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**Post-copulatory sexual selection allows females to alleviate the fitness costs
incurred when mating with senescing males**

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Abstract

Male senescence has detrimental effects on reproductive success and offspring fitness. When females mate with multiple males during the same reproductive bout, post-copulatory sexual selection that operates either through sperm competition or cryptic female choice might allow females to skew fertilization success towards young males and as such limit the fitness costs incurred when eggs are fertilized by senescing males. Here, we experimentally tested this hypothesis. We artificially inseminated female North African houbara bustards with sperm from dyads of males of different (young and old) or similar ages (either young or old). Then, we assessed whether siring success was biased towards young males and we measured several life history traits of the progeny to evaluate the fitness costs due to advanced paternal age. In agreement with the prediction, we found that siring success was biased towards young males, and offspring sired by old males had impaired hatching success, growth and post-release survival (in females). Overall, our results support the hypothesis that post-copulatory sexual selection might represent an effective mechanism allowing females to avoid the fitness costs of fertilization by senescing partners.

Keywords: offspring growth, offspring survival, paternal age, reproductive senescence, siring success, sperm selection

Introduction

Reproductive senescence refers to the age-dependent decline in breeding success, involving physiological and behavioural changes [1,2]. In males, reproductive senescence is often associated with poor ejaculate quality [3–5], potentially impairing male fitness through reduced fertilization success [6]. However, the effect of paternal age extends well beyond the probability to fertilize eggs, since offspring sired by old fathers have been shown to suffer from reduced fitness, both under laboratory and natural conditions [7,8]. Negative effects of paternal age on offspring fitness can arise because of the accumulation of *de novo* mutations in the highly replicative male germline or because of epigenetic modifications [9–12]. Therefore, while paternal age has a direct effect on male fitness, it can also affect female fitness, due to poor offspring performance [1].

Given the potentially deleterious effects of male age on offspring fitness, it has been suggested that females should avoid mating with senescing males [13,14]. Other authors have, however, suggested that age might also be considered as a reliable signal of male quality, and females mating with old males might gather direct (i.e., experienced partners providing better parental care) or indirect (i.e., genetic) benefits for the progeny [15,16]. The idea that females might gather genetic benefits from mating with old males has, nevertheless, been criticized on several grounds. Indeed, longevity does not necessarily reflect fitness if there are negative correlations between fitness-linked traits expressed at early and late life [16,17], and inherited genes have all the same age, irrespective of individual age [18]. A handful of studies have experimentally investigated whether females show any preference for young or old partners and both types of response (as well as no response at all) have been reported [19–22]. This is perhaps not so surprising given that different processes might be at play in different species. For instance, the rate of senescence might differ between pre- and post-copulatory traits; with some species having faster decline of pre-copulatory traits [23], others having faster decline of post-

66 copulatory traits [5]. Therefore, female preference for young or old males might be modulated
67 by male age-specific investment in maintenance of traits associated with mating and
68 fertilization success. Predicting any adaptive mate choice based on age should explicitly take
69 into account the net effect of paternal age on fitness of the progeny [24].

70 Preference for or avoidance of old males can be achieved during pre-copulatory mate
71 choice. However, this requires that females can reliably use phenotypic attributes of potential
72 mates to assess their age [21,22]. Post-copulatory sexual selection [25] might also allow females
73 to discriminate between males of different ages. When females copulate with more than one
74 male, a widespread mating system in animals, different ejaculates compete for the fertilisation
75 of the ova (sperm competition) [26], and females might actively bias fertilisation success
76 towards sperm of preferred males (cryptic female choice) [27]. Therefore, if young males
77 produce sperm with superior competitiveness ([20,28]; but also see [29]) or females can actively
78 select sperm from young males, post-copulatory sexual selection might be an effective
79 mechanism allowing females to avoid fertilization by old males [13].

80 Here, we aimed to test this hypothesis, and to this purpose, we conducted an artificial
81 insemination experiment in a bird species, the North African houbara bustard (*Chlamydotis*
82 *undulata undulata*), kept in a conservation breeding program. Artificial insemination offers the
83 possibility to remove the effects of pre-copulatory sexual selection and to solely focus on post-
84 copulatory sexual selection. In the North African houbara bustard, the combination of
85 polyandry [30] and the storage of sperm for several weeks [31] offers the potential for post-
86 copulatory sexual selection to operate. In this species ejaculate quality (e.g., number of sperm
87 in the ejaculate, sperm motility) reaches peak value at the age of 4-6 years and then declines
88 with advancing age [5]. When eggs are fertilized by senescing males they have a lower
89 probability to hatch and, when they do, chicks have an impaired growth [32]. We artificially
90 inseminated females with sperm from dyads of males of different ages (one at prime age, one

in the senescence stage), while two other groups of females were inseminated with sperm from dyads of males of similar ages (either young or old). In addition to the probability to fertilize eggs when sperm of young and old males compete in the female reproductive tract, we also assessed the fitness consequences for the offspring sired by a young or an old father, in terms of hatching success, growth rate, early survival under captive conditions and long-term post-release survival in the wild.

