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Individual heterogeneity determines sex differences in mortality in a monogamous bird with reversed sexual dimorphism

Fernando Colchero*,[1,2], Alix Eva Aliaga[3,4], Owen R. Jones[1,3] and Dalia A. Conde[1,3,5]

[1]Max-Planck Odense Center on the Biodemography of Aging, Campusvej 55, 5230 Odense M, Denmark; [2]Department of Mathematics and Computer Science (IMADA), University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark; [3]Department of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark; [4]Amphi Consult, Forskerparken 10, 5230 Odense M, Denmark; and [5]Species 360, 7900 International Drive, Suite 1040, Bloomington, MN 55425, USA

Summary

1. Sex differences in mortality are pervasive in vertebrates, and usually result in shorter life spans in the larger sex, although the underlying mechanisms are still unclear. On the other hand, differences in frailty among individuals (i.e. individual heterogeneity), can play a major role in shaping demographic trajectories in wild populations. The link between these two processes has seldom been explored.

2. We used Bayesian survival trajectory analysis to study age-specific mortality trajectories in the Eurasian sparrowhawk (*Accipiter nisus*), a monogamous raptor with reversed sexual size dimorphism. We tested the effect of individual heterogeneity on age-specific mortality, and the extent by which this heterogeneity was determined by average reproductive output and wing length as measures of an individual's frailty.

3. We found that sex differences in age-specific mortality were primarily driven by the differences in individual heterogeneity between the two sexes. Females were more heterogeneous than males in their level of frailty. Thus, a larger number of females with low frailty are able to survive to older ages than males, with life expectancy for the least frail adult females reaching up to 4·23 years, while for the least frail adult males it was of 2·68 years.

4. We found that 50% of this heterogeneity was determined by average reproductive output and wing length in both sexes. For both, individuals with high average reproductive output had also higher chances to survive. However, the effect of wing length was different between the two sexes. While larger females had higher survival, larger males had lower chances to survive.

5. Our results contribute a novel perspective to the ongoing debate about the mechanisms that drive sex differences in vital rates in vertebrates. Although we found that variables that relate to the cost of reproduction and sexual dimorphism are at least partially involved in determining these sex differences, it is through their effect on the level of frailty that they affect age patterns of mortality. Therefore, our results raise the possibility that observed differences in age-specific demographic rates may in fact be driven by differences in individual heterogeneity.

Key-words: Bayesian survival trajectory analysis, cost of reproduction, individual heterogeneity, sex differences in mortality, sexual dimorphism

Introduction

Recent studies have revealed a great diversity of age-specific patterns of mortality in wild populations (Jones *et al.* 2014). These age-specific trends in vital rates are an integral component of the regulation of wild populations (Schindler *et al.* 2012; Sæther *et al.* 2013), and thus it is fundamental to understand the mechanisms that determine them. Although these patterns are measured at the population level, many of the mechanisms that drive them

*Correspondence author. E-mail: colchero@imada.sdu.dk

occur at the individual level (Lescroel *et al.* 2009). In particular, sex-biased mortality and individual differences in frailty or vitality, also known as individual heterogeneity, are two of the most important sources of variability in vital rates within populations (Vaupel, Manton & Stallard 1979; Vaupel & Yashin 1985b; Stover, Kendall & Fox 2012; Noonburg *et al.* 2015). Disentangling the interaction between these two processes and how they contribute to observed population-level mortality trajectories has seldom been explored. This represents an important challenge for studies of population dynamics and life-history evolution, and requires detailed individual-level data and appropriate statistical modelling.

The principle of energy allocation (Cody 1966; Williams 1966) suggests that natural selection maximizes fitness by optimizing the allocation of a finite energy pool among processes that include reproduction and survival. The diversity of life-history strategies seen in the natural world thus reflects different solutions to this optimization problem that are reached under different conditions. Since the costs of reproduction vary between the sexes, the optimal energy allocation strategy can also be expected to be sex dependent (Williams 1957; Clutton-Brock & Parker 1992; Bonduriansky *et al.* 2008). Consequently, when one sex allocates relatively more resources to reproduction than the other (e.g. via parental care or mate acquisition), fewer resources will be available for maintenance in that sex and survival probability will be reduced leading to sex-biased mortality (Williams 1957; Bonduriansky *et al.* 2008). Several comparative studies have explored this phenomenon, focusing on factors including mating system and sexual body size dimorphism as potential underlying mechanisms (Promislow 1992; Promislow, Montgomerie & Martin 1992; Liker & Székely 2005; Clutton-Brock & Isvaran 2007). The earlier studies proposed that male-biased mortality was related to sexual size dimorphism in birds (Promislow, Montgomerie & Martin 1992) and polygynous mammals (Promislow 1992), and suggested that female-biased mortality in monogamous species resulted from a decreased male allocation to reproduction. Other studies have focused on the distribution of parental care between the sexes and male–male competition intensity as drivers of the observed patterns of sex differences in mortality (Owens & Bennett 1995; Toigo & Gaillard 2003; Liker & Székely 2005). Others have examined the role of the duration of the effective breeding in males and their capacity to allocate energy to sexual traits (Clutton-Brock & Isvaran 2007; Lemaitre & Gaillard 2013) or male-biased parasitism (Moore & Wilson 2002). The collected cross-species work on this topic shows an association between male-biased mortality and both polygynous mating systems and pronounced body size dimorphism. However, studies on sex differences in the costs of reproduction within individual species are often equivocal, although there are notable exceptions (Michener & Locklear 1990; Madsen & Shine 1993; Hoffman *et al.* 2008). The exceptions to the expected pattern may stem from an obscuring effect of variation in vital rates both among species and within populations. Much of this variation can be attributed to individual heterogeneity as a measure of individual 'quality' (Cam & Monnat 2000), which influences total energy available to an individual. This means that if variation in individual condition is not accounted for, allocation to particular processes may appear to be positively correlated when trade-offs are expected (Clutton-Brock 1985; Van Noordwijk & de Jong 1986; Jennions, Møller & Petrie 2001; Moyes *et al.* 2009).

