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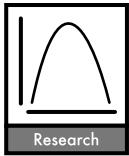
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Landscape fragmentation influences winter body mass of roe deer

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Body size of large herbivores is a crucial life history variable influencing individual fitness-related traits. While the importance of this parameter in determining temporal trends in population dynamics is well established, much less information is available on spatial variation in body size at a local intra-population scale. The relatively recent increase in landscape fragmentation over the last century has led to substantial spatial heterogeneity in habitat quality across much of the modern agricultural landscape. In this paper, we analyse variation in body mass and size of roe deer inhabiting a heterogeneous agricultural landscape characterised by a variable degree of woodland fragmentation. We predicted that body mass should vary in relation to the degree of access to cultivated meadows and crops providing high quality diet supplements. In support of our prediction, roe deer body mass increased along a gradient of habitat fragmentation, with the heaviest deer occurring in the most open sectors and the lightest in the strict forest environment. These spatial differences were particularly pronounced for juveniles, reaching >3 kg (ca 20% of total body mass) between the two extremes of this gradient, and likely have a marked impact on individual fates. We also found that levels of both nitrogen and phosphorous were higher in deer faecal samples in the more open sectors compared to the forest environment, suggesting that the spatial patterns in body mass could be linked to the availability of high quality feeding habitat provided by the cultivated agricultural plain. Finally, we found that adults in the forest sector were ca 1 kg lighter for a given body size than their counterparts in the more open sectors, suggesting that access to nutrient rich foods allowed deer to accumulate substantial fat reserves, which is unusual for roe deer, with likely knock-on effects for demographic traits and, hence, population dynamics.

For large herbivores, body mass is typically a reliable indicator of phenotypic quality. Body mass influences most life history traits, including early survival (Clutton-Brock et al. 1992, Gaillard et al. 1997, Loison et al. 1999), age at first reproduction (Saether and Haagerud 1985, Williamson 1991, Langvatn et al. 1996), litter size (Hewison 1996, Hewison and Gaillard 2001) and longevity (Gaillard et al. 2000a), and so can be considered as a good proxy for fitness related traits (Clutton-Brock 1991).

Body mass of large herbivores typically varies in time, particularly in relation to the conditions individuals experience during the early stages of life (cohort effect sensu Albon et al. 1987). For example, the quality and fate of a given cohort is tightly linked to population density during early development (Clutton-Brock et al. 1992, Rose et al. 1998, Pettorelli et al. 2002, Kjellander et al. 2006), conditioning the temporal dynamics of the population. However, spatial variation in environmental conditions (e.g. habitat quality) may play a similar role in influencing the quality of individuals, leading to spatial structure in

demographic traits, even at local scales (Conradt et al. 1999, Coulson et al. 1999, Focardi et al. 2002, Pettorelli et al. 2002, 2003), with important consequences for population dynamics (Milner-Gulland et al. 2000).

The roe deer is considered as originally a forest dwelling species, but which has recently undergone a demographic explosion leading to a rapid increase in both numbers and geographical range across Europe (Andersen et al. 1998). This expansion has led to the colonisation of new biotopes, with roe deer now present in agricultural, montane, Mediterranean garrigue and moorland environments (Linnell et al. 1998). Populations have particularly flourished in the modern agricultural landscapes which are widespread across Europe, where the fragmented mosaic of wood lots, hedgerows, meadows and cultivated crops seems particularly favourable (Hewison et al. 2001, Jepsen and Topping 2004). However, little is known about the demographic performance of roe deer in such contexts.

In this paper, we analyse variation in the body mass and condition of juvenile and adult roe deer living within an

agricultural landscape (7500 ha) which includes a gradient of local landscape structure. That is, the local environment varies in terms of woodland fragmentation, from a purely forested area, through more fragmented landscapes to a predominantly agricultural plain within a single study site (see also Hewison et al. 2007). We, therefore, looked for spatial variation in body mass and condition in relation to local landscape structure, notably woodland fragmentation. While much attention has been focused on the community and population-level effects of landscape fragmentation (Debinski and Holt 2000), as well as on body mass variation at a broad spatial scale (for example, geographical gradients and Bergmann's rule, Herfindal et al. 2006), there is currently little information on the relationship between fragmentation and indices of phenotypic quality such as body size at a local scale (but see Schmidt and Jensen 2003, Lomolino and Perault 2007).

Although little empirical information exists, roe deer of the open agricultural plain ("field roe deer") may attain higher body mass than their forest dwelling counterparts (Fruzinski et al. 1982). In addition, it has been suggested that deer populations are currently over-shooting the woodland carrying capacity because they are able to supplement their diet in these agro-system landscapes (Seagle 2003). Hence, we hypothesised that body mass should increase with landscape openness (prediction 1), probably due to the availability of nutrient rich foods provided by meadows and cultivated crops. In red deer, for example, the availability of meadows has been shown to be an important factor determining body mass, both in time and space (Mysterud et al. 2002), and may also affect lifetime reproductive success (see McLoughlin et al. 2007 in roe deer). As juveniles are commonly more susceptible to variation in environmental conditions (see Gaillard et al. 2000b for a review), we also hypothesised that spatial differences in body mass should be most pronounced for this age class (prediction 2).