Materials and methods

Breeding programme management

All birds used in this study are part of the Emirates Center for Wildlife Propagation (ECWP), a conservation breeding programme located in eastern Morocco, aiming at reinforcing natural populations of the North African houbara bustard (see ESM for a description of the ecology of the species). This programme relies entirely on artificial inseminations [31] and follows strict rules where breeding is designed to maintain genetic diversity within the captive flock [33]. Ejaculates are routinely collected and immediately assessed for quality (see ESM for details). Females are regularly checked for reproductive status and inseminated with freshly collected semen when ready to lay.

Experimental groups and artificial inseminations

The study was conducted during the 2016 breeding season. We used 92 females [mean age (\pm sd) = 4.5 ± 1.7 years, min-max = 3-8 years, corresponding to the peak of breeding performance in females], split into three groups (female age did not differ between groups: Kruskal-Wallis test: $\chi^2_2 = 0.63$, $p = 0.732$): 30 females were inseminated with a mix of semen from a dyad of young [mean age (\pm sd) = 3.5 ± 1.0 years, min-max = 3-6 years] and old [mean age (\pm sd) = 13.0 ± 1.0 years, min-max = 12-16 years] males (hereafter called young-old group); 33 females were inseminated with a mix of semen from a dyad of young males (young

group, same mean age and range as above); 29 females were inseminated with a mix of semen from a dyad of old males (old group, same mean age and range as above). In total, 71 males (31 young, 40 old) were used in the experiment, and the semen of each male was used 2.6 ± 2.7 times (mean \pm sd, min-max = 1-19).

Male age categories were chosen based on the pattern of senescence that has been previously reported in the North African houbara bustard [5]. Nevertheless, to make sure that the same pattern of age-associated decline in ejaculate quality was observed among males that were available in the captive flock in 2016, we ran a linear mixed effect model confirming that ejaculate quality (i.e. proportion of motile sperm and number of sperm in the ejaculate) reached peak values at the age of 4-6 years and then declined (Table S1; Fig. S1A,B in ESM).

One obvious consequence of this age-associated decline in ejaculate quality is that, when mixing ejaculates of young and old males, each age category might potentially contribute with different number of sperm of different quality. Previous work has already shown that when females are inseminated with mixes of sperm, paternity is systematically skewed towards males that contribute the most to the mix [34]. Therefore, we wished to go beyond the simple “the more (or better) sperm, the higher the chance to fertilize the eggs” paradigm. To do this, we equalised the number of sperm that each male contributed to the mixes and made sure that ejaculates from young and old males had similar motility (t value = 1.488, $p = 0.140$; Table S2 in ESM). As such, the sample of old males used for the study was not randomly drawn from the total population of old males present in the captive breeding (Tables S3 and S4 in ESM).

Females were inseminated once with $32.9 \times 10^6 \pm 8.3$ sperm (mean \pm sd), which is close to the mean number of sperm per ejaculate produced by the 71 males used in the study ($29.8 \times 10^6 \pm 20.9$). Inseminations took place between February 8th and April 18th and there was no difference in insemination date among experimental groups (one-way ANOVA: $F_{2,89} = 0.132$, $p = 0.876$).

We collected up to the first five eggs laid. However, note that not all 92 females laid five eggs (see ESM for details), and therefore a total of 401 eggs were collected. Number of eggs laid did not differ among experimental groups (generalized linear model with a Poisson distribution of errors: $F_{2,89} = 0.17$, $p = 0.844$). Eggs were laid between February 13th and June 3rd and laying date did not differ among experimental groups (linear mixed effects model: $F_{2,86.4} = 1.30$, $p = 0.279$). Three hundred seventy-four eggs out of the 401 laid eggs were incubated following a standardized protocol (see ESM for details, including fertility assessment).

