OXFORD

The distribution of the Lansing Effect across animal species

Edward R. Ivimey-Cook[1], [iD], Sarema Shorr[2], Jacob A. Moorad[2], [iD]

[1]Institute of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow, United Kingdom
[2]Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, United Kingdom
Corresponding author: Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, United Kingdom. Email: jacob.
mourad@ed.ac.uk

Abstract

Maternal senescence is the reduction in individual performance associated with increased maternal age at conception. When manifested on adult lifespan, this phenomenon is known as the "Lansing Effect." Single-species studies report both maternal age-related increases and decreases in adult lifespan, but no comprehensive review of the literature has yet been undertaken to determine if the Lansing Effect is a widespread phenomenon. To address this knowledge gap, we performed a meta-analysis of maternal aging rates taken from all available published studies. We recovered 78 estimates from 22 studies representing 15 species. All studies taken together suggest a propensity for a Lansing Effect, with an estimated average effect of maternal age on offspring's adult lifespan of between -17% and -22%, depending upon our specific choice of model. We failed to find a significant effect of animal class or insect order but given the oversampling of insect species in the published literature and the paucity of vertebrate studies, we infer that only rotifers and insects yet demonstrate a tendency toward expressing the phenomenon.

Keywords: offspring lifespan, maternal age, meta-analysis, aging, senescence

Senescence is the association between increased age and the deterioration of organismal function as manifested upon key components of fitness such as survival and fertility (termed actuarial and reproductive senescence, accordingly), but it can also be observed in many other traits that may affect survival and reproduction (functional senescence). Most discussions of senescence relate the ages and phenotypes of the same individuals, but recent attention has begun to focus on the social effects of aging, or how the age of one individual affects the outcomes of one or more others. Relevant social interactions can involve the ages of grandmothers (Hawkes, 2003; Moorad & Walling, 2017), mothers (Rogers, 1993), siblings (Hamilton, 1966), and even residents of the same population (Ronce & Promislow, 2010), but most studies involve maternal age effects because maternal-offspring relationships are generally considered to be the most important social interactions across a great diversity of plant and animal species (Mousseau & Fox, 1998). Most of these studies focus on two effects of maternal age: pre-adult survival and lifespan.

The most closely studied of these manifestations of aging has been pre-adult survival, likely because this trait is more convenient to study than lifespan and because it is understood to be a key component of fitness. Evolutionary genetic models predict widespread maternal senescence for this trait, especially at older maternal ages (Moorad & Nussey, 2016), and a recent survey of the published literature finds a high prevalence of this sort of aging across all well-studied animal groups, with birds representing a notable exception (Ivimey-Cook & Moorad, 2020). The second well-studied aspect of maternal aging is its manifestation upon the offspring's adult lifespan (which together with juvenile survival describes the total

lifespan). A decrease in longevity associated with an increase in maternal age at birth is known as the "Lansing Effect" in recognition of Albert Lansing's observations of the phenomenon in parthenogenic rotifers (Lansing, 1947). Follow-up studies failed to replicate Lansing's results in rotifers (Comfort, 1953; King, 1983), but many other studies have found mixed evidence for a Lansing effect in numerous species, including humans (Galipaud & Kokko, 2020; Monaghan et al., 2020).

While awareness of the Lansing Effect appears to be high (Monaghan et al., 2020), the study of maternal age effects on offspring lifespan lags behind the study of pre-adult survival in two important respects. First, evolutionary biology lacks a formal predictive genetic model of the phenomenon. Second, our current understanding of the prevalence of the Lansing Effect is only anecdotal: we lack a rigorous synthesis of the published literature that can summarize its prevalence and magnitude across studies and species. As the need to satisfy the first gap in our understanding should be evaluated somewhat by lessons to be learned by addressing the second, we have untaken a meta-analytic review of the evidence for the Lansing Effect across published studies. Our primary focus is to determine if the manifestation of a Lansing Effect is a general tendency across animal species. A secondary goal is to identify predictors for maternal age effects on lifespan, such as environment, offspring sex, and phylogeny.

Methods

This meta-analysis followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Figure S1). We searched for relevant published

studies using the databases Web of Science (Carloni, 2018) and Scopus (Baas et al., 2020) and the search terms provided in Supplemental Table S1 between June and August 2022. All studies were screened manually using the Rayyan web-based application (Ouzzani et al., 2016) and included in our study if they presented some measure of outbred offspring adult lifespan on maternal age (and their standard errors (SEs)) from one of three sources:

(1) Direct estimates of linear maternal age effects on offspring lifespan (with associated SEs). Slopes were taken directly from the source paper if they were unfettered by estimates of higher-order contributions of age or another variable. However, this case occurred only twice (Gavrilov & Gavrilova, 2001; Ivimey-Cook & Moorad, 2018). Some studies only fit polynomial functions or other higher-order interactions involving maternal ages. As we were interested only in the linear effects of age, we ignored these results and derived slopes using other methods.

(2) If raw data were provided, slopes were subsequently estimated by fitting a simple linear model that regressed offspring lifespan against maternal age class. We did this for five studies (Angell et al., 2022; Bouwhuis et al., 2015; Dowling et al., 2014; Kroeger et al., 2020; Lind et al., 2015). Where possible, and if the model converged, appropriate random effects (for instance, maternal ID) were incorporated to provide a clearer estimate of maternal aging.

