the energetic of milk production (Oftedal 1985), but only a few have analyzed behavioral strategies that females adopt to meet these energetic demands in the wild (Clutton-Brock et al. 1982). Thus, females has to daily forage in habitats of good quality to offset the costs of reproduction and insure their survival as well as the one of their offspring while simultaneously minimizing the risk of predation of their offspring (Linnell et al. 1995), but foraging and protection are rarely maximized in the same habitat type (Lima and Dill 1990; Houston et al. 1993; Brown 1999). Thus, for example, bighorn sheep move to poorer quality pasture, compromising their energy intake, in order to reduce predation risk to their neonates (Festa-Bianchet 1988). Lactating Grevy's zebras (*Equus grevyi*) also use inferior pasture, but they do this in order to maintain access to water (Ginsberg 1989). Despite these few studies, how females change their behavior according to their status (i.e. presence or absence of offspring) is still widely unknown.

Therefore, our aim in this exploratory study was to test whether the presence of fawns and their growth modify the foraging and spatial behavior of mothers. To do that, we focused on the trade-off tactics of females between resources acquisition and risk avoidance (Chapter V) and the early survival and growth of their fawns. We supposed that females with fawns (successful early fawns' survival) would express a trade-off meaning they would favor their acquisition of resources of high quality despite a potential higher predation risk. In the same way, we supposed that the fawns' growth may influence the females' trade-off tactic

with females having fawns in good condition (i.e. a higher growth) foraging more in open habitats.

## MATERIAL AND METHODS

Between 2004 and 2013, newborn fawns (97% less than 20 days old, average age at capture = 6.3 days) were caught by hand each year between the end of April and the middle of June, but more intensively since 2009 (30 fawns caught between 2004 and 2008, with none in 2005 and 2006, and then more than 100 fawns were caught since 2009), mostly by observing the behavior of the mother. Among others things, we weighed (with a precision of 50 g), aged fawns using 3 age-classes (<3, 3–5, and  $\geq 6$  days old) and equipped them with an expandable very high frequency (VHF) radio collar (Biotrack). Since 2013, we try to catch a second time each fawn to weigh it to obtain its body mass and then, estimate its growth. We have weighed 33 fawns but only 15 had a known mother. Subsequently, fawns were located each day from marking to the end of the summer (1.5 locations per day per individual on average) by radio-telemetry and triangulation. The radio-collars were equipped with a mortality sensor, providing us with information about the current fate of each fawn. When a mortality signal was detected, we immediately recovered the dead animal and, where possible, ascertained the cause of its death.

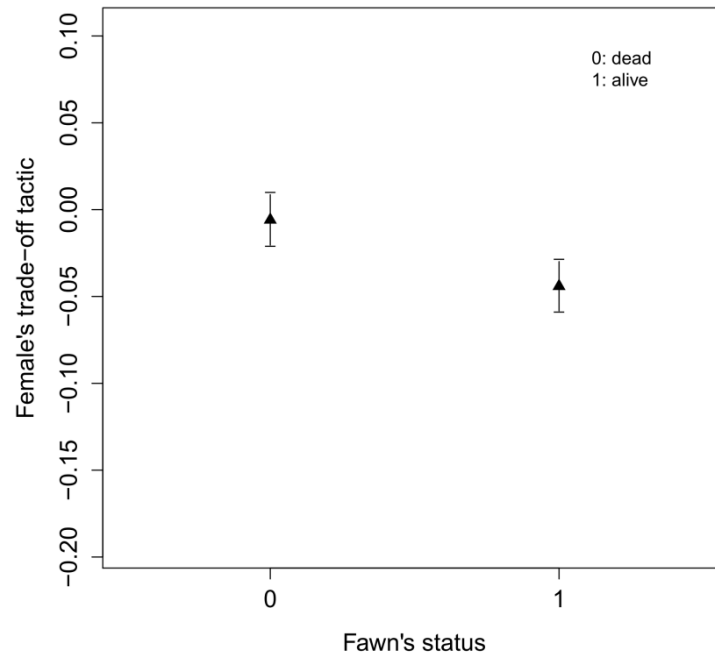
We excluded fawns with unknown mothers and fawns of mothers with missing data for the trade-off between resource acquisition and risk (i.e. missing average speed or proportion of time using the secure habitat which was most of the time due to electronic problem of the GPS collar, see Chapter V). We firstly investigated the relationship between the survival of fawns (explanatory variable) and the fact that their mothers have to cope with a trade-off (dependent variable). Then, we realized a second analysis focusing solely on females that expressed a risk-resource trade-off (dependent variable). Besides, we performed the same analyses with, this time, the fawns' growth as the explanatory variable. Thus, we performed analyses using linear models (LM) with the survival or the growth of fawns as the explanatory variable and the females' trade-off tactics or the strength of their trade-off as the dependent variable. To describe each mother's trade-off tactic, we extracted the female-level slope of the relationship describing feeding efficiency in relation to the use

of secure habitat in spring (March to June; see Chapter V). Finally, we obtained 45 fawns for which we had their survival and their mother's trade-off tactic (positive or negative slope) and 28 fawns when we solely kept females having a negative slope (i.e. expressing a trade-off). We had 14 fawns with both their growth and their mother's trade-off tactic and 8 fawns when we focused on females expressing a trade-off. Survival was estimated on the four first month of life of fawns (see Monestier et al. 2015). Model selection was based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002). All analyses were performed in R version 2.15.1 (R Development Core Team 2013).

## RESULTS

### *Fawns' survival and their mother's trade-off tactic*

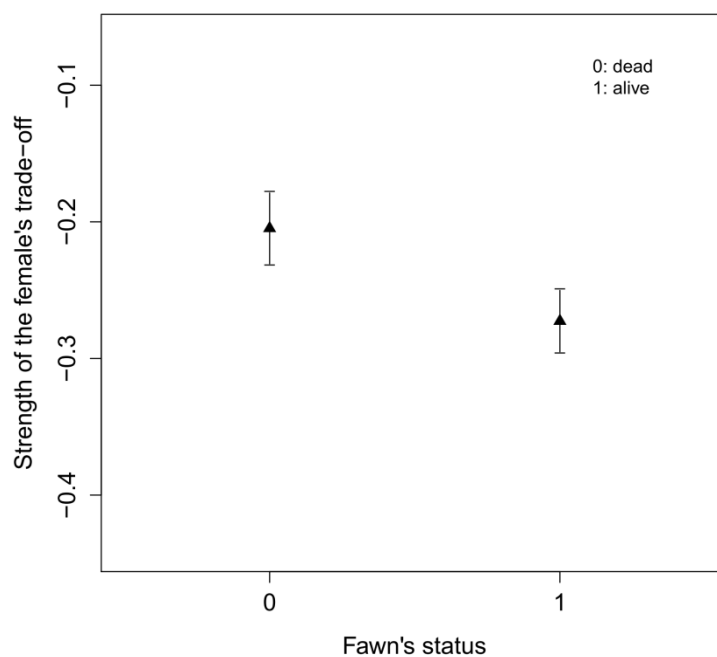
The model with the highest support describing the link between the mother's trade-off tactic and the survival of their fawns was the variable representing the survival status of the fawns (AICc weight = 0.65, AICc = -109.67,  $\Delta$ AICc to constant model = 1.27). However, the most parsimonious model was the constant model (AICc = -108.40,  $\Delta$ AICc to best model = 1.27, AICc weight = 0.35). That being said, we found that fawns surviving to their first months of life had a mother expressing a trade-off, whereas fawns which did not reach this stage had a mother which did not express a trade-off or which express a trade-off with a weak strength (Fig. 1). When focusing solely on females expressing a trade-off, the best model included the survival status of the fawn (AICc weight = 0.67, AICc = -50.58,  $\Delta$ AICc to constant model = 1.41), but the most parsimonious was the constant model (AICc weight = 0.33, AICc = -49.17,  $\Delta$ AICc to best model = 1.41). Thus, when a mother had a fawn, the strength of its trade-off between resources acquisition and risk avoidance is higher than females with no fawn (Fig. 2).



**Figure 1. Effect of the female's trade-off tactic on the early survival of its fawns.** We used linear models ('lme4' package; Bates et al. 2015) to test whether the choice of females in the trade-off (negative slope, vs. absence of trade-off when the slope is positive) between resource acquisition and risk avoidance was related to the early survival of their fawns.

0 means that the fawn is dead whereas 1 means is still alive.

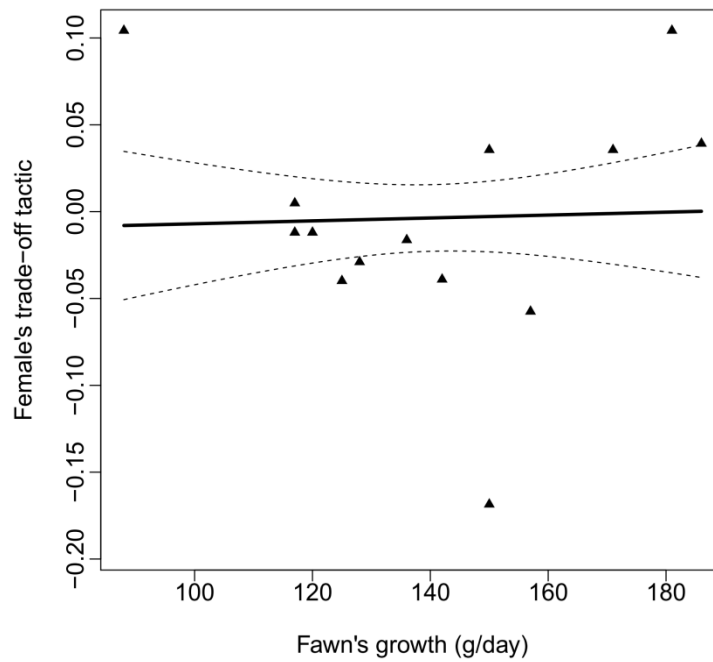
Standard deviation is represented here.



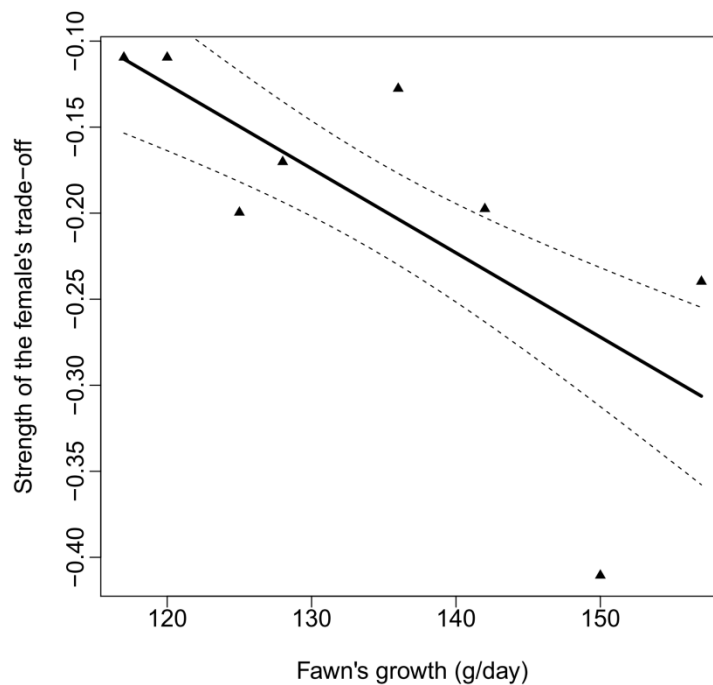
**Figure 2. Link between the strength of the female's trade-off and the early survival of its fawns.** To do that, we used linear models focusing solely on females expressing a risk-resource trade-off (i.e. negative slope) meaning these females favor their feeding efficiency in rich and risky habitats. 0 means that the fawn is dead whereas 1 means is still alive. Standard deviation is represented here.

### ***Fawns' growth and their mother's trade-off tactic***

The model with the highest support describing the link between the mothers' trade-off tactic and the growth of their fawns (Fig. 3) was the constant model (AICc weight = 1, AICc = -110.64). However, when focusing on females expressing a trade-off, we found some support for the model including the growth of the fawn (AICc weight = 0.52, AICc = -9.14,  $\Delta$ AICc to constant model = 0.13) even if the constant model was the most parsimonious (AICc weight = 0.48, AICc = -9.01,  $\Delta$ AICc to best model = 0.13,  $\Delta$ AICc to constant model = 0.00). It seemed that the strength of the mothers' trade-off increased with higher fawns' growth (Fig. 4).



**Figure 3. Effect of the female's trade-off tactic on the growth rate of its fawns.** We used linear models ("lme4" package; Bates et al. 2015) to test whether the choice of females in the trade-off (negative slope, vs. absence when the slope is positive) between resource acquisition and risk avoidance was related to the growth of their fawns. Standard deviation is represented here.



**Figure 4. Link between the strength of the female's trade-off and the growth of their fawns.** To do that, we used linear models focusing solely on females expressing a risk-resource trade-off (i.e. negative slope) meaning these females favor their feeding efficiency in rich and risky habitats. Standard deviation is represented here.



## DISCUSSION

Our aim in this exploratory study was to test whether the presence of fawns and their growth modify the foraging and spatial behavior (i.e. the trade-off tactic) of their mothers. Generally speaking, the constant model was the model retained according to the parsimony criteria. However, we found some support for a link between the mothers' trade-off tactic and their fawns' growth and a more pronounced link between the mothers' trade-off tactic and their fawns' survival.

As we supposed it, females with newborns (i.e. fawns with a successful early survival) expressed a trade-off between resources acquisition and risk avoidance favoring their food acquisition in highly nutritious habitats even though these habitats were riskier than closed habitats (Myserud and Ostbye 1999; Verdolin 2006; Stankowich 2008). Moreover, we found that both the early fawns' survival and their growth tend to increase the strength of their mothers' trade-off. These findings seem consistent with the available literature on deer. Indeed, energetic needs are especially acute in late gestation and weaning in mammals (Clutton-Brock 1989) to offset the costs of milk production. Consequently, foraging in open habitats may allow females to respond to their needs and to produce milk in sufficient quantity or quality to feed their fawns. Staying in closed habitats would reduce predation risk especially from red foxes which kill often fawns in open habitats (Panzacchi et al. 2010), but this would decrease the acquisition of resources of good quality since open habitats such as meadows are more attractive and nutritious during spring than closed habitats (Abbas et al. 2011). Diet plays a major role in the survival and growth of fawns. On the contrary, females without fawns (unsuccessful early fawns' survival) or with fawns with a low growth so, with fawns probably not in good conditions, would have lower energetic needs because, for example in the case of females without fawns, females did not have to offset for the costs of milk production anymore. Thus, energetic needs are not for the 'mother-offspring' pair but only for the female. As their needs are lower, females may forage for shorter periods of time in risky habitats and spend more time in closed and more secure habitats.

In addition, we previously highlighted (Chapter V) that females expressing a trade-off between resources acquisition and risk avoidance had a higher level of vigilance which allows them to detect earlier risk (as predators) for themselves but also for their fawns.

Moreover, we found that proactive females favored their fawns' survival in open habitats (Monestier et al. 2015). These females are supposed to be bold (Koolhaas et al. 1999) allowing them to take risk to forage in rich sites, favoring their feeding efficiency rather than their security for example (Chapter V), and they are also assumed to be more aggressive which allows them to improve their survival and the one of their offspring. Panzacchi et al. (2010) showed that high female aggressiveness and short mother-fawn distance are associated with increased offspring survival during the hiding phase in open habitats because ungulate females may aggressively defend and protect their fawns (Ozoga and Verme 1986; Lingle et al. 2005). Thus, fawns' presence seemed to modify their mothers' spatial behavior favoring their acquisition of resources of good quality. Moreover, these females taking more risks in open habitats seemed to be able to protect their fawns toward potential predation risk in some extent.

Hence, even if results were not really significant due to a weak sample size, we could conclude with caution saying that it seems that fawns' presence and growth modify their mother's behavior in spring. To conclude, we previously found that females' behavior influence their fitness and, with this exploratory work, we showed that fawns' presence and their growth impact their mothers' behavior too. Therefore, the links between females' behavior and fitness work in both ways. These findings are promising and encourage us to continue the demanding field campaigns to perform future analyses with larger sample size.