We have previously shown that deer density 100 ha^{-1} of woodland habitat was similar across this landscape (Hewison et al. 2007) and so, in the present analysis, we supposed that any differences in phenotypic quality must be generated by landscape-related differences in food availability and/or quality. Hence, we tested this hypothesis (prediction 3) by investigating spatial variation in diet quality as indexed by levels of nitrogen and phosphorous in faecal samples (for studies of the relationship between dietary and faecal nitrogen and phosphorous, see Erasmus et al. 1978, Howery and Pfister 1990, Ueno et al. 2007) in relation to landscape openness.

Finally, roe deer are generally considered income breeders (sensu Jönsson 1997), which stock few fat reserves (Hewison et al. 1996), relying instead on energy intake to offset the costs of reproduction (Andersen et al. 2000). From this point of view, any variation in body mass should be strongly determined by body size rather than condition (fat stores) (Toïgo et al. 2006). We, therefore, hypothesised that all individuals should follow a single allometric relationship such that heavier deer are also proportionately larger (prediction 4). To test this hypothesis, we examined the allometric relationship between body mass and body size (indexed as hind foot length) for deer living along the gradient of local landscape structure.

Methods

Study site

The study was carried out in a fragmented agricultural landscape of the Aurignac canton ($43^{\circ}13'N$, $0^{\circ}52'E$), situated in the Comminges region of south-west France (Hewison et al. 2007). It is a hilly region, rising to a maximum of 380 m a.s.l., which has undergone substantial modification over the last century due to intensification of agricultural practice, with a loss of hedges and copses, the planting of new crop types (corn, sorghum) and an increase in average field size. Note, however, that during the present study, landscape modifications were minor compared to the marked contrasts in structure across the landscape (e.g. extent of wooded habitat was 15.79% in 1990 and 15.97% in 2000, Pekkarinen et al. in press; <forest.jrc.ec.europa.eu/ForestResources/ForestMap/>). It is a mixed landscape of open fields and small woodland patches (average size 3 ha), with a central larger forest of 672 ha. The primary land use is pastoral for sheep and cattle grazing, with agricultural crops on the increase. The human population is present throughout the site, in small villages and farms distributed along the extensive road network which covers the study site. The climate is oceanic with an average annual temperature of $11-12^{\circ}C$ and 800 mm precipitation, mainly in the form of rain.

The total study area covers ca 7500 ha, of which about one fifth is wooded (Fig. 1). The natural vegetation of the area is classified as a south west European lowland-colline downy oak forest (Bohn et al. 2002). At present, the landscape is characterised by woodland patches (14% of the area) dominated by oak *Quercus* spp., often associated with hornbeam *Carpinus betulus*, while the central forest (7% of the area) is a mixed species forest of Douglas-fir *Pseudotsuga menziesii*, pine *Pinus* spp., oak *Quercus* spp. and hornbeam *Carpinus betulus*. The understorey is dominated by brambles *Rubus* spp., common honeysuckle *Lonicera periclymenum*, ivy *Hedera helix* and butcher's broom *Ruscus aculeatus*. Meadows cover ca 34% of the total area, of which 38% are dominated by *Dactylis glomerata* and *Festuca arundinacea*, 27% by *Festuca rubra* and *Agrostis capillaris*, 15% by ray grass *Lolium perenne*, 11% by *Holcus lanatus* and *Lolium perenne*, and 9% by lucerne *Medicago* sp. and clover *Trifolium* sp. With the exception of ray grass, the meadows also contain forbs such as the legumes *Potentilla* sp., *Sanguisorba* sp., *Geranium* sp., and *Taraxacum* sp. which are palatable for roe deer. About 33% of the total area is now cultivated, mostly with wheat and barley (51%), sunflower (15%), maize (10%), soya (5%), sorghum (8%) and rape (4%). Hedges cover 7% of the total area and contain numerous ligneous shrubs and trees (*Prunus spinosa*, *Cornus* sp., *Lonicera* sp., *Quercus* sp., *Rubus* sp., *Rosa* sp., *Crataegus* sp., *Hedera helix*, *Ligustrum vulgare*), grasses, sedge and forbs (*Gallium* sp.).

The roe deer population is hunted on a regular basis by drive hunts with dogs during autumn–winter (September–January) and stalking during summer (June–August, bucks only). The hunting teams are organised in relation to the boundaries of one, or a few, communes. Deer density in the central forest was estimated at around 34 deer 100 ha^{-1} in the winter of 2005, while density 100 ha^{-1} of woodland in the surrounding fragmented landscape was of a similar level

