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Research

Heterogeneity in individual quality in birds: overall patterns and insights from a study on common terns

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While life-history theory predicts a tradeoff between reproduction and survival, positive covariance, indicative of heterogeneity in individual quality, is often reported among individuals from natural populations. We review longitudinal studies of wild bird populations that test the relationship between annual reproductive success and lifespan and find the majority to report a positive correlation, while none reports a negative correlation. Heterogeneity in individual quality in resource acquisition, masking resource-based tradeoffs, therefore appears to be common in birds. Considering that there is little evidence for heritable variation in fitness, heterogeneity in individual quality among adults may be due to life-long effects of developmental conditions. In a 20-year case study on common terns *Sterna hirundo*, we test for life-long effects of cohort quality and within-cohort nest quality, but find no significant effects on long-term proxies of quality. Since other studies do find strong life-long effects of developmental conditions, we suggest that the brood reduction strategy adopted by common terns, causing the majority of offspring to die rapidly after hatching, efficiently reduces variation in offspring quality at independence. As such, a brood reduction strategy may contribute to reduced heterogeneity in adult survival in stochastic environments, both suggested to be more common and adaptive in long-lived species. Further study is required to assess heterogeneity in individual reproduction, especially in relation to environmental stochasticity and species' life-history strategies, in order to assess whether the relative strength of selection in early and late life may indeed affect the magnitude of heterogeneity in individual quality over life, and how this is mediated by parent–offspring conflict.

Introduction

The key principle of life-history theory is that organisms are faced with limited resources, such that they need to choose how to allocate their time, energy and nutrients between the many different processes that enhance their fitness (Williams 1966, Kirkwood 1977, Stearns 1992). The resulting tradeoffs between costly processes such

as reproduction and self-maintenance are predicted to be resolved such that the conversion of resources into fitness is maximised. In accordance, experiments in which individuals were manipulated to increase investment in reproduction have revealed these individuals to suffer from decreased survival (Dijkstra et al. 1990, Boonekamp et al. 2014) and fitness (Daan et al. 1990, Tinbergen and Daan 1990).

Rather than negative associations, correlative studies of life history variation in natural populations, however, often report positive associations between reproductive performance and survival (Hamel et al. 2009, Bouwhuis et al. 2010b). This apparent discrepancy can be explained by consistent individual variation in resource availability: if individual variation in resource acquisition exceeds that in relative allocation, individuals that show increased investment in reproduction may also show increased investment in survival, and any within-individual tradeoff is masked (van Noordwijk and de Jong 1986, Descamps et al. 2016). The resulting positive correlations between fitness components among individuals are indicative of heterogeneity in individual quality (Wilson and Nussey 2010).

In this synthesis we use the framework of life-history theory and assume that heterogeneity in individual quality is equivalent to individual variation in resource acquisition, where the term resource acquisition encompasses all processes (e.g. food availability, competitive ability, metabolic efficiency) that determine the amount of resources an individual has at its disposal to convert into fitness. We focus on questions regarding 1) the evidence for heterogeneity in individual quality in wild bird populations, 2) its underlying causes, and 3) interspecific variation in the extent of heterogeneity in relation to life-history strategy. In addition, we present a case study in which we investigate how cohort effects translate to individual heterogeneity in life-history trajectories using a 20-year longitudinal dataset on common terns *Sterna hirundo*. Our synthesis is focused on studies on wild bird populations, since several such populations of species exhibiting a wide range of life-history strategies have now been monitored for multiple decades and it is relatively easy to estimate annual reproductive success and lifespan of individual birds in a standardized way. Nevertheless the insights are not restricted to birds and of general applicability.