(3) For all other cases, we assumed that observations of offspring lifespan were independent of one another and distributed normally. We applied an optimization procedure to estimate the slopes of least-squares regressions and their associated SE using maternal-age-specific means and SEs taken from the publications (see Supplementary Material for further explanation). Data were extracted from the main text, supplementary information, figures, and tables of the selected studies. In cases where data were only shown in figures, the packages *metaDigitise v1.01* and *shinyDigitise v0.1.0* (Ivimey-Cook, 2022; Pick et al., 2019) were used within *R v4.1.0* (R Core Team, 2021) to extract relevant information. Information on sample size, error, and maternal age-specific means were required.

We note that the "Lansing Effect" has a definition that varies across the published literature. For this review, we have strictly defined it as an effect manifested on adult lifespan for two reasons. First, this definition matches that offered by Comfort, (1953), who coined the term and applied it to study the "mean expectation of life from eclosion." Second, the effect of maternal age on offspring pre-adult survival has already been covered at length in a previous paper by Ivimey-Cook and Moorad (2020). Incidentally, Lansing's (1947) work was not included in the meta-analysis owing to its absence of precision estimates.

Our analyses took the form of three multi-level meta-analysis models, each applied to two overlapping age ranges. Species, study, and replicate ID were fit as nested random effects in each. The first model used slope estimates to test for an overall effect size of maternal age on lifespan. The second model extended the first to evaluate and correct for the presence and effects of publication bias, which if left uncorrected, could produce a large and spurious overall effect size purely as a result of

the systematic absence of studies reporting statistically insignificant results. Following recommendations by Nakagawa et al. (2022), publication bias was examined statistically by regressing point estimates against their respective sampling variance. An additional moderator of mean-centered publication year was added to the above model to test and account for time-lag bias (an association between the date of publication and effect size). The intercept fit to this model is interpreted as the overall average slope that is ideally unbiased by time lag and publication bias. Noble et al. (2017) suggest that the comparison between this intercept and one derived from a model that does not include these moderators can be interpreted as a test for result robustness. Monaghan et al. (2020) point out that highly concave aging trajectories may make it difficult to resolve Lansing Effects if offspring lifespan from young mothers are included in simple linear regressions. For this reason, we apply all models to data from two ranges of maternal ages. *All* contains the complete data extracted from each study. *Old* is comprised of data from maternal ages determined by one of two methods, depending upon the study and species. For the two vertebrates species, *old* ages are those that exceed the generation time T, or the average age of mothers at birth (estimates for T were taken from Felsenstein (1971) for *Homo sapiens* and Sæther et al. (2013) for *Sterna hirundo*) (N.B. a third species was included in the analysis, *Marmota flaviventris*, however, the raw data age classes were scaled and standardized and as the mean value was not provided, we were unable to truncate at T). Whilst no theory yet exists to make general predictions relating to the age of onset of a Lansing Effect, evolutionary models of maternal age effects predict that T should predict the age of onset for maternal senescence on juvenile survival (Moorad & Nussey, 2016). *Old* mothers were restricted to the last two ages for invertebrate species, as estimates of T were either unavailable or highly sensitive to environmental conditions, particularly temperature (Cui et al., 2018). All ages are considered *old* in studies that considered only two ages classes; we assume that the relevant published experimental designs chose older ages with which to investigate this phenomenon that is associated with late life.

The third model was used to evaluate the influence of moderator variables. These factors were:

1. The species "group", defined as Order for insects and Class for non-insects;
2. Paternal-age-controlled (PAC: yes or no; N.B. species were assumed to be paternal age controlled when sperm was not involved in fertilization, for instance, in asexual species or in species that reproduce by parthenogenesis, e.g., daphnia and aphids);
3. Offspring sex (male, female, or combined/other; in some cases, the sex of the offspring was unclear, such as in the nematode worm *Caenorhabditis elegans,* in this case, they were placed in the "other" category).

The effect of laboratory or natural environment was initially considered as a moderator, but this was rejected due to the low number of slopes that were able to be estimated from field studies and the large number of human studies, which cannot be accurately considered to be in "natural" environments (Table 1), and the large prevalence of certain classes only present in the laboratory (e.g., insects—see Table 1). As insect species were far better represented in the literature than non-insect species (10 vs. 5 species), the former

were grouped at a lower taxonomic rank to allow for the finer-scaled comparisons. This model was applied independently to both age ranges and fit with and without bias moderators.

All aforementioned factors were fit into our model as fixed effects with species, study, and replicate number fit as nested random effects to account for the non-independence of slopes (Nakagawa & Santos, 2012; Nakagawa et al., 2021b). All subsequent analyses and visualizations were carried out in *R v4.1.0* (R Core Team, 2021), using the *metafor v3.0.2* (Viechtbauer, 2010), *ggplot2 v3.3.5* (Wickham, 2011), *emmeans v1.7.1-1* (Lenth et al., 2019), and *orchaRd v0.0.0.9* (Nakagawa et al., 2021a) packages.

Associated R code and meta-data can be found at: https://github.com/EIvimeyCook/Lansing_Meta.