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Photo by C. Demussy



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## **Chapter VII**

### **Discussion**

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The interest for the study of personality or behavioral syndromes in ecology is now recognized and is experiencing a boom (Réale et al. 2010). Indeed, it is currently in the context of numerous frameworks, from production to conservation for example. Moreover, this inter-individual variability in behavior among individuals plays a crucial role in the whole life of individuals, affecting their life-history traits such as their dispersal (Dingemanse et al. 2003; Cote and Clobert 2007; Debeffe et al. 2014), or their territory quality and size (Civantos 2000; Both et al. 2005). However, few attempts have been made to study inter-individual differences in life-history traits from a personality point of view and their consequences in wild populations (Wilson et al. 1994), which means that the importance of personality for fitness remains largely unknown (Wilson et al. 1994; Dingemanse and Réale 2005; Smith and Blumstein 2008).

Thus, with this thesis we focused our research on the inter-individual variability in individual behavior in a wild population of a large herbivore, and we explored its potential impact on components of individual fitness.

## **Which traits? And what are their links between each other?**

A first and consequent difficulty when we want to study personality or behavioral syndromes is to identify the traits of interest, together with their precise definition. This may seem obvious, but this is one of the reasons why personality was ignored for a long time in ecology (Réale et al. 2007). Indeed, historically, personality studies focused on humans and there were some doubts on the possibility of studying personality in non-human animals without falling into the trap of anthropomorphism (Grootuis and Carere 2005). Réale et al. (2007) suggested focusing more precisely on five behaviors to study inter-individual differences in animal behavior. Despite this simplification, studying these behaviors in the wild remains challenging, and so little unexplored to date.

Our first goal was to highlight inter-individual differences in behavior by exploring which of the 'Big Five' behavioral dimensions could be pertinent in a large herbivore such as roe deer, and identifying which parameters could suitably index a given personality trait. Moreover, we wanted to test for the existence of behavioral syndromes (i.e. correlated behaviors reflecting between-individual consistency in behavior within a given behavioral



context or across multiple contexts, Sih et al. 2004). To do that, we carried out two studies: one in the wild (Chapter III) and one in captivity (Chapter IV). With both, we found consistent inter-individual differences in behaviors. Beyond the fact that we wanted to study a particular personality trait in captivity: the neophobia-neophilia dimension, we wanted to calibrate our measures/indices of personality collected in the wild using the same behavioral and physiological measures collected in captivity. As matter of fact, most studies on inter-individual variability in behavior are performed in captivity for practical reasons. Maybe the most commonly recognized reason is that captivity allows the experimenter to control the conditions under which the behaviors of individuals are measured (Campbell et al. 2009). However, some researchers suggest that studies of personality in captivity may be misleading, notably because individuals are conditioned to captive conditions so that they may have modified their initial or “wild-type” behavior (Butler et al. 2006). That being said, a recent study that aimed to improve knowledge regarding the expression of behaviors in the wild and in captivity suggested that both exploration and neophobia of blue tits in a foraging context appeared similar in both contexts (Herborn et al. 2010a) . We cannot mimic this approach exactly for a large wild herbivore such as roe deer, but our calibration study followed the same logic as that of Herborn et al. (2010). Indeed, we found that behavioral (behavioral score) and physiological (temperature, immunology) parameters differed consistently among individuals in a stressful situation in both the wild and captivity, and that they were correlated with measures of neophobia in captivity. Thus, we could be more confident that behavioral and physiological parameters expressed during a stressful situation may index inter-individual variability in personality. Indeed, it is particularly interesting to carry out such calibration measures on behavior in captivity in order to remove a certain number of doubts regarding the expression and indexing of personality traits in the wild.

In addition, we found, once again, in both the wild and in captivity, that certain personality traits were inter-correlated: the shyness-boldness (or the reactivity-proactivity) dimension appeared to be related to the activity dimension in the wild population study, while the shyness-boldness (or the reactivity-proactivity) dimension appeared to be linked to the neophobia-neophilia dimension in captivity, suggesting the existence of behavioral syndromes (*sensu* Sih et al. 2004). It was very encouraging to identify such behavioral syndromes, irrespective of whether the study occurred in the wild or, all the more so, in

captivity, because it is recognized that inter-individual differences in behavior do generally not concern a single personality trait, but rather several traits, resulting in a behavioral syndrome (Sih et al. 2004b). We can easily understand this finding by illustrating it with an example in humans. Five factors are usually used in human psychology to characterize an individual (Gosling and John 1999; McCrae and Costa 1999). Thus, an individual with a high level of impulsivity is not solely characterized by its level of impulsivity. He/she has also the pleasure to be, for instance, extrovert and closed to experience (i.e. with little creativity or imagination). Indeed, it would be simplistic to think that only one trait defines us and explains all our differences with other individuals. It is more likely that a huge number of traits are correlated with each other, acting as a whole which, in the end, defines such inter-individual differences in behavior. Thus, we identify a multi-dimensionality in the behavioral expression of individuals with the existence of behavioral syndromes, but also with intra-individual correlations among levels (i.e. correlations between behaviors and physiological parameters for instance). In the Chapter IV, we found that the behavioral score, temperature, and hematocrit level were positively correlated to each other and negatively to the neutrophils-lymphocytes ratio (N/L ratio). As it was suggested by Koolhaas et al. (1999,2010), behavior expressed during a given situation is the first parameter we can observe, but this behavior is the result of a kind of 'chain reaction' from neurotransmitters to behavior (Bond 2001). For instance, several studies carried out in captivity on rodents showed such correlations between behavior and neurotransmitters. For instance, during defensive burying tests, rodents have the choice between proactivity and reactivity. In general, defensive burying is accompanied by aggressiveness, high plasma noradrenaline and relatively low plasma adrenaline and corticosterone (i.e. individuals are proactive), while freezing behavior is associated with lower level of aggressiveness, relatively low plasma noradrenaline and high plasma corticosterone levels (i.e. individuals are reactive; De Boer et al. 1990; Korte et al. 1992). Thus, evidence is accumulating that a differential HPA axis reactivity may explain some of the behavioral differences even if it is highly unlikely that all differences in coping style can be reduced to one single causal factor (De Boer et al. 1990; Korte et al. 1992; Koolhaas et al. 1999).

Thus, as in many species (in the three-spined stickleback: Huntingford 1976; Bell and Sih 2007; Dingemanse et al. 2007; damselfishes (*Pomacentrus* sp.): Biro et al. 2010;

freshwater crayfish (*Cherax destructor*): Biro et al. 2014; great tits: Verbeek et al. 1996; Marchetti and Drent 2000; Carere et al. 2005; Herborn et al. 2010; North American red squirrel: Boon et al. 2007; Boon et al. 2008; bighorn sheep: Réale et al. 2009), consistent inter-individual differences in several dimensions of personality exist in roe deer. That being said, we were not able to take either the aggressiveness or the sociality of individuals into account in this thesis. Generally, aggressiveness in males is studied focusing on their home-range size (Civantos 2000) and/or their social status as most aggressive males are supposed to become socially dominant (Benus et al. 1988). Aggressiveness in females may be studied during the raise of offspring with for example the defense of their offspring or the defense of the site where their offspring are (Kontinen et al. 2009). To study aggressiveness of a large herbivore such as roe deer which is wary in the wild seems quite complicated. Moreover, in captivity, to avoid any risk of injury, individuals are separated in groups in different enclosures to reduce any potentially aggressive behavior. During field campaigns, we may sometimes observe aggressive acts of an individual towards one of its conspecifics, but the probability that individuals are identifiable is very low. Moreover, it is not always simple to distinguish aggression from social interactions such as intimidation, notably when it is expressed during play. That being said, during the territoriality period, we could realize an experiment to test for their aggressiveness. After locating a focal male, then, we could use playbacks of barking and observe its reaction characterizing its barking behavior (i.e. whether it barks) and its spatial behavior (i.e. does it go in the direction of the barking sounds or rather does it avoid them going further?).

However, inter-individual variability in sociality should be somewhat easier to measure. Sociality has been studied in a huge number of species (from mosquitofish (*Gambusia holbrooki*) to vervet monkeys (*Chlorocebus pygerythrus*)) measuring, for example, the attractiveness of a given individual to another one or any changes in the individual behavior. Indeed, the presence of conspecifics might restrict individual behavioral responses via conformity or enhance differences in behavior by facilitation (King et al. 2015). Moreover, sociality is known to affect life-history traits such as dispersal (Cote and Clobert 2007) or other personality traits such as exploration (Dingemanse and de Goede 2004). Exploration of novel items is facilitated by the presence of conspecifics in several species. For instance, zebra finches (*Taeniopygia guttata*) feed more quickly in a flock rather than when

alone (Coleman and Mellgren 1994). Capuchin monkeys (*Cebus apella*) increase their acceptance of novel food after witnessing group members eating that food (Addessi and Visalberghi 2001). A similar pattern has been found in young children who more readily eat novel food after observing peers eating that food (Birch 1980). In common ravens (*Corvus corax*), the presence of a sibling has been found to increase latency to approach novel objects, though it additionally increases the frequency of manipulation, at 3 and 6 months of age (Stöwe et al. 2006). As regards roe deer, this species is rather solitary or lives in small groups including generally the mother and its offspring of the year (Hewison et al. 1998). However, they are able to live in large groups of ten or more individuals in open agricultural plains (Cibien et al. 1989; Gerard et al. 2002). One possibility could be to conduct experimental designs in captivity to test for inter-individual variation in sociability in roe deer. In captivity, we could study this aspect during foraging activities. Thus, we could observe the foraging behavior of an individual when it is alone in a trial and compare it to its behavior when it is with other conspecifics. This would allow us to know whether the focal individual has changed its behavior and how.

## **Which mechanisms favor consistent inter-individual differences in behavior? The role of the environment in fragmented and human-impacted landscapes...**

Several mechanisms have been suggested to understand why differences in behavior occur among individuals of the same species or population and to explain their consistency in time or among contexts (Houston and McNamara 1999; Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008; Luttbeg and Sih 2010). Most of them are theoretical, and we lack empirical studies focusing on the sources of this behavioral variability, especially in the wild. Thus, our second goal was to identify some sources of variability in behavior in roe deer living in the wild.

Chapter V and VI focused on this aspect. We found that the behavioral trade-off between resource acquisition and risk avoidance favored consistent inter-individual differences in behavior which could be described as a gradient from risk-prone to risk-averse

individuals. Moreover, the individual's level of vigilance mediated this trade-off. Indeed, we found that both the probability of facing a trade-off and its strength tended to increase with the vigilance level, meaning that females facing a more important trade-off are more vigilant individuals. These findings were in line with theoretical studies presented in the Introduction section (Stamps 2007; Wolf et al. 2007) showing that life-history trade-off favor the existence and consistency of behavioral differences among individuals. For instance, during a field experiment, Biro et al. (2004,2006) investigated the trade-off between growth and mortality in farmed salmonids (*Oncorhynchus mykiss*) selected for high growth rate. This selection lead to an increase in risk taking during their foraging activities. When they were released in natural lakes, Biro et al. (2004,2006) observed that these fish took more risk while foraging, and so grew faster. However, they paid a cost through a lower survival rate in the presence of predators. In our study, we found that deer using more open and risky habitat had higher feeding efficiency than individuals spending more time in closed and more secure habitats, but were more exposed to potential predation risk as humans and disturbance created by human activities or again the presence of domestic pets generate disturbance similar to predation risk (Myserud et al. 1999a,1999b; Frid and Dill 2002; Stankowich 2008). Moreover, risk-prone individuals (i.e. individuals prioritizing their feeding efficiency by exploiting rich but risky habitats rather than their security) had a higher vigilance level which should allow them to detect potential predation risk more rapidly (Lima and Dill 1990; Hopewell et al. 2005) but, they seemed to pay a cost for this high vigilance level in closed habitat, since their feeding efficiency decreased strongly. This second result seems to indicate that a behavioral type for a given trait may be advantageous in a given context, but maladaptive in another one.

We found another result along these same lines in Chapter VI where we showed that the coping style type (proactivity vs. reactivity) of a female seemed more advantageous in some habitats. Indeed, proactive mothers increased their early fawns' survival in open habitats whereas reactive females improved their fawns' survival in closed habitats which show, once again, that a given behavioral type is not the best whatever the context. We suggest that spatial habitat heterogeneity could be involved, because patch resources richness and predation risk vary depending on habitat type. Indeed, recent theoretical models have demonstrated that, under variable food conditions, the involvement of

behavioral traits in life-history trade-offs may lead to the maintenance of individual differences in behavioral phenotype (Stamps 2007; Wolf et al. 2007). For example, fluctuation in food resources and/or predation risk may involve temporal environmental variability (Boon et al. 2007) and/or spatial environmental variability which could lead to consistent inter-individual differences in behavior.

Thus, all these results together indicate that the hypothesis that one behavioral type performs best irrespective of environmental conditions seems not to reflect the reality of what happens in natural and wild environments. Hence, environmental variation in its broader sense is an important source of heterogeneity promoting consistent inter-individual differences in behavior. Moreover, the underlying mechanisms may be more complex due to interactions between the environment and behavioral type and genes (Dingemanse et al. 2010). Indeed, individuals of a particular behavioral type can search for specific habitats (niche picking mechanism; Stamps and Groothuis 2010a,b). They might also influence their environment meaning individuals in the same population create or encourage different sets of experiences for themselves (niche construction mechanism; Plomin et al. 1977). At the same time, the environment might also influence an individual's behavior. Generally, there are good examples of personality-environment correlations in humans (Plomin et al. 1977), but this concept is not well understood in natural populations of non-human animals. We will begin to address this question of no one best behavioral type in the continuing long-term study of the roe deer population living in the wild. Indeed, we will assess the spatial distribution of deer according to their behavioral syndrome. More precisely, we will first characterize the behavioral syndrome of individuals in different contexts (indexing, for instance, their response to a stressful event or during a baseline risk context) and then, we will study their spatial behavior and habitat use for the year following their capture thanks to GPS collars. With these data, we will assess the impact of the link between inter-individual variation in behavioral type and fitness components on the maintenance of behavioral tactics. Moreover, there is some evidence suggesting that particular behavioral profiles occur more frequently in some environments than in others (Dingemanse and de Goede 2004; Stamps and Groothuis 2010; Pearish et al. 2013), and we found that fitness consequences of personality depended notably on environmental variability. Therefore, we suppose that, in our fragmented landscape, a given behavioral syndrome or more generally

an individual's behavior will occur more often and will perform better in a given habitat. For example, the environment may influence the individual's behavior via the predation risk if different individual's behaviors are more likely to survive in different habitats. Open risky habitats in agricultural landscape are particularly interesting for deer during spring and summer (Hewison et al. 2009; Abbas et al. 2011), so that we suppose proactive individuals would be more able to acquire food of good quality as they take more risks spending more time in these habitats, for example, whereas reactive individuals would avoid risks when it is possible. In addition, proactive individuals are more aggressive and we found that they have higher level of vigilance which allows them to flee more rapidly or to better defend their offspring from predators as foxes. Thus, proactive individuals may occur more frequently in open habitats whereas reactive ones will be more present in closed habitats.

## **What are the functions of personality? Fitness consequences of inter-individual behavioral variations**

Despite a growing number of studies carried out within the personality or behavioral syndrome framework showing that individual behavioral differences are widespread across a large number of taxa (Gosling 2001), and that these consistent differences are linked to variation in life-history traits (see Réale et al. 2007,2010 for reviews), the functional consequences of personality (and even more so, behavioral syndromes) in wild populations (Herborn et al. 2010c) in terms of their importance for fitness remains largely unknown (Wilson 1998; Dingemanse and Réale 2005). An explicit illustration of this lack of empirical studies linking personality and fitness was provided by Smith and Blumstein (2008)'s study listing 31 studies that have actually investigated the link between behavioral differences and fitness components, with only 19 carried out on wild populations. Here, our final aim was to explore the potential links between inter-individual differences in behavior and individual fitness in a long-term monitored wild population of a large herbivore, the roe deer.