Evidence for heterogeneity in individual quality in natural bird populations

Several methods have been employed to estimate heterogeneity in individual quality and to separate it from purely stochastic between-individual variation in lifespan and reproductive performance (Bonnet and Postma 2016, Cam et al. 2016). Since we are specifically interested in heterogeneity in overall quality rather than in single underlying traits (see Gimenez et al. 2017 for a review on heterogeneity in single traits in the context of capture–recapture models), we have opted to compile all longitudinal studies on birds that tested whether variation in individual annual reproductive

performance (i.e. the number of fledged or recruited offspring) was explained by variation in individual lifespan. This analytical approach, advocated by van de Pol and Verhulst (2006), is widely used to correct for individual heterogeneity in longitudinal studies of (avian) senescence (Bouwhuis and Vedder 2017), which has the benefit that the correlation between annual reproductive performance and lifespan has been routinely reported, regardless of its direction or significance. Do note that by compiling studies using this approach, we assume that an individual's lifespan can only explain its reproductive performance if variation in both traits is not purely due to chance (but see Tuljapurkar et al. 2009, Steiner et al. 2010 for a different perspective).

All studies that have tested the effect of individual lifespan on annual reproductive success in a wild bird population, and cite the original study by van de Pol and Verhulst (2006), are listed in Table 1. From this table, it is evident that a positive correlation between lifespan and annual reproductive success frequently occurs among bird species, as it is reported in 9 out of 14, i.e. in 64%, of species. Moreover, the absence of a positive correlation between lifespan and annual reproductive success, as observed in the other five species, may not necessarily reflect less heterogeneity in individual quality to occur in these species for two reasons. First, as evident from the listed studies on blue-footed boobies, pied flycatchers and great tits, lifespan is not necessarily consistently correlated with all measures of reproductive success. In these three species, measures that integrate the quality of produced offspring (their recruitment process) are positively correlated with lifespan, while the number of fledglings produced is not. Hence, the absence of positive covariation between survival and the annual number of fledglings produced may reflect high quality parents to invest their surplus of resources into offspring quality rather than quantity. Second, similar to the life-history tradeoff between reproduction and survival potentially being masked by between-individual variation in resource acquisition (van Noordwijk and de Jong 1986, Descamps et al. 2016), heterogeneity in individual quality, as exemplified by a positive correlations between reproduction and survival, may be masked by variation in resource allocation. Our long-term study on common terns provides an example of such variation in resource allocation masking heterogeneity in quality. As Table 1 reports, studies within the van de Pol and Verhulst analytical framework provided no evidence for a relationship between annual fledgling production and lifespan (Bouwhuis et al. 2015, Zhang et al. 2015a), while positive between-individual covariance between reproduction and survival became apparent in a follow-up study in which variation in resource allocation was better accounted for (Zhang et al. 2015b). New work shows that part of the underlying variation in resource allocation can be attributed to individuals increasing their investment in reproduction in years that are favourable for reproduction at the population level, at the expense of adult survival to the next breeding season (Vedder et al. unpubl.). Such an increase in allocation to reproduction in good years is indeed

Table 1. Overview of studies testing for an effect of individual lifespan on repeated measures of individual annual reproductive success in wild bird populations.

Species	Measure of reproductive success	Significant lifespan effect?	Reference
Wandering albatross <i>Diomedea exulans</i>	breeding success	no	Froy et al. 2013
Blue-footed booby <i>Sula nebouxii</i>	breeding success	no	Kim et al. 2011
	recruitment success	positive	Torres et al. 2011
Black kite <i>Milvus migrans</i>	fledgling production	positive	Blas et al. 2009
Common kestrel <i>Falco tinnunculus</i>	fledgling production	positive ^a	Lopez-Idiaquez et al. 2016
Black-legged kittiwake <i>Rissa tridactyla</i>	breeding success	positive	Aubry et al. 2009
Common tern <i>Sterna hirundo</i>	fledgling production	no	Bouwhuis et al. 2015, Zhang et al. 2015a
Tawny owl <i>Strix aluco</i>	fledgling production	no	Millon et al. 2011
Barn swallow <i>Hirundo rustica</i>	fledgling production	positive ^b	Balbontin et al. 2007, 2012
Seychelles warbler <i>Acrocephalus sechellensis</i>	fledgling production	no	Hammers et al. 2012
Pied flycatcher <i>Ficedula hypoleuca</i>	fledgling success	no	Potti et al. 2013
	recruitment success	positive	Potti et al. 2013
Collared flycatcher <i>Ficedula albicollis</i>	fledgling production	positive	Evans et al. 2011
Great tit <i>Parus major</i>	fledgling production	no	Bouwhuis et al. 2009
	recruit production	positive	Bouwhuis et al. 2009
Wood thrush <i>Hylocichla mustelina</i>	fledgling production	positive	Brown and Roth 2009
House sparrow <i>Passer domesticus</i>	fledgling production	no	Schroeder et al. 2011
	recruit production	no	Schroeder et al. 2011