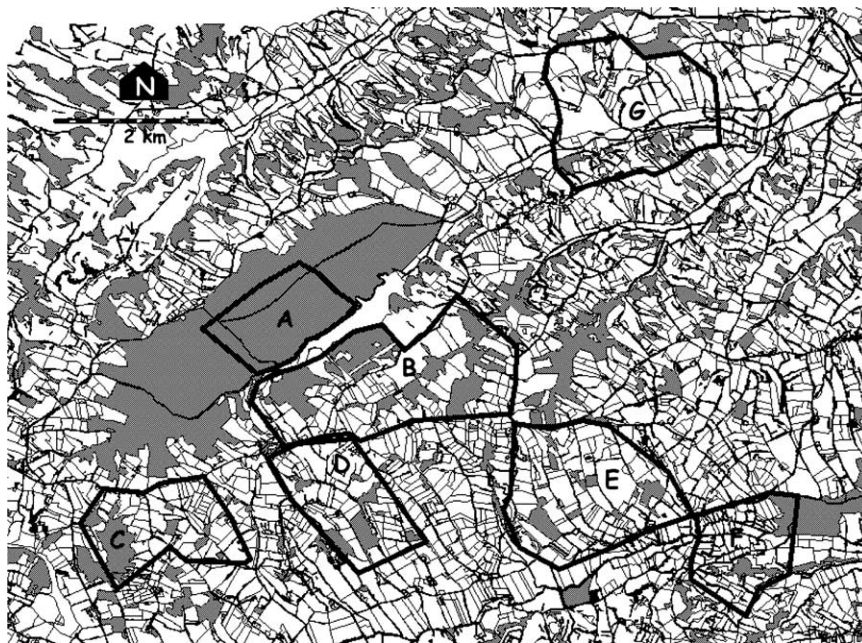


Figure 1. Map of the study site (situation in 2007) illustrating the varying degree of woodland fragmentation across the landscape at the seven catch sites. Woodland and hedgerows are depicted in grey, the line in the top left corner measures 2 km. For analysis, we identified three sectors based on landscape characteristics: 1 = a forest sector (catch site A), 2 = a woodland sector (catch site B), and 3 = an open agricultural sector (catch sites C–G) (see text for further explanation).

(31.6–52.4, Hewison et al. 2007). Standardised car transects during winter (counts of all deer seen along a 42 km circuit of the study site, repeated at dawn and dusk 6–10 times yr^{-1} , February–March) indicate a relatively stable population from 1992 to 2001, followed by a fall in 2002 and a subsequent increase to previous levels (unpubl.).

Study population and data collection

From 1996 to 1997 and then from 2001 to 2008 (i.e. a total of 10 sampling years), roe deer were caught during winter (from 16 November to 27 March) using large-scale drives of between 30 and 100 beaters and up to 4 km of long-nets positioned at one of seven spatially distinct capture sites (Fig. 1), with 90% of deer caught at four of these sites (A, B, F and G on Fig. 1). For each animal we recorded its weight (with an electronic balance to the nearest 0.1 kg), its sex and the length of its hind foot (with a customised slide ruler to the nearest mm; measurement was repeated by two independent observers to ensure minimal measurement error). Juveniles (less than one year-old) are distinguishable from older deer by the presence of a tricuspid third pre-molar milk tooth (Ratcliffe and Mayle 1992). Tooth wear was used to assign older deer to one of the following classes: 1.5 yr of age, 2.5–3.5 yr of age, 4.5–6.5 yr of age and older than 6.5 yr of age. However, because errors are common using this technique (Hewison et al. 1999), we retained only two adult age classes for the analysis (yearlings and adults of >2 yr of age, see below). From 2003 onwards, a sample of faecal pellets was extracted directly from the anus of the deer and stored in a freezer. Deer were then equipped with ear tags and, for some, a radio-collar (for home range and habitat use studies) and released on site. A total of 268 deer were caught, 119 in the

central forest and 149 in the surrounding fragmented landscape. Of these, 45 were re-captured on at least one further occasion (max. = 5 re-captures).

The level of faecal nitrogen and phosphorous was subsequently evaluated for a total of 120 deer. The faecal pellets were first thawed, ground to a powder (0.5 mm) and oven-dried at 80°C for 48 h. Then, using the ground milled faecal material, total N content (N%) was determined with a CN gas analyser (LECO Corporation, St Joseph, MI, USA), while total P content (P%) was obtained after wet digestion in $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ using the ceruleomolydic blue method (Murphy and Riley 1962).

Statistical analysis

The seven capture sites were grouped into 3 landscape units based on contrasting landscape structure in terms of woodland extent and the relative proportions of meadows and cultivated fields (Fig. 1). Thus, we identified a forest block (sector 1: catch site A; $n=119$ deer), a partially wooded area (sector 2: catch site B; $n=38$ deer) and an open agricultural area with highly fragmented woodland (sector 3: catch sites C–G; $n=111$ deer). The landscape characteristics of these sectors are provided in Table 1. Because single catch sites were small (400 ha or less) compared to roe deer home range size (generally between 50 and 150 ha in this study, unpubl.), individual deer caught at a given site were assumed to range over a large proportion of that landscape. Note, we could not analyse our data at the individual level, as all deer caught at a given catch site would then be assigned identical landscape characteristics, leading to problems of pseudo-replication.

We then used general linear models to investigate variation in body mass and condition among sectors

Table 1. Landscape characteristics of the three sectors of contrasting landscape structure (1 =forest sector; 2 =woodland sector; 3 =open agricultural sector).