Chapter VI was devoted to this aspect and we found some promising results indicating that personality or behavioral syndromes in wild roe deer may impact their fitness. First, we found that the coping style type of mothers influenced the early survival of

their offspring in a context-specific manner with a higher fawns' survival of proactive mothers in open habitats and a higher fawns' survival of reactive mothers in closed habitats. Then, we found that females with their fawns expressed a strong response in terms of the 'resource acquisition – risk avoidance' trade-off probably to offset the costs of milk production and, finally, to improve their fawns survival and growth. All these results were consistent with Smith and Blumstein (2008)'s study suggesting fitness consequences of behavioral differences. However, most of the studies they listed suggested a linear relationship between personality traits and fitness, which was not the case in our studies. Indeed, we found some support for context-specific fitness consequences. Thus, we showed that the spatial environmental variability in food resources and/or predation risk, and the trade-off expressed by individual females may shape and maintain behavioral differences through links with fitness components. Our results suggest the evolutionary mechanisms maintaining variation in behavior within populations may comply with the trade-off hypothesis (Sih et al. 2004) in that individual fitness varies depending on the context of the situation. For example, a general trend is that bolder individuals have greater reproductive success than shyer ones, but have shorter life span (see Smith and Blumstein 2008 for the review). That being said, this result is more pronounced in wild fish in which the tendency to inspect predators has often been used as an indicator of boldness (Godin and Dugatkin 1996). Consequently, shyer individuals have a reduced short-term reproductive success, but they live for a longer time, which may result in equal fitness. Besides, a potential explanation for the linear relationship between personality traits and fitness indicated by Smith and Blumstein (2008) could be that most studies have been carried out in captivity, which by definition removes variation in the environment. Moreover, conditions in captivity are different from those encountered in natural environments which may modify the link between personality traits and fitness. For example, the density is most of the time higher in captivity, so that both agonistic and social interactions may increase and shape the individual's behavior. This could result in a higher number of breeding attempts due to, for example, a larger number of sexual partners and so potentially a higher reproductive success associated to this behavioral type.

Hence, in this chapter we showed that long-term studies are important in the study of fitness consequences of behavioral differences, so that we need more long-term studies



of individually identifiable animals focusing on this aspect in wild populations because environmental heterogeneity (spatial and temporal heterogeneity) seems to play a marked role in both the individual's behavior and in the individual's performance. Moreover, to work in the personality framework, we need repeated data. It is possible to estimate the behavior consistency within a year but, it is interesting to estimate repeatability across several years and to compare it with repeatability estimate within a year. Indeed, we previously found that docility estimates remain stable across time (Debeffe et al. 2015), but it is more generally found that short-term repeatability (i.e. repeatability estimates performed over short time intervals) yield higher estimates than long-term repeatability (i.e. repeatability estimates over long time intervals; see Bell et al. 2009 for a meta-analysis). For instance, repeatability varies in relation to age, although predictions for age-dependent variations are not straightforward (Bell et al. 2009).

Consequently, personality and behavioral syndromes may also have, ultimately, repercussions for demography and population dynamics. As presented in the Introduction section, some individual characteristics such as age are systematically taken into account in demographic modeling. In contrast, the individual's behavior is not included in such analyses yet. However, we have seen that the behavioral differences among individuals may shape their whole life history, including their fitness, and so, partly the fate of their offspring. Consequently, the behavior of individuals may certainly also have an impact on their population dynamics, so it would be wise to consider this aspect in demographic analyses, with potential repercussions for conservation and/or management. Thus, we plan to perform a demographic analysis on our population of wild roe deer divided into two different parts. The first one will focus on the demographic responses of populations to contrasted degrees of landscape fragmentation. To do that, we will generate the first estimate of population growth rate for roe deer living in a fragmented agricultural landscape. Then, we will compare this to growth rates of different European populations (already known) to attempt to understand the impact of the among population variability in landscape structure and environmental context (fragmented landscape vs. mainly woodlands, etc.) and temporal variability (different rates of climate change) on population performance. Finally, given the importance of the environmental context for observed variation in vital rates and behavior between deer living in predominantly forested habitat

(other study sites) compared with those living in the open agricultural plain (our study site), we will quantify variation in growth at the within-population scale. Thus, with this demographic analysis, we could explore, whether after accounting for environmental variability, the individual behavioral variation plays a significant role *in fine* in their population demography. This approach will give us vital knowledge as regards the impact of behavioral differences not solely at the individual scale, but also at a population level.

In addition, in our study, when we considered individual demographic performance, we focused on individual reproductive success, and offspring growth rate and survival. Thus, focusing on offspring, a logical next step is the study of both the heritability and ontogeny of behavior. Indeed, to understand the maintenance of inter-individual differences in behavior, we need to characterize its repeatability, or consistency, but also its heritability. Thanks to studies carried out in laboratory, there is some evidence for heritability of behavior from parents to their offspring (Hemsworth et al. 1990; Drent et al. 2003; van Oers et al. 2004). However, performing heritability analyses on wild animals is particularly challenging and, to our knowledge, extremely scarce. That being said, Dingemanse et al. (2002) found that exploratory behavior was heritable from parents to their juveniles in great tits. This study, performed with wild animals in an open field test in the laboratory, was really promising, showing that it may be possible to obtain heritability estimates in wild animals. Initially, in the context of this thesis, I planned to test for heritability of the behavioral differences expressed during a stressful situation (indexed either as shyness-boldness or proactivity-reactivity coping style) from the mother to its offspring, but I was not able to do so because of time and logistical constraints. However, this question is a priority for future research. Since 2004, we have caught new-born fawns each spring and since 2012, we have characterized their behavior during the spring capture event. More precisely, we record their behaviors at four different stages: before the capture event, after catching but before handling, during handling, and, finally, at release. As during winter catches, from this information we can obtain a behavioral score indexing the fawns' responsiveness to an acute stress (i.e. capture event). Furthermore, 15 days after each fawn's first capture, we attempt to catch them again to collect the same behavioral and morphological data, in particular for measuring individual growth rate, a crucial parameter determining the fawn's fate. Finally, the following winter, during regular catch events, we try to re-catch these same fawns so

that we can assess their behavior under the same conditions as their mother. Hence, we could use mother-offspring regressions during regular winter catching to test for the heritability (in its broader sense) of the behavioral score expressed during stressful situation. We could also estimate more precisely the phenotypic variance from some of its components as the genetic variance and the maternal variance using pedigrees or matrices of genetic distances (using genetic markers as SNP for example) and animal model. Therefore, we could estimate heritability and this one would be potentially more precise and more accurate because we could distinguish genetic variance from others sources of variability. However, this approach is quite difficult to implement in our study site since roe deer live in wild environments meaning we can not always obtain all the necessary data for both the mother and its fawn. In addition, the behavioral score measured at three different periods will allow us to test for the ontogeny and consistency of the fawns' behavior. Indeed, during its first two months of life, the fawn's fate is highly dependent on its mother's maternal care (Andersen et al. 2000; Gaillard et al. 2000; Van Moorter et al. 2009), and so we could hypothesize that its behavior also is highly dependent on that of its mother. Then, as the animal gains independence following emancipation from its mother at around 10-11 months of age, we might suppose that behavioral measures collected later in life will reflect more its own behavior as it will more able to move and feed nearby its mother but alone. In this ontogeny context, it has been demonstrated that morphological traits as body mass were highly determined by the maternal effect early in life, but that this influence of maternal effect decreased over time whereas the influence of the genetic effect increased over time (Wilson et al. 2005). Therefore with these findings, we could imagine to observe the same evolution of maternal effect on the ontogeny of a behavioral trait. This study up set of long-term monitoring of individually identifiable animals in a population of large herbivores should allow us to explore to what extent behavioral traits are inherited and so to predict their evolution.

## Here the last words... because there are always last words...

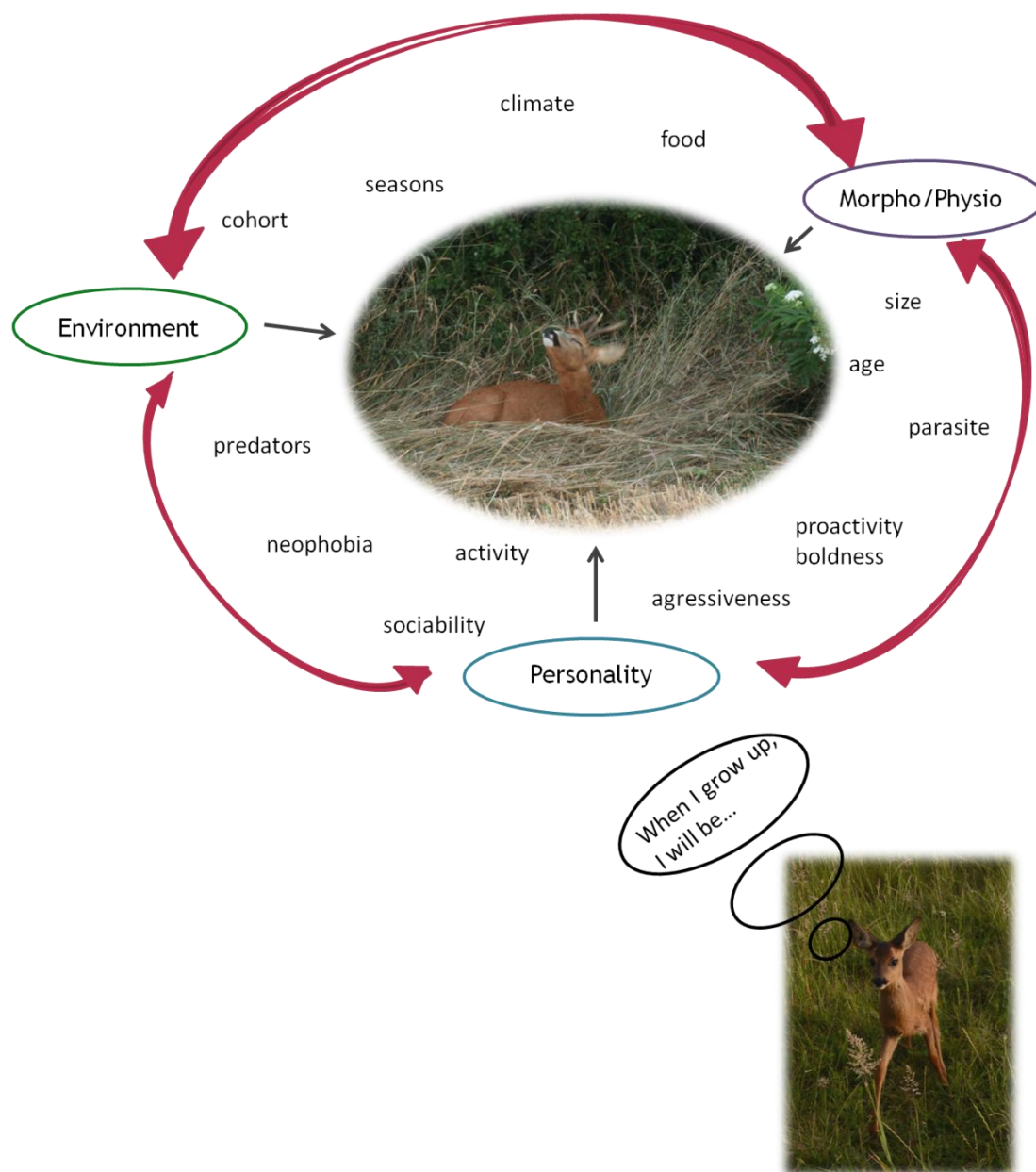
'Personality' a promising word full of mystery...

This is an intriguing phenomenon which is infiltrating ecology and evolution more and more. Despite little interest until the end of the XX<sup>th</sup> century, it is now recognized that personality (and others terms referring to inter-individual differences in behavior) exists in a large range of species (Gosling 2001) and plays an important role for the whole life history of organisms. With this thesis, I hope that I have contributed in some small way to an increase of knowledge showing that inter-individual variability in behavior also exists in wild large herbivores, with the study of roe deer, and seems to result from diverse sources of variability. Thus, environmental heterogeneity, morphological or physiological individual characteristics and personality traits act as a whole (Fig. 1). Moreover, behavioral inter-individual differences affect fitness components in a context-specific manner. These findings support the fact that one behavioral type that performs as the best one is not a real representation of what happens in natural systems. Indeed, few studies were carried out in wild environments, but these studies seemed also to indicate non-linear relationships between behavior and fitness (see Réale and Festa-Bianchet 2003; Dingemanse et al. 2004; Boon et al. 2007). Besides, this idea is beginning to be considered in the public domain. As a matter of fact, for a long time, it was assumed that being bold was the best behavior. We could imagine that being impulsive (see McRae and Costa 1992 for the five behaviors defined in human beings) would be relevant when working in finance for instance, whereas being highly impulsive working in a social job may be not really suitable... That depends on the context...

To conclude, a lot of questions remain without answer, and I am convinced that the study of personality is solely starting irrespective of the study species. Indeed, questions about personality and its link with fitness go above and beyond our study model. These questions are in fact universal and interest a very large public, not solely researchers. We often speak about the link between research and society and the difficulty of communicating our research to people working in totally different fields. Well, I guess that the personality framework is of common interest. How and why individuals differ in their reactions to the same situation interests researchers, but more generally people. Who are we? What are the

consequences of this or that behavior for us? but also for our population or species? Everyone asks himself these questions. They are universal and have been considered by man since historic times. I am still searching for these answers and I hope I will pursue my research on roe deer or other species first...

To be continued...



**Figure 1. Illustration of potential sources for behavioral differences among individuals and their relationships.** The environmental heterogeneity includes variability in food resources, predators, climate changes, density-dependence, social context etc. Morphological and physiological heterogeneity includes individual characteristics such as age, size, mass, body condition etc. Personality refers to all consistent inter-individual differences in behavior (i.e. temperament, coping style or behavioral syndrome). Photos by B. Lourtet (adult deer) and O. Couriot (fawn).

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## **Chapter VIII**

### **References**

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## **Chapter IX**

## **Appendices**

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## Appendix 1



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## Original Article

# Is a proactive mum a good mum? A mother's coping style influences early fawn survival in roe deer

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Individual differences in behavior may strongly shape life-history trajectories. However, few empirical studies to date have investigated the link between behavioral traits and fitness, especially in wild populations. We measured the impact of coping style in female roe deer (*Capreolus capreolus*) on early survival of their offspring. Specifically, we expected offspring of proactive mothers, which should be more mobile and aggressive, to survive better than those of reactive females, which should be more passive and react less in stressful contexts. To test this prediction, we accounted for confounding effects of variation in early survival linked to habitat heterogeneity, as we also expected bed-site selection to impact fawn survival. Fawn survival was highly dependent on the interaction between habitat use and the coping style of the mother. As expected, fawns of proactive mothers survived better in open habitats. However, unexpectedly, fawns of reactive mothers had the highest survival in closed habitats. Our findings provide clear evidence that interindividual differences in the coping style of the mother can markedly impact early offspring survival and, thereby, female fitness, in wild populations of mammals. Moreover, we provide evidence that fitness consequences of coping styles are habitat-dependent, providing a possible mechanism for the maintenance of within-population variation in behavior.

**Key Words:** body temperature, habitat use, individual differences, juvenile survival, maternal care.

## INTRODUCTION

It is increasingly recognized that, within populations, individuals exhibit consistent behavioral differences over their lifetime, and that these differences may have important ecological and evolutionary implications (Wilson et al. 1994; Réale et al. 2007). When these behavioral differences are manifested in stressful situations characterized by risky or challenging environments, they are generally interpreted within the “coping style” framework (Koolhaas et al. 1999). Koolhaas et al. (1999) defined a coping style as “a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals.” Two distinct coping styles are generally identified, although these stress responses are more likely best described by a continuum. Proactive individuals are fast explorers, highly aggressive, impulsive in decision-making, novelty seekers and take risks

in the face of potential dangers (Koolhaas et al. 1999, 2010). They are thus assumed to cope actively with the source of stress through a “flight-or-fight” response. In contrast, reactive individuals show the opposite physiological patterns and tend to react to challenges by freezing. From a physiological viewpoint, proactive individuals show a high sympathetic reactivity and a low hypothalamus-pituitary-adrenal (HPA) axis responsiveness compared with reactive individuals (Koolhaas et al. 1999). However, the associations between physiological traits and behavioral traits are still poorly documented. Fast explorers may have a lower HPA (Montiglio et al. 2012), which is associated with increased frequency and variation in heart rate (Visser et al. 2002). Similarly, Groenink et al. (1994) showed that a high rectal temperature reliably indicates stress-induced hyperthermia (SIH), which has been repeatedly associated with personality. For instance, in great tits (*Parus major*), bold individuals (assumed to be proactive, Schjolden et al. 2005) had lower body temperature and respiration rate during handling than shy individuals (Carere and van Oers 2004). It

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is widely recognized that coping styles relate the level of boldness and aggression to the magnitude of the physiological response to stress (Koolhaas et al. 1999; Frost et al. 2013). Consequently, proactive individuals are also assumed to be bold and aggressive, whereas reactive individuals should be shy and less aggressive.

