Early development, recruitment and life history trajectory in long-lived birds

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ABSTRACT

Lindström (1999) synthesized knowledge about "early development and fitness in birds and mammals", interesting tracks and challenges for future studies. Today there is unambiguous evidence that Lindström's first statement holds in long-lived birds: "It is obvious that adverse environmental conditions might have immediate effects […]." However, whether there are "long-term fitness consequences of conditions experienced during early development" (Lindström's second statement) is unclear for long-lived birds. The extent to which the disadvantage of frail individuals at independence is expressed predominantly in terms of higher mortality and disappearance from the population before recruitment, or persists after recruitment, is still an open question. Due to rarity of relevant data and the fact that most studies are retrospective, heterogeneity in methods and time scales hampers identification of general patterns. Nevertheless, several studies have provided evidence of a relationship between early conditions and future reproductive parameters, or lifetime reproductive success. Evidence from large mammals suggests substantial long-term individual and population effects of early conditions, including trans-generational maternal effects. Evidence from short-lived birds also suggests long-term individual consequences, and maternal effects have been documented in long-lived ones. Despite logistical and financial difficulties inherent in long-term studies, they are the only way of addressing Lindström's second statement. Existing long-term longitudinal data sets should be re-analyzed using recently developed capture-mark-recapture models handling state uncertainty and unobservable heterogeneity in populations. Statistical methods designed to estimate lifetime reproductive success or incorporate pedigree information in standard situations of studies of wild vertebrates with imperfect detection offer new opportunities to assess long-term fitness consequences of early development in long-lived birds.

Keywords: life history evolution, longitudinal studies, long-term effects, population dynamics

INTRODUCTION

Background. A decade ago, in a paper entitled "Early development and fitness in birds and mammals", Lindström (1999) stated that "It is obvious that adverse environmental conditions might have immediate effects [...]. However, the long-term fitness consequences of conditions experienced during early development have been documented only recently". Long-lasting effects of early conditions are receiving growing attention because large differences in lifetime reproductive success among individuals may result from differences in the conditions under which growth or ontogeny from birth to recruitment take place (de Kogel 1997; Hamel et al. 2009; Metcalf and Monaghan 2001; Newton 1989; van de Pol et al. 2006 a). In addition, it has been shown that life history characteristics such as senescence rate may vary with conditions during development (Nussey et al. 2007). Individuals may compensate adverse early conditions by growing fast when conditions improve, but may incur delayed costs and reduced longevity (Metcalfe and Monaghan 2001, 2003). Here the main question we will focus on is whether there is evidence of long-term *fitness* consequences of early conditions in long-lived birds (evidence of morphological or physiological consequences isn't 'sufficient'). It is not our intention to provide a full review of the literature on the topic. We recognize that our perception of current knowledge on the subject in the literature led us to express a subjective opinion inspired by a large number of studies addressing small parts of the problem in a large range of species; of course, the same body of material may inspire different opinions in other researchers.

A flurry of traits, mechanisms and consequences. As summarized in Burness et al. (2000), in mammals and birds, the environment experienced during ontogeny may have morphological, behavioral and life history consequences. Individuals experiencing harsh conditions during development (e.g., parasite load, weather, food availability) may exhibit smaller structural size and mass at independence, lower survival probability in the first year, and lower recruitment probability (Boag 1987; Braasch et al. 2009; de Kogel 1997; Dijkstra et al. 1990; Hall

et al. 2001; Magrath 1991; McDonald et al. 2005; Naef-Daenzer et al. 2001; Perrins 1965; Richner 1989; Sedinger et al. 1995; Szép and Møller 1999; Tinbergen and Boerlijst 1990; van der Jeugd and Larsson 1998; Verboven and Visser 1998). There is some indication that fledging date, structural size or mass at independence influence the probability of acquiring a territory as well (Both et al. 1999; Drent 1983). If they reach reproductive status, individuals may exhibit lower reproductive fitness components (e.g., smaller egg or clutch sizes; Braasch et al. 2009; Gorman and Nager 2004; Haywood and Perrins 1992; Potti 1999; Schluter and Gustafsson 1993). Differences in reproductive success may sometimes result from use of lower-quality breeding habitat (see Verhulst et al. 1997 for an example in a long-lived bird, the Oystercatcher *(Haematopus ostralegus*) or access to lower-quality mates because of lack of attractiveness of secondary sexual characters (Blount et al. 2003; de Kogel and Prijs 1996; de Kogel 1997; but see Walling et al. 2007 in a different taxon). Variation in the quality of the rearing environment is assumed to result in differences in the physiological condition (Burness et al. 2000) or morphology of individuals reared in that environment, which in turn may result in differences in survival probabilities, and possibly variation in the adult physiological or morphological phenotype (de Kogel and Prijs 1996; Haywood and Perrins 1992; Perrins 1965; Schluter and Gustafsson 1993; but see Lendwai et al. 2009). Differences in personalities (and correlated fitness differences) may also arise from early environment (Dingemanse et al. 2004; Dingemanse and Réale 2005; Krause et al. 2009; Stamps and Groothuis 2010). Alternatively, there may not be any observable trait associated with lower survival (or at least one we know how to identify and measure), which may result in a "cryptic" structure of populations (Fox and Kendall 2002; Kendall and Fox 2002). Last, evidence has been found in long-lived species that offspring early survival depends on sex under stressful conditions (e.g., Nager et al. 2000).