Results

We extracted or estimated a total of 78 slopes (k) derived from 22 published studies (n) of 15 species (s). Of these, 54 estimates (69.2%) came from studies with more than two maternal age classes. All derived estimates of the slopes (and SEs) are provided in the Supplemental Section (Supplementary Table S2). Twenty estimates came from field studies ($n = 7$, $s = 4$; although we note that humans are classified into this "natural" field category), and the remaining 58 effect sizes came from laboratory studies ($n = 15$, $s = 11$) (Table 1). While the dominant field organism was *H. sapiens* ($k = 14$, $n = 4$), the most studied species in the laboratory was *Drosophila melanogaster* ($k = 28$, $n = 4$). As expected, insect species dominated the laboratory environment ($k = 51/58$), and a study of the antler fly (*Protopiophila litigata*, Angell et al., 2022) provided the only estimate derived from a natural insect system (Table 1). Strong associations between taxonomy and environments, namely, the observation that insects are rarely studied in the field and mammals and birds are rarely studied in the laboratory, resemble those reported in a recent review of the relationship between maternal age and early offspring survival (Ivimey-Cook & Moorad, 2020).

We fit all extracted slopes to a progression of three models (Models 1–3) using all available maternal ages (Table 2—All). Model 1 is the intercept-only model; this indicates a clearly negative value for the estimates (–0.17) with 95% confidence intervals that do not overlap zero (95%CI = –0.25, –0.08; $p = .0003$). Differently put, offspring lifespan is observed to decline by 17% of the increase in maternal age. Model 2 adds estimates for the effects of publication bias and time lag. Neither of these effects has a statistically significant effect on the slopes ($p = .763$, $.554$, accordingly), but including these moderators decreases the intercept from –0.17 to –0.18, and the confidence intervals associated with the intercept widen but still do not overlap zero (95%CI = –0.29, –0.08). However, these estimates may be conservative: Stanley and Doucouliagos (2014) report that the estimate of the intercept will be a downwardly biased indicator of the magnitude of the true mean, which, in this case, suggests that the true mean effect of maternal age (once publication and time lag biases are accounted for) is less than –0.17 (i.e., the true effect is more negative).

Focusing our analysis only on the last two maternal age classes (Table 2—old) increased the negative effects of maternal age (from –17% to –22%) and moved the confidence intervals further from zero (95%CI = –0.31, –0.13). Dropping studies that had only two ages classes decreased the overall effect from "old" mothers from 22% to 20%, but nevertheless, the effect remained significant and did not overlap zero (–0.28, –0.11).

Next, we considered the effects of species group, PAC, and offspring sex (Model 3). We fit this model with and without time lag and publication bias moderators and for all ages and the terminal interval. As before, we find no detectable effect of the bias moderators, and the choice of which ages to include has little effect on the results. Table 3 summarizes results from the version of the model without bias moderators and with *All* age classes; other results are provided in the Supplement (Supplementary Table S3). A comparison of marginal means for all groups (Figure 1) finds the strongest evidence for a Lansing Effect in Orthopterans, Hemipterans, Coleopterans, Chromoadorea (nematode worms), and rotifers. Dipterans and birds show a similar pattern when all ages are considered, but the Lansing Effect diminishes when these are analyzed over only the terminal ages. Neither mammalian group appears to present tendencies for Lansing Effects. However, it should be emphasized that no differences among these groups are statistically

Table 1. Joint distribution of major species groups and laboratory/field environments described by all extracted studies.

	Laboratory	Field
Birds	-	$k = 2$, $n = 1$, $s = 1$
Mammals	-	$k = 16$, $n = 5$, $s = 2$
Insects	$k = 51$, $n = 13$, $s = 9$	$k = 2$, $n = 1$, $s = 1$
Other invertebrates	$k = 7$, $n = 2$, $s = 2$	-

Table 2. Meta-analytic mean slope unadjusted (Model 1) and adjusted (Model 2) for publication bias (standard errors) and time-lag bias (mean-centered years) with corresponding 95% confidence intervals, *t*, and *p* values. Estimates for the effects of bias are derived from Model 2.

Ages	Fixed effect		Estimate	95% CI	*t* value	*p* value
all	Intercept	Unadjusted	–0.17	[–0.25, –0.08]	–3.79	.0003
		Adjusted	–0.18	[–0.29, –0.08]	–3.63	.0005
old		Unadjusted	–0.22	[–0.31, –0.13]	–4.76	.000001
		Adjusted	–0.22	[–0.31, –0.12]	–4.57	.00002
all	Time-lag		–0.001	[–0.006, 0.003]	–0.60	.554
old			0.0009	[–0.004, 0.006]	0.38	.703
all	Publication bias		0.20	[–1.12, 1.52]	0.30	.763
old			–0.063	[–0.52, 0.40]	–0.27	.787

significant in any version of the model. Considering both the estimates and the sample sizes of slopes taken from the various animal groups, it appears that the overall support for a general Lansing Effect may be driven by an oversampling of insects, where there appears also to be the greatest prevalence of negative slopes. A visual comparison of these marginal means found no evidence to suggest that focusing only upon *old* ages increased the statistical signatures of a tendency toward a Lansing Effect.

Controlling mate age (PAC) appears to diminish the strength of the Lansing Effect, but that effect is not statistically significant ($p = .375$). We might expect this direction of effect if parental ages are positively correlated *and* if a Lansing-like Effect acts through paternal age, but we lack the means to test this suggestion here. Finally, we note that the Lansing Effect appears to manifest nearly identically upon females (females, in particular, show a significant difference when compared to pooled offspring sex; $p = .045$) and males and more strongly on specific sexes than on mixed-sex offspring. We have no explanation for this last pattern except to suggest, with no evidence, that experiments that pool sexes when reporting lifespan might differ in other respects from those that segregate by sex.