Most work on characterizing coping styles has been carried out under controlled laboratory conditions (Koolhaas et al. 1999; Øverli et al. 2007), whereas evidence from field tests are much scarcer and have so far been conducted on semicaptive populations (e.g., Rödel et al. 2006; Hoffman et al. 2011). Furthermore, there is a crucial lack of empirical studies on the effect of coping styles on individual performance and, hence, on their consequences for population dynamics. From a meta-analysis of studies performed on domestic, captive and wild animals, Smith and Blumstein (2008) concluded that bolder and more aggressive individuals generally have higher reproductive success than shyer or less aggressive individuals. For example, in bighorn sheep (*Ovis canadensis*), boldness is positively related to both weaning rate (Réale et al. 2000) and survival (Réale and Festa-Bianchet 2003). Hence, coping styles are likely to be associated with interindividual differences in reproductive success, as reported in the Ural owl (*Strix uralensis*) in which proactive and aggressive females produced more recruits (Kontiainen et al. 2009).

Large herbivores are widespread in most temperate ecosystems and are the subject of a number of detailed long-term monitoring studies of behavior and population dynamics (e.g., Gaillard et al. 2013 on roe deer, Hallett et al. 2004 on Soay sheep *Ovis aries*, Coulson et al. 2004 on red deer *Cervus elaphus*, Garel et al. 2007 on mouflon *Ovis gmelini*, Toigo et al. 2007 on ibex *Capra ibex*, Servant et al. 2011 on wild boar *Sus scrofa*). These studies have shown that spatial and temporal variation in juvenile survival is a key component of the population demography of large herbivores in the wild (see Gaillard et al. 2000 for a review). Environmental factors such as predation and population density during the preweaning stage are critical for shaping variation in juvenile survival. Likewise, climatic conditions during late gestation and early lactation also influence juvenile survival through their effects on plant biomass and quality and, thereby, the availability of food for the mother (Gaillard et al. 2000). In addition, maternal physiological and morphological traits such as size, age, and previous reproductive success strongly impact juvenile survival, generating marked individual differences in female reproductive success (Gaillard et al. 2000). However, whether a mother's coping style influences juvenile survival in wild large herbivores remains virtually unknown (Smith and Blumstein 2008).

We aim here to fill this gap in our knowledge of the link between the coping style of the mother and her reproductive success by investigating the impact of individual differences in coping styles of female roe deer on the early survival of their fawns in an intensively studied roe deer population. Roe deer females are income breeders (sensu Jönsson 1997) such that females do not store fat reserves, relying instead on current energy intake to offset the costs of reproduction (Andersen et al. 2000). For income breeders, the trade-off between foraging and risk of predation should be particularly acute (Bongi et al. 2008) because females have to forage intensively while simultaneously minimizing the risk of predation of their offspring (Linnell et al. 1995). Hence, females with newborns generally isolate themselves from conspecifics. This behavior is associated with lower disturbance by conspecifics and reduced risk of predation (Schwede et al. 1993). Females also often range less widely during the first months after parturition (Said et al. 2009). Moreover, roe

deer are hidiers (sensu Lent 1974) where, apart from short visits for suckling (3–7 times/day), the fawns lie hidden, secluded from the mother for most of the time up to the age of 6–8 weeks (Espmark 1969). Thus, high female aggressiveness and short mother-fawn distance are associated with increased offspring survival during the hiding phase in open habitats (Panzacchi et al. 2010). Bongi et al. (2008) found that females tend to select denser habitats with high cover and concealment, which may contribute to increase offspring survival. However, the extremely high energetic needs of roe deer females during lactation are expected to constrain them to use habitats where predation risk for fawns is high (Panzacchi et al. 2010). Hence, during the hider phase, a fawn's survival mostly depends on its mother's ranging behavior (van Moorter et al. 2009) and care (Andersen et al. 2000; Gaillard et al. 2000). Maternal care behavior is likely highly variable among individuals (Nowak et al. 2000) but, to our knowledge, although some information is available for birds (Kontiainen et al. 2009; Ringsby et al. 2009; Westneat et al. 2011; Betini and Norris 2012), no study has yet investigated how variation in coping styles among mothers impacts the survival of their offspring in any large mammal in the wild.

When faced with a challenge, proactive individuals are risk-takers that respond with high levels of general activity and aggression and low attack latency, whereas reactive individuals show high attack latency and a lack of initiative (Koolhaas et al. 1999, 2010). Ungulate females aggressively defend and protect their fawns (Truett 1979; Ozoga and Verme 1986; Lingle et al. 2005), and this is also the case in roe deer during attack by foxes (Jarnemo 2004). Consequently, we first hypothesized that the coping style of the mother should influence the survival of her fawns. In the absence of direct observations of maternal roe deer behavior in response to predation in our study area, we assumed that reactive mothers would not defend their fawns as strongly as proactive mothers against predators. Second, we hypothesized that the spatial behavior of the mother should impact the choice of bed-site by the fawn and thus affect its early survival, which is highly dependent on bed-site characteristics (van Moorter et al. 2009). Hence, fawns of females that mostly used habitats with protective cover should have access to the most secure bed-sites and should thereby have higher early survival. Finally, Boon et al. (2007) showed that the aggressiveness of the mother impacted the survival of her offspring in red squirrel (*Tamiasciurus hudsonicus* Erxleben), but that these effects varied across life-history stages and over time (i.e., temporal heterogeneity in the influence of behavior on individual performance). Furthermore, there is also some evidence that specific behavioral profiles occur more frequently in some environments than in others (Dingemanse et al. 2003; Stamps and Groothuis 2010; Pearish et al. 2013). Consequently, we hypothesized that fawn survival should be impacted by the coping style of the mother in a context-specific manner (i.e., spatial heterogeneity in the influence of behavior on individual performance), although we had no clear prediction as to the form of this relationship.

## MATERIAL AND METHODS

### Study site

The study was carried out at Aurignac (7500 ha) in the south-west of France (43°13'N, 0°52'E). The climate is oceanic with Mediterranean tendencies, with an average annual temperature of 11–12 °C and total precipitation of 800 mm. This hilly region is a mixed landscape mostly covered by open habitats interspersed with small woodland patches (mean  $\pm$  SD: 2.9  $\pm$  7.6 ha) and 2 main



forests (672 ha and 515 ha). Meadows and cultivated fields occupy 31.9% and 36.2%, respectively, of the total surface area of the study site. Woodland covers 19.3 % of the total study site and is dominated by oak (*Quercus spp.*) (see Hewison et al. 2009 for further details).

#### Data collection for roe deer mothers

Each winter between 2003 and 2013, roe deer were caught from November to March (i.e., at least 6 weeks before parturition, Gaillard et al. 1993) using drive netting. Roe deer capture and marking procedures were performed according to French laws for animal welfare and approved by the French administration. Once the deer was caught in the net, it was tranquilized with an intramuscular injection of acepromazine (Calmivet 3cc). Then, we transferred the animal to a small wooden retaining box designed to minimize risk of injury and to limit stress. At the end of the capture event, each individual was weighed with an electronic balance, sexed, aged according to tooth eruption, marked with 2 plastic ear tags and equipped with a GPS collar (Lotek 3300 GPS).

Between 2009 and 2013, we recorded the behavior at capture, during handling and at release for 121 females. Of these, 86 were adults (i.e., older than 1 year at first winter capture), which generally give birth every year (Hewison 1996; Andersen et al. 1998). We attributed a score of 1 (occurrence) or 0 (absence) for each of the following behaviors: 1) the individual struggled in the net (see also Réale et al. 2000), 2) it turned upside down in the box, 3) it attempted to remove its collar at release, and 4) it fell (i.e., stumbled and fell to the ground) at release. In addition, we attributed a score of 1 if 5) the individual struggled and panted on the table during marking, or a score of 0.5 if it struggled only (otherwise 0), and a score of 1 (high speed running), 0.5 (moderate running), or 0 (trotting) in relation to 6) its flight behavior at release. Indeed, flight speed at release is commonly used for the assessment of temperament in cattle (Müller and von Keyserlingk 2006). An index of proactivity was then calculated as the sum of the scores for these 6 behavioral items describing a stress profile gradient ranging from 0 to 6, potentially taking 13 different values (9 over the recorded range), with 6 indicating a priori highly proactive individuals. We also measured the rectal temperature for each female (using a Digitemp Color thermometer with a precision of 0.1 °C, potentially taking 36 different values, over the recorded range). Following Montané et al. (2003)'s study showing that body temperature of roe deer decreases over time from capture to 45 min after capture before stabilizing, we recorded temperature more than 1 h after the capture event in all cases. We recorded the temperature of each individual at the beginning and at the end of the marking procedure, and used the mean of these 2 values (difference: range = [-0.4–0.7], mean = 0.1, and median = 0.0) to index the female's stress response based on the existence of a positive correlation between the HPA axis and SIH (Moe and Bakken 1997; Korhonen et al. 2000). Thus, we assumed that a high index of proactivity and a low rectal temperature indicated more proactive individuals, whereas a low index of proactivity and a high rectal temperature typified more reactive individuals.

#### Data collection for roe deer fawns

Between 2004 and 2013, newborn fawns (97% less than 20 days old, average age at capture = 6.3 days) were caught by hand each year between the end of April and the middle of June, but more intensively since 2009 (30 fawns caught between 2004 and 2008, with

none in 2005 and 2006, and then 114 fawns caught since 2009), mostly by observing the behavior of the mother. We marked fawns only once the mother had fed it and moved away. We first weighed (with a precision of 50g), sexed and aged fawns using 3 age-classes (<3, 3–5, and ≥6 days old) and then marked them with 2 metallic ear tags and an expandable very high frequency (VHF) radio collar (Biotrack). The age of fawns was established in relation to daily monitoring of the mother's appearance (size of her belly, presence/absence of udders) and behavior (reaction to a whistle mimicking the call of a fawn), which provided information on the approximate date of birth, and in relation to the fawn's behavior (Julien et al. 1992). Roe deer females generally give birth to 2 fawns per litter (Hewison and Gaillard 2001), but even when we located both fawns of a single litter, we manipulated and marked only one of the siblings as the fate of litter mates is highly interdependent, especially in poor cohorts (Gaillard et al. 1998). We also recorded the characteristics of the site where fawns were found in terms of habitat type (woodland, crops, natural meadows, or artificial meadows such as ray grass, *Lolium perenne*). Subsequently, fawns were located each day from marking to the end of the summer (1.5 locations per day per individual on average) by radio-telemetry and triangulation. The radio-collars were equipped with a mortality sensor, providing us with information about the current fate of each fawn. When a mortality signal was detected, we immediately recovered the dead animal and, where possible, ascertained the cause of its death.

#### Statistical analyses

##### *Proactivity index and rectal temperature of the mother: repeatability and intercorrelation*

Of the 39 mothers, we assessed the within-individual consistency of the proactivity index and of rectal temperature based on a subsample including only the 18 mothers that were caught at least twice between 2009 and 2013 (10 caught twice, 7 caught 3 times, and 1 caught 4 times) by calculating their repeatability with mixed models (Nakagawa and Schielzeth 2010). Bell et al. (2009) reported in a meta-analysis that repeatability of behavioral traits (excluding physiological traits such as body temperature) has an average value of 0.37. Repeatability coefficients, that is, intraclass correlation coefficients, were calculated using the "rpt.remlMM" function of the "rptR" package (Schielzeth and Nakagawa 2011) in R version 2.15.1 software (R Development Core Team 2013), which estimates repeatability as the ratio of between-individual variance to total variance with linear mixed-effects models (with individual identity as a random factor) using the restricted maximum likelihood (REML) method. Because it is widely employed in behavioral ecology, for comparative purposes we also used the Lessells and Boag (1987)'s method to estimate repeatability. Finally, because we had no a priori idea of the expected relationship between temperature and coping style, except for small mammals (Moe and Bakken 1997; Korhonen et al. 2000), we also tested this correlation in our sample of female roe deer.

##### *Early survival of fawns*

To assess the influence of the mother's coping style on early fawn survival, we excluded fawns with unknown mothers and fawns of mothers with missing data for either rectal temperature or the proactivity index. Analyses were thus based on 57 fawns that were monitored over their first spring–summer during 8 different years, belonging to 39 different females. To investigate the relationship between early fawn survival and habitat use, we used the broad scale habitat type in which the fawn was found. We checked that

the habitat type where fawns were found reliably described the habitat used during their first month of life using the VHF locations (between 7 and 37) of fawns collected during that period. On average, 75% of these locations fell within the habitat recorded at marking. In addition, we accounted for possible confounding effects of age, body development at capture, cohort effects, and spring weather conditions, all of which have been reported to influence markedly early survival of roe deer fawns (Gaillard et al. 1997; da Silva et al. 2009). Body development was calculated from the residuals of the simple linear regression between age and body mass at capture (see Gaillard et al. 1993 for further details). We tested for cohort effects by including the year of birth of the 57 fawns. To assess annual spring weather conditions, we used the number of degree-days higher than 7 °C from February to April as a proxy of the precocity of spring which has recently been shown to affect strongly roe deer population dynamics (Gaillard et al. 2013), and especially early fawn survival (Plard et al. 2014).

We estimated early fawn survival by fitting Cox proportional hazard models, which are the most widely used in multivariate analyses of survival (Cox 1972; Therneau and Grambsch 2000). The model was written as:

$$h(t) = \exp(\beta_1 X_1 + \dots + \beta_p X_p) h_0(t) \quad (1)$$

where  $h(t)$  is the hazard function at time  $t$  and measures the risk that a fawn dies at a given time,  $X_p$  are the covariates influencing early fawn survival (i.e., age, early body development and number of degree-days in the baseline model, plus rectal temperature and proactivity index of the mother, plus certain 2-way interactions in the most complex model),  $\beta_p$  are the regression coefficients of these respective covariates, and  $h_0(t)$  is the baseline hazard function. We carried out the analyses on the first 105 days of the fawns' life, which roughly corresponds to the period from the median date of parturition to weaning. We added the age at capture of each fawn to the total number of days of monitoring, allowing us to start the analyses from the birth date of each fawn.

The baseline model included the fawn's age at capture (discrete variable, 3 modalities), its index of body development (continuous variable, range = [-718.0–490.1], mean = 0.00, and median = 6.097) and the number of degree-days higher than 7 °C in the spring of capture (continuous variable, range = [55–64], mean and median = 59.5). Then, we investigated the potential effect of the mother's coping style on the survival of her offspring by adding the mother's proactivity index (continuous variable, range = [0.0–4.0], mean = 2.07, and median = 2.00) and the mother's rectal temperature (continuous variable, range = [37.0–40.5 °C], mean = 38.75 °C, and median = 38.80 °C) to the baseline model. In addition, we tested for the potential effect of habitat use on early survival by adding the habitat type recorded at fawn capture to the baseline model (discrete variable, 4 modalities: woodland, crops, natural meadows, and artificial meadows). Finally, because early fawn survival may be impacted by the coping style of the mother in a context-specific manner, either across space or through time (Smith and Blumstein 2008), we also tested for the effects of the four 2-way interactions between the mother's proactivity index with both habitat type and cohort, and between the mother's rectal temperature with both habitat type and cohort on early fawn survival. In all cases, models that included an interaction also included the main effects of the variables involved in that interaction.

We checked the assumption of proportional hazards that is critical to Cox proportional models through an analysis of residuals (Grambsch and Therneau 1994). We used model diagnostics based

on scaled Schoenfeld residuals and checked the hypothesis of log-linearity and identified the most influential observations. Model selection was based on the second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002) and Akaike weights to identify the model that best described the data. All analyses were performed in R version 2.15.1 (R Development Core Team 2013) using the survival package (Therneau 2014).

## RESULTS

### Proactivity index and rectal temperature of the mother: repeatability and intercorrelation

The proactivity index did not deviate from a Gaussian distribution on a statistical basis ( $W = 0.960$ ,  $P$  value = 0.086), ranging between 0.0 and 4.0, with a median value of 2.0 and a mean of 2.1. The rectal temperature was also normally distributed ( $W = 0.980$ ,  $P$  value = 0.474), ranging between 37.0 and 40.5 °C, with both a median and a mean of 38.8 °C. There was suggestive evidence for consistent individual differences in the proactivity index (rpt. remLMM method:  $r = 0.201$ , 95% confidence interval = [0, 0.592]; Lessells and Boag method:  $r = 0.193$ , 95% confidence interval = [0.027, 0.636]). In contrast, rectal temperature was highly repeatable (rpt. remLMM method:  $r = 0.704$ , 95% confidence intervals = [0.185, 0.909]). Rectal temperature and the proactivity index were weakly, but significantly from a statistical viewpoint, positively correlated across mothers ( $P$  value = 0.037,  $r = 0.26$ , Appendix 1).