Today, an increasing body of research has stressed the importance of accounting for sources of variability that may affect the condition of individuals (i.e. their level of frailty) within populations when studying the effect of the cost of reproduction on mortality (Aubry *et al.* 2009; Chambert *et al.* 2013; Lim, Senior & Nakagawa 2014). Thus, this heterogeneity in individuals' condition, which affects their capacity to allocate to survival and reproduction, sometimes referred to as frailty, can greatly influence the patterns in vital rates at the population level (Vaupel, Manton & Stallard 1979; Vaupel & Yashin 1985a; Hamel *et al.* 2009; McDonald *et al.* 2014; Vaupel & Missov 2014). A number of studies have used reproductive effort as a proxy for individual heterogeneity. For instance, Cam & Monnat (2000) found that, in kittiwakes, birds that failed a breeding attempt in a given year had lower probabilities both of survival and of breeding in the following year, most likely as the result of individual heterogeneity. In the same species, Aubry *et al.* (2011) not only confirmed this result but also found that the cumulative reproductive effort, as a measure for individual heterogeneity, was positively related to survival. Similar results have been found in red deer (Moyes *et al.* 2006), Nazca boobies (Townsend & Anderson 2007), great tits (Nicolaus *et al.* 2011) and Monteiro's storm petrel (Robert *et al.* 2012). However, in most of these studies the effect of individual heterogeneity was evaluated either on just one sex, or the sexes were not differentiated. Thus, two important questions remain; (i) what role does individual heterogeneity play in determining sex differences in mortality? And (ii) how much of this heterogeneity is explained by average reproductive output and by measures of sexual size dimorphism?

Here, we analyse sex differences in age-specific mortality on the Eurasian sparrowhawk (*Accipiter nisus*, Linnaeus), and the role that measures of adult size (i.e. adult wing length) as well as average reproductive output play as proxys for individual heterogeneity. The Eurasian sparrowhawk is a monogamous species with strong reversed sexual size dimorphism, where females are larger than males (Newton & Marquiss 1979). These characteristics make it an appropriate species to test hypotheses on the mechanisms that drive sex differences in mortality. We used Bayesian survival trajectory analysis (Colchero & Clark 2012; Colchero, Jones & Rebke 2012) to test the following hypotheses: (i) being monogamous but with sexual size dimorphism favouring females, both sexes will have similar levels of mortality; (ii) as with other long-lived birds (Cam & Monnat 2000; Townsend & Anderson 2007; Aubry *et al.* 2011), mortality will be negatively related to reproductive effort; (iii) using wing length as a proxy of an individual's frailty, individuals with lower adult wing length will have higher risk of mortality. To test these hypotheses we compared the performance of different models of mortality, some of which explicitly incorporate a measure of individual heterogeneity.

Materials and methods

STUDY SPECIES

We used a 28 years (1971–1999) capture–mark–recapture dataset gathered by the British ornithologist Ian Newton from two populations of the Eurasian sparrowhawk in the United Kingdom. These data are freely available as part of the Long-term Individual-based Time Series (LITS) project (Jones *et al.* 2008). The dataset contains information on individual identity, sex, breeding (e.g. clutch size, hatch year), sites (e.g. land-use) and wing length, in addition to recapture and/or observation dates. In this species, body size tends to be larger in females than in males (Newton & Marquiss 1979).

