Disentangling Pre- and Postnatal Maternal Age Effects on Offspring Performance in an Insect with Elaborate Maternal Care

Edward Ivimey-Cook* and Jacob Moorad

Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, United Kingdom

ABSTRACT: Maternal effect senescence has attracted much recent scientific interest. However, the age-related effects of pre- and postnatal maternal age are often conflated, as these naturally originate from the same individual. Additionally, many maternal effect senescence studies fail to account for potential biases associated with selective disappearance. Here we use a cross-fostered laboratory population of a burying beetle, *Nicrophorus vespilloides*, to examine both the effects of female pre- and postnatal maternal age on offspring life-history traits and the postcare outcomes of mothers while accounting for selective disappearance of postnatal caregivers. Neither pre- nor postnatal maternal age affected offspring longevity or larval weight at hatching, and postnatal age had no effect on postcare maternal outcomes except to confirm the presence of actuarial senescence. There was weak evidence for concave relationships between two larval traits (dispersal weight and survival) and the age of egg producers. Selective disappearance of caregivers had no clear effect on any of the measured offspring traits. Contrary to predictions from evolutionary theory, maternal effect senescence and reproductive effort increases do not always manifest, and current theory may be insufficient to account for the true diversity of aging patterns relating to maternal care.

Keywords: aging, cross-fostering, maternal effects, *Nicrophorus vespilloides*, selective disappearance, senescence.

Introduction

Senescence is often described as an age-related physiological deterioration associated with increasing mortality risk and decreasing reproductive rates (Finch et al. 1990; Jones et al. 2014). The deleterious effect of changes on individuals' own fitness-related traits has long been explained by the evolutionary theory of aging (Williams 1957; Hamilton 1966). However, maternal effect senescence—the detrimental effects of increasing maternal age that are manifested in the traits of their offspring—is a fundamentally different form of aging that has attracted recent interest (Heidinger et al. 2016; Moorad and Nussey 2016; Warner et al. 2016; Lippens et al. 2017). The most noted offspring outcomes are reduced offspring juvenile survival (Hercus and Hoffmann 2000; Sharp and Clutton-Brock 2010) and adult longevity (Lansing 1947; Priest et al. 2002; Fox et al. 2003). Evolutionary theory predicts deleterious effects of maternal aging on early offspring survival accompanied by an age-related increase in genetic variance for maternal effects (Moorad and Nussey 2016), but no such evolutionary model has been developed to explain the negative maternal age effect on offspring adult longevity. However, this phenomenon has been observed frequently enough to be given a term, the "Lansing effect," after an early observer, Albert Lansing (Comfort 1953).

Some life-history theory predicts that reproductive effort—or the proportion of available resources allocated to reproductive processes—should increase with age as the potential to realize future costs to reproduction lessens (Williams 1966*b*; Charlesworth and Leon 1976; Clutton-Brock 1984). This is expected to mitigate the observed expression of reproductive senescence. Reproductive effort has been reported to increase with age in several taxa, including species of birds (Pugesek 1981; Velando et al. 2006), mammals (Ericsson et al. 2001; Paterson et al. 2016), fish (Poizat et al. 1999), and invertebrates (Kight et al. 2000; Creighton et al. 2009; Hargrove et al. 2018). In species that provide elaborate parental care, it has been argued that the increased reproductive effort is manifested as larger and more successful offspring at the cost of reduced parental condition (Bijleveld and Mullers 2009). However, many studies fail to find age-related increases (Dugdale et al. 2011; Martin and Festa-Bianchet 2011; Conover 2013; Kuczynski et al. 2015).

* Corresponding author; email: e.r.ivimey-cook@sms.ed.ac.uk.

ORCIDs: Ivimey-Cook, http://orcid.org/0000-0003-4910-0443; Moorad, http://orcid.org/0000-0003-1222-5525.

Age-related changes in maternal effects can be caused by altered prenatal (e.g., egg-mediated) and postnatal (e.g., care-mediated) contributions to offspring condition (Beamonte-Barrientos et al. 2010; Lemaître and Gaillard 2017). However, distinguishing between the two can be extremely difficult in many systems because the providers of prenatal and postnatal care are often the same individuals (Lock et al. 2007; Beamonte-Barrientos et al. 2010). Nevertheless, it is important to decouple these effects in order to understand better the proximate mechanisms of maternal effect changes with age that are mediated through changes in egg quality or rearing capabilities (Beamonte-Barrientos et al. 2010). In species with complex parental care, it is important to consider both aspects of maternal effects, as pre- and postnatal age can each have a large influence on offspring fitness (Lock et al. 2007). Cross-fostering, where offspring born to one parent are raised by another, is a useful method for decoupling these two effects (Lynch and Walsh 1998). Applied to studies of senescence, cross-fostering offers a way to reveal potential divergent age-related effects of pre- and postnatal maternal effects. This approach has been used to study maternal age effects in the blue-footed booby, *Sula nebouxii*, where both the age of egg producers and carers were found to independently decrease growth rates of second chicks (laying-mother age [years]: $\beta = -1.00$ mm day^{-1}; rearing-mother age [years]: $\beta = -1.80$ mm day^{-1}; Beamonte-Barrientos et al. 2010).

While evolutionary models predict age-related changes in individual traits, demographic models suggest that among-individual variation (individual heterogeneity) can cause age-specific means for fitness-related traits to increase because of selective disappearance of frail individuals (Vaupel et al. 1979; Vaupel and Yashin 1985; van de Pol and Verhulst 2006). As a result, age-related changes in trait values may reflect changes in the identities of the individuals that make up the population rather than longitudinal changes in individuals caused by aging. This phenomenon has been shown to influence the perceived effects of age on fitness traits in various mammal and bird species (Cam et al. 2002; Nussey et al. 2006, 2011). Fortunately, the effects of selective disappearance can be corrected for statistically in longitudinal studies of aging (van de Pol and Verhulst 2006; van de Pol and Wright 2009; Nussey et al. 2011). If left uncorrected, inferences about the effects of aging on individuals may be unreliable (Hayward et al. 2013). Controlling for the effects of heterogeneity has only seldom been applied to maternal effect aging research (e.g., Hayward et al. 2013; Berger et al. 2015; Fay et al. 2016). There is a general need for an integration of methodologies that combine cross-fostering with the ability to control for selective disappearance.