Discussion

A Lansing Effect could be said to exist in any single study that finds a negative association between maternal age and offspring longevity, but a multi-study view can provide new evolutionary or ecological insights, such as a characterization of the central tendency of the phenomenon over groups of species or the identification of modifiers that may provide new understanding of the causes of the Lansing Effect. The primary goal of this study was to determine if the sum of published data was sufficient to detect a tendency across animal populations to exhibit Lansing Effects. Overall, we found clear evidence that such a tendency exists: a unit increase in maternal age translates to a decrease in offspring lifespan of 17–22% of that unit. However, that negative tendency appears to be driven by observations of insects and, to a lesser degree, rotifers, which are oversampled compared to the other animal groups that offer little to no tendencies themselves.

Mammal species (predominantly humans) did not demonstrate a statistically significant deleterious maternal age effect on offspring lifespan that is consistent with a general Lansing Effect. In fact, humans exhibited near-zero effect sizes (although we note that a similar pattern was found in birds prior to accounting for selective disappearance). This is surprising given that the conspicuous maternal care provided in these species should present more opportunities for deleterious effects of increased age to manifest. However, it could be that post-natal mechanisms of maternal care are more amenable to improvement with age owing to the accumulation of experience, and this effect mitigates or even overwhelms senescence for pre-natal maternal inputs into offspring survival. This sort of conflict between sources of aging effects has been suggested as important for understanding juvenile mortality in seabirds (Aubry et al., 2009, 2011; Froy et al., 2013). Finally, we note that post-natal parental care has been suggested to buffer against the deleterious effects of the environment (Grew et al., 2019; Pilakouta & Smiseth, 2016; Schroeder et al., 2012). If true, then it may seem logical to expect that animals such as mammals should have lower rates of maternal senescence if one were to consider old maternal age as a poor environment. However, this argument neglects the possibility that buffering ability might also senescence, and this would serve to reinforce the deleterious effects of increased maternal age in systems with maternal care (see Moorad & Ravindran, 2022 for a fuller discussion of buffering in the context of selection and the evolution of aging).

Clearly, we need far more relevant studies of vertebrate species featuring varying degrees of post-natal care if we wish to understand the prevalence (let alone the causes) of the maternal age effects on lifespan in birds and mammals. Reproductive experience (or parity) should be controlled for experimentally or statistically, and further attention should also focus on species and systems that can allow us to disentangle taxonomy and environment, for example by studying vertebrates in the laboratory or insects (or other invertebrates) in the wild.

Our results correspond very roughly to those of a recent review of maternal age effects on juvenile survival (Ivimey-Cook & Moorad, 2020) in the sense that the most negative effects of age appear to manifest in invertebrates. Mammals are

Table 3. Full model output from a multi-level mixed effect model across all species and ages with moderator variables acting on slopes. Note that the reference categories are Aves, mixed offspring sex, and uncontrolled mate age; the Intercept is the estimated mean for their combination. Effects are shown unadjusted for publication and time lag bias.