The two populations correspond to two different study areas in Scotland: Eskdale and Annandale. A total of 699 individuals were recaptured: 228 females and 121 males in Annandale; 262 females and 88 males in Eskdale. Individuals were either caught directly from their nests (i.e. chicks and adults) or near their nests (i.e. adults) (Newton & Rothery 1997). Individuals were caught between late April and early June, which correspond to 2 weeks before females laid their eggs, to the end of the incubation period (Newton, Rothery & Wyllie 2008). Fledgling occurs in July while during the post-fledging period, which lasts for 3–4 weeks, chicks are still fed by their parents, until they disperse mainly in August (Newton & Rothery 2000). Great variation in adult survival and reproduction has been reported in both populations (Newton, Wyllie & Rothery 1993), with a decline in population numbers in Annandale between 1970 and 1980 and overall constant conditions in Eksdale (Wyllie & Newton 1991; Newton, Rothery & Wyllie 2008).

During the breeding season, female weights vary from 258 to 262 g in August–September, to 325 g in May, at the peak of the egg laying period (Newton, Marquiss & Village 1983). Male weights vary considerably less, from 143 g in August, to 155 g in March. The clutch sizes fluctuate from one to seven eggs, where typically higher clutch sizes are associated to heavier females.

We estimated average reproductive output for a given individual i as

$$\mathrm{Repr}_i = \frac{1}{T_i}\sum_{t\in\tau_i} y_{it},$$

where τ_i is the set of years for which individual i was recorded breeding with length T_i (i.e. number of occasions individual i was recorded breeding) and y_{it} is the number of hatchlings produced by that individual at time t.

We standardized the wing length variable as

$$\mathrm{Wing}_i = \frac{w_i - \bar{w}}{s_w},$$

where w_i is the wing length (in mm) for individual i, $\bar{w}$ and s_w are the sample mean and the sample standard deviation of the wing lengths for all the individuals in the population (subsequently we provide average measures together with their standard deviations). Since females had consistently larger wing lengths than males ($\bar{w}_f = 237{\cdot}2 \pm 10{\cdot}04$ mm, $\bar{w} = 200{\cdot}6 \pm 8{\cdot}38$ mm, Welch's one-sided t-test P-value <0·0001), most of the Wing_i values for females were positive while those for males were negative.

STATISTICAL ANALYSIS

To understand sex differences in age-specific mortality patterns of the Eurasian sparrowhawk and how they are affected by individual level covariates such as average reproductive output and adult body size, we used the R package BaSTA (Colchero & Clark 2012; Colchero, Jones & Rebke 2012). The models in BaSTA use a Bayesian framework to allow users to explore different functional forms of age-specific mortality when age information is scarce or entirely missing, which is typical from capture–mark–recapture/recovery datasets. This package is based on the principles of survival analysis, which require defining a random variable X for age at death, where any given age is represented by $x \geq 0$. A typical age-specific survival analysis requires us to define the mortality or hazards rate as

$$\mu(x|\boldsymbol{\beta}) = \lim_{\Delta x \to 0} \frac{\Pr(x < X < x + \Delta x | X > x, \boldsymbol{\beta})}{\Delta x}, x \geq 0 \qquad \text{eqn 1}$$

where $\boldsymbol{\beta}$ is a vector of mortality parameters to be estimated, and the cumulative hazards function given by

$$H(x|\boldsymbol{\beta}) = \int_0^x \mu(t|\boldsymbol{\beta})\mathrm{d}t. \qquad \text{eqn 2}$$

From eqns (1) and (2), a number of demographic functions are derived, particularly the survival function

$$S(x|\boldsymbol{\beta}) = \Pr\{X > x|\boldsymbol{\beta}\} = \exp[-H(x|\boldsymbol{\beta})], \qquad \text{eqn 3a}$$

the cumulative distribution function (CDF) of ages at death

$$F_X(x|\boldsymbol{\beta}) = \Pr\{X \leq x|\boldsymbol{\beta}\} = 1 - S(x|\boldsymbol{\beta}), \qquad \text{eqn 3b}$$

and the probability density function (PDF) of ages at death

$$f_X(x|\boldsymbol{\beta}) = \frac{\mathrm{d}}{\mathrm{d}x}F_X(x|\boldsymbol{\beta}) = \mu(x|\boldsymbol{\beta})S(x|\boldsymbol{\beta}) \qquad \text{eqn 3c}$$

We explored two functional forms for the mortality function in eqn (1). These included the Gompertz mortality model (Gompertz 1825), which is given by

$$\mu_0(x|\boldsymbol{\beta}) = \exp(\beta_0 + \beta_1 x), \qquad \text{eqn 4a}$$

where $\beta_0 \in \mathbb{R}$ and $\beta_1 > 0$. Here, β_0 is the baseline mortality (i.e. when $x = 0$) and mortality increases exponentially with age at a rate determined by parameter β_1. This model can be extended into a logistic mortality model (Vaupel, Manton & Stallard 1979; Vaupel & Missov 2014) which accounts for individual heterogeneity in frailty. The logistic mortality model is given by