Offspring traits

Chick body mass (± 1 g) and size (head-skull length ± 0.5 mm), were measured at day 1, 9, 18, 26, 40, 60 and 90 post-hatching (see ESM for details on rearing conditions). Survival in captivity was monitored daily up to October 26th. Survival in the wild was monitored for 142 birds. To this purpose, birds were fitted with a GPS satellite transmitter (GPS - PTT), two weeks prior to release. At that time, birds were at least 4-month-old [mean age (\pm sd) = 190 ± 18 days, min-max = 145-233 days]. They had become sexually dimorphic and could therefore be sexed (77 males and 65 females). All birds were released on October 27th 2016. Age, body mass and body size at release did not differ between birds sired by young and old fathers (Table S5 in ESM). Survival was monitored until March 2019 (i.e. 28 months post-release). For each bird, we also computed the maximal distance travelled as the distance (in kilometres) between the release location and the furthest location from release. This measure served as a proxy of movement behaviour (dispersal and/or exploration).

Paternity analyses

We genotyped 13 microsatellite loci designed for the species. Paternity was assigned using CERVUS 3.0. Individuals were included in parentage analyses whenever they were genotyped at a minimum of 11 loci, and only paternities assigned with a confidence level of 95% were considered (see ESM for further details).

Statistical analyses

Analyses were performed with R 3.1.3 [35].

Siring success within the young-old group was estimated as the probability for each egg to be fertilised by a young or an old male. Siring success was therefore analysed using a generalized linear mixed effects model ('glmer' function of the 'lme4' package) with a binomial distribution of errors. We tested whether the intercept significantly deviated from 0.5, which represents the null-hypothesis of equal siring probability between young and old males. Maternal identity and males' identities within dyads were included as random effects (to take into account the non-independence of offspring produced by the same mother and the repeated use of the sperm of certain males among dyads, respectively).

Hatching success was analysed using a generalized linear mixed effects model with a binomial distribution of errors ('glmer' function of the 'lme4' package), while hatchling body mass and size, and offspring growth, were analysed using linear mixed effects models ('lmer' function of the 'lme4' package) with a normal distribution of errors. In all models, paternal age was included as a fixed effect, whereas maternal identity and males' identities within dyads were included as random effects.

When analysing offspring growth, we also included offspring age and the interaction with paternal age as fixed effects. We tested for linear and quadratic effects of offspring age on growth by comparing two models including age, or age and squared age, respectively, based on their AICc. A linear effect of age received the best statistical support for body mass, while for body size, the best model included the squared age term. Offspring identity nested within maternal identity was also included as a random effect to take into account the repeated measurements on the same chicks over time and the non-independence of chicks produced by the same mother.

An information theoretic model averaging approach was used to test for the significance of fixed effects as predictors of the response variables using the function ‘dredge’ of the ‘MuMIn’ package. Significance of each effect was based on the p -value of the corresponding conditional model-averaged coefficient. For generalized linear mixed effects models with a binomial distribution of errors, we also systematically checked whether data were overdispersed. For all models the ratio between residual deviance and residual degrees of freedom was comprised between 1.17 and 1.3, and the test proposed by Bolker [36] showed no evidence for overdispersion.

Offspring survival under captive conditions and after release in the wild was analysed using a mixed effects Cox model (function ‘coxme’ of the ‘coxme’ package). The model on survival in captivity included paternal age as a fixed effect, and maternal identity and males’ identities as random effects. For the model on post-release survival, we could also include offspring sex and the interaction between paternal age and offspring sex as fixed effects, because released birds were old enough to be sexed based on sexual dimorphism. Among the 142 birds that were released in the field with PTTs, 18 were lost and were censored in the survival analysis. Offspring movement (as log-transformed maximal distance travelled from the release site) was analysed using a linear mixed effects model. Offspring age, sex, paternal age and the two-way interactions were included as fixed effects, while maternal identity and males’ identities as random effects.

Results

Siring success when females are inseminated with sperm of young and old males

Females that were inseminated with a mix of sperm from young and old males laid 118 fertile eggs, and paternal identity could be assigned for 86 of them. Based on these 86 offspring,

we found that old males had significantly lower within-dyad siring success compared to young males (33.7% *versus* 66.3%; z value = 2.220, p = 0.026; Fig. 1).

Given that the paternity of 27% of laid eggs could not be assigned, one possibility could be that the differential siring success reflects differential embryo mortality (all eggs for which paternity could not be assigned had early embryo mortality). To address this issue, we ran another model that was restricted to the first egg laid by each female, for which the rate of paternity assignment was high (28 out of 29). This restricted model confirmed that siring success was significantly lower for old compared to young males (25% *versus* 75%; z value = 2.517, p = 0.012; Fig. 1).

Fitness consequences for offspring sired by young or old males

Eggs fertilized by old males had a lower probability to hatch compared to eggs fertilized by young individuals (58% *versus* 70%, n = 331 eggs from the three experimental groups; z value = 2.146, p = 0.033; Table S6 in ESM).