^aonly in males, ^bresults were inconsistent between studies, ‘success’ refers to a per offspring measure while ‘production’ refers to the number of offspring fledged, or recruited, to the natal population.

predicted for long-lived species in a stochastic environment (Erikstad et al. 1998) and fits with the observation that, in our system, years with high fledging success are characterized by high food availability (Dänhardt and Becker 2011). In general, it is therefore noteworthy that none of the studies listed in Table 1 reports a negative relationship between reproductive success and lifespan, which would be predicted by life-history theory in the absence of heterogeneity in quality (van Noordwijk and de Jong 1986, Descamps et al. 2016). This suggests that individual heterogeneity in quality is always at least as large as variation in resource allocation and allows us to conclude that individual heterogeneity in quality more likely is common, rather than an exception, in wild bird populations.

Causes of heterogeneity in individual quality

Why individuals show consistent variation in their reproductive performance and survival poses an intricate question, in respect to which several ideas have been put forward. While the relative magnitude of the correlation between individual lifespan and annual reproductive success itself, or factors explaining it, have not yet become the subject of study in this respect, any positive correlation between lifespan and reproductive performance should translate to variation in lifetime reproductive success, which is a suitable proxy for quality and fitness and has received at least some empirical attention.

Variation in fitness components may have a genetic basis (Postma 2014), though any genetic basis may be more likely to reflect genetic variation in the share of resources allocated to a trait and thus variation in life-history strategy, rather than genetic variation in the ability to acquire resources. In fact, evolutionary theory predicts little heritability of resource

acquisition and the ability to converse resources into fitness, since selection would, by definition, rapidly deplete such heritable variation (Fisher 1930). Accordingly, studies on wild birds have found traits closely associated with lifetime reproductive success to generally exhibit low heritability (Gustafsson 1986, Merilä and Sheldon 2000, McCleery et al. 2004, Teplitsky et al. 2009, Wheelwright et al. 2014). However, the low heritability of these traits was not found to result from low levels of additive genetic variance, but from greater variance explained by other, unspecified, sources (Merilä and Sheldon 2000, McCleery et al. 2004, Wheelwright et al. 2014; but see Teplitsky et al. 2009).

Between-individual variation in the quality of developmental conditions may constitute one of the most important environmental sources of consistent variation in performance of individuals (reviewed by Lindström 1999, Cam and Aubry 2011). Various studies of wild birds have linked variation in lifetime reproductive success to developmental conditions, such as parental age (Bouwhuis et al. 2015, Schroeder et al. 2015), hatching or fledging date (Visser and Verboven 1999, Saino et al. 2012) and natal cohort or habitat quality (Reid et al. 2003, van de Pol et al. 2006). Such effects are typically referred to as ‘silver spoon’ effects and one idea regarding the underlying mechanism is that an individual’s state at age t is positively related to its state at age $t+1$, leading to cascading effects of poor developmental conditions throughout life (Caswell 2001, Beckerman et al. 2002, Cam et al. 2016). Yet, why natural selection would not prevent such cascading effects from occurring, by favouring mechanisms that would buffer against mechanistic cascades, is poorly addressed.