$$\mu_0(x|\boldsymbol{\beta}) = \frac{\exp(\beta_0 + \beta_1 x)}{1 + \beta_2 \frac{e^{\beta_0}}{\beta_1}(e^{\beta_1 x} - 1)}, \qquad \text{eqn 4b}$$

where $\beta_0 \in \mathbb{R}$ and β_1, $\beta_2 > 0$. Vaupel, Manton & Stallard (1979) showed that this model is the population level equivalent of the gamma-Gompertz model, which incorporates the effects of individual differences in frailty on mortality as $\mu(x|z, \boldsymbol{\beta}) = z\exp(\beta_0 + \beta_1 x)$ for $x \geq 0$ and $z > 0$. The gamma-Gompertz model, which assumes that the level of frailty does not change during an individual's lifetime, defines the random variable Z as gamma-distributed individual frailty with values given by $z > 0$ and mean $\mathrm{E}(Z) = 1$. In their proof they demonstrate that $\mathrm{Var}(Z) = \beta_2$. In other words, the third parameter in the logistic model represents the level of variation in frailty within a population. If $\beta_2 = 0$ all individuals in the population share the same level of frailty, namely $z_i = 1$ for $i = 1, \ldots, n$ and the model becomes a simple Gompertz mortality model. If, on the other hand, $\beta_2 > 0$ then the level of frailty varies among individuals.

The models in BaSTA allow us to evaluate the effects of covariates under a proportional hazards framework as

$$\mu(x, \mathbf{w}|\boldsymbol{\beta}, \boldsymbol{\gamma}) = \exp(\boldsymbol{\gamma}^T \mathbf{w})\mu_0(x|\boldsymbol{\beta}), \quad \text{for } x \geq 0, \mathbf{w} \in \mathbb{R}^p, \tag{eqn 5}$$

where $\mathbf{w}$ is a vector of covariates of length p, and $\boldsymbol{\gamma} \in \mathbb{R}^{\mathrm{p}}$ is a vector of parameters linking the covariates to the overall mortality. For our analysis these covariates included average reproductive output (Repr) and wing length (Wing).

In addition, BaSTA allows us to evaluate the effect of categorical covariates on mortality parameters. For instance, let y_i be an indicator for sex such that $y_i = 1$ if individual i is a female and $y_i = 0$ otherwise. Thus, for an individual i we have the Gompertz mortality in eqn (4b) which would be

$$\mu(x_i|y_i, \boldsymbol{\beta}) = \exp\left[\underbrace{(\beta_{0f}y_i + \beta_{0m}(1 - y_i))}_{\beta_0} + \underbrace{(\beta_{1f}y_i + \beta_{1m}(1 - y_i))}_{\beta_1} x_i\right] \tag{eqn 6}$$

for $i = 1,\ldots,n$, where, β_{0f}, $\beta_{0m} \in \mathbb{R}$, β_{1f}, $\beta_{0m} > 0$ and the subscripts f and m refer to females and males respectively.

We tested 10 nested models where the full model of mortality as a function of the covariates included the following variables and interactions

$\mu(x) = f(\mathrm{Sex} + \mathrm{Sex} : \mathrm{Repr} + \mathrm{Sex} : \mathrm{Wing} + \mathrm{Repr} : \mathrm{Wing})$,

where Repr = average reproductive output, Wing = adult wing length, and the interaction between the two variables is represented as Sex : Repr.

Because the sampling effort primarily focused on adult birds and hence juvenile birds were under-represented, we estimated mortality patterns only for adults [i.e. individuals that were 2 years of age or older, based on estimates of age at sexual maturity by Newton, Marquiss & Village (1983)].

The R package BaSTA performs Metropolis sampling within an MCMC algorithm (Metropolis *et al.* 1953; Clark 2007). For each model, we ran eight parallel chains with 105 000 iterations, a burn-in of 5001 and thinned every 200 iterations. We evaluated convergence based on Gelman *et al.*'s (2013) potential scale reduction, while we calculated deviance information criterion (DIC) as a measure of model fit (Spiegelhalter *et al.* 2002; Celeux *et al.* 2006). In addition, we applied a calibration of the Kullback–Leibler discrepancies (KLD) (Kullback & Leibler 1951; Burnham & Anderson 2001) proposed by McCulloch (1989) to test the difference between the posterior distributions of corresponding parameters for the two sexes. This calibration provides a value $k_\beta \in [0{\cdot}5, 1]$ for a given parameter β as a measure of the amount of overlap between the posterior distributions of the estimates for β_f and β_m for females and males, respectively. A value of $k_\beta = 0{\cdot}5$ means that there is full overlap between both posterior distributions, while $k_\beta = 1$ implies that there is no overlap.

In addition, we estimated life expectancy at age 2 as $e_2 = \int_2^\infty S(x)\mathrm{d}x/S(2)$, for each sex based on the model with the lowest DIC value.