We performed an aging experiment with a species of burying beetle, *Nicrophorus vespilloides*, with conspicuous postnatal maternal care. This species provides an ideal study system for discriminating between pre- and postnatal maternal effects because larvae can be cross-fostered (Lock et al. 2004, 2007; Head et al. 2012). Furthermore, while both parents can simultaneously provide care, the removal of one parent does not detrimentally effect average larval body weight or survival in the laboratory (Smiseth et al. 2005). Using a cross-fostered experimental design, we aimed to decouple the prenatal (egg producer) and postnatal (carer) effects of different maternal ages on life-history traits of their offspring and fitness-related outcomes of care-giving females. Existing models of maternal effect senescence (Moorad and Nussey 2016) predict that as maternal age increases into late age, we should see corresponding declines in offspring survival. This theory makes no explicit predictions regarding other offspring traits, but it is reasonable to predict that similar evolutionary arguments should predict that offspring adult longevity and larval dispersal weight will decrease with increasing maternal age. Previous *N. vespilloides* research is consistent with this expectation by showing that increased maternal age reduced the number of hatched larvae (Creighton et al. 2009), dispersed larvae, and total weight of brood at dispersal (Ward et al. 2009; Cotter et al. 2010). We may also expect that old egg producers will negatively impact the life history of the carer if they produce low-quality offspring. In fact, cross-fostered *N. vespilloides* females have been shown to provide more care when given lower-quality larvae to care for (Mattey et al. 2018), and it is possible that providing this additional care comes at a cost. Last, we corrected for selective disappearance statistically by adding carer longevity as a factor to our analyses of postnatal effects; this is a novel approach to aging research into postnatal maternal effects in a controlled laboratory population.

Material and Methods

Study System

Nicrophorus vespilloides breed and feed on small, dead vertebrates. Breeding pairs prepare the carcass by removing all hair, feathers, or scales and roll the carrion into a ball before burying it in the soil (Scott 1998). The female lays eggs in the surrounding soil. Two to three days later, larvae hatch and move to the carcass, where they can self-feed and be provisioned and cared for by their parents until independence, which occurs after 4 or 5 more days. Parental care in this species is characterized by the regurgitation of carrion from parents to larvae, defense of the larvae and carcass from conspecifics and other competing species, and the secretion of an anal exudate that inhibits fungal growth on the carcass. Larvae disperse into the surrounding soil after they become independent from parental care and pupate into adults (eclose) 21 days later.

The beetles used in this study were taken from an outbred laboratory population maintained at the University of Edinburgh originally derived from a colony in the Netherlands kindly provided by Daniel Rozen in 2013. Genetic diversity has since been maintained and enhanced by annual additions of wild beetles trapped from natural populations around Edinburgh. Beetles were individually housed in clear plastic boxes, kept at 21°C on a 16L:8D cycle, and fed small pieces of organic beef twice a week.

Experimental Age Classes

Female beetles were sampled from the population at four different posteclosion age ranges: young, midlife, old, and very old (comprising 11–18, 32–39, 53–60, and 77–87 days, respectively). Females are seldom reproductively active before 10 days after eclosion (Cotter et al. 2010), and female virgins that are older than very old are exceedingly rare. Female ages were also selected to represent differing rates of cumulative survival in virgin females (94%, 80%, 26%, and 1%; J. Moorad, unpublished data) and thus presumably represent highly varied magnitudes of selection for age-specific maternal care that covers nearly the full potential life span of the beetle (Moorad and Nussey 2016). We used virgin beetles for two reasons. First, differences among individuals in past reproductive allocation could contribute unnecessarily to trait variance even if the previous number of reproductive events was considered as a correlate in the statistical models. Second, with multiple matings, female age will be necessarily confounded with reproductive history, and the strong correlation between age and mating experience can cause additional statistical problems. One such problem could be that reproductive experience and increased age both have negative effects, and conflating the two effects will overestimate the true effects of age.

Experimental Procedures

We used a cross-fostered design to assess offspring performance in relation to varying carer and egg producer age. Virgin females from the four age classes were mated with virgin males aged approximately 2 weeks after eclosion. The males' ages were standardized in order to reduce variation caused by effects of paternal age. We supplied each pair with a mouse carcass weighing 20.71–25.99 g (Livefood Direct, Sheffield). Females were weighed before breeding, after egg laying, and after providing care. Males were removed 72 h after introduction to the carcasses and mating, and females with carcasses were placed into new breeding containers (absent of any eggs or larvae) in preparation for them to receive a mixed brood of larvae from other females. The old mating boxes (those which had previously contained females, carcasses, and eggs) were checked for newly hatched larvae every 2 h for 5 minutes until no new larvae were found (~72 h). Females that recently produced hatched larvae are capable of caring for other larvae, provided that these have hatched at roughly the time point as their own. If larvae appear on the carcass too early or too late, females will perceive them as not theirs and kill them (Müller and Eggert 1990). Infanticide from cross-fostering did not appear to have occurred in this experiment because no mothers eliminated whole broods of larvae. Previous work involving several *Nicrophorus* species used similar cross-fostering techniques (Rauter and Moore 2002*a*; Lock et al. 2004, 2007; Head et al. 2012; Steiger 2013).

We pooled larvae from same-age mothers (Rauter and Moore 2002*b*; Crook et al. 2008; Rozen 2008; Arce et al. 2012). *Nicrophorus vespilloides* females produce highly variable brood sizes (Smiseth and Moore 2002), and considerable asynchrony in larval hatching is frequently observed (Smiseth et al. 2008; Ford and Smiseth 2016). Pooling larvae produced by different mothers into mixed broods was a tractable approach to generating suitable numbers of experimental broods with constant family size. From these, we randomly sampled larvae to construct mixed broods of 15 larvae each to control for initial effects of density. A brood size of 15 larvae struck a reasonable balance between obtaining sufficient numbers of mixed broods while falling within the range of normal brood sizes produced by *N. vespilloides* (range = 2–47; Smiseth and Moore 2002; Smiseth and Parker 2008). Each mixed brood was placed under the care of unrelated mothers of various age classes and allowed to develop in the presence of their foster mother (the carer). At dispersal, larvae were counted and individually weighed using an Ohaus Pioneer PA114 analytical balance (repeatability = 0.1 mg). Mated females and eclosed offspring were then individually housed, regularly fed (with raw organic beef twice a week), and checked for death (three times a week) until all beetles had died. In total, we set up 147 matings, with 55 females caring for a brood (table 1). The other 92 females provided no care and donated larvae after mating ($n = 55$), had eggs that did not hatch ($n = 15$), or were omitted because the matings and females could not be used ($n = 22$).

Table 1: Numbers of caregiving and egg-producing beetles in each experimental age class

Age class	Young egg producer	Midlife egg producer	Old egg producer	Very old egg producer
Young carer	5 (75)	6 (90)	6 (90)	5 (75)
Midlife carer	8 (120)	2 (30)	3 (45)	…
Old carer	5 (75)	6 (90)	4 (60)	…
Very old carer	5 (75)	…	…	…

Note: Numbers of larvae are in parentheses.

We used ASReml v.4.1 (Gilmour 1997) to construct univariate generalized linear mixed effect models using data observed at the level of the offspring (table 2) to independently measure both carer age and egg producer age effects on larval weight at dispersal and offspring adult longevity (both with Gaussian error structures). Next, we fit a multivariate mixed effect model using data that were collected at the level of the carer to evaluate the effects of the caregivers' and egg producers' age on traits related to fitness. Dependent variables were larval weight at hatching (pooled over all broods of 15 larvae), residual life span of carer (days survived after mating), carer weight change (difference between postcare and precare body weight), and number of larvae surviving to dispersal. Note that the two univariate models fit using data collected at the level of the offspring feature offspring outcome traits as dependent variables, while the multivariate model fit using data collected at the level of the carer features dependent variables that describe both offspring and carer traits. All models were fit twice: once with first-order effects of carer and egg-producer age and once with all three possible second-order interactions involving these ages. Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad .941d66f (Ivimey-Cook and Moorad 2018).