In contrast, life-history theory predicts that individuals that have fewer resources available during development should allocate a greater share of their resources to traits that

promote immediate survival or reproductive success, at the expense of investment in somatic maintenance or future reproductive success (Williams 1957, 1966, Kirkwood 1977). Because unavoidable extrinsic mortality causes the number of individuals that would benefit from such an allocation strategy to outweigh the number of individuals that live long enough to experience the costs, this strategy could be favoured by natural selection (Medawar 1952, Williams 1957, Kirkwood 1977). In this case, late-life negative consequences of a poor start would not result from cascading effects, but from adaptive buffering against resource limitation in early life at a price paid later in life. Empirical studies seem to support this life-history perspective, for example with findings of individuals being able to accelerate early-life growth at a later cost (Metcalf and Monaghan 2001), but it is difficult to distinguish between cascading effects and adaptive buffering, as early-life buffering may be incomplete and also lead to a progressive increase of fitness consequences of developmental conditions over life, seemingly correlating an individual's state at age t to its state at age $t+1$.

A case study on common terns

To add to the empirical studies that quantify early-life effects on individual quality in birds, we analyse data from an individual-based longitudinal study on common terns. The common tern is a Nearctic and Palearctic colonially breeding and migratory seabird (Becker and Ludwigs 2004). The data (Vedder and Bouwhuis 2017) we present come from a study population located in the Banter See at Wilhelmshaven on the German North Sea coast (53°36'N, 08°06'E), where the presence and reproductive performance of individual common terns has been monitored following a standard protocol since 1992 (Becker et al. 2008). For birds fledged between 1992 and 2010 ($n=3896$), we investigate whether cohort effects translate to between-individual variation in reproduction and survival. Specifically, we test whether common terns fledged in years with varying levels of average colony-wide reproductive performance (range 0.12–1.57 fledglings/brood, Fig. 1) differ in 1) local 'prospecting probability', the probability of a fledgling to be observed in the population during adulthood, 2) local 'recruitment probability', the probability of a prospector to attempt reproduction in the colony, as defined by it reaching the incubation stage at least once, 3) 'age at first prospecting and recruitment', and, for birds that recruited, 4) 'lifespan', with birds being assumed to have died when they have not been recorded in the colony for at least two seasons (see also Bouwhuis et al. 2015, Zhang et al. 2015b), and 5) 'lifetime reproductive success', assessed as the total number of fledglings produced. Moreover, and within the same statistical framework (van de Pol and Wright 2009), we investigate whether within-cohort variation in natal quality (expressed as the deviation in the number of fledglings of each brood (range 1–3) from the overall annual average colony-wide reproductive performance) relates to variation in these traits (1–5). In order to pinpoint at which life stage potential selection occurs, our analytical approach is sequential: each life

Figure 1. Variation in cohort quality between 1992 and 2010.

stage is analysed only for individuals that survived to the previous life stage.

Our data are highly suitable for our purpose because the numerous locally-hatched birds are individually marked with rings and transponders and return with a high probability, after which they are highly philopatric, so that they can be followed throughout life. An automated detection system edging the colony records the presence of transponder-marked individuals, including prospectors and non-breeders. All transponder-marked breeders are additionally linked to a breeding attempt by placing an antenna around each clutch for at least 24 h during incubation, which is shared between partners. Three-times weekly checks of each clutch provide detailed information on reproductive performance of breeders: laying date, clutch size, and brood size are recorded and chicks are individually marked with metal rings upon hatching, while transponders are injected shortly prior to fledging. The detection probability of breeders is almost 100%, and their re-sighting probability, not conditional of survival, is 90% (Szostek and Becker 2012). The number of breeding pairs at the colony has ranged between 90 and 650 between 1992 and 2016.