### Early fawn survival

Overall, 25 out of 57 (43.9%) fawns survived to 105 days. Of the 32 fawns which died, 10 died from predation, 4 died due to poor maternal care (abandonment, malnutrition), 7 died from human activity causes (5 from mowing and 2 from vehicle collisions), 3 died due to health problems (disease, cachexia), 2 died from accidents (falling into a ditch), and 6 died from unknown causes. There was no statistically significant variation in the proactivity index of the mother among these 6 categories of mortality causes ( $F_{5,36} = 2.05$ ,  $P$  value = 0.10). However, mothers whose fawns were predated tended to have a lower proactivity index than those whose fawns died of other causes ( $F_{1,36} = 2.93$ ,  $P$  value = 0.10). There was also no statistically significant relationship between the proactivity index of the mother and the age of the fawn at capture ( $F_{2,34} = 0.87$ ,  $P$  value = 0.43), indicating that there was no age-related sampling bias with respect to maternal coping style that might explain any link between fawn survival and the proactivity index. Similarly, there was no evidence of any habitat-related sampling bias because fawns were distributed more or less randomly across habitat types with respect to the proactivity index of their mother (see Appendix 2).

In addition to the baseline factors (number of degree-days > 7 °C, age at capture, early body development) that all influenced early fawn survival, the Cox proportional hazard model of early fawn survival with the highest support included the 2-way interaction between habitat type and proactivity index of the mother, plus an additive effect of mother's rectal temperature (AICc = 217.10,  $\Delta$ AICc = 2.16, AICc weight = 0.55, Table 1).

As expected, early survival decreased with time, with the sharpest decrease in survival occurring during the first 20 days of the fawns' life (Appendices 3, 4, 5). All things being equal, fawns that were older ( $\geq 6$  days old) at capture survived better than younger (<6 days old) fawns (93% of fawns vs. 53% of fawns reached

105 days of life, Appendix 3). As expected, fawns with a fast body development survived better than fawns with slow body development (68% of fawns for the heaviest fawns vs. 1% of fawns for the

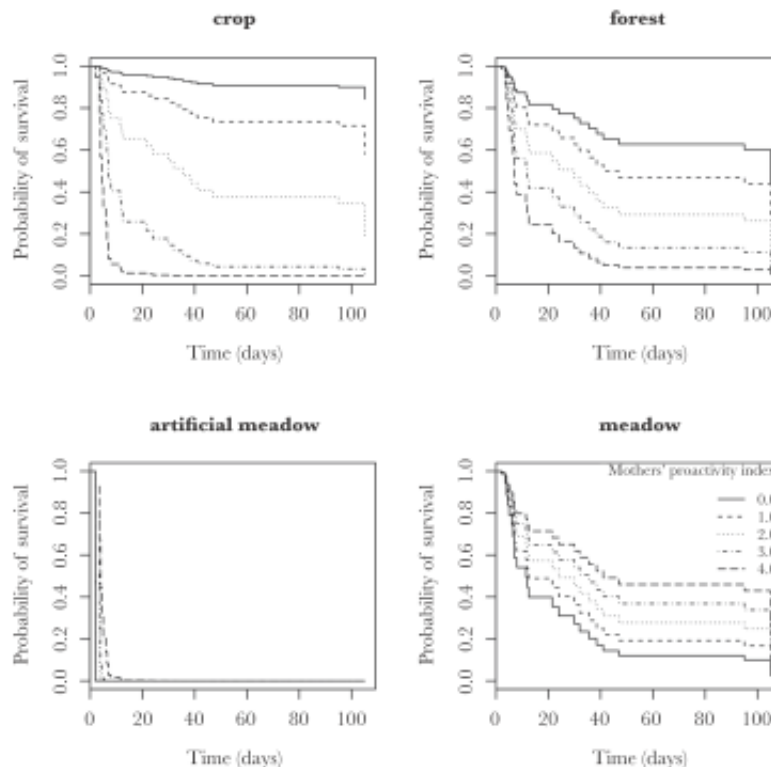
**Table 1**  
Candidate Cox proportional hazard models fitted to investigate variation in the probability of fawns surviving to 105 days of age

Models	<i>K</i>	AICc	ΔAICc	AICcWt
Baseline model + habitat × PI + <i>T</i>	12	217.10	0.00	0.55
Baseline model + habitat + PI + <i>T</i>	9	219.26	2.16	0.32
Baseline model + cohort + habitat × PI + <i>T</i>	16	220.29	3.20	0.09
Baseline model + cohort	8	223.93	6.83	0.01
Baseline model + habitat × PI + habitat × <i>T</i>	15	224.64	7.54	0.01
Baseline model + PI + habitat × <i>T</i>	12	224.82	7.73	0.01
Baseline model + cohort + habitat + PI + <i>T</i>	13	226.81	9.71	0.01
Baseline model	4	228.70	11.60	0

The baseline model includes the number of degree-days, early body development, and the fawn's age at capture. To this baseline model, we then added the cohort effect (cohort), the proactivity index of the mother (PI), and the rectal temperature (*T*) of the mother, as well as the habitat type where the fawn was caught (habitat). AICc is the value of the corrected Akaike's Information Criterion and *K* is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for ΔAICc and on the Akaike weights. Only models with an AICc lower than that of the baseline model are presented.

lightest fawns reached 105 days of life, Appendix 4). Likewise, as expected, early survival of fawns decreased with increasing number of degree-days (7% of fawns at 64 degree-days vs. 94% of fawns at 47 degree-days reached 105 days of life, Appendix 5).

In addition to this support for the variables in our baseline model, we found that habitat type and proactivity index of the mother both shaped early fawn survival. Fawns born to mothers with a high proactivity index survived much better than fawns born to mothers with a low proactivity index when they principally used natural meadows (44% of fawns for mothers with a proactivity index of 4.0 vs. 10% of fawns for mothers with a proactivity index of 0.0 reached 105 days of age, Figure 1). In contrast, early survival was lower for fawns born to mothers with a high proactivity index than for fawns born to mothers with a low proactivity index when they principally used either forest (4% of fawns for mothers with a proactivity index of 4.0 vs. 61% of fawns for mothers with a proactivity index of 0.0 reached 105 days of age) or crops (0% of fawns for mothers with a proactivity index of 4.0 vs. 90% of fawns for mothers with a proactivity index of 0.0 reached 105 days of age). No fawns born to mothers that principally used artificial meadows survived beyond 12 days of age (*N* = 6), irrespective of the proactivity index of their mother. In addition, fawns born to mothers with a low rectal temperature survived slightly less well (33% of fawns for mothers with a rectal temperature of 37.0 reached 105 days of age) than fawns born to mothers with a high



**Figure 1**

Probability of a roe deer fawn surviving to 105 days of life in relation to the proactivity index of its mother and to the habitat type (4 modalities: crops, forest, artificial meadows, natural meadows) in which the fawn was found. The proactivity index potentially varies between 0 and 6, but the highest observed value was 4. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, fawn age at capture), the interaction between habitat type and the proactivity index of the mother, plus an additive effect of the mother's rectal temperature.

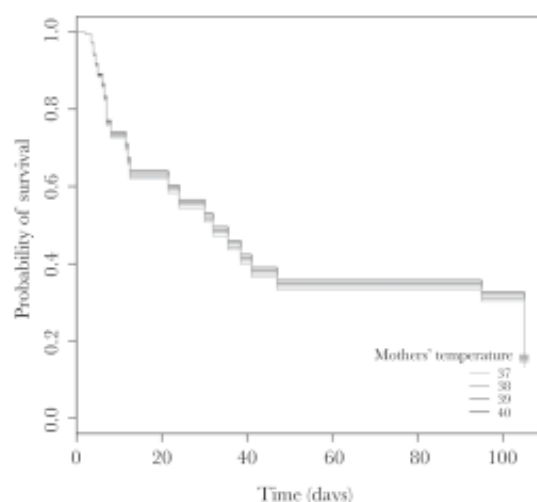


rectal temperature (37 % of fawns for mothers with a rectal temperature of 40.0 reached 105 days of age, Figure 2). Finally, contrary to our expectation, we found no evidence for a cohort effect on early survival, and no temporal variation in the influence of the mother's proactivity index or rectal temperature on early survival.

## DISCUSSION

### Overview

The central aim of our study was to investigate how variation in the mother's coping style and space use impact the early survival of her offspring. We detected consistent individual differences in both behavioral and physiological components of coping style, with roe deer mothers ranking along a continuum of the proactive-reactive response to stress. As expected, we found that the coping style of the mother affected early survival of her fawns. However, the pattern of variation in early fawn survival in relation to the coping style of their mother was context-specific. Compared with more reactive mothers, mothers with a more proactive coping style were more likely to wean a fawn in open meadows, but less likely to do so in forest or crops. Our findings therefore demonstrate that inter-individual differences in the coping style of mothers have a habitat-specific influence on offspring survival, and hence on female fitness, in wild populations of mammals. Boon et al. (2007) found that maternal personality impacted both survival and growth rate of offspring in red squirrels, but that these effects varied across life-history stages and among years, that is, temporal heterogeneity in the influence of personality on individual performance. Here, we detected spatial heterogeneity in the influence of the coping style of mothers on an important fitness component, early offspring survival, in roe deer. We suggest that both these forms of heterogeneity



**Figure 2** Probability of a roe deer fawn surviving to 105 days of life in relation to the rectal temperature of its mother. We used a Cox proportional hazard model with temperature as an explanatory variable with values ranging between 37 and 40 °C. This representation was obtained from the best model that included the baseline factors (number of degree-days, early body development, and fawn age at capture), the interaction between habitat type and the proactivity index, plus an additive effect of the mother's rectal temperature.

may potentially contribute to the maintenance of behavioral variation in wild populations.

### Proactivity index and rectal temperature of the mother: repeatability and intercorrelation

In a meta-analysis, Bell et al. (2009) reported that behavioral traits are generally repeatable with an average value of 0.37. In comparison, relative to this average value for repeatability, we found that the level of proactivity was only a moderately repeatable trait ( $r = 0.201$ ,  $CI = [0, 0.592]$ ), whereas rectal temperature was highly repeatable ( $r = 0.70704$ ,  $CI = [0.185, 0.909]$ ). In addition, in our study, these 2 maternal traits covaried positively, although the relationship was weak. The fact that the correlation between rectal temperature and the proactivity index was positive was unexpected based on previous studies on small mammals (Moe and Bakken 1997, Korhonen et al. 2000), but there has been no equivalent study to date on ungulates. This unexpected result could be due to the fact that body temperature at capture reflects the combination of 2 physiological components: in a nonstressed situation, body temperature is a proxy of individual metabolic rate (Biro and Stamps 2008), whereas in a situation of stress, body temperature rises and indicates "SIH" (Bakken et al. 1999; Korhonen et al. 2000). Hence, temperature at capture might reflect the effects of among-individual differences in metabolic rate modulated by the stress response (see Debeffe et al. 2014).

Phenotypic correlations among such traits are typical of the proactive-reactive syndrome (Koolhaas et al. 1999; Sih et al. 2004). We thus identified a gradient of coping style, varying from mothers with a marked behavioral (i.e., a high proactivity index) and physiological (i.e., a high rectal temperature) response to capture (i.e., the most proactive) to those with a low level of response (i.e., the most reactive). We have recently shown elsewhere that both this proactivity index and rectal temperature contribute to shape a dispersal syndrome among juvenile roe deer (Debeffe et al. 2014) and a risk management syndrome among adults (Bonnot et al. 2015), suggesting that they reliably index consistent interindividual variation in behavior. However, further work on a larger sample size will be necessary to obtain reliable estimates of repeatability for these traits so as to better apprehend how well they index a behavioral syndrome in roe deer more generally.

### Early fawn survival in relation to age, body development, and spring conditions

The results from our baseline model support previous studies that reported effects of age, body development and spring conditions on early survival in populations of large herbivores (see Gaillard et al. 2000 for a review). Older fawns at capture survived better than younger ones. In large herbivores, most mortality occurs within the first few weeks of life (e.g., Guinness et al. 1978). Within this critical period, the mortality risk is especially high during the first few days of life, when newborns are subject to thermoregulation problems, abandonment by the mother, disease, and, in some hider species, predation because newborns are immobile and isolated from the mother for most of the time. High quality and quantity of food resources are key for early survival in most large herbivores (Gaillard et al. 2000), which grow very fast from birth to weaning (Pontier et al. 1989). Using the number of degree-days as a proxy of plant phenology (Plard et al. 2014), we found that fawn survival decreased with increasing number of degree-days. Energetic needs of mammalian mothers peak during late pregnancy and early

lactation (Clutton-Brock et al. 1989) so that the match between maternal energy requirements and the peak of resource availability is crucial to offspring survival. As roe deer birth timing is highly repeatable (Plard et al. 2013) and quite constrained (Gaillard et al. 2013), early vegetation flush leads to an increase in early fawn mortality (Plard et al. 2014) and, thereby, to lower population growth rate (Gaillard et al. 2013). These negative effects of early springs were reported for forest roe deer, but our study indicates that this relationship holds even for populations living in more open landscapes. Likewise, our results also support previous observations of a positive influence of fast early body development on early survival of roe deer fawns in forest populations (da Silva et al. 2009).

#### Early fawn survival in relation to the mother's coping style and habitat type

The neonatal period is a critical phase for juvenile survival in most mammals and depends heavily on the nature and quality of the interactions between the mother and her offspring (Nowak 1996). In some species, mothers or other members of the group may actively defend the young (Leuthold 1977), sometimes directly attacking a predator and/or attempting to disrupt its chase (Jarnemo 2004; Lingle et al. 2005). These antipredator behaviors vary in relation to the hunting tactic of the predator (ambush vs. coursing), predator abundance and diversity, and habitat type. For example, Panzacchi et al. (2010) concluded that meadows are an especially risky habitat for roe deer fawns because the density of small rodents is generally high. Because of this, meadows are hunting hot spots for red foxes (*Vulpes vulpes*), so that predation risk of fawns is likely to be higher in this habitat. Our findings support this hypothesis, as fawns born to more proactive mothers survived better than those born to more reactive mothers when in open meadow habitat (natural meadows). We suggest that this is because, when attacked by fox, proactive mothers are more mobile and aggressive, and so successfully defend their fawn, compared with reactive mothers who are more passive and display a high attack latency. However, none of the 6 fawns monitored in artificial meadows survived beyond 12 days of age, irrespective of the mother's coping style. This presumably occurred because fawns in this habitat type were killed by mowing, the second most important mortality factor for roe deer fawns in agricultural landscapes (Jarnemo 2002). In contrast, in closed habitats (i.e., forest and crops), fawns born to more proactive mothers survived less well than those born to more reactive mothers.

The marked influence of habitat type on the success of a given mother's coping style that we describe above is likely related to habitat-specific differences in the trade-off between resource acquisition and predation risk (Bongi et al. 2008; Boon et al. 2008). The requirement for high quality forage is particularly acute for income breeders like roe deer (Bongi et al. 2008), so that risky tactics (e.g., in terms of exposure to fawn predation risk) may potentially be the most rewarding in terms of fitness. The quality of food resources for roe deer is far better in open habitats (Hewison et al. 2009; Abbas et al. 2011), so that females should preferentially select meadows. However, the risk of predation is also highest in open habitats (Panzacchi et al. 2010). As a result, females raising their fawns in meadows play a high risk-high benefit tactic, where the pay-off is greater if females actively defend their fawns. Our results indicate that this is the case for more proactive mothers who are better able to raise their fawns successfully in high risk open meadows, presumably because they respond more actively to the attack of a predator by actively defending their fawns (Jarnemo 2004), but also possibly because they are more attentive in general, thus also

minimizing mortality due to other causes. In forest habitats, food resources are less plentiful and predation risk is much lower than in open habitats because alternative prey such as rodents are less abundant. Furthermore, closed habitats provide visual obstruction so that antipredator behaviors such as vigilance may be less efficient and active defence of the fawn may be more difficult and/or inefficient. In this context, the best antipredator tactic for the mother may be to range further away from the fawn's bed site during feeding, so as not to provide cues of the fawn's location to predators (Fitzgibbon 1993). Because food resources are of lower quality in closed habitats (Hewison et al. 2009), females have to spend more time on food acquisition, especially during the energetically demanding early lactation period. In this case, the pay-off associated with the low risk-low benefit tactic adopted by the more reactive mothers is maximized in closed habitat. Although the above interpretation of our results is coherent with expectations, we did not have any direct observations of maternal behavior during attempted predation to confirm that this was the behavioral mechanism underlying the observed relationship between coping style and fawn survival. Future work should focus on how maternal care tactics, and specifically antipredation behaviors, vary between habitats and among individuals in relation to variation in coping styles.