Hatchling body size was slightly lower for chicks sired by young fathers, while hatchling body mass and size-corrected body mass were not affected by paternal age (Tables S7 and S8 in ESM).

We assessed growth rate of chicks during their first 3 months of life, in terms of body size, body mass and size-corrected body mass (Table S7 in ESM). Growth rate of body size did not differ between chicks sired by young or old fathers (Table S9 in ESM). However, offspring sired by young fathers had higher body mass growth and size-corrected body mass growth (Table 1). The slope relating body mass to offspring age was steeper for chicks sired by young fathers (offspring age \times paternal age interaction; Table 1). The model that also included body size (providing therefore a measure of size-corrected body mass) showed a significant three-way interaction between offspring age, paternal age and body size (Table 1). To visualize the effect of paternal age on size-corrected body mass growth, we computed the residuals of body

mass on body size and plotted them against chick age for the two paternal age groups. The figure shows that chicks sired by young fathers initially gained more mass for their size compared to chicks sired by old fathers (Fig. 2).

Offspring survival was high in the captive breeding (86% of chicks were alive prior to release) and did not differ between individuals sired by young and old fathers (mixed effects Cox model: $z = -0.240$, $p = 0.810$).

Among the 142 birds that were released in the field with PTTs in October 2016, 79% had died 28 months later (March 2019). A mixed effects Cox model showed that survival was affected by the interaction between paternal age and offspring sex ($z = -2.280$, $p = 0.022$; Table S10 in ESM), with female offspring sired by young fathers having the highest survival rate (Fig. 3). To investigate whether the effect of paternal age on female survival was due to a differential propensity to move further away from the release site, we ran a linear mixed effects model on the log-transformed maximal distance covered by each individual (mean \pm sd = 37.7 ± 62.9 km, min-max: 2.3-483.8 km, $n = 142$). This model showed that paternal age did not affect offspring movement (Table S11 in ESM), suggesting that the effect on survival was not mediated by differences in exploratory/dispersal behaviour.

Discussion

We found that when females were concomitantly inseminated with sperm from young and old males, egg fertilization success was biased towards young males. We also found evidence showing that when eggs are fertilized by old males, hatching rate was reduced, chick's growth rate was decreased, and long-term survival in the wild was lower for female offspring. Therefore, this work supports the hypothesis that post-copulatory sexual selection, that operates when females mate with multiple males, may allow females to limit the fitness cost incurred when eggs are fertilized by the sperm of senescing males [13].

The North African houbara bustard is an ideal candidate to test the hypothesis that post-copulatory sexual selection might allow females to avoid the cost of egg fertilization by old mates, because females are polyandrous (and the decision to mate with several males is under female control), old males produce ejaculates with fewer sperm of lower motility, and paternal age is associated with fitness costs for the progeny. Here, we used a very stringent experimental approach where young and old males used to prepare the mixes of semen had similar ejaculate quality and similarly contributed to the mixes in terms of sperm motility and number. Our decision to use a non-random sample of old males has pros and cons. Among the cons, we might speculate about the possible consequences if there are trade-offs among ejaculate attributes and/or between ejaculate attributes and other phenotypic traits [6,37,38]. An intriguing possibility would be that, if there is a trade-off between sperm motility and longevity, sperm of old birds with high motility might also have the shortest longevity, possibly due to their higher mutation load, which might account for their poorer fertilization success. Further work is definitely needed to explore how age affects the strength of the trade-offs among different ejaculate attributes, as well as between traits involved in pre- and post-copulatory sexual selection. Additional ejaculate attributes (e.g. sperm velocity) measured using computer-assisted sperm analysis might contribute to investigate these trade-offs.

This last point brings us also to the difficulties to properly identify and fully tease apart any male and female effects as drivers of the observed fertilization bias in favour of young males. We controlled for two obvious traits that are known to contribute to the probability of egg fertilization when sperm from different ejaculates compete, but there are many more phenotypic attributes that we could not control for (for instance, how long sperm from young and old males live once in the female reproductive tract, sperm morphology, etc.). In addition to the phenotypic attributes, when studying the effect of male age, one should also control for any possible mutation load and/or epigenetic changes that are known to occur in the highly

replicative male germ line. Therefore, in line with the conclusions of a recent review article [27], we think that it is extremely challenging to tease apart male (traits leading to higher sperm competitiveness) from female effects (active female sperm selection). The difficulties to identify the mechanism underlying the biased fertilization success do not, however, preclude to conclude that females, by mating with multiple males may open the way for post-copulatory selection to operate and, as such, limit the risk of being fertilized by senescing mates.