Increased interest in physiological 'paths'. There is currently increased interest in physiological mechanisms ('paths') responsible for the long-term consequences of early

development (e.g., Merilä and Svensson 1997; Thomas et al. 2007). There is evidence that early life development can directly affect the immune system and physiology through trans-generational effects, both positively and negatively. Müller et al. (2009) have shown that maternal hormones in bird eggs enhanced post-natal growth rate on the one hand, but decreased asymptotic mass and reduced survival probability on the other hand. Groothuis et al. (2005) have experimentally shown that yolk androgens suppress immune function but simultaneously stimulate growth in Black-headed Gull chicks (*Larus ridibundus*). Thus, "mothers face a trade-off between these costs and benefits and may tune hormone deposition to prevailing conditions that influence chick survival". Maternal yolk androgens have also been shown to affect a number of adult or juvenile traits including social dominance, neophobia, dispersal, male sexual characters, and male attractiveness (e.g., Eising et al. 2006; Gil 2003; Rubolini et al. 2006; Tobler and Sandell 2007; Tschirren et al. 2007). Stress, through elevated glucocorticosteroids during early life can also impair physiological development. In a wild population of White Storks (*Ciconia ciconia*), developing juveniles that released more corticosterone in response to a common stressor experienced lower survival and recruitment a few years later in life (Blas et al. 2007). In the same vein, pathogen exposure during the development of immunocompetence can affect an individual's ability to fight off pathogens later in life (Franceschi et al. 2000), which may influence reproductive performance and survival chances throughout life (Finch and Crimmins 2004). Boulinier and Staszewski (2008) reviewed evidence of transfer of antibodies from mother to offspring, and Gasparini et al. (2007) found evidence of variation in such transfers according to food availability in a wild long-lived bird species, the Kittiwake (*Rissa tridactyla*).

Caloric restriction during the earliest stages of life (i.e., foetal development in utero) can impair development, and is thought to increase risks of disease later in life. In humans, reduced fetal growth is strongly associated with a number of chronic conditions later in life including coronary heart disease, stroke, diabetes, and hypertension ('the Barker hypothesis'; Barker 1994). Some human cohort studies support the Barker hypothesis (e.g., Doblhammer and Vaupel 2001)

while others have found greater support for an effect of exposure to infectious diseases in the first year of life on the ability to fight pathogens later in life (i.e., the 'inflammatory exposure hypothesis'; Bengtsson and Lindström 2000; Finch and Crimmins 2004). Because of the intricate connection between endocrine and immune systems in animals, these two hypotheses may be difficult to disentangle (Franceshi et al. 2000), but nevertheless are likely to have similar demographic consequences.

'Population' and 'individual' consequences. Long-term individual consequences of conditions during development have been extensively addressed in short-lived birds as early as four decades ago (Haywood and Perrins 1992; Gustafsson and Sutherland 1988; Perrins 1965; van Noordwijk et al. 1988). Similarly, a number of long-term longitudinal studies of large mammals have addressed the relationship between early life development and population dynamics (Albon et al. 1987; Forchhammer et al. 2001; Saether 1997), as well as the individual fitness consequences of early life environmental conditions (Kruuk et al. 1999; Festa-Bianchet et al. 2000; Gaillard et al. 2000; Nussey et al. 2007; Rose et al. 1999). Population phenomena resulting from early conditions shared by individuals in a cohort are considered 'indirect effects' and suspected to be common (Benton et al. 2006). For example, Benton et al. (2006) hypothesized that stages (e.g., age classes) "which are reduced in density may lead to compensatory increases in the density of other stages (Cameron and Benton 2004; Moe et al. 2002)." Population consequences of early conditions have probably received more attention in large mammals than long-lived birds (Albon et al. 1987; Seather 1997; but see Votier et al. 2008). Such consequences may result from delayed effects of increased mortality at early stages of life in some cohorts (individuals born in the same year), which leads to smaller (future) population size for example. Early conditions can also translate into lower future reproductive performance and population productivity of young raised under poor conditions. In other words, population consequences of early conditions sometimes imply long-term consequences of these conditions

at the individual level, but they may result solely from early disappearance of frail individuals from the population before breeding (phenotypic mortality selection). Individuals from a given cohort affected by adverse early conditions may die early, when survivors (that recruit and breed) do not necessarily differ from other individuals in the breeding segment of the population. Alternatively, early conditions may have long-lasting effects on individuals without necessarily affecting survival; such frail individuals may recruit but exhibit poorer reproductive performance for example. Of course, the two scenarios may hold simultaneously (Rose et al. 1999).

LONG-LIVED SPECIES

Despite increased interest in this topic because of identification of possible causes of population dynamics and life history phenomena (Lindström 1999), knowledge and understanding of long-term consequences of early conditions is undoubtedly unbalanced in short- *versus* long-lived birds (Meathrel and Carey 2007). There is no clear definition of short- or long-lived species; here long-lived species will be (loosely) referred to as species where a substantial proportion of individuals defer breeding (beyond age one) and where mean reproductive longevity (i.e., after recruitment) may reach 4 years or more (based on estimates available in the literature). In long-lived bird species, the extent to which the disadvantage of individuals that are 'frail' at independence is expressed predominantly in terms of higher mortality before recruitment (Braasch et al. 2009; Nevoux et al. 2010), or persists after recruitment (Reid et al. 2003) is still unclear. Here 'frailty' may concern many different phenotypic traits: structural size, body condition, physiological state, morphology, personality, etc.

