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Report

Male Reproductive Senescence Causes Potential for Sexual Conflict over Mating

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Summary

The realization that senescence, age-dependent declines in survival and reproductive performance [1–4], pervades natural populations has brought its evolutionary significance into sharper focus [5, 6]. However, reproductive senescence remains poorly understood because it is difficult to separate male and female mechanisms underpinning reproductive success. We experimentally investigated male reproductive senescence in feral fowl, *Gallus gallus domesticus*, where socially dominant males monopolize access to females and the ejaculates of multiple males compete for fertilization [7]. We detected the signal of senescence on multiple determinants of male reproductive success. The effect of age on status was dependent upon the intensity of intrasexual competition: old males were less likely to dominate male-biased groups where competition is intense but were as likely as young males to dominate female-biased groups. Mating and fertilization success declined sharply with male age largely as a result of population-level patterns. These age-dependent declines translated into sexually antagonistic payoffs: old males fertilized more eggs when they were dominant, but this resulted in females suffering a drastic reduction in fertility. Thus, male senescence causes potential for sexual conflict over mating [8], and the intensity of this conflict is modulated socially, by the probability of old males dominating reproductive opportunities.

Results and Discussion

Quantifying reproductive senescence hinges on disentangling male- and female-driven mechanisms underpinning age-dependent variation in reproductive success. This is challenging because in most species, females can mate with multiple males and variation in reproductive success is determined not only by behavioral interactions over mating but also after mating, by the differential fertilizing efficiency of rival ejaculates [9]. Here, we addressed this challenge by experimentally investigating male reproductive senescence and its repercussions for male and female reproductive success in a seminatural population of domestic fowl, *Gallus gallus domesticus*. Natural fowl populations are characterized by overlapping generations [10] and intense sexual selection on males both before and after mating [7]. Socially dominant males have privileged access to mating opportunities [11, 12], but females often mate multiply, forcing the ejaculates of different males into sperm competition [12–14]. First, we experimentally assessed the impact of male senescence on six established components of male reproductive success: (1) social status, (2) copulation propensity, (3) semen transfer, (4) ejaculate size, (5) sperm swimming velocity, and (6) ejaculate fertilizing efficiency under sperm competition. Second, we measured the impact of male aging on male and female reproductive success by quantifying differential fertilization success and the proportion of eggs fertilized in replicate groups.

By experimentally manipulating the sex ratio of replicate groups of nine birds, we studied the relationship between male age and male social status under different intensities of intrasexual competition, and we found a signal of senescence in male social status only under intense competition. In groups in which six males competed over access to three females (6:3), socially subordinate males were older than males of higher status (Kruskal-Wallis, $\chi^2_2 = 8.035$, $p = 0.018$, $n_{groups} = 10$). However, in the more relaxed competition of female-biased groups (3:6), male social status was independent of male age ($\chi^2_2 = 1.72$, $p = 0.42$, $n_{groups} = 10$; see Table S1 available online for an alternative analytical approach with qualitatively similar results). In addition, male age had a consistent impact on different measures of male mating performance. When experimentally exposed to unrestricted mating opportunity with successive females, older males displayed a lower propensity to copulate (general linear mixed model [LMM], age: $F_{1,56} = 20.81$, $p < 0.0001$; Table S2; Figure 1A), suffered from reduced probability of semen transfer (generalized linear mixed model [GLMM], age: $F_{1,48} = 12.70$, $p = 0.0008$; Table S3; Figure 1B), and ejaculated fewer sperm than young males (LMM, age: $F_{1,67} = 43.12$, $p < 0.0001$; Table S4; Figure 1C). In addition, there was a tendency for older males to ejaculate sperm of lower swimming velocity (LMM, age: $F_{1,54} = 3.39$, $p = 0.071$; Table S5; Figure 1D). We further investigated age-dependent declines in sperm fertilizing efficiency through a sperm competition experiment in which the same number of sperm from two males, one "old" (i.e., age 6–8 years, mean age = 7 years, standard deviation [SD] = 0.76) and one "young" (i.e., age 2–3 years, mean age = 2.75 years, SD = 0.46; see Supplemental Experimental Procedures), were simultaneously inseminated artificially in the same female. Even after controlling for age-dependent differences in male mating performance and number of sperm inseminated, the ejaculate of the young males had on average a strong fertilizing advantage, accounting for 77% (±10% standard error [SE]) of the paternity of a clutch, which deviated significantly from an even (i.e., 50%) paternity share expected in the absence of age-specific differences in sperm fertilizing efficiency (generalized linear model [GLM] of young male paternity, intercept tested versus 0.5: $t = 2.64$, $df = 7$, $p = 0.0335$).