Sector	Habitat area (ha)	%	Number of habitat patches	Mean patch size, ha (SD)
Sector 1 (259 ha)				
– woodland	153	100	1	–
Sector 2 (397 ha)				
– woodland	139	35.0	20	6.9 (9.3)
– hedgerows	8	2.1	81	0.1 (0.1)
– meadows	153	38.5	87	1.8 (3.2)
– cultivated fields	86	21.6	43	1.9 (1.8)
Sector 3 (1217 ha)				
– woodland	153	12.5	75	2.0 (3.9)
– hedgerows	77	6.3	356	0.2 (0.7)
– meadows	411	33.8	327	1.3 (1.6)
– cultivated fields	520	42.7	249	2.1 (3.1)

(3-level factor), including sex as a 2-level factor to account for the fact that roe deer are slightly sexually dimorphic (Andersen et al. 1998). Because the vast majority of deer were caught only once and to avoid pseudo-replication problems, for animals that were re-captured on more than one occasion, we used the data taken during the first capture event only for this analysis. We analysed data for juveniles (<1 yr of age) and older deer separately. For juveniles, we included the date of capture (Julian date running from 1 September, JD = 1, to 31 March, JD = 212) in the model to account for the fact that these animals continue to grow during their first winter (Hewison et al. 2002). For adults, we included age class in the model using only the two classes defined above (yearlings vs adults of > 2 yr of age).

We first looked for a relationship between body mass and landscape structure by analysing variation in body mass between the 3 sectors and between the 2 sexes for juveniles and older deer separately. For juveniles, we included year of capture in the models as a random factor in a mixed model procedure in order to control for possible confounding cohort effects (*sensu* Albon et al. 1987). For adults, however, as these animals were first caught as adults and hence exact age was not known, potential cohort effects associated with their year of birth could not be controlled for. Note, also, that year of capture is unlikely to have any marked effect on adult body mass, as a capture year comprises a mix of different cohorts and as the body mass of roe deer adults varies little with age (Hewison et al. 1996), being overwhelmingly determined by conditions in the year of the animal's birth (cohort) (Pettorelli et al. 2002).

Subsequently, we investigated spatial variation in body condition by analysing the allometric relationship between body mass and body size (see also Toigo et al. 2006), regressing the natural log of body mass on the log of hind foot length for juveniles and adults separately. For juveniles, we pooled data for both sexes as dimorphism is low or absent at this age (see Results, also Gaillard et al. 1996, Hewison et al. 2002) and, as roe deer of this age are still growing, we expected both sexes to follow a single allometric relationship. For the analysis of adult deer, we removed all yearlings (1.5 yr of age, $n = 25$) as these animals were also still growing and clearly much lighter than older adults. We then looked for differences in this relationship as

a function of landscape structure by comparing the slope and intercept of the allometric relationship for the forest sector with that of the more open fragmented landscape (combining data from sectors 2 and 3, as there were not enough data to retain 3 sectors because hind foot length data were not available for all captured deer) for both sexes.

Finally, we looked for spatial variation in diet quality by using general linear models to investigate spatial variation in the level of faecal nitrogen and phosphorous across the landscape. We used a simple analysis of variance on arc-sine transformed values for each faecal parameter, with sector fitted as a 3-level factor.

In all cases, we fitted the most general model as a starting point, including the main factors and all 2 and 3-way interaction terms. We then proceeded to simplify this model by successive withdrawal of the non-significant terms in a backward stepwise procedure (see Crawley 1993 for details). The final selected model was considered as the model where no further terms could be withdrawn without significantly reducing the explanatory power of the model. All calculations were performed with R software (R Development Core Team 2007).

Results

Body mass variation

For juveniles, we found no significant two-way interaction between the predictor variables sex and sector in their influence on body mass changes of juveniles over the winter (Log-likelihood ratio = 1.90, $p = 0.387$). Similarly, we found no two-way interaction between sex and sector on body mass at a given date (Log-likelihood ratio = 0.47, $p = 0.789$) and over winter body mass changes did not differ between the sexes (Log-likelihood ratio = 0.37, $p = 0.543$) or between sectors (Log-likelihood ratio = 1.18, $p = 0.555$). Indeed, body mass of juveniles did not change significantly over the winter (Log-likelihood ratio = 1.04, $p = 0.307$). However, body mass varied significantly between the sexes (Log-likelihood ratio = 5.22, $p = 0.022$) and among the 3 sectors (Log-likelihood ratio = 26.82, $p < 0.001$). Male juveniles weighed on average 0.8 kg (SE = 0.38) more than females. Juveniles were lightest in the forest sector, were on average 2.0 kg (SE = 0.59) heavier in the woodland sector

and 3.1 kg (SE = 0.43) heavier in the open agricultural sector (Fig. 2).