| Fixed effect	Estimate	95% CI	*t* value	*p* value
Intercept	0.14	[−0.56, 0.84]	0.40	.692
Chromadorea-Rhabditida	−0.26	[−1.28, 0.76]	−0.51	.611
Insecta-Coleoptera	−0.22	[−0.92, 0.47]	−0.64	.524
Insecta-Diptera	0.02	[−0.61, 0.65]	0.06	.949
Insecta-Hemiptera	−0.36	[−1.05, 0.33]	−1.04	.301
Insecta-Orthoptera	−0.61	[−1.60, 0.39]	−1.22	.227
Mammalia-Primates	0.22	[−0.36, 0.80]	0.75	.455
Mammalia-Rodentia	0.59	[−0.22, 1.39]	1.46	.149
Monogononta-Ploima	−0.24	[−0.93, 0.44]	−0.70	.484
Female	−0.46	[−0.92, 0.01]	−2.04	.045
Male	−0.40	[−0.86, 0.05]	−1.77	.082
PAC	0.14	[−0.17, 0.44]	0.89	.375
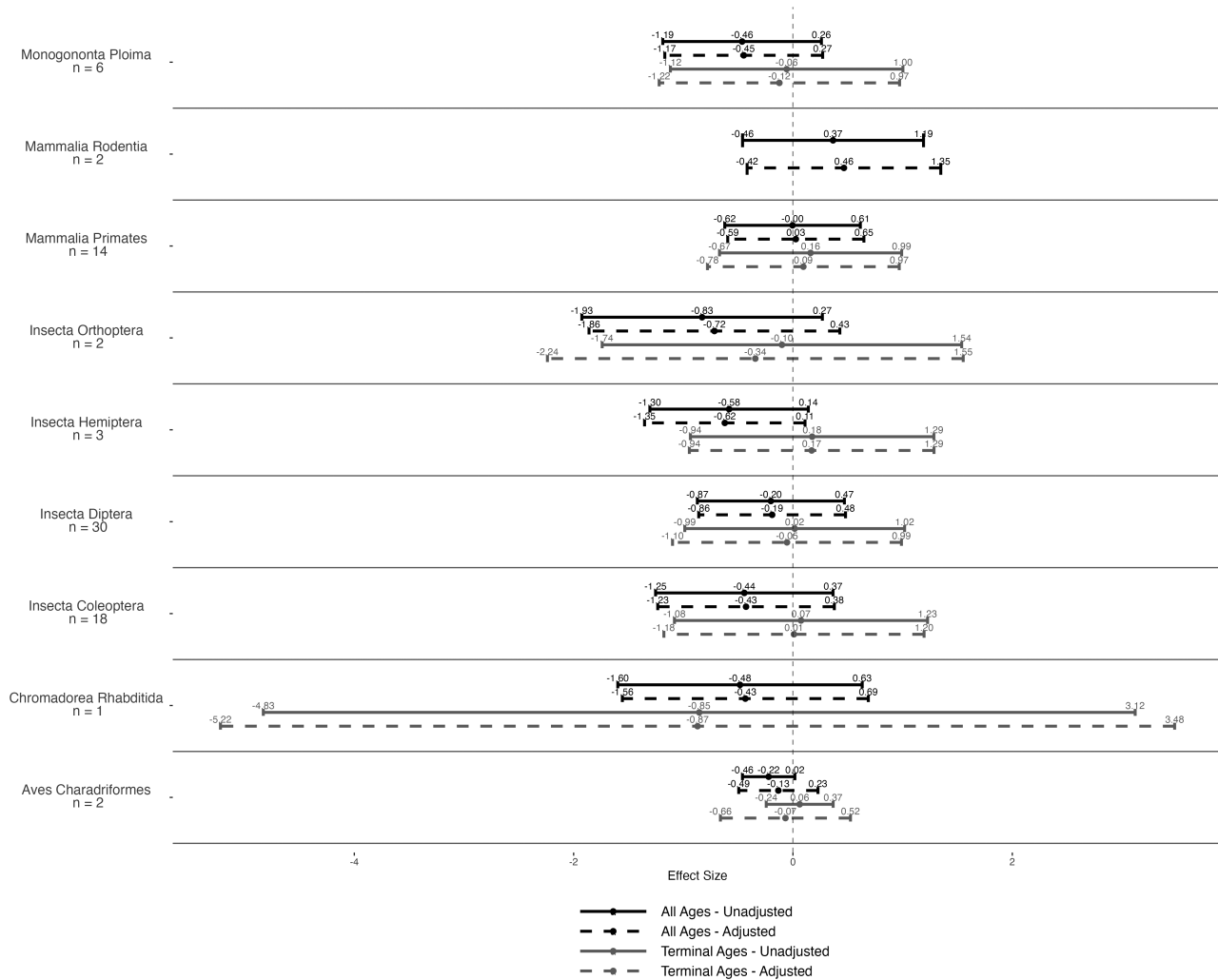
Figure 1. The marginal means of slope estimates for species groups (*n* = species) with corresponding 95% confidence intervals. Note that the rodent intervals only reflect all ages because old age classes could not be determined from the source paper.

intermediate in both meta-analyses, but whereas the previous study had the sufficient statistical power to bound grouped effect sizes away from each other (e.g., invertebrates and mammals had negative effects, and birds had positive effects), this study did not. The current study found considerably less relevant metadata than the juvenile survival study; it is much more difficult to measure lifespan than juvenile survival in most laboratory and wild animal populations, and this difference is likely reflected in the quantity and precision of estimates that are available from the published literature. This current study extracted 78 estimates from 15 species, with a median number of offspring for each aging rate estimate of 362 (all ages). This compares poorly with the study by Ivimey-Cook and Moorad (2020) featuring 273 estimates from 97 animal species and a median number of offspring per aging rate estimate of 5000. This discrepancy underscores the need for more studies of the Lansing Effect to be performed on more species.

Although the current study failed to detect statistically significant differences among species groups, our observations of a general tendency toward a Lansing Effect and similar rankings of species groups when we consider the strength of the two different manifestations of maternal senescence merit attention from evolutionary theory. Does the theory predict that age-specific selection that acts on maternal effect genes

for offspring lifespan invariably weakens with age similar to how we expect age-specific selection for direct effect genes to relax (Charlesworth, 1994; Hamilton, 1966; Moorad & Ravindran, 2022), or does this pattern of selection have a maximum at some later maternal age, as we expect is the case for genes that affect juvenile survival (Moorad & Nussey, 2016)? It might seem intuitive to expect that selection for a Lansing Effect should have dynamics that are more similar to the latter, and this would help explain the rough congruence between the rankings of animal group aging rates. We might also like to know how different life histories lead to the evolution of among-species variation in the Lansing Effect (assuming, of course, that such variation actually exists). Proper answers to these questions await the development of the relevant evolutionary genetic theory. Such development might build upon the population genetic models of Moorad and Nussey (2016), who considered population growth, age structure, and incomplete relatedness between mothers and offspring, by extending age-specific maternal gene effects to offspring age-specific survival at all ages. Further work could explore the effects of genetic trade-offs, either between age-specific survival and reproduction within individuals or between mothers and offspring, to explore how these shape the ways that selection drives the evolution of the Lansing

Effect. Moreover, maternal age is known to affect offspring life history in other ways, such as lifetime reproductive success and fitness (Bock et al., 2019; Kroeger et al., 2020; Monaghan et al., 2020). If expressions that describe selection for age-specific maternal genetic effects on offspring age-specific reproduction can be derived, then predictive models for the evolution of these offspring endpoints can also be provided.