A current challenge of senescence studies in natural populations is to establish the extent to which population-level trends are determined by age-specific declines of individual organisms and by alternative population-level mechanisms, such

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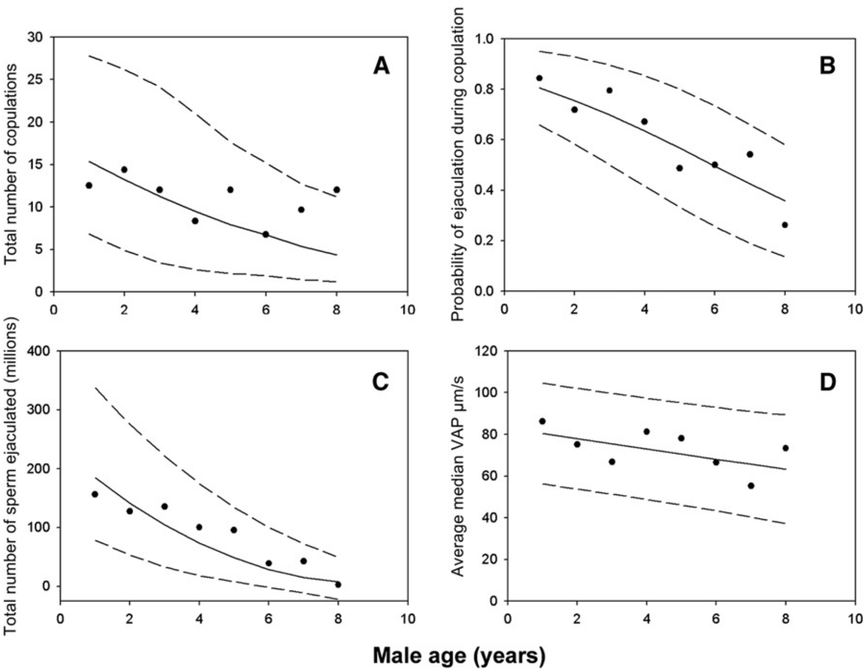

Figure 1. Cohort Patterns of Mating Performance

(A) Copulation propensity.

(B) Probability of ejaculation.

(C) Total number of sperm ejaculated.

(D) Sperm swimming velocity (average path velocity, VAP).

Solid lines represent predicted values from the model; dashed lines represent confidence intervals.

as the selective disappearance of high-performing individuals [15, 16]. We found high individual variation in age-specific trajectories of reproductive performance (Figures 2A–2D) and used within-subject centering to disentangle changes within individuals from population-level processes. The extent to which age-dependent declines were explained by individual declines varied across different reproductive traits. Using a "mean-centered" analytical approach (see Supplemental Experimental Procedures), we found no evidence of significant within-individual decline in copulation propensity (LMM, mean-centered copulation propensity: $F_{1,7} = 1.05$, $p = 0.340$; Table S6; Figure 2A). However, patterns of semen transfer failure (GLMM, mean-centered semen transfer failure: $F_{1,11} = 3.34$, $p = 0.0959$; Table S7; Figure 2B) and the total number of sperm ejaculated were associated with a nonsignificant tendency for individual declines (LMM, mean-centered total sperm number: $F_{1,8} = 4.38$, $p = 0.068$; Table S8; Figure 2C). There was also no evidence of significant within-individual declines in sperm swimming velocity (LMM, mean-centered sperm swimming velocity: $F_{1,15} = 1.14$, $p = 0.302$; Table S9; Figure 2D). Together, these results indicate that age-dependent declines in male reproductive performance are explained largely by population-level processes; however, they do not eliminate the possibility that some reproductive traits, such as the size of the ejaculate delivered, might also suffer from individual senescence.