For older deer, the three-way interaction between sex, age class and sector in their influence on body mass of adults was not significant ($F_{1,164} = 0.04$, $p = 0.851$). Similarly, we found no significant two-way interaction between sex and age ($F_{1,165} = 2.25$, $p = 0.135$), age and sector ($F_{2,165} = 1.21$, $p = 0.300$) or sex and sector ($F_{2,165} = 0.38$, $p = 0.686$). However, body mass varied significantly between the sexes ($F_{1,170} = 15.33$, $p < 0.001$), between age classes ($F_{1,170} = 38.60$, $p < 0.001$) and among the 3 sectors ($F_{1,170} = 8.93$, $p < 0.001$). Male adults weighed on average 1.3 kg (SE = 0.32) more than females and yearlings weighed on average 2.8 kg (SE = 0.46) less than older adults. Deer were lightest in the forest sector, were on average 1.6 kg (SE = 0.49) heavier in the woodland sector and 1.3 kg (SE = 0.34) heavier in the open agricultural sector (Fig. 3).

Allometric relationship between body mass and hind foot length

For juveniles, the slope of the mass-size allometric relationship differed significantly between the forest sector and the fragmented landscape (sectors 2 and 3 combined) (Log-likelihood ratio = 8.89, $p = 0.003$). Hind foot length increased by 3.7 cm (SE = 0.31) per kg of body mass in the forest, but by 2.4 cm (SE = 0.45) in the fragmented landscape. Thus, although juveniles from the forest sector were consistently lighter for a given body size than juveniles from the fragmented landscape, this difference was particularly marked for very small individuals (Fig. 4a).

For older deer, we found no significant two-way interaction between the predictor variables sex and sector (2 modalities: forest vs fragmented landscape) in their influence

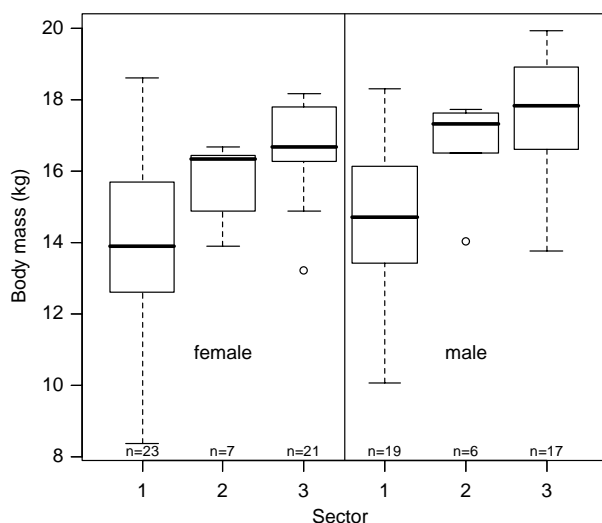


Figure 2. Body mass of juvenile (8–10 months old) roe deer across the three sectors of contrasting landscape structure (1 = forest sector; 2 = woodland sector; 3 = open agricultural sector). Circles represent outlying data points, the box encompasses the first to the third quartiles, inside the box the horizontal line represents the median and the whiskers are located at $1.5 \times \text{IQR}$ (inter-quartile range) below the first quartile and at $1.5 \times \text{IQR}$ above the third quartile.

on the slope ($F_{1,92} < 0.01$, $p = 0.989$) or the intercept ($F_{1,93} = 1.16$, $p = 0.284$) of the mass-size allometric relationship among adults. Similarly, the allometric relationship did not differ in slope between the sexes ($F_{1,93} = 1.74$, $p = 0.190$) or between the forest sector and the fragmented landscape ($F_{1,93} = 0.08$, $p = 0.774$). The allometric relationship was significant ($F_{1,97} = 18.95$, $p < 0.001$) and indicated that hind foot length increased by 1.3 cm (SE = 0.30) per kg of body mass. There was, however, a significant difference in the intercept of this relationship between the sexes ($F_{1,97} = 5.39$, $p = 0.022$) and between the forest sector and the fragmented landscape ($F_{1,97} = 4.43$, $p = 0.038$). Males were on average 1.0 kg (SE = 1.02) heavier for a given body size than females, and adults from the forest sector were on average 1.0 kg (SE = 1.02) lighter for a given body size than adults from the fragmented landscape (Fig. 4b).

Spatial variation in diet quality

There was significant variation in both faecal nitrogen ($F_{2,117} = 33.10$, $p < 0.001$) and faecal phosphorus ($F_{2,117} = 22.67$, $p < 0.001$) among the three sectors. For both elements, the most marked difference was between the forest sector and the other 2 more open sectors, although there was also a trend for both elements to increase slightly with increasing landscape openness (Fig. 5).

Discussion

We found pronounced variation in body mass of both juvenile and adult roe deer along a gradient of habitat fragmentation within a single study site, with the heaviest deer occurring in the most open sectors and the lightest in