Depending on the fitness component considered, studies of long-term fitness consequences of early conditions in different species have provided some indication that fitness consequences are either not perceptible before recruitment (post-fledging survival and recruitment probability; Hipfner 1999; Drummond et al. 2003), not detectable after recruitment,

170 or no longer detectable after recruitment even if earlier fitness consequences might have been
171 detected (Nevoux et al. 2010). Alternatively, Van de Pol et al. (2006 a) found evidence of long-
172 term consequences of the quality of the habitat experienced during growth in Oytercatchers on
173 both survival probability and reproductive success, through the quality of the habitat they recruit
174 in. Similarly, Cam et al. (2003) found evidence of long-term consequences of the length of the
175 rearing period on reproductive success after recruitment in Kittiwakes. Reid et al. (2003; 2008)
176 also found evidence of a relationship between early cohort conditions and future breeding
177 success in Choughs (*Pyrrhocorax pyrrhocorax*), or between natal location and adult survival. In other
178 words, there is substantial heterogeneity in results according to the species, study design and
179 methods used to collect or analyze data. Nevertheless, studies of long-lived birds share some
180 common challenges and features (see below).

181 ***Specific methodological challenges***. Most studies of the consequences of early
182 conditions in long-lived birds have addressed relatively short-term fitness consequences on
183 fitness compared to the time scale at which reproduction takes place (e.g., survival from hatching
184 to fledging or survival just after fledging; Viñuela 1999). Due to extended pre-breeding period
185 (sometimes longer than 10 years in seabirds; e.g., Jenouvrier et al. 2008) and 'insufficient'
186 duration of research projects (relative to the mean longevity in the studied species), most studies
187 have focused on the following traits: post-fledging juvenile survival, survival from independence
188 to recruitment, or recruitment probability (Hario and Rintala 2009; Meathrel and Carey 2007).
189 Longer term consequences of conditions during development have rarely been addressed
190 (Nevoux et al. 2010). Naturally, a large number of studies of short-lived birds also have focused
191 on pre-breeding survival and age of first breeding (e.g., Lindén et al. 1992; Magrath 1991;
192 Verboven and Visser 1998).

193 Ironically, despite the specific interest of studies of stages immediately following
194 dependence on parents (and the possible short-term influence of the quality of rearing

195 environment and parental care on fitness components), survival after independence is one of the
196 most difficult demographic parameters to estimate in long-lived birds (especially seabirds, but not
197 exclusively). Indeed, many long-term studies assume or observe that yearlings (or sometimes
198 older) usually do not return to colonies or breeding locations that year (e.g., Croxall et al. 1990;
199 Jenouvrier et al. 2008), they sometimes ignore resightings of pre-breeders because they are too
200 few (e.g., Nevoux et al. 2010), and recapture probability at age 1 is set to 0 in capture-mark-
201 recapture models (e.g., Votier et al. 2008). In addition, a common limitation is the confounding
202 of mortality and permanent emigration out of the study area; the latter is particularly difficult to
203 assess in species with large distribution areas (e.g., Koenig et al. 1996; Link et al. 2002) unless
204 (still) expensive electronic devices are used (provided such devices can be used, depending on
205 size and battery life expectancy). This is particularly problematic in situations where dispersal
206 probability varies with individual features determined during development, e.g., body mass and
207 condition in juveniles (Barbraud et al. 2003; Belthoff and Duffy 1998). Schreiber et al. (2004) and
208 Hénaux et al. (2007) provided evidence of a relationship between early conditions at the colony
209 scale and natal dispersal probability in a long-lived bird.

210 ***Cohort effects as 'proxies' of early conditions.*** Cohort studies can be helpful
211 when individual traits at fledging (i.e., traits assumed to reflect conditions during development;
212 e.g., body condition, structural size, etc.) are not measured. There is a long tradition of such
213 studies in long-lived birds and large mammals (e.g., Albon et al. 1987; Cam et al. 2005;
214 Christensen 1999; Nevoux et al. 2010; Reid et al. 2003). The long-term fitness consequences of
215 early conditions can be addressed by investigating whether individuals born in different years
216 exhibit similar fitness components at later age (age-specific survival, recruitment probability,
217 success probability after recruitment). 'Early conditions' are then defined as conditions
218 experienced by groups of newborns (weather, food availability, population, density, or simply
219 'year', etc.; Crespin et al. 2006). Benton et al. (2006) emphasized that "The way that traits covary

means that individuals that experience common environmental conditions can carry the signature of those conditions throughout life. This is especially true of exposure to early environments, which can lead to marked differences in the life histories of cohorts of organisms born at different times (Bateson et al. 2004; Beckerman et al. 2002; Lindström 1999; Loison et al. 2004; Reid et al. 2003; Solberg et al. 2004)." To determine whether cohort effects reflect the influence of conditions in the year of birth on a later fitness component (e.g., recruitment probability), or a relationship between the fitness component addressed and the conditions in the year it is assessed (e.g., food availability in the year of recruitment; Spear et al. 1993), accounting for year effects is necessary. However, cohort, age, and year effects cannot be completely separated.