Finally, we quantified the extent to which these age-dependent declines in male reproductive performance impacted on male and female reproductive success in replicate groups in which two males competed over access to three females. Consistent with our experimental findings that male age has little effect on male status in female-biased populations (see above), we found that old males were as likely to become socially dominant as their younger counterparts (GLMM, age: $F_{1,15} = 0.05$, $p = 0.833$). However, reproductive skew among competing males was strongly influenced by an interaction between male age and status. In groups where the dominant male was young, the old subordinate male failed to gain any paternity. In groups where the dominant male was old, on the other hand, the young subordinate male was able to steal some of the paternity (mean ± SE = 29% ± 14%) despite his subordinate status (GLMM, age of dominant male: $F_{1,14} = 8.14$, $p = 0.0128$; effect size: old = 0.31 ± 0.08, young = 0.69 ± 0.09; $n_{groups} = 16$, $n_{eggs\ fertilized} = 114$, $n_{eggs\ laid} = 237$; Figure 3A). Importantly, an interaction between male age and social status also had drastic consequences for female reproductive success. Whereas a relatively high proportion (73% ± 7%) of the eggs were fertilized in groups dominated by a young male, on average only 54% (±10%) of the eggs in groups dominated by an old male were fertilized, representing a 27% fertility cost (GLMM, age of dominant male: $F_{1,14} = 5.13$, $p = 0.0399$; effect size: old = 0.45 ± 0.08, young = 0.73 ± 0.08; $n_{groups} = 16$, $n_{eggs\ fertilized} = 136$, $n_{eggs\ laid} = 237$; Figure 3B).

Most research on senescence has focused on declines in survival, and less is known about the proximate mechanisms that govern male reproductive senescence and their evolutionary implications. However, reproductive senescence might represent a significant source of variation in individual fitness [17], with important consequences for sexual selection and sexual conflict in age-structured populations [18]. Taken together, the results of our study (1) demonstrate a strong signature of aging on multiple aspects of male reproductive function in a bird population, (2) reveal that such declines are explained largely by population-level mechanisms, and finally (3) indicate that male reproductive senescence has the potential to foster conflict over mating between aging males and their partners.

From an evolutionary standpoint, senescence is ultimately due to the inability of Darwinian selection to purge deleterious mutations acting late in life [1–4]. This has led to the assumption that senescence plays a limited role in individual fitness variation in natural populations, where extrinsic mortality is expected to prevent individuals from reaching old age [19, 20]. However, extensive evidence has recently challenged this assumption by demonstrating age-dependent declines in fitness and/or physiological performance in many vertebrate and invertebrate organisms [5, 21–23], which indicates that senescence is a ubiquitous and biologically relevant evolutionary force.

We show here that multiple reproductive traits with an established link to reproductive success display marked patterns of steady age-dependent declines at population level. These patterns are likely to be relevant to natural fowl populations. Red junglefowl, *Gallus gallus ssp.*, the wild ancestor of the domestic fowl [24], can live up to 30 years in captivity [25], and in seminatural populations exposed to predation