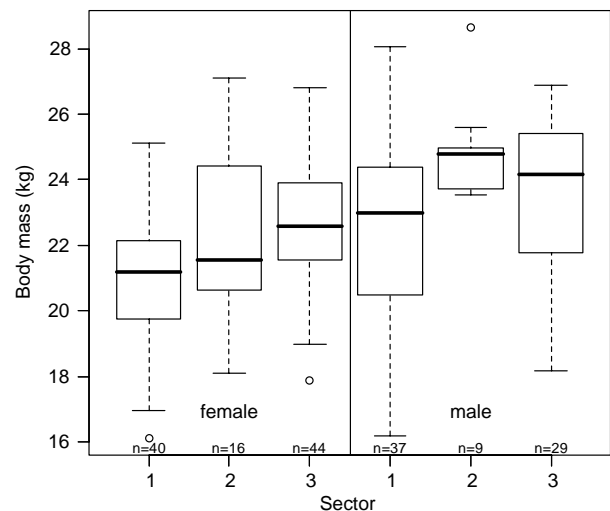


Figure 3. Body mass of adult male and female roe deer across the three sectors of contrasting landscape structure (1 = forest sector; 2 = woodland sector; 3 = open agricultural sector). Circles represent outlying data points, the box encompasses the first to the third quartiles, inside the box the horizontal line represents the median and the whiskers are located at $1.5 \times \text{IQR}$ (inter-quartile range) below the first quartile and at $1.5 \times \text{IQR}$ above the third quartile.

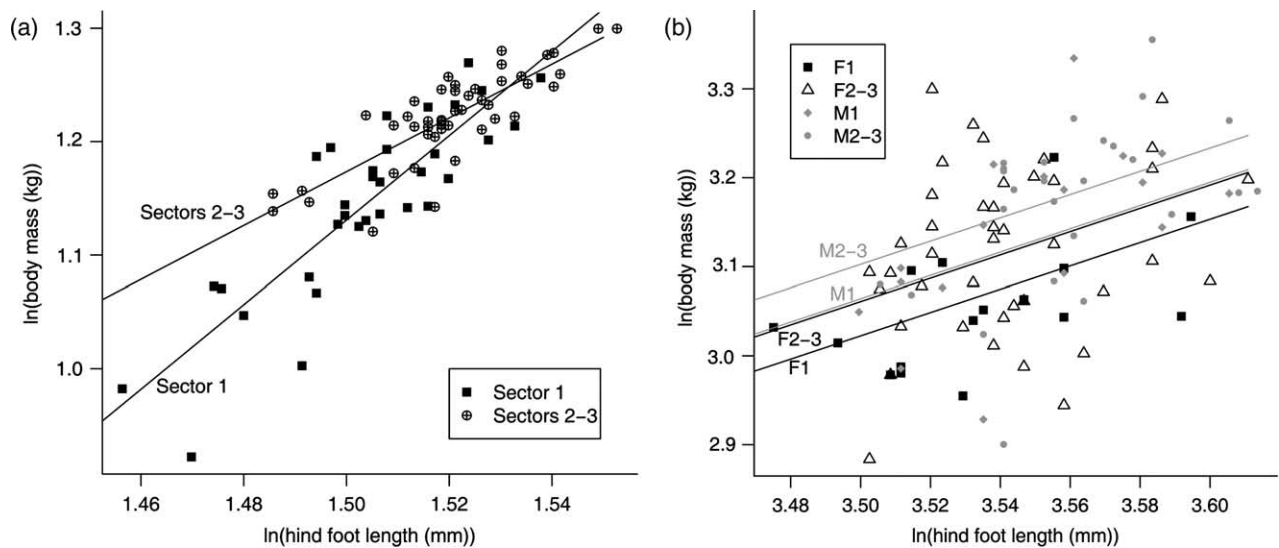


Figure 4. The allometric relationship between body size (hind foot length) and body mass of (a) juvenile (8–10 months old) and (b) male and female adult roe deer living in the central forest (sector 1) or in the surrounding fragmented landscape (sectors 2 and 3 combined).

the strict forest environment, supporting our first prediction. In agreement with previous work (Pettorelli et al. 2002, 2003), we found that the spatial pattern of body mass variation was similar between the sexes, which is expected for a species with relatively low sexual dimorphism (Andersen et al. 1998). In support of our second prediction, these spatial differences in body mass were particularly pronounced among juveniles, reaching more than 3 kg (ca 20% of total body mass) between the two extremes of this gradient. This is of a similar range to observed body mass variation among cohorts over time in response to marked changes in environmental conditions in 2 long-term monitored roe deer populations (Kjellander et al. 2006). Pettorelli et al. (2003) also found that body mass of

roe deer fawns varied to a similar degree over time (among years) and through space, with a 2 kg range across the studied woodland population. Differences of this magnitude certainly have an impact on the fate of individual roe deer, potentially influencing over-winter survival (Gaillard et al. 1993a) and future reproductive output (Hewison 1996, Hewison and Gaillard 2001). In agreement with our third prediction, this landscape-related variation in phenotypic quality was mirrored by the pattern of spatial differences in diet quality as indexed by faecal nitrogen and phosphorous levels. In contrast, our fourth prediction that, because roe deer are income breeders with low levels of stored fat (Andersen et al. 2000), all individuals living along the gradient of local landscape structure should follow a