Extreme heterogeneity in traits affected by early development and fitness components. Many hypotheses have been put forward concerning traits that may be affected by early conditions, most of which relate to pathogens and energetic stress associated with breeding phenology and food abundance, the efficiency of parental care, or the number of siblings competing for parental care. However, we won't venture to describe any 'general relationship' between early conditions and traits in long lived birds, or any 'universal' pool of traits influenced by early development. Ludwigs and Becker (2006) reviewed 22 studies of post-fledging survival in long-lived seabirds and found that 10 pre-fledging traits potentially covary with survival ("clutch size, hatching order, hatching date, fledglings per brood, growth rate, body size, chick peak mass, fledging mass, body condition, fledging age"). Additional papers (including on geese) confirm the profusion of traits, fitness components, and relationships between such traits and fitness. A relationship between fledging date and fledging survival in Guillemots (*Uria aalge*; Harris et al. 2008) and Sooty Terns (*Onychoprion fuscatus*, formelly *Sterna Fuscata*; Fear 2002), but not body condition (Harris et al. 2008). A relationship between fledging size (wing length), and marginally mass, survival up to recruitment, and age of first return in Tufted Puffins (*Fratecula cirrhata;* Morrison et al. (2009). A relationship between body mass, structural size at

fledging (tarsus length) and pre-breeding survival in Barnacle Geese (*Branta leucopsis;* van der Jeugd and Larsson 1998), but not date of birth. A relationship between body mass at fledging and recruitment probability in Common Terns (*Sterna hirundo;* Ludwigs and Becker 2006), but not clutch size, hatching order, number of fledglings per brood, or recruitment of fledged young. In Western Gulls (*Larus occidentalis)*, neither hatching order, hatching date, brood size had consequences on age-specific survival from independence to recruitment, nor recruitment probability (Spear et al. 1993). Similar results were found concerning body mass in Black Brant (*Branta bernicla*; Sedinger et al. 2004). In contrast, Cam et al. (2003) concluded that there was a relationship between the length of the rearing period in Kittiwakes, pre-breeding survival and recruitment probability. In the Short-tailed Shearwaters (*Puffinus tenuirostris*), Meathrel and Carey (2007) concluded that none of the intrinsic factors (parental quality, the size and weight of the egg) "seemed to explain why some chicks returned to prospect and breed, while others did not. […] analyses were unable to detect which intrinsic factors could be important to recruitment in this species." They suggested that "factors operating outside the breeding season and away from the Bass Strait islands may determine whether or not a chick survives to return to breed".

Heterogeneity across life histories. Ludwigs and Becker (2006), and Meathrel and Carey (2007) hypothesized that specific differences in life histories explain why some phenotypic traits before fledging influence post-fledging survival or recruitment probability in some seabird species, but not in others. In some species, fledglings experience the transition from breeding site to the open sea alone, when parents still provide care in some others. Meathrel and Carey (2007) emphasized that in tube-nosed seabirds "all species for which a relationship between fledging weight and post-fledging survival or recruitment has been documented, become independent of their parents just before fledging, such as the Short-tailed Shearwaters who desert their young up to a month before fledging (Serventy 1967), so whether or not they return as adults is independent of direct parental investment after fledging". Along this line, Ludwigs and

Becker (2006) highlighted that "Terns benefit from prolonged parental guidance after fledging (Burger, 1980; pers. obs.). In this respect, they could be described as intermediate between auks, which leave the colony under parental care at a pre-fledging stage (Harris et al., 1992; Hedgren, 1981; Lloyd, 1979), and Shearwaters, which are all but independent at fledging (Mougin et al. 2000; Perrins et al. 1973; Sagar and Horning 1998). Chicks of Common Murres (Harris et al. 1992; Hedgren 1981)) and Razorbills (*Alca torda*) (Lloyd, 1979) leave the colony long before independence, and are fed by their parents for a long period at sea before reaching their 'independence' mass. That may well be one reason why, in the Alcidae, no evidence has been found for any influence by pre-fledging body mass on survival after fledging" (but see Harris et al. 2008). Similarly, Stienen and Brenninkmeier (2002) hypothesized that parental provisioning after fledging buffers juvenile against growth disadvantages that they experienced prior to leaving their colony (see also Fear 2002). Parents can buffer environmental variation to some extent (e.g. increase foraging effort when resource availability decreases; Erikstad et al. 1998). As emphasized by Ludwigs and Becker (2006) and Meathrel and Carey (2007), relevant measurable traits are likely to be species-specific, or at least specific to classes of species sharing common ecological and lifestyle characteristics.

Methodological heterogeneity. The difficulty in identifying 'general patterns' in the literature partly reflects methodological differences across studies in data collection and analysis. For example, in a study of Barnacle Geese, van der Jeugd and Larsson (1998) hypothesized that they did not find evidence of hatching date on post-fledging survival because of the time of capture: hatching dates in the sample of young birds that survived to the age of capture wasn't representative of the whole population. Indeed, many other studies have documented a relationship between hatching date and post-fledging survival (e.g., Harris et al. 1994; 2008; Korpimäki and Lagerström 1988). Concerning data analysis, analytical methods to estimate age- and state-specific survival probability (e.g., pre-breeders versus breeders), recruitment probability,

295 and breeding probability after recruitment, have drastically changed over the past three decades:
296 current methods allow investigators to account for imperfect detection of individuals *in natura*
297 (Williams et al. 2002), or to base their study on a local detection rate close to one (new techniques
298 of remote and electronic recording of individuals, e.g. Dittmann et al. 2003, Becker et al. 2008,
299 Braasch et al. 2009, Limmer and Becker 2010). Some studies of fitness consequences of early
300 conditions have used such approaches, have estimated detection probability and provided
301 estimates of fitness components not confounded with detection rate (e.g., Cooch 2002; Nevoux
302 et al. 2010; Reed et al. 2003; Votier et al. 2008; van der Jeugd and Larsson 1998; Votier et al.
303 2008;), whereas some others haven't (mostly relatively old studies that could not yet benefit from
304 those approaches; e.g., Croxall et al. 1990; Spear and Nur 1994), making comparisons among
305 studies difficult.