#### Coping styles, fitness, and the maintenance of behavioral variation

Only a few studies to date have provided empirical evidence of an influence of interindividual variation in behavior on fitness in the wild (Smith and Blumstein 2008), and only one has reported that a given behavioral phenotype is favored in some ecological conditions, but not in others, governed by life-history trade-offs (Boon et al. 2007). These authors found that both the direction and magnitude of the influence of maternal aggressiveness on offspring survival differed among years in North American red squirrel, likely in response to marked yearly variation in food availability. Our findings that the direction and magnitude of the influence of the mother's coping style on offspring survival differ across the landscape provide clear evidence of spatially dynamic associations between behavioral phenotype and fitness components. These combined results imply that both temporal and spatial variation in resource acquisition and allocation contribute to ensure that no given behavioral phenotype is consistently associated with the highest fitness. The exact mechanisms by which variation among individuals in behavioral traits is maintained in the wild are largely unknown. A potential explanation for differences in fawn survival that we reported in relation to their mother's behavior could involve genetic factors. Indeed, the aggressiveness of mothers toward their offspring, the responsiveness of mothers toward signals from their offspring or the nursing behavior of mothers can be under genetic control (Grandinson 2005). However, our findings directly suggest that spatial habitat heterogeneity could be involved. Indeed, recent theoretical models have demonstrated that, under variable food conditions, the involvement of behavioral traits in life-history trade-offs may lead to the maintenance of individual differences in behavioral phenotype (Stamps 2007; Wolf et al. 2007).

Depending on the strength of spatial variation in the fitness advantages associated with a given level of proactivity, one may hypothesize that certain behavioral phenotypes should predominate in a given habitat (see Dingemans et al. 2004; Bergmüller and Taborsky 2010). For example, in chipmunks (*Tamias striatus*), the most exploratory and docile individuals established their home ranges in those areas that were most frequented by humans (Martin and Réale 2008). Further studies investigating correlations between behavior

and environment are needed so as to better understand their ecological and evolutionary implications in terms of the maintenance of interindividual behavioral variation (Ravigné et al. 2003). In particular, we lack empirical case studies that directly link interindividual variation in behavioral phenotype with fitness components across variable environments. Our work provides evidence that spatial heterogeneity in fitness pay-offs for different coping styles may promote the maintenance of behavioral variation in wild populations.

**SUPPLEMENTARY MATERIAL**

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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## Appendix 2

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## Short- and long-term repeatability of docility in the roe deer: sex and age matter



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Behavioural consistency is a key assumption when evaluating how between-individual differences in behaviour influence life history tactics. Hence, understanding how and why variation in behavioural repeatability occurs is crucial. While analyses of behavioural repeatability are common, few studies of wild populations have investigated variation in repeatability in relation to individual status (e.g. sex, age, condition) and over different timescales. Here, we aimed to fill this gap by assessing within-population variation in the repeatability of docility, as assessed by the individual's response to human handling, in a free-ranging population of European roe deer, *Capreolus capreolus*. Docility was an equally repeatable behaviour at both short- and long-term timescales, suggesting that this behavioural trait is stable across time. Repeatability did not differ markedly between age and sex categories but tended to be higher in juvenile males than in juvenile females. Finally, contrary to expectation, individual variation in the repeatability of docility was not correlated with individual body mass. Further studies are required to assess the life history consequences of the individual variation in docility we report here.

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Interest in the study of behavioural differences between individuals has increased markedly over recent years (Bell, 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012) and consistent behavioural differences between individuals over time and/or across different ecological contexts have been documented within populations in a large variety of taxa (Bell, 2007; Bell, Hankison, & Laskowski, 2009). These consistent behavioural differences can indeed have profound effects on life histories (Bell, 2007; Biro & Stamps, 2008; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). For instance,

annual adult survival is related to exploration behaviour in great tits, *Parus major* (Dingemanse, Both, Drent, & Tinbergen, 2004). In the common lizard, *Lacerta vivipara*, socially tolerant individuals grow faster and reproduce better than intolerant individuals (Cote, Dreiss, & Clobert, 2008). Similarly, boldness and docility are linked to survival and reproductive success in bighorn sheep rams, *Ovis canadensis* (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009), and to weaning success in bighorn sheep ewes (Réale, Gallant, Leblanc, & Festa-Bianchet, 2000).

Behavioural consistency can be assessed by evaluating repeatability (Hayes & Jenkins, 1997), where repeatability is defined as the proportion of observed behavioural variation within a population that is accounted for by individual differences (Bell et al., 2009). This then requires that behavioural traits be assessed repeatedly in the same individuals. The vast majority of studies that have assessed behavioural repeatability have been conducted under

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somewhat unrealistic laboratory conditions (e.g. see Bell et al., 2009 for a review), whereas repeatability measures of behavioural traits in the wild are less common (e.g. Martin & Réale, 2008a in eastern chipmunks, *Tamias striatus*; Réale et al., 2000 in bighorn sheep; Montiglio, Garant, Thomas, & Réale, 2010 in house mice, *Mus musculus*, and eastern chipmunks; Garamszegi, Eens, & Janos, 2009 in collared flycatchers, *Ficedula albicollis*, Nakagawa, Gillespie, Hatchwell, & Burke, 2007 in house sparrows, *Passer domesticus*).

Despite the importance of individual behavioural differences for understanding the evolution of life history tactics (Sih et al., 2012), the individual characteristics that influence repeatability are still to be fully understood and require further investigation (Bell et al., 2009). Using a meta-analysis based on 114 studies (466 estimates assessed in the laboratory versus 293 in the field) investigating the repeatability of various behavioural traits, Bell et al. (2009) found that within-population variation in repeatability depends on the focal behavioural trait, as well as the species under study, and is affected by (1) time elapsed between measurements, (2) age, (3) sex and (4) ecological conditions.

Behavioural repeatability generally decreases as the time elapsed between successive measurements increases (Bell et al., 2009; David, Auclair, & Cezilly, 2012; Gifford, Clay, & Careau, 2014). This is probably because, with time, there is more opportunity for individuals to experience developmental modifications and fluctuating environments (Stamps & Groothuis, 2010), and also because their phenotype may be influenced by different genes at different ages (Charmantier, Perrins, McCleery, & Sheldon, 2006). Thus, experimental trials performed over short time intervals (i.e. short-term repeatability) generally yield higher estimates of repeatability than those carried out over longer time intervals (i.e. long-term repeatability) for a large range of traits, including docility (Bell et al., 2009; David et al., 2012; Gifford et al., 2014).

Repeatability also varies in relation to age, although predictions for age-dependent variations are not straightforward (Bell et al., 2009). Assuming that behavioural repeatability has an ontogenetic component (Stamps & Groothuis, 2010; i.e. it develops progressively over a lifetime), the behaviour of older individuals should be more repeatable than that of younger ones (De Kort, Eldermire, Valderrama, Botero, & Vehrencamp, 2009). For instance, behavioural repeatability in humans increases with age up to 50 years old before reaching a plateau (Roberts & DelVecchio, 2000). Hence, higher repeatability of docility is expected among adults.

Behavioural repeatability may differ between the sexes under the action of sexual selection (Schuett, Tregenza, & Dall, 2010). Indeed, behaviours shaped by sexual selection should provide reliable, honest, and thus consistent, cues, so that they can reliably be interpreted by conspecifics (Bell et al., 2009; Schuett, Godin, & Dall, 2011). For instance, in two kangaroo rat species (*Dipodomys* spp.), food-hoarding behaviour, a behavioural trait that may partially underpin alternative mating tactics, has been reported to be more repeatable in males than in females (Jenkins, 2011). Surprisingly, however, based on the published literature, Bell et al. (2009) concluded that females generally tend to display more repeatable behaviours (except for mate choice-related behaviours) than males. Hence, between-sex differences in repeatability may depend on the behavioural trait under scrutiny, with males being more repeatable for behaviours linked to mate choice and subject to intrasexual competition (Schuett et al., 2010).

Repeatability may also vary among individuals within a given sex or age class. At the population level, a behavioural consistency estimate that is statistically different from 0 for a given trait in a given age and sex category does not mean that all individuals are equally consistent for that trait (Bell et al., 2009). Indeed, individual variation in predictability, or within-individual variability,

once variation due to sex and/or age differences has been accounted for, is widespread (Briffa, 2013; David et al., 2014; Stamps, Briffa, & Biro, 2012) and may have consequences for fitness-related traits. For instance, in hermit crabs *Pagurus bernhardus*, within-individual variation was higher in a risky situation, suggesting that animals benefit by behaving unpredictably under predation threat (Briffa, 2013). Such flexibility is assumed to be costly (DeWitt, Sih, & Wilson, 1998; Niemela, Vainikka, Forsman, Loukola, & Kortet, 2013) and should therefore vary as a function of individual body condition (David & Giraldeau, 2012; David et al., 2014). For example, zebra finches, *Taeniopygia guttata*, in higher body condition are less consistent in their producer tactic use in a producer–scrounger foraging game (David et al., 2014). A link between body condition and variation in docility may thus be expected.

The objective of this study was thus to test the effect of the above factors on the repeatability of docility in European roe deer, *Capreolus capreolus*. Docility is a commonly measured behavioural trait (Benhajali et al., 2010; Martin & Réale, 2008a; Réale et al., 2000) often associated with the shy–bold behavioural gradient (Réale et al., 2007). Indeed, docility has often been linked with other behavioural traits such as activity and exploration (Ferrari et al., 2013; Martin & Réale, 2008a) and with physiological parameters such as hypothalamo-pituitary-adrenal reactivity (Montiglio et al., 2010) or the level of cortisol (Martin & Réale, 2008b). Docility has been reported to be a repeatable behavioural trait in several studies, both in captivity (e.g. David et al., 2012; Mazurek et al., 2011) and in the field (Ferrari et al., 2013; Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Réale et al., 2000, 2009). Moreover, docility is linked to fitness components in bighorn sheep (Réale et al., 2000, 2009), while it also influences the productivity of livestock farming enterprises (Norris, Ngambi, Mabelebele, Alabi, & Bényi, 2014). For instance, fearful cows produce lighter calves at birth that grow less well than those produced by nonfearful (i.e. docile) cows (Turner, Jack, & Lawrence, 2013). Because docility may be part of a behavioural syndrome (i.e. a suite of correlated behaviours reflecting between-individual consistency in behaviour across multiple situations; Sih, Bell, & Johnson, 2004), variation in docility may thus have important consequences for life history traits. Information about which factors influence the repeatability of docility remains scarce, however. In yellow-bellied marmots, *Marmota flaviventris*, Petelle et al. (2013) reported that boldness was repeatable only in yearlings, whereas docility was repeatable in all age classes. Repeatability of docility was also shown to be higher when measured over the short term than over the long term (Bell et al., 2009; David et al., 2012).

In this study, we investigated the repeatability of docility taken as the behavioural responses to human manipulation at capture in a free-ranging, wild population of European roe deer in central Sweden. The response of roe deer to human handling during capture is assumed to reliably reflect docility (Le Neindre et al., 1995; Réale et al., 2000). The roe deer is a medium-sized (20–30 kg), slightly dimorphic and weakly polygynous ungulate in which adults of both sexes are highly sedentary (Andersen, Duncan, & Linnell, 1998). Roe deer life expectancy in the wild at 1 year of age is around 10–12 years in the absence of hunting, but varies among populations (Veiberg et al., 2007). Despite being primarily a forest-dwelling species, roe deer have colonized almost all types of habitats since the early 1980s, including human-modified landscapes (Andersen et al., 1998; Hewison et al., 2001), and express a high degree of behavioural plasticity (Jepsen & Topping, 2004). Here, we investigated whether the repeatability of docility varies in relation to the time elapsed between successive measurements, age, sex and body mass. We expected (1) short-term repeatability estimates to be higher than long-term ones, (2) repeatability to be

higher in adults than juveniles, and (3) repeatability to be similar in both sexes as docility is a priori not related to mate choice (Andersen et al., 1998). Finally, as individual body mass is stable over most of a roe deer's lifetime (Hewison et al., 2011) and constitutes a reliable indicator of body condition and, more generally, of phenotypic quality (Toigo, Gaillard, Van Laere, Hewison, & Morellet, 2006), we expected (4) within-individual variation in behaviour (i.e. predictability) to decrease with decreasing body mass due to the presumed costs of behavioural flexibility.

## METHODS

### Ethical Note

All captures and handling were done in accordance with Swedish and European laws for animal welfare. All procedures were approved by the Ethical Committee for Animal Experiments in Uppsala, Sweden (permit numbers C302/12 and C289/09) and adhered to legal and ethical requirements for research on wild animals in Sweden and the European Union. Roe deer captures in our study site have been performed since 1973, and all animals used for this study were captured in the context of a long-term ongoing project on roe deer ecology. Some animals were fitted with a VHF or GPS collar to meet the objectives of other projects, including predator–prey interactions, herbivore–plant interactions, migration, disease ecology and veterinary medicine, and roe deer–human interactions using a variety of scientific methods and technical and analytical approaches.

### Study Area

The study was carried out from 2008 to 2013 at Grimsö Wildlife Research Area (GWRA; 130 km<sup>2</sup>), located in south-central Sweden (59°40'N, 15°25' E) within the southern part of the Nordic taiga. The area is covered mainly by mixed conifer forest (74%), while bogs, mires and fens cover 18% and farmland 3%. For a more detailed description of GWRA see Kjellander, Gaillard, and Hewison (2006). Daily mean temperatures range from 20 °C in summer to –10 °C in winter. The ground is generally snow covered from December to March.

### Behaviour at Capture

Each winter from 2008 to 2013, roe deer were caught in wooden box traps (L6 Rådjursfälla M/Öster Malma, dimensions: 130 × 62.5 cm and 100 cm high) baited with specific forage intended for deer (Renfor, manufacturer Lantmännen, Nyköping, Sweden). Roe deer captures spanned 185 days, from 12 November to 25 March, with 11 February as the median date. Hence, this capture period did not overlap with the phases of reproduction (i.e. the birth period in May–June and the rutting period in mid-July to mid-August; Sempéré, Mauget, & Mauget, 1998) or the period of male

territoriality (late March to early September; Liberg, Johansson, Andersen, & Linnell, 1998). Each individual was sexed, marked with plastic ear tags and weighed to the nearest 0.1 kg. Juveniles (<1 year old) were identified from the presence of a tricuspid third premolar milk tooth that is only present in individuals less than 1 year old (Cederfund, Kjellander, & Stålfelt, 1991) and distinguished from adults (≥1.5 years old). During manipulation, we measured docility for each roe deer using a handling score ranging from 0 to 4, a commonly used method for quantifying this behaviour (Behajali et al., 2010; Le Neindre et al., 1995; Norris et al., 2014; Réale et al., 2000). The score was based on several behavioural component measures that indexed how much resistance roe deer showed during handling (see Table 1 for more details), and was assessed by the same experienced handler (L.J.) at each capture. Note that the absolute value of this score has no direct interpretation; rather it represents the judgement of an experienced handler as to how stressed an animal was during handling relative to other individuals in the population.

Between winter 2007–2008 and winter 2012–2013, 262 roe deer were caught for a total of 1569 capture events, but only individuals captured at least twice with recorded behavioural data were included in the analyses ( $N = 130$  individuals for a total of 532 capture events, mean  $\pm$  SE number of captures per individual =  $4.09 \pm 2.81$ , range 2–22; Fig. 1). A given individual could potentially be caught several times during a given winter ( $N = 117$  individuals) and/or during successive winters ( $N = 65$  individuals).