Parameters with the potential to confound the relationships between maternal ages and offspring outcomes were included in the mixed models as fixed and random effects. These fixed effects were carcass size (because resource availability is known to effect larval fitness; Trumbo 1990) and carer age at death in order to account for selective disappearance that might otherwise mask signatures of senescence (van de Pol and Verhulst 2006). When used as a predictor, age at death was defined according to the interval at which the event occurred (added as a four-level factor to identify age intervals between reproductive opportunities: between young and midlife, between midlife and old, between old and very old, and beyond very old). In longitudinal studies, the effects of selective disappearance are usually modeled by fitting linear or quadratic functions of longevity (Bouwhuis et al. 2009; Millon et al. 2011; Nussey et al. 2011; Hayward et al. 2013). This practice is appropriate when phenotypic observations and deaths are distributed continuously over ages, but it is not the best approach for analyses of controlled experiments in which phenotypes are collected in relatively few discrete age ranges at regular intervals. There are two reasons for this. First, the categorical approach used here accommodates more complex age functions (three parameters originating from four age intervals vs. two parameters from a quadratic function). Second, variation in age at death that occurs within intervals (e.g., different ages at death that all occur between young and midlife) or outside all the intervals (different ages of death after very old) should not contribute to model fitting. This constraint is appropriate because all individuals that die within intervals are all equally dead at the onset of the next age class, and their precise timing of removal within intervals should be noninformative. In this case, implementing age as a continuous effect (as is often done in studies of natural populations) would inappropriately allow within-interval variation to influence parameter estimates. Our experiment allowed us to correct for the effects of selective disappearance of caregivers but not egg producers, as the mixed-brood design made the identification of egg producers impossible.

The effects of block (as the experiment was split into nine experimental blocks) and carer identification (ID) were added as nested random effects (carer ID nested within block). The latter was included to account for possible effects of pseudoreplication as individual mothers care for multiple offspring. The full multivariate model that fit linear age effects failed to converge, indicating a non–positive definite variance-covariance structure for block effects. We ran univariate analyses for each female trait with and without the random effect of block to learn whether we could justify dropping block effects from the full model. The P values from a likelihood ratio test between the two models were as follows: larval weight at hatching, $P = .240$; carer

Table 2: Summary of mixed models

		Full model	
Level	Response variable	Fixed effects	Random effects
Offspring	Larval weight at dispersal	Carer age + egg producer age + carcass weight + age of carer at death	Block/carer identification
Offspring	Offspring adult longevity	Carer age + egg producer age + carcass weight + age of carer at death	Block/carer identification
Carer	Larval weight at hatching, residual life span of carer, weight change of carer, no. larvae surviving to dispersal	Carer age + egg producer age + carcass weight + age of carer at death	Block (for trait 4)

Note: Quadratic forms of the models add all possible second-order interactions involving carer age and egg producer age (two squared terms and one cross product).

residual life span, $P = .357$; carer weight change, $P = 1.000$; and number of larvae surviving to dispersal, $P = .031$ (for likelihood ratio test results, see table S1; tables S1–S4 are available online). These results justified rerunning the unconstrained full model while including block effects only for the number of larvae surviving to dispersal.

For each of the six traits of interest, comparisons were made between three models that fit maternal age effects in different ways: (1) no effect of carer and egg producer age (the null model), (2) first-order effects of carer and egg producer age (the linear model), and (3) all first- and second-order effects of both ages (the quadratic model). Because restricted maximum likelihood methods are not appropriate for model comparisons, maximum likelihood was used instead. For larval weight at hatching, residual life span, and carer weight change, there was no need to fit random effects in the model because (1) observations were made at the level of the carer (no carer ID effects) and (2) block effects were shown to be statistically insignificant (no block effect). Consequently, general linear models were applied using R v.3.3.3 (R Development Core Team 2016). The other traits required models that included random effects: all models required block effects, and offspring longevity and dispersal weight required carer ID effects. For these traits, we applied a mixed model approach using lme4 v.1.1–15 (Bates et al. 2015). Models were compared using Akaike information criterion values.

Results

Two carers were lost after care, but their offsprings' data have been included in the offspring-level analyses because postcare maternal longevity had no detectable effect on offspring outcomes. These females were excluded from the multivariate analysis. Model selection indicated that (1) null models were best for describing offspring adult longevity, larval weight at hatching, and female weight; (2) a linear model best described residual life span of the carer; and (3) quadratic models best described larval weight at dispersal and number of larvae surviving to dispersal (table 3; for full model selection comparison, see table S2).

Larval Weight at Dispersal

In the linear model, egg producer age was shown to have a negative effect on larval weight at dispersal, while carer age was shown to have a positive effect. However, neither effect was statistically significant (table 4; fig. S1(a); figs. S1–S6 are available online). In the quadratic model, there were detectable positive linear and negative quadratic effects of egg producer age. Carer age had no detectable effects on larval weight at dispersal (table 4; fig. S1(b)). There was a statistically significant negative effect of age of carer at death (2–5 weeks) on larval weight at dispersal in the quadratic model. No other measured covariates affected larval dispersing weight.

Offspring Adult Longevity

In the linear model, egg producer age was shown to have a negative effect on offspring adult life span, while carer age was shown to have a positive effect, but neither was statistically significant (table 5; fig. S2(a)). No linear or quadratic effects of egg producer and carer age on offspring adult life span (table 5; fig. S2(b)) were detected in the quadratic model. No other measured covariates affected offspring adult longevity in either model.

Traits Assessed at the Level of the Carers

In the linear model, neither carer age nor egg producer age affected any of the measured carer-level traits (table 6; fig. S3(a)–S6(a)), with the sole exception of a negative relationship between carer age and postcare residual life span. Incidentally, we should not expect any meaningful effects of carer age on larval weight at hatching because this experimental design ensures that carers do not influence offspring development until after hatching. In the quadratic model, there was neither linear nor quadratic effects of carer age on any of the measured carer-level traits (fig. S3(b)–S6(b)). However, egg producer age had a positive linear and a negative quadratic effect on the number of larvae surviving to dispersal (tables 6, S3(b)). Furthermore, carer age and egg producer age interacted to cause a statistically significant negative effect on this trait. Age of carer at death (2–5 and 8–11 weeks) affected the residual life span of the carer

Table 3: Summary of Akaike information criterion comparison for model selection

Traits	Null	Linear	Quadratic
Larval weight at dispersal	−2,644.117	−2,642.683	**−2,647.966**
Offspring adult longevity	**4,911.746**	4,914.960	4,915.163
Larval weight at hatching	**−372.415**	−370.567	−365.987
Residual life span of carer	513.974	**485.546**	486.427
Weight change of carer	**−211.259**	−210.798	−205.476
No. larvae surviving to dispersal	273.494	274.992	**269.105**

Table 4: Effect of age on larval weight at dispersal

Model and covariate	Effect size estimates (mg day^{-1})	SE (mg day^{-1})	z-score	P
Linear:				
Carer age	.152	.235	.647	.518
Egg producer age	−.239	.206	−1.159	.246
Carcass weight	3.466	3.036	1.142	.254
Age of carer at death (weeks):				
2–5	−49.780	28.720	−1.733	.083
5–8	9.806	20.180	.486	.627
8–11	4.275	12.600	.339	.734
11+	.000	.000	.000	...
Quadratic:				
Carer age	.459	1.180	.389	.697
Egg producer age	**2.690**	**1.201**	**2.240**	**.025**
Carer age × egg producer age	−.007	.014	−.514	.607
Carer age^2	−.001	.011	−.117	.907
Egg producer age^2	**−.034**	**.012**	**−2.934**	**.0033**
Carcass weight	3.296	2.940	1.121	.262
Age of carer at death (weeks):				
2–5	**−57.020**	**28.890**	**−1.974**	**.048**
5–8	24.220	20.640	1.173	.241
8–11	5.559	11.380	.488	.625
11+	.000	.000	.000	...