306 Due to relative rarity of relevant data sets to address long-term consequences of early
307 conditions in long-lived bird species and to the fact that many studies are retrospective (i.e., *a*
308 *posteriori* use of data not necessarily collected for that purpose), heterogeneity in methods used
309 and time scales considered hampers identification of general patterns. The first statement in
310 Lindström (1999) clearly holds: "It is obvious that adverse environmental conditions might have
311 immediate effects […]." Evidence has been found of effects lasting up to recruitment in species
312 delaying recruitment for several years. However, whether there are "long-term fitness
313 consequences of conditions experienced during early development" (Lindström's second
314 statement) is still an open question in the vast majority of long-lived bird species. In a review
315 focusing on humans, Ulijaszek (1996) defined 'early conditions' as follows: "what constitutes an
316 early environmental influence is anything that happens before full developmental maturity is
317 achieved". Humans have extended childhood and in most societies extended parental care, a
318 feature suggested as creating substantial differences between mammals and birds in long-term

consequences of conditions during development (see Reinhold 2002 concerning maternal effects for example). However, at least some recent results from wild long-lived bird species have provided evidence that conditions during the rearing period (e.g., length of the rearing period, habitat quality), and possibly the efficiency of parental care, both have long-term consequences on fitness components (e.g., Cam et al. 2003; Van de Pol et al. 2006 a). Importantly, assessment of lifetime consequences of early conditions in long-lived birds is still extremely rare (e.g., Reid et al. 2003). In a study of lifetime reproductive success in Oystercatchers, Van de Pol et al. (2006 a) provided evidence that "long-term effects of early conditions contributed more to overall fitness differences than short-term consequences, contrary to common conceptions on this issue. Short-term effects of early conditions lead to the large underestimation of fitness consequences".

WHERE TO NEXT?

New analytical methods. Future studies should gain insight into whether early conditions have long-lasting effects on fitness in long-lived birds by re-analyzing available long-term data sets using homogeneous analytical approaches. In the 1990's, statisticians started developing methods to estimate 'state-specific' fitness components (survival probability, recruitment probability, breeding probability and success after recruitment) from individually marked individuals in situations where not all individuals alive and present in the study area were observed (multistate capture-recapture models; Arnason 1973; Hestbeck et al. 1991; Nichols and Kendall 1995; Schwarz et al. 1993). Such models are required to estimate survival probability in pre-breeders and breeders of the same age for example, i.e., individuals in different reproductive 'states', where individuals change state in a stochastic manner. In species with delayed maturity, failure to observe, contact or capture individuals for several years raises substantial difficulties in studies of consequences of early conditions on fitness. To handle such situations, several authors treated the pre-breeding stage as an unobservable state (e.g., Crespin et al. 2006; Jenouvrier et al. 2008; Nevoux et al. 2010). Simultaneously, statisticians started developing approaches to handle

344 uncertainty in state assignment (Kendall 2004). Such approaches are relevant when observers
345 cannot assess with certainty whether individuals breed, or not, a common situation in bird studies
346 where individuals breed unsuccessfully and no longer attend breeding sites for example; they may
347 be considered as non-breeders (possibly pre-breeders), or floaters.

348 A recent extension of multistate models developed by Pradel (2005; see also Choquet et
349 al. 2009), 'Multievent models' are especially designed to handle state uncertainty. Importantly,
350 Rouan et al. (2009) developed a method (derived from Multievent models) to estimate lifetime
351 reproductive success when breeding status cannot always be assessed. Other approaches to
352 construct sequences of discrete states using hidden Markov chains have been applied in
353 molecular ecology or weather forecasting for example (Cappé et al. 2005) and can be used in the
354 capture-mark-recapture setting (see Dupuis 1995 for one of the first applications not extended
355 yet to inferences about lifetime reproductive success). This development should prove
356 particularly useful to re-investigate long-term consequences of early conditions in long-lived birds
357 using available data sets. Indeed, the method handles a major feature of capture-mark-recapture
358 studies of wild vertebrates (imperfect detection), and doesn't require that all individuals are
359 monitored over their entire life (i.e., right censored data can be used).

360 Another recent development of capture-mark-recapture models may prove useful to
361 assess long-term fitness consequences of early conditions. A difficulty inherent in longitudinal
362 studies of fitness components is disentangling within-cohort phenotypic mortality selection and
363 genuine variation of these components throughout life (Vaupel and Yashin 1985). To address this
364 question, accounting for unobserved heterogeneity in populations (Jones et al. 2010) is common
365 in human demography (see Vaupel et al. 1979 for one of the first papers on the topic). Recently,
366 Gimenez and Choquet (2010), Marzolin et al. (2011), and Royle (2008) have combined capture-
367 mark-recapture models with models accounting for such heterogeneity and re-analyzed a
368 'famous' data set collected by Marzolin (2002; European Dipper *Cinclus cinclus*; cited in virtually

any textbook on capture-mark-recapture modeling). This approach will help investigators re-analyze existing long-term data sets (including ones continuing at present) and assess whether the consequences of early conditions persist throughout life, or if early conditions mostly affect survival in younger age classes, with frail individuals progressively disappearing from populations via within-cohort phenotypic mortality selection. In addition, this approach can be used to address whether models incorporating measurable covariates (describing early conditions) perform better than models also accounting for unobserved heterogeneity, and thus assess the contribution of early conditions to differences in fitness components among individuals (Aubry et al. 2011; Cam et al. 2002 a; Jones et al. 2010). Although very data hungry, statistical models accounting for the stochastic change in individuals 'state' and individual covariates may allow disentangling long-term effects of early conditions and short-term carry over effects (Harrison et al. 2011).