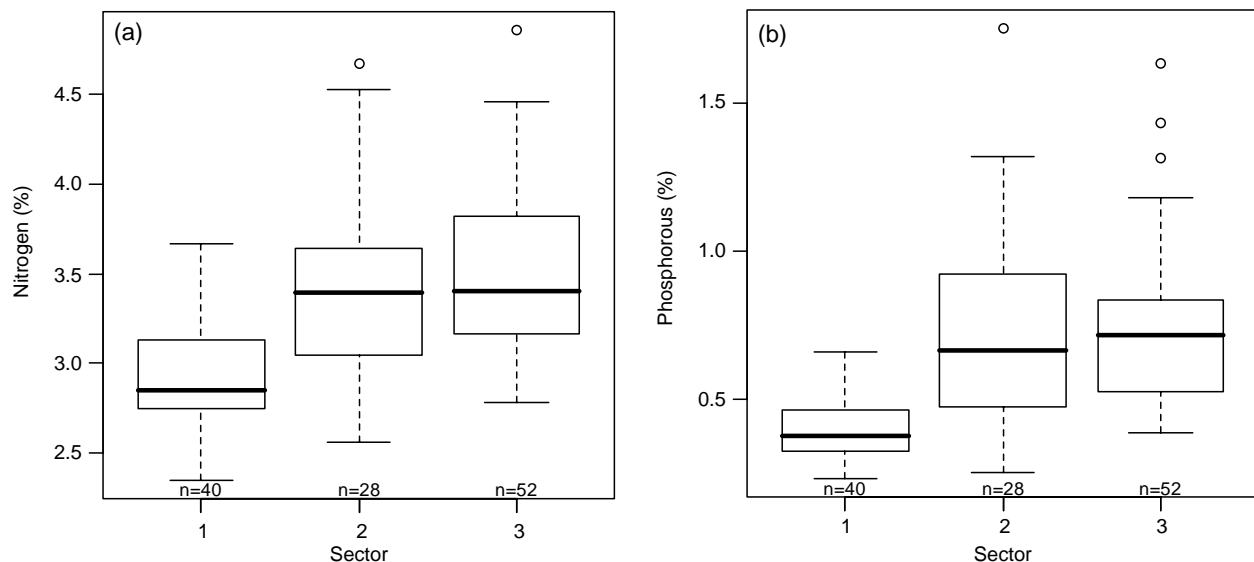


Figure 5. The levels of (a) nitrogen and (b) phosphorous in the faecal samples of roe deer caught in the three sectors of contrasting landscape structure (1 = forest sector; 2 = woodland sector; 3 = open agricultural sector). Circles represent outlying data points, the box encompasses the first to the third quartiles, inside the box the horizontal line represents the median and the whiskers are located at $1.5 \times$ IQR (inter-quartile range) below the first quartile and at $1.5 \times$ IQR above the third quartile.

single allometric body mass-body size relationship was not supported. Rather, we found that, for a given body size, adult deer in the forest sector were ca 1 kg lighter than those in the fragmented landscape. This suggests that access to the nutrient rich foods provided by the meadows and cultivated crops of the agricultural plain allowed deer to accumulate substantial fat reserves (Mysterud et al. 2002), with likely knock-on effects for demographic traits and, hence, population dynamics.

The spatial differences in phenotypic quality that we observed among sectors of differing local landscape composition are most probably due to habitat-related variation in early growth rates, both in utero and during the first summer of life (Cook et al. 1996, Gaillard et al. 1996, Hewison et al. 2002). This is supported by the pattern of increasing levels of faecal nitrogen and phosphorous along the gradient of habitat fragmentation (Blanchard et al. 2003), with a marked contrast between the central forest sector and the rest of the more open landscapes (Fig. 5). Higher resource availability and/or quality provides for accelerated growth and, hence, higher body mass and size at the onset of winter (Coté and Festa-Bianchet 2001, Ericsson et al. 2002), leading to higher body mass also among adults (Pettorelli et al. 2002). In particular, high abundance of preferred plant species is likely a strong determinant of spatial variation in body mass (Pettorelli et al. 2001, 2003) and, therefore, fitness related traits (Pettorelli et al. 2005, McLoughlin et al. 2007). For example, Pettorelli et al. (2003) found that the heaviest roe deer fawns within the Chizé forest were associated with oak stands that were rich in hornbeam, star of Bethlehem *Ornithogalum* sp. and bluebells *Hyacinthoides* sp., whereas the lightest were found in beech stands *Fagus sylvatica* with butcher's broom, wild madder *Rubia peregrina* and brambles. Habitat-related variation in both abundance and quality of food was likely very high in our study site, particularly between the forest environment on the one hand and the fertilised meadows and cultivated fields on the other. Fertilisation is carried out on our study site in both the meadows and the cultivated fields and results in higher biomass and increased leaf nitrogen content, leading to a higher intake rate among herbivores (Delagarde et al. 1997). Indeed, wild herbivores may often prefer to feed in fertilised plots (e.g. moose and hare, Ball et al. 2000). At a coarse spatial scale, Mysterud et al. (2002) found a positive link between red deer body mass and the proportion of meadows in the landscape. In our study site, roe deer feed on plants from the forest, meadows and cultivated areas (unpubl.), hence, it is likely that roe deer with access to fertilised meadows and crops obtained a higher quality diet than those living in the forest. This is of particular importance for a small-sized ruminant such as the roe deer which is limited by rumen size and, hence, must be selective for high quality forage (Duncan et al. 1998). To better identify the habitat-related parameters which are driving spatial differences in body mass across the landscape, it will be necessary in the future to collect data on body mass, ranging behaviour and diet quality at the individual scale.