Note: z-scores were derived by dividing effect sizes by standard errors, and P values were calculated from these. Effects that were significant to a threshold of $\alpha = 0.05$ are in bold.

in both the linear and quadratic models. No other measured covariates affected the measured traits at the level of the carer (see tables S3(a), S3(b)).

Discussion

For three of the six traits investigated here (offspring adult longevity, larval weight at hatching, and weight change of carer), model comparisons and estimated effect sizes clearly indicate the absence of significant maternal age effects. Our results show a clearly negative effect of carer age on the residual life span of carers, but this simply reflects actuarial senescence, or an increase in mortality risk with increasing age (Finch et al. 1990). If older egg producers make lower-quality offspring and these placed a greater burden on older caregivers, then we might expect a negative interaction between the ages of egg producers and carers. While we did estimate a negative interaction effect, it was not statistically significant. For two traits (larval weight at dispersal and number of survived larvae), model selection indicated that the quadratic models were best and the linear models were worst. In both cases, quadratic estimates suggest convex relationships between larval outcomes and egg producer age (there was also a negative interaction effect on larval survival between the ages of egg producers and carers). This quadratic pattern to aging has been observed in both mam-

mal (Weladji et al. 2002; Nussey et al. 2006; Dugdale et al. 2011; Linares 2013; English et al. 2014) and bird species (Bouwhuis et al. 2009, 2010; Torres et al. 2011; Drummond and Rodríguez 2015). However, there are reasons to view our results with skepticism. First, we estimate a large number of quadratic effects (three effects for each of the six traits), and we expect that some estimates may be statistically significant only owing to chance. It might be appropriate in this case to correct for multiple comparisons. A Bonferroni correction (Bonferroni 1936) reduces the threshold for rejecting the null model of no quadratic effect to $\alpha = 0.0028$. The effects of egg producer age^2 fail to reach this threshold, but the interaction of carer age and egg producer age on number of larvae surviving to dispersal satisfies this condition. We note that the statistically significant effect of carer age on residual carer life span (actuarial senescence) remains after a Bonferroni correction (12 estimated linear age effects, $\alpha = 0.0042$). Second, we must be circumspect when interpreting quadratic effects of egg producer age because our experimental design did not allow us to correct for selective disappearance of egg producers. This phenomenon is discussed more generally below, but applied to this situation, we would expect that the preferential removal of poor mothers early in life could lead to the observed concave functions of larval weight and survival against age. Given a lack of meaningful linear maternal effects and only ambiguous quadratic effects,

Table 5: Effect of age on offspring adult longevity

Model and covariate	Effect size estimates (life span day^{-1})	SE (life span day^{-1})	z-score	P
Linear:				
Carer age	.001	.124	.006	.995
Egg producer age	−.075	.112	−.675	.500
Carcass weight	.350	1.566	.223	.823
Age of carer at death (weeks):				
2–5	−6.120	14.690	−.417	.677
5–8	−4.700	11.140	−.422	.673
8–11	−3.956	6.641	−.596	.551
11+	.000	.000	.000	…
Quadratic:				
Carer age	.777	.635	1.225	.221
Egg producer age	−.247	.654	−.378	.705
Carer age × egg producer age	−.010	.007	−1.326	.185
Carer age^2	−.006	.006	−1.039	.299
Egg producer age^2	.006	.007	.883	.377
Carcass weight	.348	1.547	.225	.822
Age of carer at death (weeks):				
2–5	−6.827	14.940	−.457	.648
5–8	−6.993	11.680	−.599	.549
8–11	−3.370	6.425	−.525	.600
11+	.000	.000	.000	…

Note: z-scores were derived by dividing effect sizes by standard errors, and P values were calculated from these.

a conservative explanation of our results is that we failed to detect pre- and postnatal maternal effect senescence for several traits related to fitness.

Because other work on *Nicrophorus* species has detected changes in offspring outcomes with maternal age, it is important to carefully evaluate our negative findings against these, with a particular emphasis placed on assessing the relative statistical power of our analysis. To interpret statistically nonsignificant results, evaluating the effect size and their relative confidence intervals is preferred to posthoc power analyses (Colegrave and Ruxton 2003). We do this by asking whether effect sizes reported in previous *Nicrophorus vespilloides* studies fall within the 95% confidence intervals estimated here using linear models. However, some comparisons are impossible because our study was the first to evaluate the effects of maternal age on many traits. Furthermore, previous studies very rarely report effect size estimates (preferring instead to emphasize significance). Consequently, in some cases, we had to estimate previous effect sizes using age-class data presented in graphical form in the source papers (for details, see table S4). Ward et al. (2009) reported that larval dispersal weight changed by −1.97 mg day^{-1} of maternal age for multiply mated females. Cotter et al. (2010) surveyed brood weights at dispersal from virgin females bred at different ages, but they did not report larval number in their analysis. This study observed a total brood weight change of −30 mg day^{-1} of maternal age. A generous

larval density estimate of 1.88 g^{-1} (see Smiseth and Moore 2002) suggests a per-larval effect size of −1.60 mg day^{-1} of maternal age. Both of these estimates lie far beyond the 95% confidence intervals estimated here for egg producer and carer age effects (95% CI = −0.64 to 0.16 mg day^{-1} and −0.31 to 0.61 mg day^{-1}, respectively; table 4). The Ward et al. (2009) study reported that larval survival declined 0.0087 day^{-1} of maternal age; the estimated 95% confidence intervals for this effect here was −0.0048 to 0.0011 day^{-1} and −0.0054 to 0.0012 day^{-1} for the two maternal age effects (see estimates in table 6 divided by 15 for the initial brood size). In general, type 2 errors can always be a concern with reports of negative results, but these comparisons make clear that any true effect in our population is much smaller than other published estimates from previous comparable studies.