Individual 'quality'. The concept of 'quality' (of parents, eggs, offspring) is pervasive in studies of conditions during growth and their consequences on offspring fitness (e.g., Bize et al. 2002; Vergara et al. 2010). In birds, early conditions start at the egg stage. Meathrel et al. (1993), and Meathrel and Carey (2007) illustrated the importance of the 'quality' hypothesis in studies of consequences of conditions during development: "egg size in seabirds is commonly held to be an important index of egg quality because it is thought to reflect the quantity of nutrient reserves available to the chick during embryonic development and at hatching (Boersma 1982)." "High rates of survival for chicks hatching from large eggs may be a consequence of egg size per se, or of the ability of high quality parents to lay eggs and to subsequently provide superior care to nestlings (Meathrel et al. 1993). Both egg size and offspring survival are likely to be affected by parental attributes, in particular those of the maternal parent (Nager et al. 2006)." Maternal expenditure (egg size) is logically assumed to be related to traits (morphological, physiological) of the young at birth (hatching), but there is unambiguous evidence that offspring

394 traits at independence also depend on parental care in long-lived birds, which may have long-
395 lasting effects on offspring fitness. For example, in an experimental study of Oystercatchers, Van
396 de Pol et al. (2006 b) found evidence that there was a relationship between rearing conditions
397 (environmental or parental quality), but not egg size, and offspring survival over 50 days.

398 Despite the difficulty inherent in definition and measurement of 'individual quality'
399 (Bergeron et al. 2010; Lailvaux and Kasumovic 2011; Wilson and Nussey 2009), the hypothesis
400 that parents differ in 'quality' plays such a large part in studies of conditions during growth and
401 their consequences on offspring (e.g., Bize et al. 2002; Vergara et al. 2010; Wendeln and Becker
402 1999) that investigators should attempt to be specific about the way they use this concept. It may
403 not always be possible to 'measure' quality: in studies of primates, Hawkes (2010) and Jones *et al*
404 (2010) recently re-emphasized that investigators may not always be able to define measurable
405 criteria *a priori* to rank individuals according to the quality of care they may provide to offspring,
406 and then model-based inference should be used to account for heterogeneity in fitness among
407 parents. In addition, 'quality' rarely comes down to morphology and physiology (but see e.g.,
408 Wendeln and Becker 1999). When the conditions are met, behavioral traits that may partly reflect
409 parental experience and the pair common experience (e.g., coordination) should be considered.
410 In Common Guillemots, Lewis et al. (2006) used detailed behavioral data from parents to
411 characterize pair quality based on time spent together at the site and chick feeding rates. They
412 also used trip duration at the individual level to assess the quality of care provided by the
413 individual parent. They concluded that the pair effect on breeding success was larger than the one
414 of each parent alone. Using a longitudinal approach, Limmer and Becker (2009) found that chick
415 provisioning improves with parental experience in Common Terns. In Kestrels (*Falco tinnunculus*),
416 Vergara et al. (2010) used the duration of the post-fledging dependence period to assess parental
417 quality.

Timing of trait measurement. When fledglings' traits are measured, studies should consider carefully the questions of the time scale considered, timing of measurement of traits, and consistency (or correlation through life) in individual traits over time (e.g., Carere et al. 2005; van Oers et al. 2004 a). Festa-Bianchet et al. (2000) addressed this issue thoroughly in a study of Bighorn Sheep (*Ovis canadensis)*. They did not find evidence of a relationship between mass in 3-week old lambs and adult mass or lifetime reproductive success in ewes. However, "mass gain during lactation, possibly but not necessarily related to the amount of maternal care received, affects adult mass and reproductive success. Mass gain over several years and the number of ewes in the population strongly affects adult mass in both sexes and therefore can have profound effects on reproductive success in this long lived species with a multi-year growth period". Detailed behavioral observations are necessary to address post fledging parental care in birds and its role in transition to independence (Ashmole and Humberto 1968; Heinsohn 1991). In the Short-tailed Shearwater , Meathrel and Carey (2007) concluded that "there were only weak relationships between parental quality, the size and weight of the egg and the chick at 2 months of age". Similarly, in Common Terns, Braasch et al. (2009) found that "neither the date of hatching nor the departure age was found to affect survival. The only predictor of survival was last post-fledging body mass whereas fledging mass itself was of minor importance." In Lesser Snow Geese (a nidifugous species, *Anser caerulescens caerulescens*), there was a correlation between gosling size and adult size (Cooch et al. 1991). Sedinger et al. (1995) found similar results in Black Brant, as well as Larsson and Forslund (1987) in Barnacle Geese (*Branta leucopsis*). Geese select mates assortatively (Choudbury et al. 1992), so size is likely to influence the probability of finding a mate and breeding.