Finally, we offer some recommendations for future studies of maternal senescence. First, maternal ages that clearly define old individuals should be included in observations, and justifications for why these ages are considered such should be provided. We advocate the use of mean generation time T as a useful yardstick in this effort because it defines the mean age of parents in the population, and this determines exactly what it means for a parent to be older than average. Lastly, it should also be noted that as population demographics are likely to differ markedly due to experimental conditions (for instance, between the field and the laboratory), if possible, experimenters should endeavor to report T for each specific condition. Second, experimenters should be aware that cohorts of same-age individuals change over time for reasons owing to aging (within-individual changes) and selective appearance and disappearance (among-individual change). As many are most interested in the former, care should be taken to decouple these two components of change to avoid biasing our interpretations of the true aging rate. For selective disappearance, this is accomplished by fitting appropriate statistical models that include some aspect of age-at-death as a modifier (Ivimey-Cook & Moorad, 2018; Nussey et al., 2011; van de Pol & Verhulst, 2006), and this has become common practice in studies of conventional perspectives of aging that seek to understand the association between trait values and ages of the same individuals (Hämäläinen et al., 2014; Hayward et al., 2013; Nussey et al., 2011). Applied to maternal senescence, it is the age of maternal death that should be considered (e.g., Bouwhuis et al., 2010; Ivimey-Cook & Moorad, 2018; Lord et al., 2021; Nussey et al., 2011; Schroeder et al., 2012; van de Pol & Verhulst, 2006), but this is seldom done in practice. It should be noted that only three of the estimates used in this study derive from analyses that adequately correct for selective disappearance. Gavrilov and Gavrilova (2001), Bouwhuis et al. (2015), and Ivimey-Cook and Moorad (2018) either provide relevant estimates in the papers or sufficient data that allowed us to derive these. Unfortunately, no other study provided the necessary information to account statistically for these effects, and there is a risk that our results for other studies are biased. The direction of bias will depend upon the nature of the relationship between age-specific maternal survival and offspring lifespan, but if we assume that mothers vary in overall quality (i.e., longer surviving mothers are also better mothers, and this is reflected in longer offspring lifespan), then we might expect that such biases work to reduce the severity of the Lansing Effect. If sufficiently strong, selective disappearance may even cause the direction of aging to be reversed. In light of this, we might consider our findings to be conservative with respect to the general tendency of animal species to exhibit a Lansing Effect. It may also be that among-group differences in selective disappearance may have contributed to apparent (albeit statistically non-significant) among-group differences in the presence of a Lansing

Effect. Selective appearance can also complicate inferences of within-individual aging. For example, if high-quality mothers produce longer-lived offspring independent of their own age, and these mothers begin to reproduce earlier in life, then maternal senescence may appear stronger owing to among-individual effects. To account for this, some studies have also included age at first reproduction as a covariate (Fay et al., 2021; Hayward et al., 2015; Zhang et al., 2015).

This is the first comprehensive review of maternal senescence manifested on adult lifespan. We found a general tendency for insect and rotifer species to exhibit a Lansing Effect This is notable because it supports the notion that there are transgenerational mechanisms for the inheritance of aging; this is important to our understanding of the evolution of life histories, and it may have important implications to conservation. However, it may be premature at this point to conclude that a tendency toward a Lansing Effect exists in birds and mammals. This may change as more observational and experimental aging studies are performed and evolutionary theory is developed sufficiently to know whether natural selection tends to favor the evolution of a Lansing Effect in the general case.

Supplementary material

Supplementary material is available online at *Evolution* (https://academic.oup.com/evolut/qpac045)

Data availability

R code and meta-data are deposited at https://github.com/EIvimeyCook/Lansing_Meta

Author contributions

E.I.C. and J.A.M. conceived of the study. E.I.C. and S.S. extracted the data and performed analyses in consultation with J.A.M. All authors contributed to the drafting and revision of the manuscript. E.I.C. and S.S. should be considered joint first authors.

Conflict of interest: The authors declare no conflict of interest.

References

Angell, C. S., Janacek, R., & Rundle, H. D. (2022). Maternal and paternal age effects on male antler flies: A field experiment. *The American Naturalist*, 199, 4367–4442. https://doi.org/10.1086/718236

Aubry, L. M., Cam, E., Koons, D. N., Monnat, J. -Y., & Pavard, S. (2011). Drivers of age-specific survival in a long-lived seabird: Contributions of observed and hidden sources of heterogeneity. *Journal of Animal Ecology*, 80, 375–383. https://doi.org/10.1111/j.1365-2656.2010.01784.x

Aubry, L. M., Koons, D. N., Monnat, J. -Y., & Cam, E. (2009). Consequences of recruitment decisions and heterogeneity on age-specific

breeding success in a long-lived seabird. *Ecology*, 90, 2491–2502. https://doi.org/10.1890/08-1475.1

Baas, J., Schotten, M., Plume, A. M., Cote, G., & Karimi, R. (2020). Scopus as a curated, high-quality bibliometric data source for academic research in quantitative science studies. *The MIT Press Journals*, 1, 377–386. https://doi.org/10.1162/qss_a_00019

Bock, M. J., Jarvis, G. C., Corey, E. L., Stone, E. E., & Gribble, K. E. (2019). Maternal age alters offspring lifespan, fitness, and lifespan extension under caloric restriction. *Scientific Reports*, 9. https://doi.org/10.1038/s41598-019-40011-z

Bouwhuis, S., Charmantier, A., Verhulst, S., & Sheldon, B. C. (2010). Trans-generational effects on ageing in a wild bird population. *Journal of Evolutionary Biology*, 23, 636–642. https://doi.org/10.1111/j.1420-9101.2009.01929.x

Bouwhuis, S., Vedder, O., & Becker, P. H. (2015). Sex-specific pathways of parental age effects on offspring lifetime reproductive success in a long-lived seabird. *Evolution*, 69, 1760–1771. https://doi.org/10.1111/evo.12692

Carloni, M. (2018). Web of Science Core Collection Descriptive Document.