Why are the effect sizes reported here so much smaller than in other *Nicrophorus* studies? This may have been the result of important improvements in our experimental design that enabled us to estimate the true effects of maternal age with more rigor. Unlike other aging experiments in *Nicrophorus* sp., this experiment used virgin females. While these may be difficult to obtain, especially in the older age classes (owing to ever-decreasing rates of cumulative survival), using virgins in all age classes removes the risk of conflating the effects of breeding experience with the effect of maternal age. Second, this experiment successfully accounted for potential bias attributed to selective disappear-

Table 6: Effect of age on various offspring and carer outcomes

Model, female age, and trait	Effect size estimate (unit day^{-1})	SE (unit day^{-1})	z-score	P
Linear:				
Carer:				
Larval weight at hatching (mg)	−.077	.056	−1.363	.173
Residual life span of carer (days)	**−1.122**	**.182**	**−6.182**	**<.001**
Weight change of carer (mg)	.394	.255	1.549	.121
No. larvae surviving to dispersal	−.032	.025	−1.259	.208
Egg producer:				
Larval weight at hatching (mg)	−.035	.051	−.688	.491
Residual life span of carer (days)	−.107	.163	−.656	.512
Weight change of carer (mg)	−.097	.229	−.425	.671
No. larvae surviving to dispersal	−.028	.023	−1.209	.228
Quadratic:				
Carer:				
Larval weight at hatching (mg)	.0385	.3201	.120	.904
Residual life span of carer (days)	−1.163	.995	−1.169	.242
Weight change of carer (mg)	−.0309	1.4550	−.021	.983
No. larvae surviving to dispersal	.220	.120	1.832	.067
Egg producer:				
Larval weight at hatching (mg)	.2667	.3224	.827	.408
Residual life span of carer (days)	−1.163	.995	−1.169	.242
Weight change of carer (mg)	.1095	1.4660	.075	.940
No. larvae surviving to dispersal	**.319**	**.121**	**2.643**	**.008**
Carer^2:				
Larval weight at hatching (mg)	−.0003	.0029	−.108	.914
Residual life span of carer (days)	.0049	.0089	.550	.582
Weight change of carer (mg)	.0060	.0131	.462	.644
No. larvae surviving to dispersal	−.0017	.0011	−1.509	.131
Egg producer^2:				
Larval weight at hatching (mg)	−.0025	.0031	−.823	.411
Residual life span of carer (days)	−.0129	.0095	−1.358	.174
Weight change of carer (mg)	−.0012	.0139	−.089	.929
No. larvae surviving to dispersal	**−.0028**	**.0012**	**−2.300**	**.021**
Carer × egg producer:				
Larval weight at hatching (mg)	−.0033	.0037	−.887	.375
Residual life span of carer (days)	−.014	.011	−1.214	.225
Weight change of carer (mg)	−.0033	.0168	−.199	.842
No. larvae surviving to dispersal	**−.004**	**.001**	**−3.065**	**.0022**

Note: z-scores were derived by dividing effect sizes by standard errors, and P values were calculated from these. Effects that were significant to a threshold of $\alpha = 0.05$ are in bold.

ance. However, no contributions of selective disappearance of carers to perceived aging patterns for any offspring trait was found. This suggests that any nonrandom subset of these females that survived to old age did not bias our results by producing higher-quality offspring with higher larval dispersal weight and longevity. Heterogeneity appears to be ubiquitous in wild vertebrates systems (Nussey et al. 2011), where it appeared to act to obscure evidence of maternal effect senescence in at least one study (Hayward et al. 2013). It is unknown whether heterogeneity may have influenced the results from other laboratory *Nicrophorus* studies of aging. We note that we were unable to test for effects of selective

disappearance of egg producers because this study used mixed broods, which unfortunately prohibited adding egg producer longevity to the models. Future research should focus on fully accounting for the effects of the selective disappearance of these mothers on offspring life-history traits. Using intact broods of larvae in which the egg producers' identities are known would allow us to completely account for the effects of heterogeneity on both maternal influences.

Neither the evolutionary predictions made by Moorad and Nussey's (2016) aging models nor those from reproductive effort models (Williams 1966*a*; Hirshfield and Tinkle 1975; Charlesworth and Leon 1976; Clutton-Brock 1984)

applied to maternal effects on larval survival are supported by our results. Other studies show mixed evidence for maternal age effects on juvenile survival. Some show declines, such as in *Panthera pardus* (Balme et al. 2013), *Papio anubis* (Packer et al. 1998), *Panthera leo* (Packer et al. 1998), *Ovis aries* (Hayward et al. 2013, 2015), and *Parus major* (Perrins and Moss 2008), while others show no effect of age, such as in *Glossina palpalis palpalis* (McIntyre and Gooding 1998), *Podisus maculiventris* (Mohaghegh et al. 1998), and *Nauphoeta cinerea* (Moore and Harris 2003), or an increase, *Vanellus vanellus* (Blomqvist et al. 1997). Why this variation exists and how it is distributed across species is unclear, and these questions deserve future study. Unfortunately, there is no formal systematic review of the literature that explores how maternal age affects neonatal survival in laboratory and wild systems. Such a review could be useful to survey the diversity of maternal aging patterns, to investigate the conditions under which predictions from the evolutionary models succeed and fail, and to better contextualize results from new studies.

Moorad and Nussey's (2016) evolution models predict that maternal effect senescence is unavoidable, but these assume the presence of age-specific genetic variation for maternal effects. Mixed evidence for the existence of maternal effect senescence across species may be expected if they vary in the degree to which their maternal genetic effects are age dependent. Further research should focus on measuring genetic correlations between age-specific maternal effects to see whether these maternal effects are actually age independent. However, it is important for more studies to quantify maternal age effects more carefully. More cross-fostering experiments that control for variation in reproductive history and that take selective disappearance into account can provide the clearest estimates of these effects while correctly assigning them to pre- and postnatal causes.

The failure to detect clear age-related increases in maternal contributions to offspring survival requires explanation as well, especially because previous research in another *Nicrophorus* species, *Nicrophorus orbicollis*, has shown evidence for age-related increases in reproductive allocation to their offspring (Creighton et al. 2009; Billman et al. 2014). In fact, while Charlesworth and Leon's (1976) formal model of reproductive effort predicts increasing adaptive optima with increased age, they do not make strong predictions regarding total reproductive investment at late ages, where selection for total reproduction is weakest (Hamilton 1966). Because reproductive effort is a proportional measure of allocation, the models actually predict total reproductive investment change with age to be represented by ever-larger fractional shares of an ever-shrinking pool of resources. Following this logic, Charlesworth and Leon (1976, p. 456) are circumspect about applying their model to make inferences about reproduction effort in the very old, and they conclude that "genes affecting later life are under relatively weak selective control, so the phenotype here may be relatively far from an evolutionary equilibrium." Finally, it should be noted that maternal age effects may be made too small to be detected if declines in offspring outcomes caused by maternal effect senescence are of similar magnitude to gains attributed to increasing reproductive effort with age. This scenario harmonizes with Charlesworth and Leon's (1976) observation that there is antagonism between the evolution of reproductive senescence and reproductive effort by applying it to age-related maternal effect. This scenario is impossible to rule out with our data. However, it seems very unlikely that an exact balance of antagonistic forces should exist for every trait investigated in our study.