Ontogeny. As highlighted earlier, Ulijaszek (1996) defined 'early conditions' as follows: "what constitutes an early environmental influence is […] anything that happens before full developmental maturity is achieved". This definition of 'early conditions' in humans includes

443 ontogeny and development during adolescence. Ontogeny may concern the entire life but here
444 we focus on conditions before recruitment in birds. In a study of Eurasian Dippers (*Cinclus*
445 *cinclus*) Yoerg (1997) addressed the relationship between acquisition of adult foraging skills and
446 age at independence and concluded that transition to independence did not require full maturity.
447 This highlights the importance of learning after independence (e.g., Watson and Hatch 1999) for
448 survival and future recruitment. A common difficulty in studies of long-term consequences of
449 early conditions is that development in long-lived species encompasses several years, and
450 conditions during development also include adolescence and behavioral development before
451 sexual maturity and recruitment. This raises the question of ontogeny and learning, a biological
452 feature acknowledged as potentially important for life history evolution in vertebrates for
453 example (Charlesworth 1994). In species with delayed breeding, environmental conditions
454 experienced during the pre-breeding stage (e.g., weather conditions at sea for seabirds) may
455 override the influence of conditions during early development before independence. Individual
456 behavior during this stage may have strong consequences on fitness (survival and recruitment
457 probability for example), and may also override the influence of early conditions.

458 As emphasized by Jenouvrier et al. (2008), "recruitment to a breeding population is a
459 gradual, complex process for long-lived species with delayed maturity". It has long been known
460 that in many bird species immatures return to colonies several years before breeding (e.g., Cadiou
461 et al. 1994; Cadiou 1999; Chabrzyk and Coulon 1976; Danchin et al. 1991; Dittmann and Becker
462 2003; Dittmann et al. 2005; 2007; Halley et al. 1995; Klomp and Furness 1992; Nelson 1987;
463 Pickering 1989). The behavior, arrival dates, and activities of young birds before recruitment (i.e.,
464 in pre-breeders) may have a substantial influence on age of first breeding, and the quality of the
465 recruitment habitat (Bruinzeel and V an de Pol 2002). For example, familiarity with sites and
466 potential neighbors may facilitate accession to breeding status and successful reproduction by
467 reducing aggression (Cadiou et al. 1994; Cadiou 1999; Dittmann and Becker 2003; Dittmann et al.

2005; 2007; Halley et al. 1995;). In the Kittiwake Cam et al. (2002 b) addressed age-specific survival, recruitment probability, and reproductive success over life as a function of behavior during the pre-breeding period (activities assumed to play a part in territory acquisition and integration into the local social web), and found evidence of a relationship between both covariates and fitness components up to recruitment. There is indication that pre-breeders attending breeding locations, involved in nest building activities or coordination activities with a mate have a higher probability of recruiting than others, and of breeding successfully in the first breeding attempt (Cam et al. 2002 b). There may not be any detectable direct relationship between pre-breeding behavior and breeding success other than in the first attempt, but there is one between age of recruitment and subsequence breeding success (i.e., some indirect consequences of behavior during the pre-breeding period; Aubry et al. 2009 a b; Cam et al. 2002 b; Limmer and Becker 2010). Investigating ontogeny requires detailed behavioral studies; such data are likely to be missing in retrospective analysis of existing long-term studies. However, depending on the importance of the part played by conditions (including social conditions, competition, etc.) and pre-breeding activities in the recruitment process, behavioral observations during the pre-breeding stage may substantially help explain future reproductive trajectory (e.g., van de Pol et al. 2007). This should help address whether conditions between independence and recruitment override the influence of early conditions on fitness after recruitment. In addition, improvement of remote tracking techniques based on electronic devices may contribute to investigate pre-breeders' activities such as prospection, involvement in social activities before breeding, and conditions experienced at that stage (Becker et al. 2008; Bogdanova et al. 2011; Dittman and Becker 2003).

Heritability and parental effects. A question currently receiving growing attention is the extent to which morphological (e.g., structural size), physiological (e.g., body condition) and personality traits are determined genetically and are heritable (e.g., Authier et al. 2011;

493 Dingemanse et al. 2004; Dingemanse and Réale 2005; Drent et al. 2003; Garnett 1981; Kontainen
494 et al. 2008; Larsson and Forslund 1992; Larsson 1993; Merilä et al. 2001; Réale and Festa-
495 Bianchet 2003; Schluter and Gustafsson 1993; Stamps and Groothuis 2010; Téplitsky et al. 2008;
496 van Noordwijk et al. 1988; van Oers et al. 2005). Similarly, fitness components themselves may
497 be heritable (e.g., Charmantier 2006 a b; Kontiainen et al. 2007). In addition, Lindström (1999)
498 identified maternal and paternal effects as "important sources of individual variation in early
499 development". The recent development of quantitative genetics modeling tools has triggered
500 research on the genetic and environmental determinism of traits, and on parental effects on
501 various phenotypic traits, including fitness components (Kruuk and Hill 2008; Kruuk et al. 2008;
502 Wilson et al. 2008; 2010). Quantitative genetics approaches will be useful to assess the extent to
503 which offspring traits can be attributed to their genetic background and position in the pedigree,
504 to environmental conditions, to non-nuclear genetic maternal effects, and to non-genetic parental
505 features (Clutton-Brock and Sheldon 2010; Lynch and Walsh 1998). For example, in the Lesser
506 Snow Goose, a species with substantial variation in gosling size according to feeding conditions
507 in the rearing habitat (Cooch et al. 1991; 1993), Cooch (2002) hypothesized that "selection may
508 operate on the environmental component of body size, not on additive genetic variance of body
509 size". Future studies will benefit from recent methodological development of statistical models
510 combining the quantitative genetics 'animal model' (Postma and Charmantier 2006) and capture-
511 mark-recapture models (i.e., model designed to handle missing data resulting from non-detection
512 of animals that are alive and present in the study area; Papaix et al. 2010).