### Docility and Habituation

As pointed out by Martin and Réale (2008a), individuals might habituate to a behavioural assay when they are measured several times. This habituation may lead to a decrease in the strength of the behavioural response over trials and, as a result, bias repeatability estimates. For instance, previous experience with handling increases docility during subsequent capture in domestic cattle, *Bos taurus* (Le Neindre, Boivin, & Boissy, 1996), or decreases the intensity of the behavioural response in hole-board and handling bag tests in eastern chipmunks (Martin & Réale, 2008a) and captive zebra finches (David et al., 2012). To test whether docility was related to an individual's previous capture experience (number of capture events and time elapsed since the previous capture event), we used linear mixed models with handling score as the dependent variable, and with individual identity included as a random factor on the intercept to control for repeated measures. When comparing the model including the number of capture events for a given individual (on a log scale to achieve normality) with the null model, docility was linked to previous capture experience such that the handling score of a given individual decreased with the number of previous capture events ( $N_{\text{capture}} = 532$ ,  $N_{\text{individuals}} = 130$ ,  $t = -10.2$ , slope =  $-0.49 \pm 0.05$ ). To account for this habituation, we included the number of previous capture events for a given individual, as well as the time elapsed since the previous capture event, as fixed

**Table 1**  
Behavioural traits recorded at capture with the corresponding derived handling score

Handling score at capture	Resistance during handling	Kicking with legs	Screaming	Handling	Calm
0	No	No	No	Easy	Yes
1	No	Very few	0–2 times	Easy	Yes
2	Few	Yes	Yes	Fairly easy	Yes between screaming and kicking events
3	Yes	Yes	Yes	Difficult	No
4	Yes	Yes	Yes	Impossible	No

The score represents the judgement of an experienced handler (the same individual for all measures) as to how stressed an animal is during handling relative to other individuals in the population. The table does not include all possible combinations of behaviour but rather displays the more representative combinations of the subjective score (see Methods).



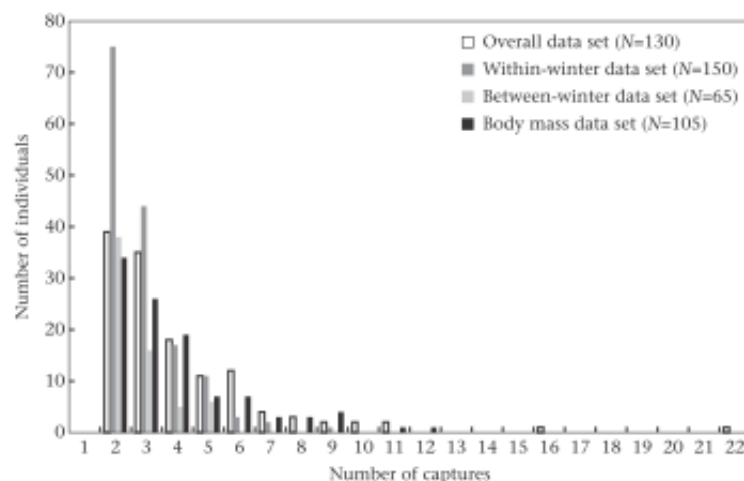


Figure 1. Sample size (number of individuals) and number of repeated measures (number of capture events for a given individual) of docility for each data subsample.

effects in the subsequent models. When this approach was not possible, we computed a 'standardized handling score' defined as the residual values from the linear regression between handling score and the log-transformed number of capture events using all available individuals and with the time elapsed since the previous capture event included as a fixed effect to control for the rate of habituation in relation to time between capture events (see Appendix Fig. A1 for the linear regression and Fig. A2 for the distributions of the standardized handling scores and handling scores, respectively). Note that because the rate of habituation did not differ between individuals (i.e. the model including individual identity with random slopes did not provide a better fit than the model without random slopes: difference in the Akaike information criterion corrected for small sample size,  $\Delta AICc = 1.3$ ), a common slope from a linear model was used to compute the standardized handling scores for all individuals. In addition, we estimated the capture rate of each individual as the total number of captures experienced by the individual during the study period divided by the number of days between the first and the last capture event and tested whether more docile individuals were captured more often than less docile ones that are potentially trap-shy. However, we did not find any relationship between an individual's handling score at first capture and its capture rate (estimated coefficient from the multinomial regression for capture rate: slope  $\pm$  SE =  $0.28 \pm 2.67$ ;  $N = 130$ ,  $Z = 0.10$ ,  $P = 0.92$ ).

#### Variation in Docility

To investigate the pattern of docility among the sexes and age classes, we fitted six candidate mixed multinomial models with handling score as a response variable using the 'ordinal' R package (Christensen, 2015; R Development Core Team, 2010;  $N_{\text{observations}} = 521$ ,  $N_{\text{individuals}} = 129$ , because we lacked age information for one individual). The most complex model included the two-way interaction between sex and age class to evaluate the support for differences in docility between the sexes and across age classes, as well as the number of previous capture events for that individual and the time elapsed since the previous capture event to control for habituation. We then computed all possible simpler models. Individual identity was included in all models as a random

intercept to control for repeated measures of docility obtained for each individual. We used a model selection procedure based on the AICc and we retained the model with the lowest AICc value, reflecting the best compromise between precision and accuracy (Burnham & Anderson, 2002). According to the rule of parsimony, when the AICc of two competing models differed by less than 2, we retained the simplest one. We also calculated AICc weights (AICcWt) as a measure of the likelihood that a given model was the best among the set of fitted models.

#### Repeatability of Docility

Repeatability and its 95% credibility intervals (95% CI) were then assessed using multivariate generalized linear mixed models with the MCMCglmm package (Hadfield, 2010) of R (R Development Core Team, 2010), and implemented in this package under the item Categorical Random interactions. To control for differences between the sexes and age classes and/or in relation to habituation, adjusted repeatability, sensu Nakagawa and Schielzeth (2010), was assessed by adding the fixed effect of age class and sex and/or the number of previous capture events experienced and the time elapsed since previous capture to the linear mixed models. The resultant values estimate repeatability as if all measurements had been taken from a single class of animals and for a given number of capture events (Nakagawa & Schielzeth, 2010). Repeatability and adjusted repeatability ( $R$ ) were calculated as the proportion of the total variance accounted for by between-individual differences using multivariate linear mixed-effect models for raw handling scores and linear mixed-effect models for standardized handling scores. First, global adjusted repeatability of raw handling scores was estimated using the entire data set ( $N_{\text{observations}} = 521$ ,  $N_{\text{individuals}} = 129$ ) and by fitting a multinomial regression for ordinal data. For comparative purposes, global adjusted repeatability for standardized handling scores was estimated using a linear mixed-effect model for Gaussian data.

#### Short- and Long-term Repeatability

Within-winter adjusted repeatability of standardized handling scores was then assessed as a measure of short-term repeatability

while controlling for sex and age differences in repeatability and using a subsample of 116 individuals that were captured several times during a given winter (range 2–9). Because some individuals were also captured several times in successive winters, the total number of data points available was 150; hence a random effect of winter nested within individual was fitted to take into account pseudoreplication. Between-winter adjusted repeatability of standardized handling scores was assessed as a measure of long-term repeatability while controlling for sex differences in repeatability and using a subsample of 65 individuals recaptured during successive winters (mean  $\pm$  SE =  $2.68 \pm 0.97$  winters, range 2–5). For each individual, the standardized handling scores were averaged for a given winter so as to retain only one measure per individual and per winter. Within-winter and between-winter adjusted repeatabilities were also estimated separately for males and females while controlling for age differences at the short-term scale only. The short-term scale corresponds to around 10% of an individual roe deer's life span, whereas the long-term scale corresponds to between 10% and 45% of an individual's life span (with an average close to 20%).

#### Age and Sex Effects on Repeatability

Finally, to evaluate differences in the repeatability of raw handling scores between the sexes and age classes, repeatability was measured for the four age–sex categories (i.e. juvenile females, juvenile males, adult females and adult males) from a single multivariate model also including the number of previous capture events experienced and the time elapsed since the previous capture event to account for habituation, and the corresponding 95% CI were compared. Individual identity was included as a random effect with an unstructured  $4 \times 4$  (co)variance matrix estimating four variance components, one for each sex and age–class category. A total of 500 000 iterations were run, including a burn-in of 50 000.

#### Within-individual Variation in Docility

To test the hypothesis that within-individual variation in docility was linked to between-individual variation in body mass, we assessed the relationship between the standard deviation of the standardized handling score of a given individual and its average body mass, while controlling for the time elapsed between measurements and the number of observations. In this analysis, a subsample of 105 individuals (for a total of 403 capture events) was used for which body mass and handling scores were recorded at least twice during the study period. We standardized body mass to account for sex and age differences by taking the residuals of the regression between body mass and these two factors (referred to as 'corrected body mass'). The standard deviation of the standardized handling score was square-root transformed to achieve normality. Because the expected relationship between within-individual variation in docility and body mass could be sex dependent due to sex-specific behavioural flexibility, the two-way interaction between sex and corrected body mass was also included in the full model. We considered the model including only the number of observations and the number of days between the first and last observations as fixed effects as our baseline model. We then fitted four more complex candidate linear models to explain variation in the standard deviation of the standardized handling score in relation to (1) mean individual corrected body mass, (2) sex, (3) both these factors and (4) their interaction, as well as the constant model (i.e. including no effect) and all the models without controlling for the number of observations and the number of days between the first and last observations. We then used a model selection procedure as described above to select the best of these 10 models.

## RESULTS

### Variation in Docility

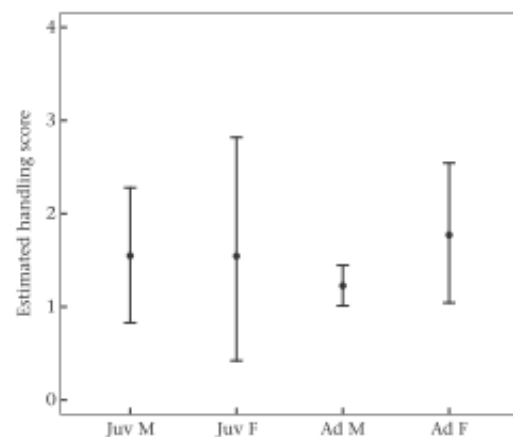
The handling scores varied between 0 and 4 with a mean  $\pm$  SD of  $1.62 \pm 0.95$  for the whole data set (Appendix Fig. A2). Estimated mean docility was between score 1 and 2 with a high standard deviation for all the four age–sex categories (mean docility  $\pm$  SD =  $1.53 \pm 0.90$  for juvenile females,  $1.71 \pm 0.95$  for juvenile males,  $1.68 \pm 0.94$  for adult females and  $1.26 \pm 0.95$  for adult males; see Fig. 2 for the numbers of scores and individuals for each category). The model with the lowest AICc included a two-way interaction between sex and age classes, plus the number of previous capture events experienced, as well as the time elapsed since the previous capture event (Table 2). Overall, females had lower docility (i.e. higher handling score) than males, but this was mainly apparent in adults (Fig. 2).

### Repeatability of Docility

Overall, docility was repeatable ( $N = 129$  individuals for 521 measures, adjusted repeatability when accounting for sex and age class variation:  $R = 0.41$ , 95% CI [0.30, 0.52] and  $R = 0.39$ , 95% CI [0.30, 0.50] using the raw and standardized handling scores, respectively).

### Short- and Long-term Repeatability

Estimates for within-winter adjusted repeatability ( $N = 116$  individuals for 150 individuals/winter and 463 measures, adjusted repeatability when accounting for sex and age classes:  $R = 0.41$ , 95% CI [0.30, 0.51]; using a random effect of winter nested within individual to account for pseudoreplication, because 20 individuals had repeated data for several winters, gave similar results:  $R = 0.43$ ) and between-winter adjusted repeatability ( $N = 65$  individuals for 170 measures; adjusted repeatability when accounting for sex:  $R = 0.31$ , 95% CI [0.13, 0.49]) of docility did not differ



**Figure 2.** Estimated mean handling score and 95% credibility intervals for each sex and age class category from the best multinomial regression. The best model included the two-way interaction between sex and age class and the number of previous capture events for that individual, as well as the time elapsed since the previous capture event, to control for habituation (number of scores and individuals:  $N_{\text{observations}} = 85$ ,  $N_{\text{individuals}} = 31$  juvenile males (Juv M);  $N_{\text{observations}} = 98$ ,  $N_{\text{individuals}} = 35$  juvenile females (Juv F);  $N_{\text{observations}} = 151$ ,  $N_{\text{individuals}} = 42$  adult males (Ad M);  $N_{\text{observations}} = 187$ ,  $N_{\text{individuals}} = 45$  adult females (Ad F)).

**Table 2**  
Performance of the six candidate mixed multinomial models for explaining variation in docility, over the 521 capture events

	k	AICc	ΔAICc	AICcWt
<b>No.<sub>catch</sub>+Δt<sub>capture</sub>+Sex+Age<sub>class</sub>+(1 ID)</b>	<b>11</b>	<b>1285.77</b>	<b>0.00</b>	<b>0.76</b>
No. <sub>catch</sub> +Δt <sub>capture</sub> +Sex+(1 ID)	9	1288.94	3.17	0.15
No. <sub>catch</sub> +Δt <sub>capture</sub> +Sex+Age <sub>class</sub> +(1 ID)	10	1290.69	4.92	0.06
No. <sub>catch</sub> +Δt <sub>capture</sub> +(1 ID)	8	1293.32	7.55	0.02
No. <sub>catch</sub> +Δt <sub>capture</sub> +Age <sub>class</sub> +(1 ID)	9	1295.14	9.37	0.01
1+(1 ID)	6	1337.96	52.19	0.00

Individual identity (1|ID) was included in all models as a random factor. The number of captures previously experienced by the individual ('No.<sub>catch</sub>') and the time elapsed since the previous capture event ('Δt<sub>capture</sub>') are included as a fixed effect in all models to control for an habituation effect. Models are ranked in increasing order of AICc. ΔAICc corresponds to the difference in AICc between the best model and a given model and AICcWt corresponds to the AIC weight of a given model, k refers to the number of model parameters. The selected model is in bold.

markedly (95% CI overlapped). However, when age class variation was accounted for, males tended to have a lower long-term than short-term repeatability (Fig. 3a).

*Age and Sex Effects on Repeatability*

Docility for juvenile females ( $R = 0.38$ , 95% CI [0.18, 0.57]), juvenile males ( $R = 0.60$ , 95% CI [0.36, 0.78]), adult females ( $R = 0.47$ , 95% CI [0.24, 0.66]) and adult males ( $R = 0.55$ , 95% CI [0.35, 0.72]) were all repeatable. Based on overlap of 95% CI, repeatability did not differ markedly between sex and age classes. However, the repeatability of docility among juvenile males tended to be higher than that of juvenile females (see Fig. 3b for the numbers of scores and individuals for each category).

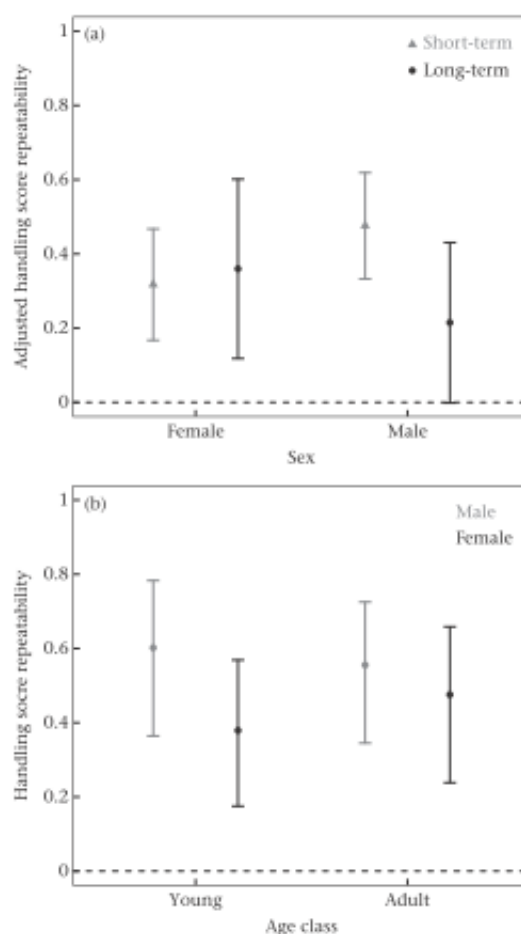
*Within-individual Variation in Docility*

The magnitude of the consistency of docility seemed to vary among individuals. From a subset of six individuals that were recaptured at least 10 times, individual trajectories of docility were indeed highly variable (see Appendix Fig. A3).

Overall, individual docility was not related to corrected individual body mass (there was no difference between the model including the effect of corrected individual body mass and the basic model correcting for habituation by including the number of previously experienced captures and the time elapsed between the previous capture event; ΔAICc between the two models = 0.01). Moreover, temporal variation in docility (estimated as the standard deviation of standardized handling scores) for a given individual was not related to its corrected body mass (slope ± SE = 0.002 ± 0.011; Fig. 4). Indeed, the best model of variation in the standard deviation of docility was the constant model (Table 3), whereas the model including the fixed effect of individual mean corrected body mass only or coupled with number of observations and time elapsed between consecutive measurements (Table 3), had no support.