Evolutionary theory makes no formal predictions regarding maternal effect senescence for other measured offspring traits, but one might expect patterns to follow qualitatively from predictions relating to juvenile survival. There is mixed evidence in the literature for maternal age affecting offspring performance aside from neonatal survival. Some systems show declines in offspring traits with maternal age: offspring longevity in *Philodina citrina* (Lansing 1947), birth weight in *Cervus elaphus* (Nussey et al. 2006), egg volume in *Diomedea exulans* (Froy et al. 2013), and offspring longevity and egg size in *Callosobruchus maculatus* (Fox and Dingle 1994; Lind et al. 2015). Other systems show no effect of aging: brood weight in *N. vespilloides* (Cotter et al. 2010), mean weight of offspring in *N. orbicollis* (Trumbo 2009), and offspring longevity in *Drosophila melanogaster* (Yilmaz et al. 2008). There is a clear need for more theory to explore the evolution of maternal effect senescence in offspring traits other than neonatal survival. For example, models that clarify the conditions under which the Lansing effect evolves would be an especially welcome addition to the literature, as this phenomenon is widely investigated (Comfort 1953; Butz and Hayden 1962; Klass 1977; Priest et al. 2002; Zehnder et al. 2007; Yilmaz et al. 2008). However, as is the case for maternal effect senescence manifested as variation in neonatal survival, there exists no systematic review of the diversity of this phenomenon.

Last, the age of the egg producer appeared to have no effect on the condition of the carer as reflected by weight change or residual life span. Specifically, larvae from older egg producers did not adversely affect the carer, and no evidence of compensation for lower-quality larvae was suggested. In some systems, age-related declines in offspring quality can often be buffered by targeted reproductive effort, where postnatal maternal effects compensate for detrimental prenatal maternal effects (Cameron et al. 2000; Lock et al. 2007). However, this targeted effort may occur only when individuals have had previous mating experience and in systems where offspring quality declines with age (Lock et al. 2007). We found no evidence for the latter condition.

There are many advantages to measuring senescence in laboratory populations, but it is not clear to what degree laboratory findings fairly represent aging in natural populations. Comparative research involving invertebrate and mammal species has shown the importance of contrasting laboratory/zoo and wild aging rates, as the two can be extremely different (Bondurianksy and Brassil 2002; Carey et al. 2008; Dukas 2008; Kawasaki et al. 2008; Rodríguez-Muñoz et al. 2010; Sherratt 2010; Tidière et al. 2017). One likely contribution to these differences is that laboratory conditions are relatively benign and free from physiological stressors, such as the need to locate and defend a resource (Scott 1998). In *Nicrophorus*, environmental stress in the laboratory can be increased to mimic natural conditions better by decreasing the resources available to the offspring or by introducing a competitor to the mother. The same principle may apply to resolving age-related increases in reproductive effort. For example, Creighton et al. (2009) found that female *N. orbicollis* females allocated more to their own body weight when placed on 20-g mice than when they were placed on 30-g carcasses, and females subsequently allocated fewer resources to current reproductive reproduction. Nevertheless, a follow-up analysis to explore these effects could shed light on the observed patterns seen in nature.

Conclusion

We performed an experiment designed to quantify the effects of maternal age on offspring traits in a laboratory population of burying beetle. Including cross-fostering and virgin females into this design and incorporating age at death into our analysis allowed us unprecedented clarity in the biological interpretations of our results. Here, these results indicate a lack of effect of pre- and postnatal maternal age on offspring outcomes. Contrary to predictions made from evolutionary theory, our results illustrate that maternal age effects do not always manifest. This highlights that current theory may be insufficient to account for the true diversity of aging patterns relating to maternal care.

Acknowledgments

Statement of authorship: E.I.-C. and J.M. conceived the ideas, designed the methodology, analyzed the data, and wrote the manuscript; E.I.-C. collected the data; and both authors contributed critically to drafts and gave final approval for publication.

Literature Cited

Arce, A. N., P. R. Johnston, P. T. Smiseth, and D. E. Rozen. 2012. Mechanisms and fitness effects of antibacterial defences in a carrion beetle. Journal of Evolutionary Biology 25:930–937.

Balme, G. A., A. Batchelor, N. De Woronin Britz, G. Seymour, M. Grover, L. Hes, D. W. Macdonald, and L. T. B. Hunter. 2013. Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. Mammal Review 43:221–237.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beamonte-Barrientos, R., A. Velando, H. Drummond, and R. Torres. 2010. Senescence of maternal effects: aging influences egg quality and rearing capacities of a long-lived bird. American Naturalist 175:469–480.

Berger, V., J.-F. Lemaître, J.-M. Gaillard, and A. Cohas. 2015. How do animals optimize the size-number trade-off when aging? insights from reproductive senescence patterns in marmots. Ecology 96:46–53.

Bijleveld, A. I., and R. H. E. Mullers. 2009. Reproductive effort in biparental care: an experimental study in long-lived Cape gannets. Behavioral Ecology 20:736–744.

Billman, E. J., J. C. Creighton, and M. C. Belk. 2014. Prior experience affects allocation to current reproduction in a burying beetle. Behavioral Ecology 25:813–818.

Blomqvist, D., O. C. Johansson, and F. Götmark. 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. Oecologia 110:18–24.

Bondurianksy, R., and C. E. Brassil. 2002. Rapid and costly ageing in wild male flies. Nature 420:377.

Bonferroni, C. 1936. Teoria statistica delle classi e calcolo delle probabilita. Pubblicazioni del R Istituto Superiore di Scienze Economiche e Commericiali di Firenze 8:3–62.

Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings of the Royal Society B 276:2769–2777.

Bouwhuis, S., A. J. van Noordwijk, B. C. Sheldon, S. Verhulst, and M. E. Visser. 2010. Similar patterns of age-specific reproduction in an island and mainland population of great tits *Parus major*. Journal of Avian Biology 41:615–620.

Butz, A., and P. Hayden. 1962. The effects of age of male and female parents on the life cycle of *Drosophila melanogaster*. Annals of the Entomological Society of America 55:617–618.

Cam, E., W. A. Link, E. G. Cooch, J.-Y. Monnat, E. Danchin, and J.-Y. Monnat. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist 159:96–105.

Cameron, E. J., W. L. Linklater, K. J. Stafford, and E. O. Minot. 2000. Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? Behavioral Ecology and Sociobiology 47:243–249.

Carey, J. R., N. T. Papadopoulos, H. G. Müller, B. I. Katsoyannos, N. A. Kouloussis, J. L. Wang, K. Wachter, W. Yu, and P. Liedo. 2008. Age structure changes and extraordinary lifespan in wild medfly populations. Aging Cell 7:426–437.

Charlesworth, B., and J. A. Leon. 1976. The relation of reproductive effort to age. American Naturalist 110:449–459.

Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist 123:212–229.

Colegrave, N., and G. D. Ruxton. 2003. Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. Behavioral Ecology 14:446–447.

Comfort, A. 1953. Absence of a Lansing effect in *Drosophila subobscura*. Nature 172:83–84.

Conover, M. R. 2013. Effects of increasing age on fecundity of old-aged Canada geese (*Branta canadensis*). Waterbirds 36:378–384.