AMOUNT OF HETEROGENEITY EXPLAINED BY THE COVARIATES

To obtain a measure of the amount of heterogeneity explained by wing length and average reproductive output, we estimated the percentage reduction in the values of β_2 (i.e. the parameter that corresponds to the variance in frailty) between the model that included only Sex as a covariate and three competing models, namely: (i) Sex + Sex : Repr; (ii) Sex + Sex : Wing; and (iii) Sex + Sex : Repr + Sex : Wing.

Results

For all the models tested, the logistic mortality model had always considerably lower DIC than the Gompertz model (highest DIC of logistic model was 5411, while lowest DIC of Gompertz model was 6416). This suggests that the effect of heterogeneity in frailty is considerable in this population. Thus, our following discussion of the results refers to the logistic model.

The model with the lowest DIC was the proportional hazards logistic mortality with the interactions Sex : Repr + Sex : Wing. This is the model that distinguishes the effects of average reproductive output and wing length between the sexes (Table 1). Importantly, the posterior densities for the baseline mortality, β_0, and the mortality rate, β_1, parameters between males and females had low Kullback–Leibler discrepancies ($k_{\beta 0} = 0{\cdot}69$ and $k_{\beta 1} = 0{\cdot}60$), which indicates high overlap in the parameter estimates of both sexes. The mortality parameter with the highest KLD value was the variance in heterogeneity

Table 1. Results of the model selection based on the values of the deviance information criterion (DIC). The model with the lowest DIC has the highest support from the data. In the second column p refers to the number of parameters estimated. The variables are: Sex = male or female; Repr = average reproductive output; Wing = wing length

Model	p	DIC
Sex + Sex : Repr + Sex : Wing	11	5257
Sex + Sex : Repr + Sex : Wing + Repr : Wing	12	5258
Sex + Repr + Sex : Wing	10	5265
Sex + Sex : Repr + Wing	10	5291
Sex + Sex : Wing	9	5301
Sex + Repr + Wing	9	5304
Sex + Wing	8	5340
Sex + Repr	8	5357
Sex + Sex : Repr	9	5363
Sex	7	5411

parameter, β_2 ($k_{\beta 2} = 0{\cdot}95$), which reveals strong differences in individual heterogeneity between the sexes, specifically indicating more heterogeneity for females (Table 2). Although the β_0 and β_1 parameters are similar in both sexes, the difference in the β_2 parameter results in higher mortality in males than in females at the population level (Fig. 1). The second best model included the interaction Repr : Wing (Table 1), however, the estimated parameter for this interaction was not different from 0 (i.e. $\widehat{\gamma}_{\mathrm{Repr:Wing}} = 0{\cdot}012 \pm 0{\cdot}11$). In other words, the interaction did not contribute any additional information.

Our results suggest that females with low average reproductive output and small wing length had proportionally higher mortality than those with high values of these traits (Table 2 and Fig 2a), while males with large wing length and low reproductive effort had higher mortality than males with opposite values (Fig. 2b). In addition, our estimates of life expectancy at age 2, e_2, for females varied from 1·91 years (± 0·12) for individuals with lowest values of wing length and average reproductive output, to 4·23 years (± 0·44) for those with higher values. Life expectancies for males ranged from 1·81 years (± 0·12) for individuals with high wing length and low average reproductive output, to 2·68 years (± 0·39) for those with low wing length and high average reproductive output.

The amount of heterogeneity explained by the two covariates indicates that wing length explained the highest percentage of heterogeneity, accounting for 44·3% (± 5·2%) in females and for 40·4% (± 24·2%) in males, while average reproductive output alone only accounted for 11·9% (± 1·2) and 24·7% (± 6·8%) for females and males respectively (Fig. 3). The combination of both covariates accounted for 49·6% (± 6·2%) and 50·0% (± 24·5%) for females and males respectively (Fig. 3). Notably, the combined effect of both covariates does not correspond to the sum of the individual effects, which suggests that these explanatory variables covary as functions of individual heterogeneity.

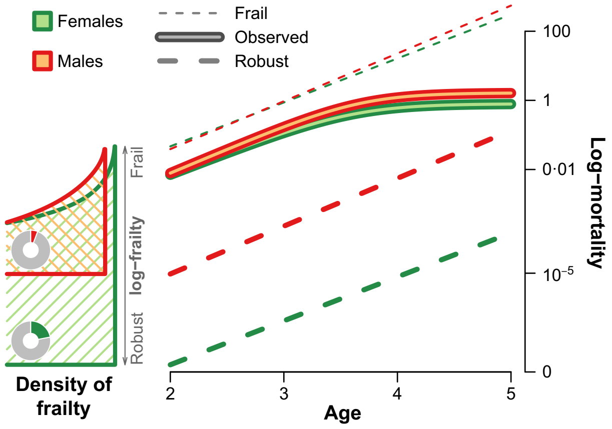

Fig. 1. Effect of the level of frailty (i.e. individual heterogeneity) on the sparrowhawk mortality. The density plots are transposed such that the frailty values (from robust to frail) are in the *y*-axis and the density values are in the *x*-axis, while the frailty values were transformed to their corresponding log-values. For display purposes, the range of the density plots was limited between 0 and 2, thus the donut plots show the percent of the area under the density plots beyond the upper level of truncation not depicted in the figure. The curves on the left show the log-mortality values; the full lines correspond to the observed level of mortality, the thick dashed line corresponds to the robust individuals (lower 95% CI of the frailty values) and the thin dashed line corresponds to the frail individuals (upper 95% CI of the frailty values).