We analyse the effect of cohort quality (the overall annual average number of fledglings produced per brood, Fig. 1) and natal within-cohort nest quality (the deviation in the number of fledglings produced in each brood from the overall annual cohort average) using mixed-effect models run in MLwiN (ver. 2.26, Rasbash et al. 2005) with binomial (1 and 2) and Poisson (3–5) distributed errors and a Markov chain Monte Carlo estimation algorithm with 100 000 iterations. In addition to the fixed linear effects of cohort quality and nest quality, models include linear covariates of year of birth and population size (estimated as the number of breeding pairs) to account for the fact that fledglings from more recent years have had fewer years to produce a successful life history

(see also Bouwhuis et al. 2015) and that post-fledging survival may be negatively affected by density-dependent processes (Fay et al. 2017), respectively. Nested random effects of year and nest are included to account for non-independent observations on fledglings originating from the same nest and cohort. We report estimates as obtained in the full models (described above and reported in the supplementary material) and the significance ($p < 0.05$, two-tailed) of fixed effects is assessed using the Wald statistic, which approximates the χ^2 -distribution.

Out of 3896 fledglings produced between 1992 and 2010, 1482 (i.e. 38.0%) prospected prior to 2017. Prospecting probability of fledglings varied with cohort quality (estimate $\pm$ SE: 0.642 ± 0.263 , $\chi^2_1 = 5.982$, $p = 0.014$), such that the probability of local prospecting increased with the average number of fledglings produced per brood in the year of hatching (Fig. 2). There was no significant effect of within-cohort nest quality (estimate $\pm$ SE: -0.091 ± 0.059 , $\chi^2_1 = 2.386$, $p = 0.122$). Age at first prospecting (average $\pm$ SD: 2.3 ± 1.0) did not vary significantly with cohort quality (estimate $\pm$ SE: -0.035 ± 0.054 , $\chi^2_1 = 0.425$, $p = 0.514$) or within-cohort nest quality (estimate $\pm$ SE: -0.026 ± 0.028 , $\chi^2_1 = 0.891$, $p = 0.345$).

Out of 1482 prospectors, 959 (i.e. 64.7%) recruited prior to 2017. Recruitment probability of prospectors did not vary significantly with cohort quality (estimate $\pm$ SE: 0.136 ± 0.265 , $\chi^2_1 = 0.264$, $p = 0.607$) or within-cohort nest quality (estimate $\pm$ SE: 0.114 ± 0.091 , $\chi^2_1 = 1.566$, $p = 0.211$). Age at recruitment (average $\pm$ SD: 3.8 ± 1.3) also did not vary with either cohort quality (estimate $\pm$ SE: -0.067 ± 0.069 , $\chi^2_1 = 0.945$, $p = 0.331$) or within-cohort nest quality (estimate $\pm$ SE: -0.002 ± 0.027 , $\chi^2_1 = 0.007$, $p = 0.933$).

Figure 2. The probability of local prospecting increases with cohort quality ($n = 1482$ prospectors out of 3896 fledglings). Data points are presented as averages ($\pm$ SE) per cohort.

Out of 959 recruited birds, 526 have not been registered in the colony for over two years and can therefore be assumed to have finalised their life histories. In total, these 526 birds attempted reproduction 3418 times (range: 1 – 18 attempts, average $\pm$ SD: 6.5 ± 3.6 attempts). Lifespan of recruits (average $\pm$ SD: 7.9 ± 3.7) did not vary significantly with cohort quality (estimate $\pm$ SE: 0.059 ± 0.062 , $\chi^2_1 = 0.905$, $p = 0.341$) or within-cohort nest quality (estimate $\pm$ SE: 0.018 ± 0.028 , $\chi^2_1 = 0.412$, $p = 0.521$). Similarly, lifetime reproductive success of recruits (average $\pm$ SD: 3.1 ± 3.4) also did not vary significantly with cohort quality (estimate $\pm$ SE: -0.097 ± 0.163 , $\chi^2_1 = 0.356$, $p = 0.551$, Fig. 3a) or within-cohort nest quality (estimate $\pm$ SE: 0.118 ± 0.074 , $\chi^2_1 = 2.548$, $p = 0.110$, Fig. 3b).