Cotter, S. C., R. J. S. S. Ward, and R. M. Kilner. 2010. Age-specific reproductive investment in female burying beetles: independent effects of state and risk of death. Functional Ecology 25:652–660.

Creighton, J. C., N. D. Heflin, and M. C. Belk. 2009. Cost of reproduction, resource quality, and terminal investment in a burying beetle. American Naturalist 174:673–684.

Crook, T. C., T. Flatt, and P. T. Smiseth. 2008. Hormonal modulation of larval begging and growth in the burying beetle *Nicrophorus vespilloides*. Animal Behaviour 75:71–77.

Drummond, H., and C. Rodríguez. 2015. Viability of booby offspring is maximized by having one young parent and one old parent. PLoS ONE 10:e0133213.

Dugdale, H. L., L. C. Pope, C. Newman, D. W. MacDonald, and T. Burke. 2011. Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence. Molecular Ecology 20:3261–3274.

Dukas, R. 2008. Mortality rates of honey bees in the wild. Insectes Sociaux 55:252–255.

English, S., A. W. Bateman, R. Mares, A. Ozgul, and T. H. Clutton-Brock. 2014. Maternal, social and abiotic environmental effects on growth vary across life stages in a cooperative mammal. Journal of Animal Ecology 83:332–342.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology 82:1613–1620.

Fay, R., C. Barbraud, K. Delord, and H. Weimerskirch. 2016. Paternal but not maternal age influences early-life performance of offspring in a long-lived seabird. Proceedings of the Royal Society B 283:20152318.

Finch, C. E., M. C. Pike, and M. Witten. 1990. Slow mortality rate accelerations during aging in some animals approximate that of humans. Science 249:902–905.

Ford, L. E., and P. T. Smiseth. 2016. Asynchronous hatching provides females with a means for increasing male care but incurs a cost by reducing offspring fitness. Journal of Evolutionary Biology 29:428–437.

Fox, C. W., M. L. Bush, and W. G. Wallin. 2003. Maternal age affects offspring lifespan of the seed beetle, *Callosobruchus maculatus*. Functional Ecology 17:811–820.

Fox, C. W., and H. Dingle. 1994. Dietary mediation of maternal age effects on offspring performance in a seed beetle (Coleoptera, Bruchidae). Functional Ecology 8:600–606.

Froy, H., R. A. Phillips, A. G. Wood, D. H. Nussey, and S. Lewis. 2013. Age-related variation in reproductive traits in the wandering albatross: evidence for terminal improvement following senescence. Ecology Letters 16:642–649.

Gilmour, A. 1997. ASREML for testing fixed effects and estimating multiple trait variance components. Proceedings of the Association for the Advancement of Animal Breeding and Genetics 12:386–390.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Hargrove, J. W., M. Odwell Muzari, and S. English. 2018. How maternal investment varies with environmental factors and the age and physiological state of wild tsetse *Glossina pallidipes* and *Glossina morsitans morsitans*. Royal Society Open Science 5:171739.

Hayward, A. D., J. Moorad, C. E. Regan, C. Berenos, J. G. Pilkington, J. M. Pemberton, and D. H. Nussey. 2015. Asynchrony of senescence among phenotypic traits in a wild mammal population. Experimental Gerontology 71:56–68.

Hayward, A. D., A. J. Wilson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2013. Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. Functional Ecology 27:184–195.

Head, M., L. Berry, N. Royle, and A. J. Moore. 2012. Paternal care: direct and indirect genetic effects of fathers on offspring performance. Evolution 66:3570–3581.

Heidinger, B. J., K. A. Herborn, H. M. V Granroth-Wilding, W. Boner, S. Burthe, M. Newell, S. Wanless, F. Daunt, and P. Monaghan. 2016. Parental age influences offspring telomere loss. Functional Ecology 30:1531–1538.

Hercus, M. J., and A. A. Hoffmann. 2000. Maternal and grand-maternal age influence offspring fitness in *Drosophila*. Proceedings of the Royal Society B 267:2105–2110.

Hirshfield, M. F., and D. W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. Proceedings of the National Academy of Sciences of the USA 72:2227–2231.

Ivimey-Cook, E. R., and J. Moorad. 2018. Data from: Disentangling pre- and postnatal maternal age effects on offspring performance in an insect with elaborate maternal care. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.941d66f.

Jones, O. R., A. Scheuerlein, R. Salguero-Gomez, C. G. Camarda, R. Schaible, B. B. Casper, J. P. Dahlgren, et al. 2014. Diversity of ageing across the tree of life. Nature 505:169–173.

Kawasaki, N., C. E. Brassil, R. C. Brooks, and R. Bonduriansky. 2008. Environmental effects on the expression of life span and aging: an extreme contrast between wild and captive cohorts of *Telostylinus angusticollis* (Diptera: Neriidae). American Naturalist 172:346–357.

Kight, S. L., M. Batino, and Z. Zhang. 2000. Temperature-dependent parental investment in the giant waterbug *Belostoma flumineum* (Heteroptera: Belostomatidae). Annals of the Entomological Society of America 93:340–342.

Klass, M. R. 1977. Aging in the nematode *Caenorhabditis elegans*: major biological and environmental factors influencing life span. Mechanisms of Ageing and Development 6:413–429.

Kuczynski, M. C., D. Bello-Deocampo, and T. Getty. 2015. No evidence of terminal investment in the gray treefrog (*Hyla versicolor*): older males do not signal at greater effort. Copeia 103:530–535.

Lansing, A. I. 1947. A transmissible, cumulative, and reversible factor in aging. Journal of Gerontology 2:228–239.

Lemaître, J.-F., and J.-M. Gaillard. 2017. Reproductive senescence: new perspectives in the wild. Biological Reviews 92:2182–2199.

Linares, J. C. 2013. Shifting limiting factors for population dynamics and conservation status of the endangered English yew (*Taxus baccata* L., Taxaceae). Forest Ecology and Management 291:119–127.

Lind, M. I., E. C. Berg, G. Alavioon, and A. A. Maklakov. 2015. Evolution of differential maternal age effects on male and female offspring development and longevity. Functional Ecology 29:104–110.

Lippens, C. C., B. Faivre, C. Lechenault, and G. Sorci. 2017. Aging parasites produce offspring with poor fitness prospects. Biology Letters 13:20160888.

Lock, J. E., P. T. Smiseth, and A. J. Moore. 2004. Selection, inheritance, and the evolution of parent-offspring interactions. American Naturalist 164:13–24.

Lock, J. E., P. T. Smiseth, P. J. Moore, and A. J. Moore. 2007. Coadaptation of prenatal and postnatal maternal effects. American Naturalist 170:709–718.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Vol. 1. Sinauer, Sunderland, MA.

Martin, J. G. A., and M. Festa-Bianchet. 2011. Age-independent and age-dependent decreases in reproduction of females. Ecology Letters 14:576–581.

Mattey, S. N., J. Richardson, T. Ratz, and P. T. Smiseth. 2018. Effects of offspring and parental inbreeding on parent-offspring communication. American Naturalist 191:716–725.

McIntyre, G. S., and R. H. Gooding. 1998. Effect of maternal age on offspring quality in tsetse (Diptera: Glossinidae). Journal of Medical Entomology 35:210–215.