Charlesworth, B. (1994). *Evolution in age-structured populations* (2nd ed.). Cambridge University Press.

Comfort, A. (1953). Absence of a Lansing effect in *Drosophila subobscura*. *Nature*, 172, 83–84. https://doi.org/10.1038/172083a0

Cui, J., Zhu, S., Bi, R., Xu, W., Gao, Y., & Shi, S. (2018). Effect of temperature on the development, survival, and fecundity of *Heliothis viriplaca* (Lepidoptera: Noctuidae). *Journal of Economic Entomology*, 111, 1940–1946. https://doi.org/10.1093/jee/toy151

Dowling, D. K., Williams, B. R., & Garcia-Gonzalez, F. (2014). Maternal sexual interactions affect offspring survival and ageing. *Journal of Evolutionary Biology*, 27, 88–97. https://doi.org/10.1111/jeb.12276

Fay, R., Ravussin, P. -A., Arrigo, D., von Rönn J. A. C., & Schaub, M. (2021). Age-specific reproduction in female pied flycatchers: Evidence for asynchronous aging. *Oecologia*, 196, 723–734. https://doi.org/10.1007/s00442-021-04963-2

Felsenstein, J. (1971). Inbreeding and variance effective numbers in populations with overlapping generations. *Genetics*, 68, 581–597. https://doi.org/10.1093/genetics/68.4.581

Froy, H., Phillips, R. A., Wood, A. G., Nussey, D. H., & Lewis, S. (2013). Age-related variation in reproductive traits in the wandering albatross: Evidence for terminal improvement following senescence. *Ecology Letters*, 16, 642–649. https://doi.org/10.1111/ele.12092

Galipaud, M., & Kokko, H. (2020). Sex, senescence, sources and sinks. *Functional Ecology*, 34, 55–64. https://doi.org/10.1111/1365-2435.13462

Gavrilov, L. A., & N. S. Gavrilova. (2001). Human longevity and parental age at conception. *Sex and longevity: Sexuality, gender, reproduction, parenthood* (pp. 7–31). Springer.

Grew, R., Ratz, T., Richardson, J., & Smiseth, P. T. (2019). Parental care buffers against effects of ambient temperature on offspring performance in an insect. *Behavioral Ecology*, 30, 1443–1450. https://doi.org/10.1093/beheco/arz100

Hämäläinen, A., M. Dammhahn, F. Aujard, M. Eberle, I. Hardy, P. M. Kappeler, M. Perret, S. Schliehe-Diecks, & C. Kraus. (2014). Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140830. https://doi.org/10.1098/rspb.2014.0830.

Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, 12, 12–45. https://doi.org/10.1016/0022-5193(66)90184-6

Hawkes, K. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology*, 15, 380–400. https://doi.org/10.1002/ajhb.10156

Hayward, A. D., Nenko, I., & Lummaa, V. (2015). Early-life reproduction is associated with increased mortality risk but enhanced lifetime fitness in pre-industrial humans. *Proceedings Biological Sciences*, 282, 20143053. https://doi.org/10.1098/rspb.2014.3053

Hayward, A. D., Wilson, A. J., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Kruuk, L. E. (2013). Reproductive senescence in female Soay sheep: Variation across traits and contributions of individual ageing and selective disappearance. *Functional Ecology*, 27, 184–195. https://doi.org/10.1111/1365-2435.12029

Ivimey-Cook, E. (2022). shinyDigitise.

Ivimey-Cook, E., & Moorad, J. (2018). Disentangling pre- and postnatal maternal age effects on offspring performance in an insect with elaborate maternal care. *The American Naturalist*, 192, 564–576. https://doi.org/10.1086/699654

Ivimey-Cook, E., & Moorad, J. (2020). The diversity of maternal-age effects upon pre-adult survival across animal species. *Proceedings of the Royal Society of London. Series B*, 287, 20200972. https://doi.org/10.1098/rspb.2020.0972

King, C. E. (1983). A re-examination of the Lansing effect. *Hydrobiologia*, 104, 135–139. https://doi.org/10.1007/bf00045959

Kroeger, S. B., Blumstein, D. T., Armitage, K. B., Reid, J. M., & Martin, J. G. (2020). Older mothers produce more successful daughters. *Proceedings of the National Academy of Sciences*, 117, 4809–4814. https://doi.org/10.1073/pnas.1908551117

Lansing, A. I. (1947). A transmissible, cumulative, and reversible factor in aging. *Journal of Gerontology*, 2, 228–239. https://doi.org/10.1093/geronj/2.3.228

Lenth, R., H. Singmann, J. Love, P. Buerkner, & M. Herve. (2019). Package "emmeans."