Discussion

Researchers have long struggled to unravel which life-history traits are the main determinants of sex differences in mortality across the tree of life. Although the evidence can be at times contradictory, the general consensus is that in polygynous species, where males are often the larger sex, males have higher mortality and shorter life spans than females, while in monogamous species, where parental care is comparable between both sexes, the differences in mortality can potentially favour males (Promislow 1992; Promislow, Montgomerie & Martin 1992). On the other hand, other researchers have explored how individual differences in frailty can affect mortality, particularly to understand how individuals bear the costs of reproduction (Aubry *et al.* 2009; Chambert *et al.* 2013; Lim, Senior & Nakagawa 2014). The connection between these seemingly unrelated topics has seldom been tackled (but see Chen & Maklakov 2014). Here, we use data on a monogamous bird with reversed sexual dimorphism to

Table 2. Parameter estimates (with description in parenthesis on their effect on the mortality function) from the model with the lowest deviance information criterion (DIC). Values include the estimate (Est.) as the average of the posterior distribution, the standard error (SE) and the lower and upper 95% credible intervals (2·5% and 97·5%) and measures of model performance such as serial autocorrelation (Autocor.) and convergence (Converg.)

Parameter	Sex	Est.	SE	2·5%	97·5%	Autocor.	Converg.
β_0 (baseline mortality)	Female	−5·00	0·51	−6·03	−4·05	0·09	0·99
	Male	−4·48	0·61	−5·69	−3·28	0·15	1·00
β_1 (rate parameter)	Female	3·85	0·43	3·05	4·71	0·11	1·00
	Male	3·56	0·48	2·67	4·52	0·11	1·00
β_2 (Variance in frailty)	Female	1·85	0·38	1·21	2·70	0·08	0·99
	Male	0·97	0·45	0·31	2·01	0·27	1·00
γ_R (propor. effect of lifetime repr. effort)	Female	−0·07	0·04	−0·14	0·01	0·01	0·99
	Male	−0·13	0·06	−0·25	−0·02	0·01	1·00
γ_W (propor. effect of wing length)	Female	−1·24	0·23	−1·69	−0·80	0·01	1·00
	Male	0·43	0·35	−0·20	1·14	0·37	1·00