In addition to the possible mechanisms that might allow the sperm of young males to outcompete sperm from senescing individuals (i.e., higher longevity in the female reproductive tract), there might also be direct mechanisms of female sperm selection [27]. For instance, it has been shown that females might control male fertilization success by ejecting sperm of non-preferred males (as in the case of sub-dominant males in the feral fowl, [39]). Obviously, such a mechanism cannot operate in the present study, because females were artificially inseminated with a mix of semen, making impossible to selectively eject the sperm of one of the two males. Other possible mechanisms might involve the selective action of the female immune system towards sperm of old males. If senescing males produce sperm carrying higher mutation load, they might be recognized by female immune cells and destroyed. Finally, the difficulty to identify and tease apart any male and female effect as drivers of the outcome of post-copulatory selection is further illustrated by the finding that the two might not be mutually exclusive and might actually interact, as in the case of the guppy (*Poecilia reticulata*) where female ovarian fluids mediate male sperm velocity [40].

Estimating siring success when females are inseminated with ejaculates of different males implies that paternity can be assigned, and this is usually achieved with genetic tools. However, when embryos have an interrupted development at very early stages, it might be impossible to retrieve enough genetic material to assign paternity. Therefore, when comparing two groups of fathers, differential siring success might arise because of differential embryo

314 mortality. In a companion study, we investigated whether post-copulatory sexual selection
315 might allow female North African houbara bustards to avoid insemination with kin. We found
316 evidence that paternity was skewed towards unrelated mates, but this skew was entirely due to
317 the low hatching success of eggs that were fertilized by males that were genetically related to
318 the female [41]. Here, we found that eggs sired by old fathers also had reduced hatching success,
319 potentially raising the same concern about differential embryo mortality as the driver of the
320 observed differential siring success between young and old males. However, when restricting
321 the analysis to first laid eggs, where paternity assignment was very successful (only one egg
322 had a missing paternity), we still found a highly skewed paternity towards young males.
323 Therefore, we are confident that our finding of differential siring success between young and
324 old males is not an artefact due to differential embryo mortality and biased paternity
325 assignment.

326 The idea that females might engage in multiple matings and let post-copulatory selection
327 to operate as to limit fertilization by senescing males is corroborated by our finding that eggs
328 fertilized by old fathers had lower hatching success and chicks sired by old fathers had reduced
329 growth rate. These findings add evidence for deleterious effects of paternal age on offspring
330 fitness, a topic that has attracted considerable attention in the last years [8,42]. In addition to
331 these short-term effects of paternal age, we also investigated whether offspring survival was
332 affected both during the period that offspring spent in the captive breeding and more notably
333 during almost 2 years and a half after their release in the wild. While early survival in the captive
334 breeding did not differ as a function of paternal age (likely the consequence of the very benign
335 environmental conditions encountered in captivity), we found a sex-dependent effect of
336 parental age on long-term survival in the wild. In particular, female offspring sired by young
337 males had better survival compared to female offspring sired by old fathers, whereas there was
338 no effect on male offspring survival. Although this is not the first study to report offspring sex-

dependent effect of parental age [8,43,44], it is difficult to precisely identify the underlying mechanisms. For instance, females generally start breeding younger than males, i.e. during their first year of life. Hence, released females might have been more exposed to environmental hazards (predation, hunting, inability to find appropriate food items) when prospecting for nest sites or during incubation, and females sired by old fathers might have performed less well than females sired by young fathers. Alternatively, although we did not find any evidence suggesting a propensity to cover longer post-release distances as a function of paternal age, differences in habitat use or other behavioural and/or physiological traits might explain the observed sex-dependent effect of paternal age on long-term survival.

To conclude, we provided experimental evidence showing that post-copulatory sexual selection can be an effective mechanism allowing females to avoid egg fertilization by senescing males and limit the associated fitness costs for the progeny. Although very challenging, further work might try to attempt identifying the possible drivers (better sperm competitiveness of young males, active female sperm preference, or both), and disentangle male and female effects of age-dependent fertilization skew.

Ethics

All birds used in the present study were bred in captivity and released into the wild in agreement with Moroccan authorities: Ministère de l'Agriculture, Développement Rural et des Pêches Maritimes, Direction Provinciale de l'Agriculture de Boulemane, and Service Vétérinaire (Nu DPA/48/285/SV) under permit number 01-16/VV; OAC/2007/E; Ac/Ou/Rn. All releases were recorded by the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification. Bird handling and sampling were performed by trained bird keepers or experimenters of the ECWP.

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Authors' Contributions

PV, LL, GL, TC, MSJ, FL, YH and GS designed the experiment; PV and AB conducted the experiment; PV performed statistical analyses; PV drafted out the manuscript, which was revised by GS and YH. All authors gave final approval for publication.