Lind, M. I., Berg, E. C., Alavioon, G., & Maklakov, A. A. (2015). Evolution of differential maternal age effects on male and female offspring development and longevity. *Functional Ecology*, 29, 104–110. https://doi.org/10.1111/1365-2435.12308

Lord, J. S., Leyland, R., Haines, L. R., Barreaux, A. M. G., Bonsall, M. B., Torr, S. J., & English, S. (2021). Effects of maternal age and stress on offspring quality in a viviparous fly. *Ecology Letters*, 24, 2113–2122. https://doi.org/10.1111/ele.13839

Monaghan, P., Maklakov, A. A., & Metcalfe, N. B. (2020). Intergenerational transfer of ageing: Parental age and offspring lifespan. *Trends in Ecology and Evolution*, 35, 927–937. https://doi.org/10.1016/j.tree.2020.07.005

Moorad, J., & Ravindran, S. (2022). Natural selection and the evolution of asynchronous aging. *The American Naturalist*, 89, 7185.

Moorad, J. A., & Nussey, D. H. (2016). Evolution of maternal effect senescence. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 362–367. https://doi.org/10.1073/pnas.1520494113

Moorad, J. A., & Walling, C. A. (2017). Measuring selection for genes that promote long life in a historical human population. *Nature Ecology and Evolution*, 1, 1773–1781. https://doi.org/10.1038/s41559-017-0329-x

Mousseau, T. A., & Fox, C. W. (1998). *Maternal effects as adaptations*. Oxford University Press.

Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, 13, 4–21. https://doi.org/10.1111/2041-210X.13724

Nakagawa, S., Lagisz, M., O'Dea, R. E., Rutkowska, J., Yang, Y., Noble, D. W. A., & Senior, A. M. (2021a). The orchard plot: Cultivating a forest plot for use in ecology, evolution, and beyond. *Research Synthesis Methods*, 12, 4–12. https://doi.org/10.1002/jrsm.1424

Nakagawa, S., Senior, A.M., Viechtbauer, W., & Noble, D.W.A. (2021b). An assessment of statistical method for nonindependent data in ecological meta-analyses: Comment. *Ecology*. 103, e03490. https://doi.org/10.1002/ecy.3490

Nakagawa, S., & Santos, E. S. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26, 1253–1274. https://doi.org/10.1007/s10682-012-9555-5

Noble, D. W. A., Lagisz, M., O'dea, R. E., & Nakagawa, S. (2017). Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular Ecology*, 26, 2410–2425. https://doi.org/10.1111/mec.14031

Nussey, D. H., Coulson, T., Delorme, D., Clutton-Brock, T. H., Pemberton, J. M., Festa-Bianchet, M., & Gaillard, J. -M. (2011). Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology*, 92, 1936–1947. https://doi.org/10.1890/11-0308.1

Ouzzani, M., Hammady, H., Fedorowicz, Z., & Elmagarmid, A. (2016). Rayyan—A web and mobile app for systematic reviews. *Systematic Reviews*, 5, 1–10. https://doi.org/10.1186/s13643-016-0384-4

Pick, J. L., Nakagawa, S., & Noble, D. W. A. (2019). Reproducible, flexible and high-throughput data extraction from primary literature: The metaDigitise r package. *Methods in Ecology and Evolution*, 10, 426–431. https://doi.org/10.1111/2041-210X.13118

Pilakouta, N., & Smiseth, P. T. (2016). Maternal effects alter the severity of inbreeding depression in the offspring. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20161023. https://doi.org/10.1098/rspb.2016.1023

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rogers, A. R. (1993). Why menopause?. *Evolutionary Ecology*, 7, 406–420. https://doi.org/10.1007/bf01237872

Ronce, O., & Promislow, D. (2010). Kin competition, natal dispersal and the moulding of senescence by natural selection. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3659–3667. https://doi.org/10.1098/rspb.2010.1095

Sæther, B.-E., et al. (2013). How life history influences population dynamics in fluctuating environments. *The American Naturalist*, 182, 743–759. https://doi.org/10.1086/673497

Schroeder, J., Burke, T., Mannarelli, M. -E., Dawson, D. A., & Nakagawa, S. (2012). Maternal effects and heritability of annual productivity. *Journal of Evolutionary Biology*, 25, 149–156. https://doi.org/10.1111/j.1420-9101.2011.02412.x

Stanley, T. D., & Doucouliagos, H. (2014). Meta-regression approximations to reduce publication selection bias. *Research Synthesis Methods*, 5, 60–78. https://doi.org/10.1002/jrsm.1095

van de Pol, M., & Verhulst, S. (2006). Age-dependent traits: A new statistical model to separate within- and between-individual effects. *The American Naturalist*, 167, 766–773. https://doi.org/10.1086/503331

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor Package. *Journal of Statistical Software*, 36, 1–48. https://doi.org/10.18637/jss.v036.i03

Wickham, H. (2011). ggplot2. *Wiley Interdisciplinary Reviews: Computational Statistics*, 3, 180–185. https://doi.org/10.1002/wics.147

Zhang, H., Vedder, O., Becker, P. H., & Bouwhuis, S. (2015). Age-dependent trait variation: The relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. *Journal of Animal Ecology*, 84, 797–807. https://doi.org/10.1111/1365-2656.12321