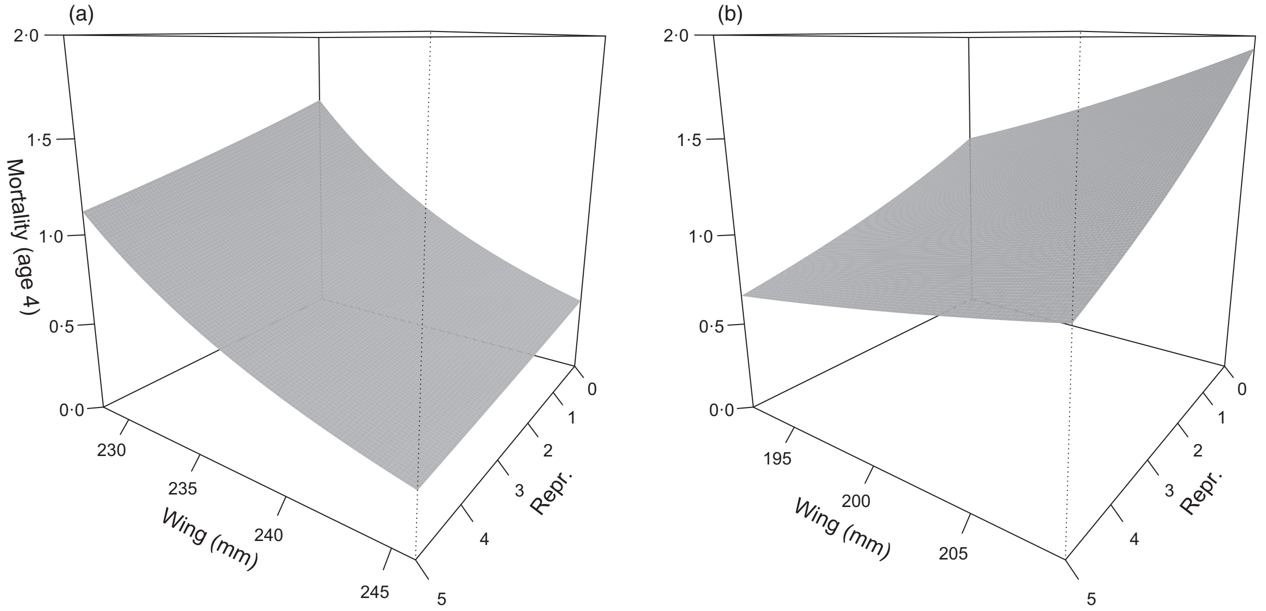

Fig. 2. Effect of average reproductive output (Repr.) and wing length (Wing) on mortality for a) females and b) males. For illustration purposes both figures depict the level of mortality at age 4. The mortality parameters were taken at the average from the posterior densities (see Table 2).

explore sex differences in mortality and how traits that relate to individual heterogeneity can be associated with these differences. Unexpectedly, our results show that the differences in mortality between both sexes are primarily driven by individual heterogeneity. Moreover, we were able to explain a high percentage of this individual heterogeneity with two uncorrelated measures, namely adult wing length, which provides a measure of an individual's physical characteristics, and average reproductive output, which is associated with the overall capacity of individuals to produce offspring. The lack of correlation between these two measures (Pearson's correlation coefficient $r_m = -0{\cdot}06$ for males and $r_f = 0{\cdot}08$ for females) and the fact that to a large extent wing length is genetically determined (Tarka *et al.* 2010), suggests that they represent two independent forces that shape the level of individual frailty, and could possibly be regarded as correlates of somatic- and germ-line investment respectively.

In terms of the specific effects of the two variables that partially explain individual heterogeneity, our results

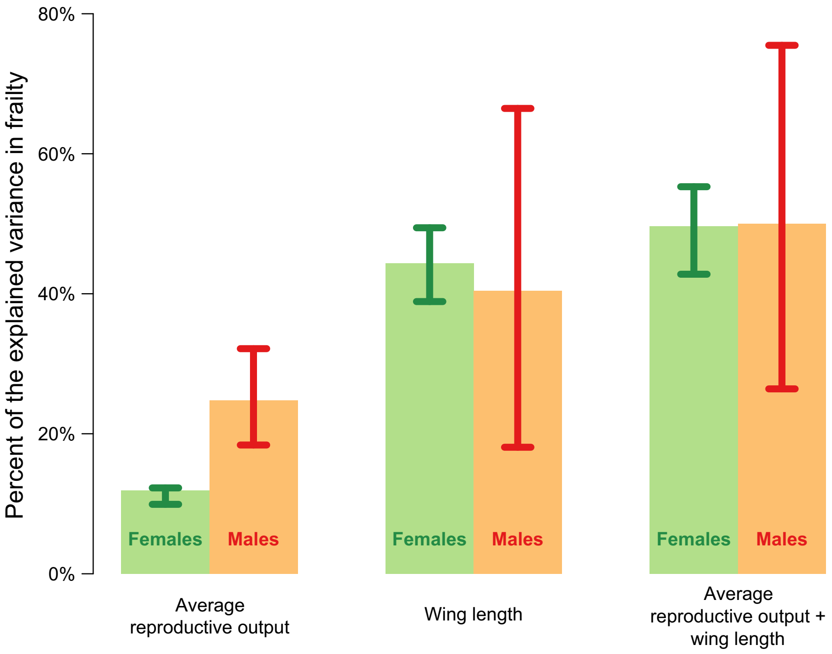

Fig. 3. Per cent of the variance in individual frailty (i.e. individual heterogeneity) for females (in green) and males (in red) explained by average reproductive output, wing length or the combined effect of average reproductive output and wing length. The per cent was calculated as $(1 - \beta_{2j}/\beta_{2S}) \times 100$, where β_{2j} is the parameter that reflects the variance in heterogeneity for the jth model and β_{2S} is the corresponding parameter for the model that only included sex as a covariate. The vertical bars depict the 95% upper and lower quantiles.

support previous findings in birds and other groups that show that measures of reproductive effort and success are negatively associated with mortality; in other words, individuals that are capable of producing more offspring are also better at surviving (Cam & Monnat 2000; Moyes *et al.* 2006; Townsend & Anderson 2007; Aubry *et al.* 2011; Nicolaus *et al.* 2011). Here, we found that this is in fact the case for both sexes, where individuals with high average reproductive output will also have higher chances of surviving and, subsequently, have higher life expectancy. However, and as we explained above, our results also highlight that our measure of average reproductive output explained only a fraction of the variation in individual frailty (about 12% for males and 25% for females). We found that adult wing length explained a larger proportion of this variation (around 40% in males and 44% in females) and, more importantly, that its effect on mortality differed between the sexes. Among females, individuals with larger wing length have lower mortality than those with lower values, while in males those with large wing length have higher mortality. Still, our measure of average reproductive output does not fully reflect the average reproductive performance of an individual, since it solely takes into account years during which that individual was observed breeding. A more appropriate measure would have been individual lifetime reproductive success (Clutton-Brock 1988) standardized by that individual's reproductive life span. It is possible that, by using the standardized LRS, we would have found a stronger effect of reproductive output on individual heterogeneity.