Data, code and materials

The datasets supporting the results are available from the Dryad Digital Repository: <https://datadryad.org/review?doi=doi:10.5061/dryad.47fd240>.

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503

Table

Table 1. Linear mixed effects models exploring the effect of paternal age on chick growth rate during the first three months of life (n = 215 chicks). Growth rate was assessed as age-dependent change in body mass and size-corrected body mass. The model on body mass included offspring age, paternal age and the two-way interaction as fixed effects and maternal identity, offspring identity nested within the maternal identity, and the identities of the two males forming the dyad as random effects. The model on size-corrected body mass also included body size (head length), as well as all the two- and three-way interactions. The old paternal age category was included in the intercept. Significant *p* values are in bold.

<i>Body mass</i>				
Fixed effects	Estimate	SE	t value	<i>p</i>
Intercept	3.510	7.062		
Offspring age	11.404	0.113	101.180	<0.001
Paternal age	-4.757	9.123	-0.520	0.930
Paternal age x Offspring age	0.333	0.145	2.300	0.022
Random effects	Variance	SD		
Offspring ID:Maternal ID	1573.300	39.653		
Maternal ID	244.800	15.647		
Male ID 1	0.006	0.079		
Male ID 2	1.5 x 10 ⁻⁴	0.012		
<i>Size-corrected body mass</i>				
Fixed effects	Estimate	SE	t value	<i>p</i>
Intercept	-383.624	23.235		
Offspring age	-17.802	1.289	-13.813	<0.001
Paternal age	-87.145	29.945	-2.910	0.376
Body size	11.093	0.579	19.157	<0.001
Paternal age x Offspring age	-3.931	1.634	-2.407	0.459
Offspring age x Body size	0.233	0.010	22.282	<0.001
Paternal age x Body size	2.392	0.749	3.196	0.151
Offspring age x Paternal age x Body size	0.027	0.013	2.071	0.039

Random effects	Variance	SD
Offspring ID:Maternal ID	434.100	20.840
Maternal ID	188.800	13.740
Male ID 1	4.2×10^{-7}	6.5×10^{-4}
Male ID 2	0.000	0.000

514

Figures

Figure 1. Within-dyad siring success (with 95% confidence intervals), considering all eggs (n = 86) and first laid eggs only (n = 28), for the two paternal age categories (young and old). The dotted line represents the random (0.5) expectation.