Natal cohort and within-cohort nest quality (in terms of the number of fledglings produced per brood) were therefore found not to underlie heterogeneity in individual quality in common terns, but to only have short-term effects: good years were followed by birds having increased prospecting probabilities, perhaps because high pre-fledging survival co-occurs with high post-fledging survival at the breeding grounds when local food availability is high. One explanation for the described ‘null result’ may be a lack of statistical power to detect long-term effects of developmental conditions. However, in the common tern dataset, the most straightforward test for a relationship between individual annual reproductive success and lifespan also yielded no significant result (Table 1, Bouwhuis et al. 2015, Zhang et al. 2015a), and evidence for heterogeneity in individual quality only became apparent with more detailed analyses (Bouwhuis et al. 2015, Zhang et al. 2015b). Hence, common terns may genuinely have comparatively little heterogeneity in individual quality.

We are not the first to report a ‘null result’ with respect to long-term effects of natal conditions. In a study on great tits, for example, no evidence was found for natal environmental conditions (density, cohort quality, beech mast crop) or natal brood characteristics (hatching date, sibling number) to be associated with late-life reproduction or lifespan (Bouwhuis et al. 2010a) and this result supplemented analyses of other life-history traits in females from the same population, which also showed that natal environmental variation had very weak effects, at most, on post-recruitment fitness components (Wilkin and Sheldon 2009). Null results, however, contrast with findings of the above mentioned studies that reported effects of parental age, natal phenology and natal cohort and habitat quality on lifetime reproductive success (Visser and Verboven 1999, Reid et al. 2003, van de Pol et al. 2006, Saino et al. 2012, Schroeder et al. 2015, Bouwhuis et al. 2015). Unfortunately, studies testing for long-term fitness effects of early life-conditions in wild birds are still relatively rare and a standard analytical approach is lacking, making it difficult to quantitatively compare studies and provide a general answer to the question of whether early-life effects are strong enough to account for heterogeneity in individual quality, but the observed variation warrants speculation on life-history drivers of interspecific variation in heterogeneity.

Figure 3. Predicted lifetime reproductive success of recruits, obtained from a model correcting for year of birth and population size, expressed as the total number of fledglings produced over life, does not vary significantly with (a) cohort quality or (b) within-cohort nest quality ($n = 526$ recruits that have not been registered in the colony for over two years and can therefore be assumed to have finalised their life histories).

Life-history drivers of interspecific variation in heterogeneity

One major caveat of studies testing for long-term effects of developmental conditions is that they typically only test for effects in adulthood, while ignoring the fraction of individuals that died before reaching adulthood as a result of early-life conditions (i.e. the ‘invisible fraction’, Grafen

1988). Although life-history theory may predict selection on offspring to favour adaptive buffering against resource limitation in early life at a price paid later in life, suggesting fitness consequences of resource limitation to be expressed more strongly later in life (Williams 1957, 1966, Kirkwood 1977), selection on parents may act in the opposite direction (Hamilton 1966). Parents facing variable and unpredictable food conditions during the phase in which offspring depend on parental care are predicted to initially produce offspring in excess and trim down offspring numbers rapidly when food is limiting (Temme and Charnov 1987, Kozłowski and Stearns 1989). In birds, this may be achieved with active infanticide, or by the parents creating a level of hatching asynchrony that causes older siblings to be able to rapidly kill or outcompete younger siblings when resources are limiting (Lack 1947, Magrath 1989, Mock and Forbes 1995). Common terns adopt the latter strategy, with the majority of hatchlings not surviving to fledging, selection on hatching order closely tracking the annual fledging success at the population level (Vedder et al. unpubl.), and offspring mortality peaking at the day of hatching (Vedder et al. 2017). We suggest that this brood reduction strategy reduces variation in offspring quality at independence, as, instead of buffering individual offspring to resource limitation, it causes rapid mortality of the individual offspring that cannot acquire enough resources, leaving only the individual offspring that were little constrained by resource availability to reach independence. Indeed, our recent study that modelled age-specific reproductive value as a function of hatching order found that the vast majority of fitness consequences of a disadvantaged start, relative to siblings, are incurred prior to fledging (Vedder et al. unpubl.). This corroborates results from studies on black-legged kittiwakes and blue-footed boobies that also adopt a brood reduction strategy in which long-term fitness effects of hatching order among individuals surviving to adulthood were found to be weak (Cam et al. 2003, Drummond and Rodriguez 2013).