Millon, A., S. J. Petty, B. Little, and X. Lambin. 2011. Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. Journal of Animal Ecology 80:968–975.

Mohaghegh, J., P. De Clercq, and L. Tirry. 1998. Effects of maternal age and egg weight on developmental time and body weight of offspring of *Podisus maculiventris* (Heteroptera: Pentatomidae). Annals of the Entomological Society of America 91:315–322.

Moorad, J. A., and D. H. Nussey. 2016. Evolution of maternal effect senescence. Proceedings of the National Academy of Sciences of the USA 113:362–367.

Moore, P. J., and W. E. Harris. 2003. Is a decline in offspring quality a necessary consequence of maternal age? Proceedings of the Royal Society B 270(suppl.):S192–194.

Müller, J. K., and A. K. Eggert. 1990. Time-dependent shifts between infanticidal and parental behavior in female burying beetles a mechanism of indirect mother-offspring recognition. Behavioral Ecology and Sociobiology 27:11–16.

Nussey, D. H., T. Coulson, D. Delorme, T. H. Clutton-Brock, J. M. Pemberton, M. Festa-Bianchet, and J.-M. Gaillard. 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. Ecology 92:1936–1947.

Nussey, D. H., L. E. B. Kruuk, A. Donald, M. Fowlie, and T. H. Clutton-Brock. 2006. The rate of senescence in maternal performance increases with early-life fecundity in red deer. Ecology Letters 9:1342–1350.

Packer, C., M. Tatar, and A. Collins. 1998. Reproductive cessation in female mammals. Nature 392:807–811.

Paterson, J. T., J. J. Rotella, J. M. Mannas, and R. A. Garrott. 2016. Patterns of age-related change in reproductive effort differ in the pre-natal and post-natal periods in a long-lived mammal. Journal of Animal Ecology 85:1540–1551.

Perrins, C. M., and D. Moss. 2008. Survival of young great tits in relation to age of female parent. Ibis 116:220–224.

Poizat, G., E. Rosecchi, and A. J. Crivelli. 1999. Empirical evidence of a trade-off between reproductive effort and expectation of future reproduction in female three-spined sticklebacks. Proceedings of the Royal Society B 266:1543–1548.

Priest, N., B. Mackowiak, and D. Promislow. 2002. The role of parental age effects on the evolution of aging. Evolution 56:927–935.

Pugesek, B. H. 1981. Increased reproductive effort with age in the California gull (*Larus californicus*). Science 212:822–823.

Rauter, C. M., and A. J. Moore. 2002*a*. Evolutionary importance of parental care performance, food resources, and direct and indirect genetic effects in a burying beetle. Journal of Evolutionary Biology 15:407–417.

———. 2002*b*. Quantitative genetics of growth and development time in the burying beetle *Nicrophorus pustulatus* in the presence and absence of post-hatching parental care. Evolution 56:96–110.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rodríguez-Muñoz, R., A. Bretman, J. Slate, C. A. Walling, and T. Tregenza. 2010. Natural and sexual selection in a wild insect population. Science 328:1269–1272.

Rozen, D. 2008. Antimicrobial strategies in burying beetles breeding on carrion. Proceedings of the National Academy of Sciences of the USA 105:17890–17895.

Scott, M. P. 1998. The ecology and behavior of burying beetles. Annual Review of Entomology 43:595–618.

Sharp, S. P., and T. H. Clutton-Brock. 2010. Reproductive senescence in a cooperatively breeding mammal. Journal of Animal Ecology 79:176–183.

Sherratt, T. N. 2010. Empirical evidence of senescence in adult damselflies (Odonata: Zygoptera). Journal of Animal Ecology 79:1034–1044.

Smiseth, P. T., C. Dawson, E. Varley, and A. J. Moore. 2005. How do caring parents respond to mate loss? differential response by males and females. Animal Behaviour 69:551–559.

Smiseth, P. T., W. Hwang, S. Steiger, and J. K. Müller. 2008. Adaptive consequences and heritable basis of asynchronous hatching in *Nicrophorus vespilloides*. Oikos 117:899–907.

Smiseth, P. T., and A. J. Moore. 2002. Does resource availability affect offspring begging and parental provisioning in a partially begging species? Animal Behaviour 63:577–585.

Smiseth, P. T., and H. J. Parker. 2008. Is there a cost to larval begging in the burying beetle *Nicrophorus vespilloides*? Behavioral Ecology 19:1111–1115.

Steiger, S. 2013. Bigger mothers are better mothers: disentangling size-related prenatal and postnatal maternal effects. Proceedings of the Royal Society B 280:20131225.

Tidière, M., J.-F. Lemaître, G. Douay, M. Whipple, and J.-M. Gaillard. 2017. High reproductive effort is associated with decreasing mortality late in life in captive ruffed lemurs. American Journal of Primatology 79:e22677.

Torres, R., H. Drummond, and A. Velando. 2011. Parental age and lifespan influence offspring recruitment: a long-term study in a seabird. PLoS ONE 6:e27245.

Trumbo, S. T. 1990. Regulation of brood size in a burying beetle, *Nicrophorus tomentosus* (Silphidae). Journal of Insect Behavior 3:491–500.

———. 2009. Age-related reproductive performance in the parental burying beetle, *Nicrophorus orbicollis*. Behavioral Ecology 20:951–956.

van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. American Naturalist 167:766–773.

van de Pol, M., and J. Wright. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. Animal Behaviour 77:753–758.

Vaupel, J. W., K. G. Manton, and E. Stallard. 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. Demography 16:439–454.

Vaupel, J. W., and A. I. Yashin. 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. American Statistician 39:176–185.

Velando, A., H. Drummond, and R. Torres. 2006. Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. Proceedings of the Royal Society B 273: 1443–1448.

Ward, R. J. S., S. C. Cotter, and R. M. Kilner. 2009. Current brood size and residual reproductive value predict offspring desertion in the burying beetle *Nicrophorus vespilloides*. Behavioral Ecology 20:1274–1281.

Warner, D. A., D. A. W. Miller, A. M. Bronikowski, and F. J. Janzen. 2016. Decades of field data reveal that turtles senesce in the wild.

Proceedings of the National Academy of Sciences of the USA 113: 6502–6507.

Weladji, R. B., A. Mysterud, O. Holand, and D. Lenvik. 2002. Age-related reproductive effort in reindeer (*Rangifer tarandus*): evidence of senescence. Oecologia 131:79–82.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398–411.

———. 1966a. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton, NJ.

———. 1966b. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687–690.

Yilmaz, M., E. D. Ozsoy, and A. N. Bozcuk. 2008. Maternal age effects on longevity in *Drosophila melanogaster* populations of different origin. Biogerontology 9:163–168.

Zehnder, C., M. Parris, and M. Hunter. 2007. Effects of maternal age and environment on offspring vital rates in the Oleander aphid (Hemiptera: Aphididae). Environmental Entomology 36:910–917.

A female *Nicrophorus vespilloides* provisions food to a begging larva. Photo credit: Per T. Smiseth.