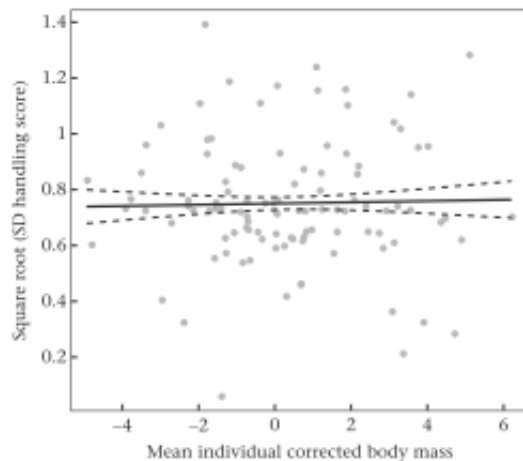
**DISCUSSION**

We investigated behavioural repeatability in an unusually comprehensive data set composed of a large number of individual roe deer for which behaviour at capture was repeatedly assessed in the wild over a reasonably long time period. Docility, a behavioural trait that we indexed through individual handling scores at capture, did not differ substantially between age classes, but female adults tended to be somewhat less docile than males. Importantly, this behavioural trait was found to be repeatable in this free-ranging population. In comparison, a very high repeatability of docility during capture was reported in a wild population of bighorn sheep ( $R = 0.65$ ; Réale et al., 2000), while a somewhat lower repeatability



**Figure 3.** Repeatability estimates and 95% credibility intervals for (a) the index of docility (standardized handling scores) over the long-term ( $N = 150$  individuals/winter for 463 measures) and short-term ( $N = 65$  individuals for 178 measures) in both sexes (with repeatability adjusted for age differences) and (b) the index of docility (handling scores) for each sex and age class derived from a single model taking into account habituation by including the number of captures previously experienced and the time elapsed since the previous capture event as fixed effects. Juvenile females:  $N = 35$  individuals for 98 measures; juvenile males:  $N = 31$  individuals for 85 measures; adult females:  $N = 45$  individuals for 187 measures; adult males:  $N = 42$  individuals for 151 measures. Juveniles are less than 1 year old; adults are 1.5 years old or more.





**Figure 4.** Relationship between temporal variation in docility for a given individual measured as the standard deviation of its standardized handling scores (square root transformed) in relation to mean individual corrected body mass ( $N = 105$ ). The factors 'number of observations' and 'time elapsed between measurements' were fixed to their mean values. The line represents the estimated relationship and the dashed lines its associated standard error.

was found in yellow-bellied marmots ( $R = 0.25$ ; Petelle et al., 2013). Although scarce, current empirical evidence thus indicates that docility is a repeatable trait in several mammal species (Montiglio, Garant, Pelletier, & Réale, 2012; Petelle et al., 2013; Réale et al., 2000, 2009), and based on some other studies is likely to be part of an overall behavioural syndrome (e.g. Montiglio et al., 2012).

Recently, Bell et al. (2009) highlighted the importance of studying patterns of variation in behavioural repeatability and of exploring the influence of factors that could influence repeatability. In accordance with previous studies (Martin & Réale, 2008a; Van Oers, Klunder, & Drent, 2005), we found that docility increased with the number of behavioural assays (i.e. an habituation effect). However, unexpectedly, we found that short-term and long-term repeatabilities did not differ markedly when accounting for age and sex. In addition, repeatability did not differ markedly between age and sex categories but tended to be higher in juvenile males than in juvenile females. Finally, also contrary to expectation, individual variability in docility was not related to body mass, a reliable measure of phenotypic quality in this species (Toigo et al., 2005).

Surprisingly, and in contrast to other studies (Bell et al., 2009; David et al., 2012; Gifford et al., 2014), the repeatability estimates of docility over both the short and long term were very similar, although males did tend to have a lower long-term repeatability. In their meta-analysis, Bell et al. (2009) reported higher repeatability for behaviours that were measured closer in time. Interestingly, variation in repeatability in relation to the size of the time window has been shown to depend on the focal behavioural trait (David et al., 2012; Gifford et al., 2014). In a study on captive zebra finches, exploratory tendencies were repeatable over the long term, whereas struggling rate was not, even though it was repeatable over the short term (David et al., 2012). The high long-term repeatability of docility we observed has also been reported in other vertebrate species (Petelle et al., 2013; Réale et al., 2000) and suggests that this behavioural trait may be stable, indexing an ecologically relevant dimension of behaviour that may be affected by natural selection. Indeed, docility may be part of a behavioural syndrome linking exploratory, social and aggressive behaviours, as well as physiological features such as long-term stress reactivity or metabolism (Careau, Thomas, Humphries, & Réale, 2008; Debeffe et al., 2014; Montiglio et al., 2012; Réale et al., 2009; Taylor et al., 2012). Moreover, like other behavioural traits, docility may have a genetic basis (Dingemans et al., 2004; Poissant, Réale, Martin, Festa-Bianchet, & Coltman, 2013; Réale et al., 2009). Given these features, docility may be affected by natural selection. For example, in bighorn sheep, age-specific selection on docility and a moderate level of selection on boldness were reported under predation pressure (Réale & Festa-Bianchet, 2003). Furthermore, because consistent behavioural traits can affect how individuals react to challenging situations (Réale et al., 2007), they may also influence individual fitness (Dingemans & Réale, 2005; Smith & Blumstein, 2008). Indeed, docility has been linked to differences in individual fitness components in bighorn sheep, with bold ewes reproducing earlier and having higher weaning success than shy ones (Réale et al., 2000, 2009). In domestic cattle, a similar relationship between docility and fitness components has also been reported (Norris et al., 2014; Turner et al., 2013). Overall, these studies indicate that docility is likely to be an ecologically relevant behaviour shaped by natural selection. This behavioural trait should therefore be recorded in field studies designed to explore the link between repeatable behavioural differences and fitness or its components.

Recent work has highlighted the importance of studying differences in consistency in relation to phenotypic attributes (Bell et al., 2009; Schuett et al., 2010), but how behavioural consistency varies in relation to age has not been intensively explored so

**Table 3**

Model selection for the linear models describing the link between temporal variation in docility for a given individual in relation to mean corrected body mass and sex for 105 roe deer

	R	AICc	$\Delta AICc$	AICcWt
<b>Constant</b>	<b>2</b>	<b>-10.63</b>	<b>0.00</b>	<b>0.34</b>
Sex	3	-10.15	0.48	0.26
Mean corrected body mass	3	-8.55	2.08	0.12
Mean corrected body mass+Sex	4	-8.07	2.56	0.09
No. days+No. observations	4	-7.32	3.31	0.06
Sex+No. days+No. observations	5	-6.57	4.06	0.04
Mean corrected body mass+No. days+No. observations	5	-6.12	4.51	0.04
Mean corrected body mass+Sex	5	-5.16	5.47	0.02
Mean corrected body mass+Sex+No. days+No. observations	6	-4.33	6.30	0.02
Mean corrected body mass+Sex+No. days+No. observations	7	-2.26	8.37	0.01

Within-individual variation in docility for a given individual was measured as the standard deviation of the standardized handling score. To control for the number of observations (No. observations) and the time elapsed between measurements (No. days) (as our baseline model), these two factors were added as fixed effects. The selected model is in bold.

far. Indeed, most previous studies of variation in repeatability of behavioural traits have focused on a single life stage (Bell et al., 2009; Stamps & Groothuis, 2010). We found that docility was a repeatable behaviour in all age–sex classes in roe deer. This result is in line with findings in yellow-bellied marmots, in which docility was repeatable irrespective of age, as well as strongly correlated across ages (Petelle et al., 2013), in firebugs, *Pyrhocoris apterus* (Gyuris, Feró, & Barta, 2012) and lake frogs, *Rana ridibunda* (Wilson & Krause, 2012) in which behaviours were repeatable within life stages. However, we found that the level of repeatability for docility in roe deer was slightly higher in juvenile males than in other sex and age class categories, providing no support for the hypothesis that maturity shapes behavioural consistency. Bell et al. (2009) reported no overall difference in behavioural repeatability between juveniles and adults, but some studies they reviewed also indicated that behaviour was consistently more repeatable in juveniles than in adults. More generally, age-related variation in repeatability seems to depend on the behavioural trait and the species considered.

Sex differences in repeatability generally occur in adults (Bell et al., 2009) so that, when excluding mate preference behaviours, females express more consistent behaviours than males (but see Schuett & Dall, 2009 on zebra finches, and Jenkins, 2011 on kangaroo rats). However, this pattern relies on those few studies that provided sex-specific estimates of repeatability, and among those, the pattern is very variable. Among juveniles, the cost of deviating from a developmental trajectory is higher for males, potentially linking consistency to sexual selection (Biro & Stamps, 2008). The juvenile stage is a key phase in the development of individual behaviour. For instance, a strong correlation of docility across ages, with docility developing mainly during the juvenile stage and then remaining stable, was reported in yellow-bellied marmots (Petelle et al., 2013). In sexually dimorphic species, young males are known to differ from females in both their growth rate and behaviour early in life (Andersson, 1994), potentially leading to the observed tendency for a higher consistency in young roe deer males.

Individuals may differ substantially in their behavioural consistency (Bell et al., 2009) such that certain individuals may be able to adjust their behaviour to varying environmental conditions better than others (Dingemanse, Kazem, Réale, & Wright, 2010). In this study, we found that within-individual variation in docility was unrelated to individual body mass, a reliable indicator of phenotypic quality in most vertebrates, including roe deer (Toïgo et al., 2006). Although it has repeatedly been suggested that behavioural flexibility should entail costs (DeWitt et al., 1998; Niemela et al., 2013), these costs have only rarely been documented in wild populations (Auld, Agrawal, & Relyea, 2010; Lind & Johansson, 2009) and, indeed, some studies failed to identify any costs (Scheiner & Berrigan, 1998; Van Buskirk & Steiner, 2009; Van Kleunen, Fischer, & Schmid, 2000). In this context, our results suggest that there is some plasticity in docility in roe deer, but that the degree of this plasticity is unrelated to individual phenotypic quality, indicating either particularly low (with all individuals being similarly flexible) or high (with all individuals being similarly consistent) costs of behavioural flexibility.

The factors shaping between-individual variation in consistency have received little attention to date (Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011) and require further investigation (Dingemanse et al., 2010; Sih et al., 2004). Notably, in the context of rapid environmental modifications due to human disturbance and global change, the ability of individuals of a given population to adapt and flourish may depend on their ability to cope with

fluctuations of their environment through the expression of behavioural flexibility. Hence, as individual differences in behavioural flexibility might have consequences for ecological and evolutionary processes (Dingemanse & Wolf, 2013), we need more studies to evaluate how predictable different behaviours are and which factors influence their level of consistency.

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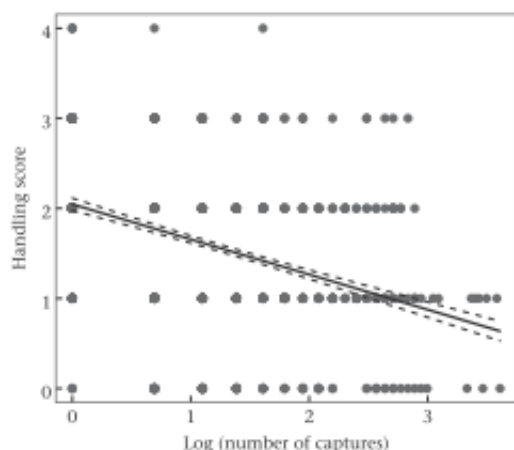
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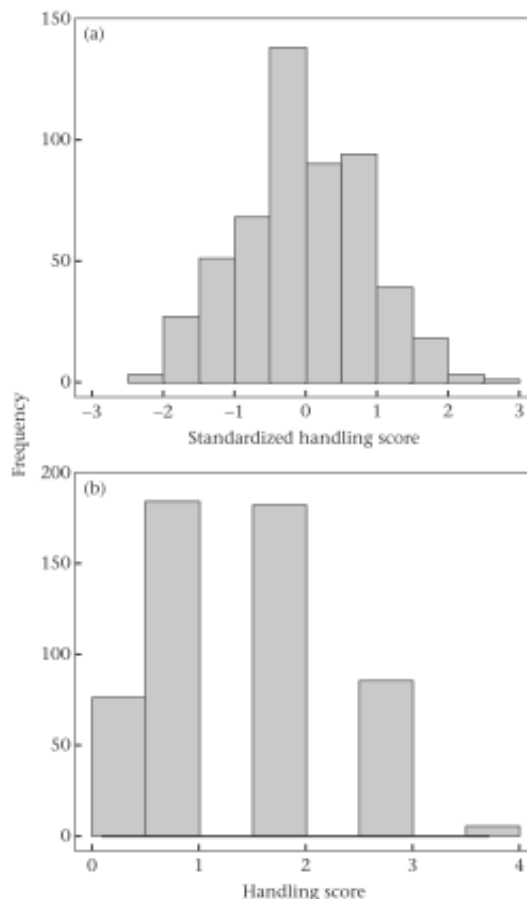
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Appendix



**Figure A1.** Linear regression between handling score (indexing docility, where low values indicate high docility) and the log-transformed number of captures using all available individuals ( $N_{\text{captures}} = 532$ ,  $N_{\text{individuals}} = 130$ ). The line represents the estimated slope of the relationship which was used to calculate the standardized handling score, and the dashed lines its associated standard error.



**Figure A2.** (a) Distribution of the handling score (to index docility) corrected for habituation, i.e. a negative link between reaction to handling during capture and the number of captures previously experienced by the individual. Note that the distribution is not normal: normality test of Shapiro–Wilk:  $W = 0.99$ ,  $P = 0.004$ . (b) Distribution of the raw handling score (normality test of Shapiro–Wilk:  $W = 0.89$ ,  $P < 0.001$ ). Note that low values indicate high docility.

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**Title:** Inter-individual heterogeneity of demographic performance and personality in roe deer (*Capreolus capreolus*)

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**Abstract:** Identifying the factors that influence the inter-individual variations of life history traits is important to understand the dynamics of natural populations, as well as to direct the conservation management of wild species. Recently, it has been shown that personality may also modify the way individuals cope with life-history trade-offs. Therefore, in this thesis, I focused on inter-individual variability in behavior in a large wild herbivore, the roe deer (*Capreolus capreolus*), and I explored its potential impact on components of individual fitness. I highlighted strong multi-dimensionality, in the behavioral expression of individuals with the existence of behavioral syndromes, but also with intra-individual correlations among levels. I also identified fitness consequences of the behavioral syndrome with, for example, an impact on the survival and growth of offspring. Thus, personality seems to affect the fate of individuals, as well as that of its offspring, and, *in fine*, the population's dynamics.

**Keywords:** behavioral ecology; roe deer; inter-individual variability; behavior; physiology; fitness

**Discipline:** Ecology, Biodiversity & Evolution

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**Titre :** Hétérogénéité interindividuelle de performances démographiques et personnalité chez le Chevreuil européen (*Capreolus capreolus*)

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**Résumé :** Il est important de pouvoir identifier les facteurs influençant la variabilité interindividuelle dans les traits d'histoire de vie pour comprendre la dynamique des populations. En parallèle, il a été montré que la personnalité pouvait modifier la manière dont les individus gèrent des compromis d'histoire de vie. C'est dans ce contexte que se situe cette étude, à savoir que l'objectif était de mesurer la variabilité interindividuelle comportementale chez le chevreuil et d'explorer ses liens potentiels avec les composants de la valeur sélective des individus. J'ai montré que cette variabilité interindividuelle comportementale est multidimensionnelle que ce soit dans l'expression du comportement des individus avec la mise en évidence de syndromes comportementaux ou dans les corrélations entre niveaux (comportemental, physiologique, hormonal) d'expression à l'échelle intra-individuelle. De plus, ces syndromes comportementaux affectent les traits d'histoire de vie de l'individu, mais aussi la survie et croissance des faons. Ainsi, la personnalité semble affecter l'avenir de l'individu tout au long de sa vie de même que sa progéniture et, *in fine*, la dynamique des populations.

**Mots clés :** écologie comportementale ; variabilité interindividuelle ; comportement ; physiologie ; valeur sélective

**Discipline :** Ecologie, Biodiversité & Evolution

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