Yet, not all bird species adopt a brood reduction strategy and, in many species, parents aim to mitigate the consequences of age-related hierarchies among offspring by providing later laid eggs with more resources (Slagsvold et al. 1984) or by hormonally priming these eggs for competition (Muller and Groothuis 2013), commonly referred to as a brood survival strategy (Howe 1976, Slagsvold et al. 1984). Whether this strategy is only effective in maximising the number of offspring that survive to independence at the expense of late-life fitness of initially disadvantaged offspring, and thereby increases heterogeneity in quality among adults, is, however, currently poorly understood. When more studies accumulate that quantify long-term effects of early-life conditions, it would be insightful to test whether adverse late-life effects of poor developmental conditions are stronger in species with a brood survival strategy and therefore whether the relative strength of selection in early and late life may affect the magnitude of individual heterogeneity over life.

So far, to our knowledge, only a single study tested whether individual heterogeneity in an essential adult fitness component was related to other traits that characterize a species general life-history strategy (Péron et al. 2016). Among five species of birds, combined with four species of mammals, less individual heterogeneity in adult survival was found in species that were larger and lived longer (Péron et al. 2016). This can be explained in terms of individuals of long-lived species adaptively prioritizing survival over reproduction, because annual survival contributes more to fitness than annual reproduction in species with a longer generation time (Pfister 1998, Caswell 2001). However, environmental stochasticity both favours a slower life-history strategy (i.e. increased adult survival at the expense of reproduction; Stearns 1976, Roff 2002) and a brood reduction strategy (Kozłowski and Stearns 1989), with the latter also being more frequently observed in larger bird species (Slagsvold et al. 1984). Ultimately, the driver of heterogeneity in quality may thus be environmental stochasticity rather than generation time per se, and a brood reduction strategy and prioritizing adult survival may contribute in conjunction to less heterogeneity in quality among adults.

Notable exceptions may occur in species with precocial offspring, in which parental investment is less divided between individual offspring. In these species, parent-offspring conflict over parental investment will be reduced, leading to the prediction that parents maintain offspring survival even under unfavourable conditions (Lazarus and Inglis 1986), which could then lead to more heterogeneity in offspring quality that is deferred into adulthood. As such, the altricial-precocial spectrum observed in birds may provide an ideal opportunity to test whether parent-offspring conflict over fitness costs of poor developmental conditions incurred early or late in life also explains variation in individual quality among adults independent of a species generation time.

With respect to temporal variation in survival, it has been found that mammalian species with a longer generation time show less variation in adult survival than in juvenile survival, while the reverse is found in short-lived species (Gaillard and Yoccoz 2003). A similar pattern has been suggested for birds (Sæther and Bakke 2000), but it remains to be investigated whether reduced temporal variation in survival comes in concert with reduced individual heterogeneity in survival, and whether species with a fast life-history strategy prioritize reproduction to the extent that reduced individual heterogeneity in reproduction would compensate for their increased heterogeneity in survival, causing no or little differences in heterogeneity in total individual quality among species with different life-history strategies. Future studies should therefore aim to quantify both individual heterogeneity in reproduction and survival in species of a wide range of life-history strategies, and assess how this relates to environmental stochasticity, both pre- and post-independence, if we are to enhance our understanding of the drivers of heterogeneity in individual quality.

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.6v29b> > (Vedder and Bouwhuis 2017).

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Supplementary material (available online as Appendix oik-04273 at <www.oikosjournal.org/appendix/oik-04273>). Appendix 1.