The fact that the relationship between habitat fragmentation and body mass seems to be more marked among juveniles than among adults might indicate that deer in the more forested landscape contexts were able to compensate for their

poor start in life (see also Fruzinski et al. 1982). However, while such compensatory growth has been documented in early life, from a roe deer fawn's first spring to its first winter (Gaillard et al. 1993b, Pelliccioni et al. 2004), this is not the case for juveniles of low body mass in their first winter (Pettorelli et al. 2002). Alternatively, the adult deer that were caught in a given landscape sector may not necessarily have originated there, as dispersal rates and distances are quite high across this landscape (unpubl.). The body mass of an immigrating individual should be more closely linked to the resource availability in the local landscape at the site of its birth rather than in its current home range, as adult body mass is strongly determined by mass at first winter (Pettorelli et al. 2002). Hence, it is likely that juvenile body mass prior to dispersal best translates landscape-related variations in resource availability over our study area.

Our data also indicate that demographic performance likely increases with landscape openness across our study site, as the ratio of average juvenile body mass to average female adult body mass increased from its lowest value in the forest sector (65%, close to that of the low demographic performance population in Chizé forest, Delorme et al. 2007) to its highest in the open agricultural sector (75%, somewhat superior to that of the high performance population of Trois Fontaines forest, Delorme et al. 2007). This ratio is hypothesised to reliably index demographic performance of roe deer populations (Delorme et al. 2007) and indicates that not only are juveniles and adults lighter in the forest sector than elsewhere, but that these light females also allocate proportionally less to reproduction. These observations highlight the potential role of woodland fragmentation in determining both temporal and spatial dynamics of deer populations and lend support to the hypothesis that they may be currently over-shooting woodland carrying capacity because they are able to supplement their diet in these agro-system landscapes (Seagle 2003).

A somewhat unexpected result of our study was that landscape structure also appeared to markedly influence body condition of roe deer. Among both juveniles and adults, individuals in the fragmented agricultural landscape were heavier in relative (for a given body size) terms than those in the central forest, indicating that the former were in better condition than the latter. This is supported by anecdotal observations of hunted carcasses which clearly carry more fat in the open landscape compared to the forest (with mesenteric and kidney fat exceeding 400 g in some cases, unpubl.). This appears surprising at first, as this species is commonly viewed as an income breeder (sensu Jönsson 1997, Andersen et al. 2000), with only few fat reserves (Hewison et al. 1996). Indeed, Toïgo et al. (2006) concluded that body mass and body size were better measures of phenotypic quality than condition for roe deer. However, this conclusion was based on an analysis of temporal variation in mass, size and condition of forest roe deer due to density-dependence and climatic factors. In contrast, Kjellander et al. (2006) observed that Swedish roe deer were not only heavier and bigger than their French counterparts in absolute terms, they were also heavier for a given body size (i.e. in better condition), indicating substantial accumulation of fat reserves. They suggested that this could reflect adaptation to increasingly seasonal environments (Lindstedt and Boyce 1985) or, alternatively, the higher quality of food resources in

northern environments (Geist 1987, see Herfindal et al. 2006 for a case study). The most likely explanation for our findings is that the roe deer in the more open sectors of the landscape are able to accumulate unusual amounts of fat because of the high quality forage available in the fertilised crops and meadows (i.e. a plastic response to habitat richness, see Peltier and Barboza 2003 for the effects of high nitrogen diets on fat deposition in muskoxen *Ovibos moschatus*). However, the agro-system is also markedly more seasonal than the forest, as resource availability varies dramatically in relation to crop planting and harvesting cycles. Hence, a more speculative suggestion would be that roe deer have adapted to these seasonal contrasts of cultivated landscapes by stocking more reserves during spring-summer and early autumn, when resources are superabundant, to cope with the dramatic fall in resource availability when crops are harvested and fields lie fallow.

Our findings clearly have implications for spatial population dynamics (see Focardi et al. 2002 for a case study on roe deer). Indeed, because much research on roe deer life history traits has concentrated on the forest environment (Gaillard et al. 1993a, 1996, 1997, Pettorelli et al. 2001, 2002, 2003), little is known about the determinants of demographic variation in the fragmented and heterogeneous landscapes which are typical of much of the current geographical range of this species. It is commonly assumed that roe deer are dependent to some degree on woodland habitat (Hewison et al. 2001) and that woodland acts as a source for colonising populations (e.g. hunting reserves). However, our data suggest that phenotypic quality, and hence performance, across heterogeneous landscapes is likely higher when deer have access to cultivated crops and meadows to supplement their diet. Hence, the pattern of source-sink dynamics in such a system is not necessarily intuitive, although the higher diet quality available in open landscapes may be counter-balanced to some degree by potentially higher fitness costs due to more intensive human activity and disturbance, particularly through hunting and collisions with vehicles (unpubl.). Managers should account for landscape-related variation in phenotypic quality when evaluating the impact of human-related pressures such as hunting and modification of agricultural practices on deer population dynamics.

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