513 The growing interest in evolutionary ecology and quantitative genetics is drawing
514 attention to maternal effects (e.g., Potti 1999; Reinhold 2002). If early conditions are commonly
515 defined as depending on the habitat and the parents, data are missing on maternal (or parental)
516 effects in long-lived birds except in physiological studies of transfers from mother to offspring
517 via egg composition (Boulinier and Staszewski 2008; Gasparini et al. 2007). Nevertheless, as

518 shown by Lewis et al. (2006), some measurable behavioral criteria can be used to assess the
519 'quality' of parental care and its relationship with parental fitness. It should be possible to address
520 its repeatability during the parent's life, and its long-term consequences on fitness of young raised
521 to independence.

522 The scarcity of long-term studies of parental effects in long-lived birds may be explained
523 by the 'age' of studies of wild birds: still insufficient to work with the pedigree of population in
524 most cases (how long does it take to have data from at least two generations of animals whose
525 mean longevity is 10, 15 years, or more?). Nevertheless, maternal effects have been suggested to
526 play a central part in the dynamics of small mammal populations (including non-cycling
527 populations; Inchausti and Ginzburg 2009; Plaistow and Benton 2009; Rossiter 1994). They have
528 been documented in several wild large mammals (Wilson and Festa-Bianchet 2009). As explained
529 by Benton et al. (2005) "Differential provisioning of offspring is a widespread phenomenon that
530 has important consequences for offspring fitness [...]. The transmission of maternal quality to
531 offspring probably also has population dynamical consequences, because it leads to a time lag
532 between the environment and the population response. In the presence of environmental
533 fluctuations, the lag created by the delayed life-history effect typically also increases population
534 variability and decreases its predictability". This type of lagged dynamical phenomenon exists in
535 long-lived birds (Thomson and Ollason 2001), but whether it is common is still unknown.

536 ***CONCLUSION***

537 There is growing interest in long-lasting effects of early development in a variety of taxa,
538 encouraged by conclusive results obtained in humans (the 'Barker Hypothesis' in 1994, or
539 hypotheses based on long-term effects of exposure to infectious diseases; Bengtsson and
540 Lindström 2000). However, as emphasized by Festa-Bianchet et al. (2000) concerning large
541 mammals "it is often assumed but seldom quantified that early conditions have long-term effects

542 on fitness. The underlying assumption is that there is a relatively strong correlation between
543 morphological, physiological, or behavioral characteristics of offspring and lifetime reproductive
544 success". Due to rarity of relevant data sets, too few studies of long-lived birds have addressed
545 the consequences of conditions during early development on fitness components over the
546 reproductive life, and lifetime reproductive success (but see Van de Pol et al. 2006 a). Whether
547 these conditions have long-term fitness consequences is still ambiguous: some studies have
548 shown that initially disadvantaged individuals do not incur long-term costs of energetic stress for
549 example (Drummond et al. 2003), or that early mortality in such individuals leads to rapid
550 disappearance from the population (Braash et al. 2009; Nevoux et al. 2010). In contrast some
551 others have found substantial lifetime reproductive success consequences of conditions during
552 development (Cam et al. 2003), including via access to higher-quality territories (Van de Pol et al.
553 2006 a). Evidence from large mammals suggests substantial long-term individual and population
554 effects of early conditions (Saether 1997; Kruuk et al. 1999), including trans-generational
555 maternal effects. Evidence from short-lived birds also suggests long-term individual
556 consequences (e.g., Gorman and Nager 2004), and maternal effects have been documented in
557 long-lived ones. Despite logistical and financial difficulties inherent in long-term studies, they are
558 the only way of addressing Lindström's second statement.

559 Existing long-term longitudinal data sets should be re-analyzed using recently developed
560 capture-mark-recapture models handling state uncertainty and unobservable heterogeneity in
561 populations (e.g., Gimenez and Choquet 2010; Pradel 2005). For example, it may be worth
562 evaluating whether some of the unique studies of reproductive success included in books edited
563 by Tim Clutton-Brock (1988) and lifetime reproduction in birds by Ian Newton (1989) have
564 continued and can provide new insight into the fate of the offspring of the individuals studied at
565 that time. One of the most difficult challenges for future studies will be determining whether
566 ontogeny and conditions experienced between independence and recruitment override the

influence of conditions during early development, or if individuals growing under unfavorable conditions disappear from the population before recruitment, or both. Although demanding, when possible ongoing studies of long-lived species should use a large number of criteria to characterize 'early conditions', i.e., not restricted to physical conditions (weather), food availability, morphological, physiological or phenological criteria; data characterizing the 'quality' of parental care should also be collected (experience, dominance status, pair coordination, e.g., Lewis et al. 2006). To assess the full range of conditions experienced before full developmental maturity, when possible, they should use a multi-disciplinary approach and address changes in individual behavior during the pre-breeding stages (prospection, habitat choice, dominance, pair formation), and characterize the social context (e.g., Van de Pol et al. 2007). In the near future electronic devices may also help collect information from individuals during the extended pre-breeding stage in a larger range of species (Bogdanova et al. 2011; Dittman and Becker 2003). Last, statistical methods designed to estimate lifetime reproductive success or incorporate pedigree information in standard situations of studies of wild vertebrates with imperfect detection probability (Papaix et al. 2010; Rouan et al. 2009) offer new opportunities to assess long-term fitness consequences of early development in long-lived birds.

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