Our results provide novel evidence on the role of sexual dimorphism in determining sex differences in mortality on birds. Specifically, the opposite effect of wing length between the sexes highlights that the mechanisms by which individual size affects mortality are sex dependent. For instance, the positive relationship between body size and survival in females can be the result of the large demands females undergo during the breeding season, when their body weight can fluctuate from 260 to 320 g on average (Newton, Marquiss & Village 1983). In addition, Newton, Marquiss & Village (1983) found that heavier females had highest breeding success and lost less body mass during the breeding season. The relationship between body size and the capacity to store fat reserves to buffer the demands of reproduction and survival through harsh or unpredictable periods was proposed by Boyce (Boyce 1979), and reviewed by Millar and Hickling (Millar & Hickling 1990). The relationship has been illustrated numerous times in both mammal (Hamel *et al.* 2009) and birds (King & Farner 1966; Nolan & Ketterson 1983). On the other hand, we found that males have the reversed effect of increased body size on mortality, where larger males have less chances to survive than smaller ones. Contrary to females, male sparrowhawks undergo much lower variations in weight during the breeding season than females, however, they are responsible for providing food for both the incubating females and the chicks (Newton, Marquiss & Village 1983; Newton & Marquiss 1984). The idea that large size and weight are not necessarily an advantage has mainly been studied in birds with respect to avoiding predation (Lima 1986; Witter & Cuthill 1993). However, one intriguing possibility is that, since males are responsible for supplying food during incubation and chick rearing, smaller males might be more efficient at catching prey and therefore have better chances of surviving (Mueller & Meyer 1985; Pérez-Camacho *et al.* 2014). This is particularly the case for birds that forage in forested areas, where a smaller size has been associated with a higher efficiency to catch preys (Storer 1966). In accordance with this hypothesis, male sparrowhawks in the two study areas used broadleave woodlands for hunting (Marquiss & Newton 1982). This dependency on smaller and more efficient male provisioning is particularly important at the beginning of the nesting season when the pair relies heavily on the availability of small tits (Newton & Marquiss 1984). As the season progresses, females can contribute to provisioning by hunting larger preys.

It has been argued that, as the result of the strength of sexual selection, the sex with higher mortality will also have a higher senescence rate (speed of change in mortality) (Clutton-Brock & Isvaran 2007; Lemaitre & Gaillard 2013). Our results clearly show that this is not the case for the sparrowhawk; the rate of change in mortality, driven by the Gompertz rate parameter β_1, is virtually the same for both sexes. It is striking that the only parameter that clearly differs between the sexes is β_2, which provides a measure of the variance in individual frailty (Vaupel, Manton & Stallard 1979). By having higher individual heterogeneity, females have a larger proportion of robust individuals that survive to older ages than males. As a consequence, at the population level this higher proportion of robust females results in a lower age-specific mortality (Fig. 1). Garratt *et al.* (2015) found that sex differences in mortality were driven primarily by viability selection on females, by which poor conditions early in life selected for more robust individuals in late-life. This mechanism could potentially explain the larger individual heterogeneity in females particularly considering the variability in environmental conditions in both populations (Newton, Wyllie & Rothery 1993; Newton, Rothery & Wyllie 2008). Thus, viability selection would cause a reduction in the pool of frail females following bad years early in life, while cohorts born in years following good environmental conditions would maintain a larger proportion of frail females. Males on the other hand, show lower individual heterogeneity and a lower proportion of robust individuals, possibly due to a lower ability to cope with environmental changes, as reflected in their low capacity to change their body weight during the breeding season (Newton, Marquiss & Village 1983). Further research on the effect of environmental conditions on survival and reproduction is needed to shed light on the selective pressures that drive these sex differences in individual heterogeneity and mortality.

Nonetheless, our results raise the possibility that observed differences in age-specific demographic rates may in fact be driven by differences in individual heterogeneity, but in a complex fashion. Although features such as sexual size dimorphism and investment in reproduction may not be directly responsible for the sex differences in mortality, they can act as fundamental building blocks of within-sex heterogeneity. We, therefore, urge researchers to carefully check for heterogeneity effects in studies relying on estimation of sex differences in mortality characteristics.

Authors' contributions

F.C. and D.A.C. designed the study. F.C. and A.E.A. wrote the first draft of the manuscript, and all authors contributed substantially to revisions. A.E.A. and F.C. performed the analyses with assistance from D.A.C. and O.R.J. All authors gave final approval for publication.

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Data accessibility

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.t89g2 (Colchero *et al.* 2017).

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