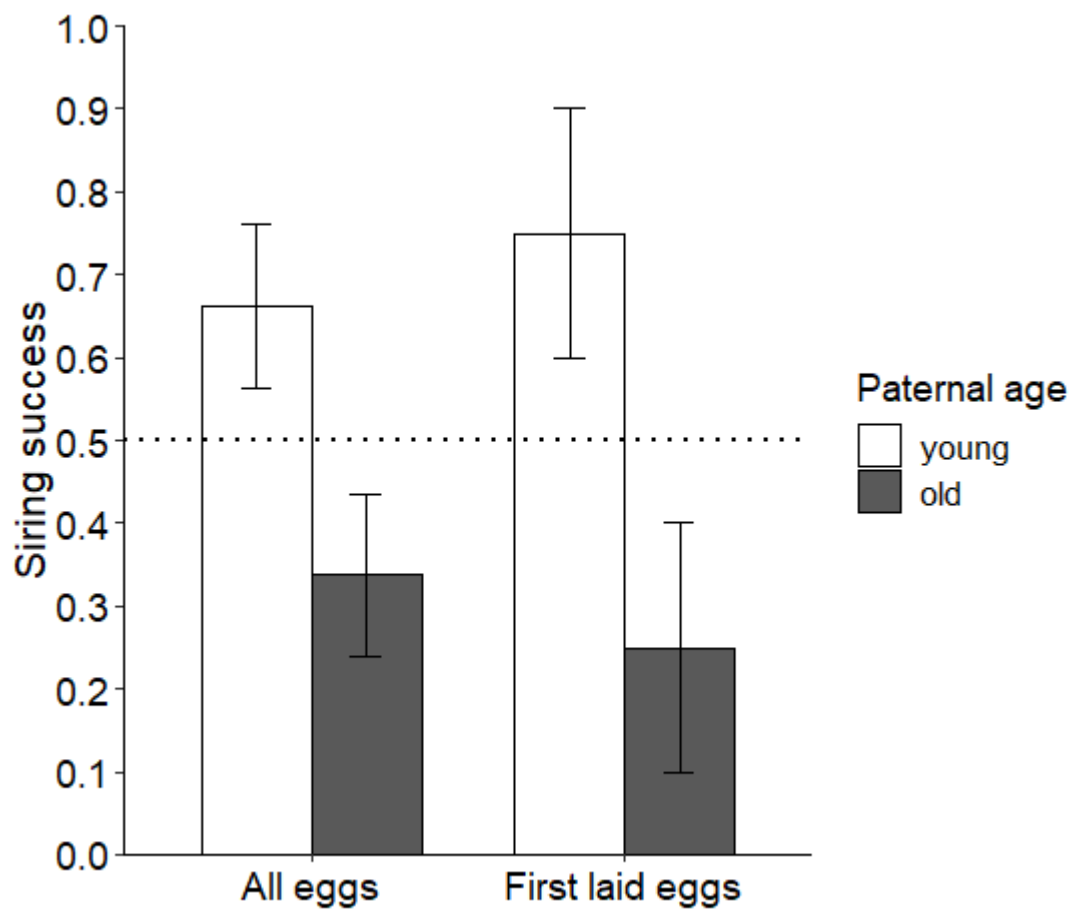
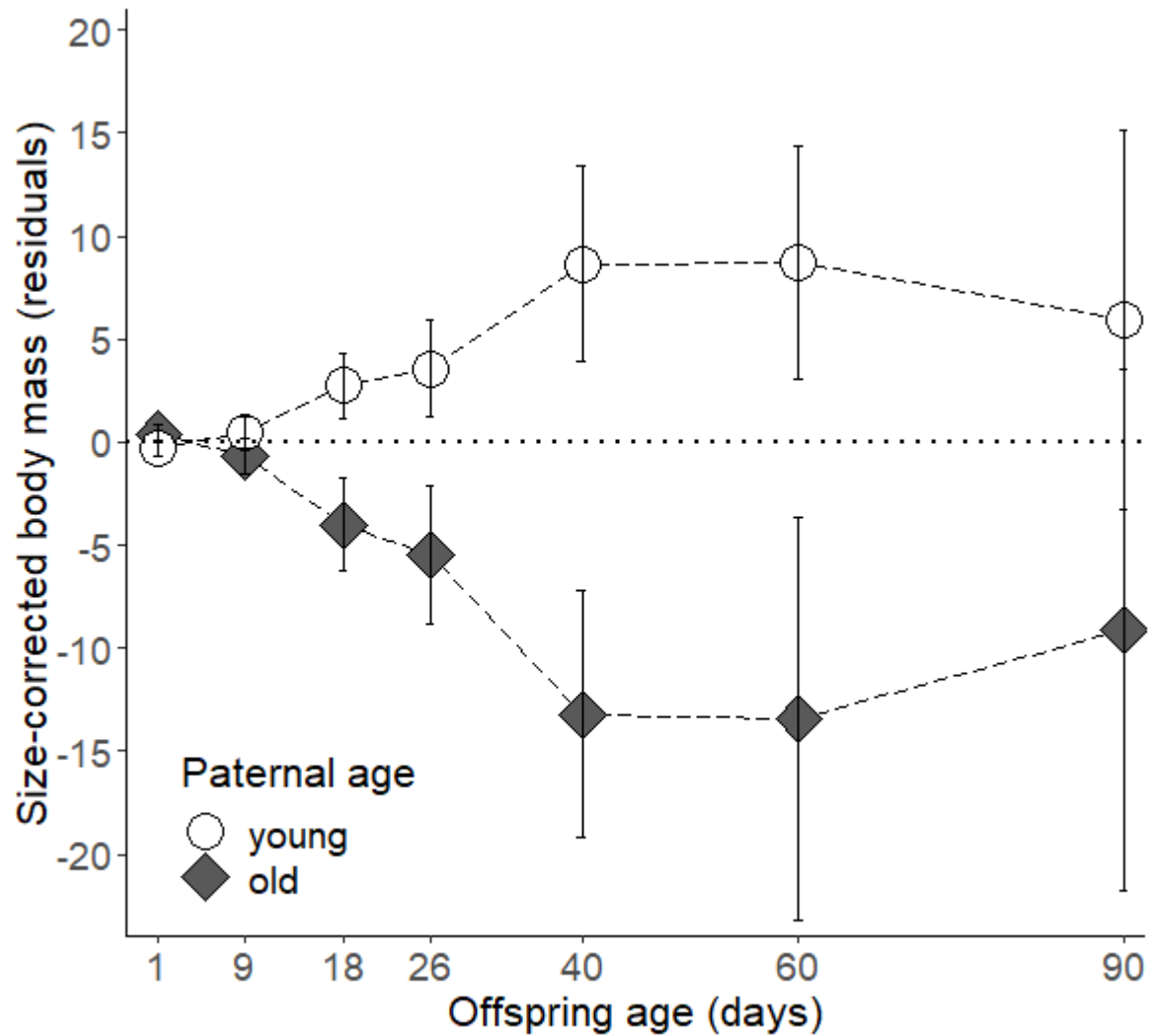
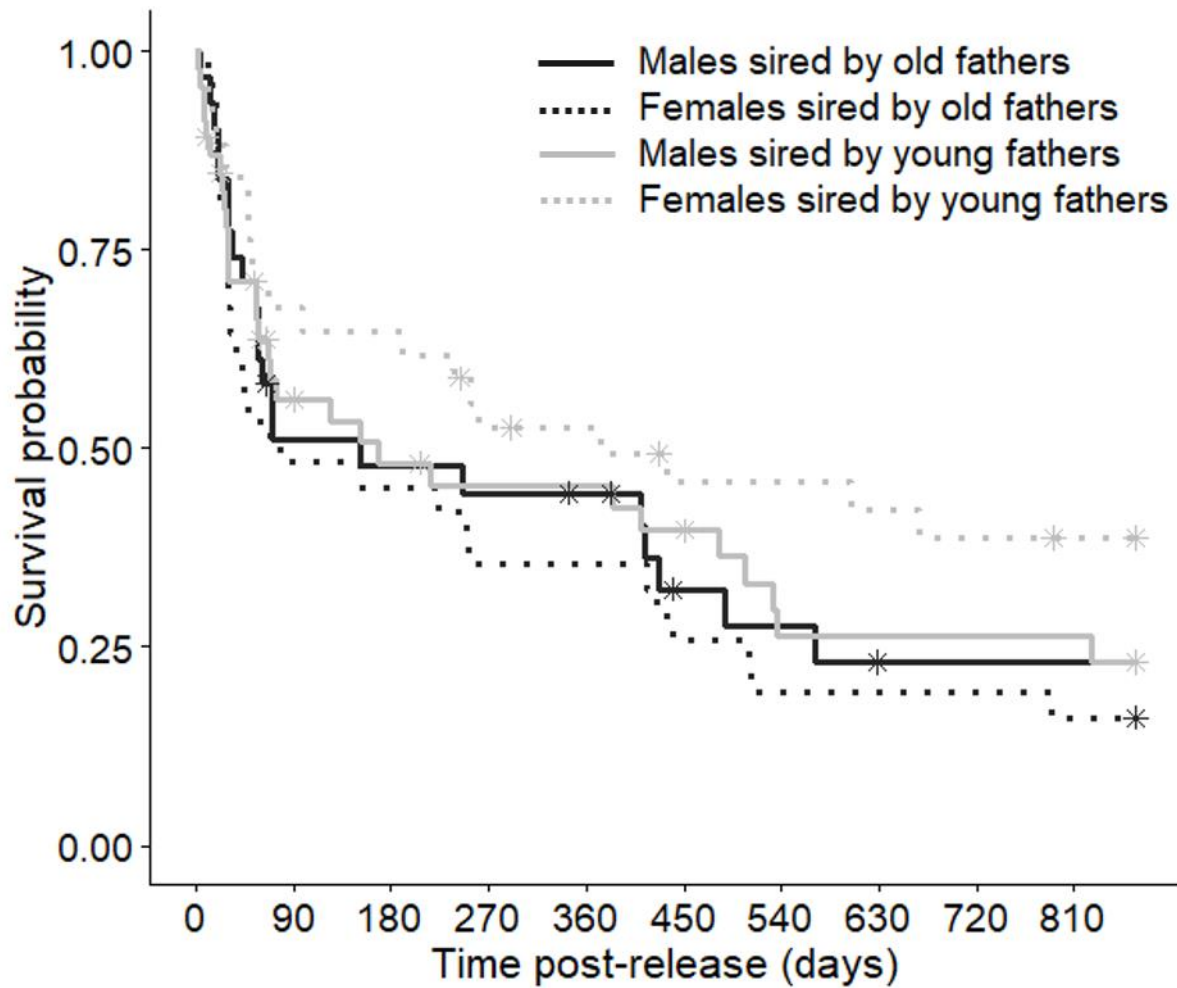


Figure 2. Age-dependent changes, during the first three months of life, in size-corrected body mass of chicks sired by young or old fathers in the North African houbara bustard. Size-corrected body mass refers to the residuals of a regression of body mass on body size (head length). Values are means \pm se.



530 Figure 3. Survival of North African houbara bustard as a function of sex and paternal age, up
 531 to 28 months post-release in the wild (n = 142). Solid lines refer to male offspring and dashed
 532 lines to female offspring. Stars represent censored observations (i.e., lost individuals).



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