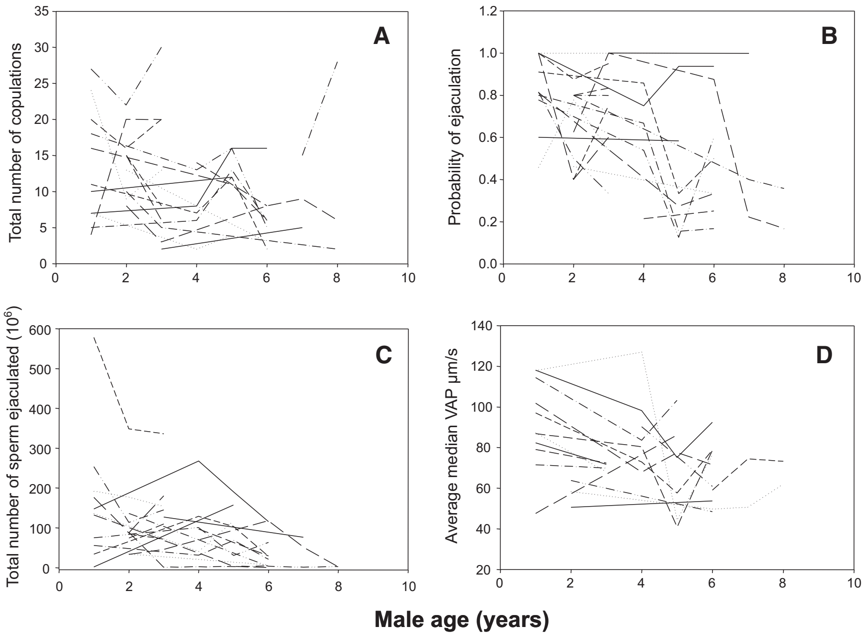

Figure 2. Longitudinal Patterns of Mating Performance

(A) Copulation propensity.
(B) Probability of ejaculation.
(C) Total number of sperm ejaculated.
(D) Sperm swimming velocity (average path velocity, VAP).

and pathogen pressures, males live at least up to 5.5 years [11], indicating that life span can be sufficiently prolonged for reproductive senescence to have considerable effects even in natural populations. That male fowl might suffer reproductive senescence had long been suspected. In the 17th century, ornithologist Francis Willughby wrote that "The cock being a most salacious bird does suddenly grow old, and becomes less fit for generation. For his spirits being spent, and the radical moisture, as they call it, consumed… his body must necessarily wax dry, and his heat of lust extinguished" [26]. By demonstrating that reproductive senescence is caused by declines in mating behaviors and ejaculate traits that impact reproductive fitness, our results lend experimental support to Willughby's original intuition.

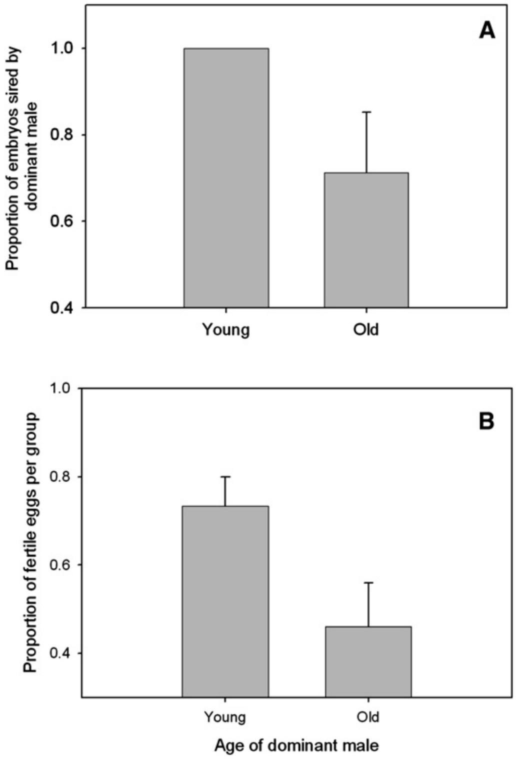

Figure 3. Sexually Antagonistic Consequences of Old Males' Status

Reproductive success of males (A) and females (B) across replicate groups comprising two males and three females. Error bars represent standard error of the mean.

Despite theoretical arguments suggesting that male reproductive function should be particularly vulnerable to senescence [18], evidence for age-dependent declines in individual reproductive traits and their fitness implications remains ambiguous (e.g., [22, 27–32]). For example, in the guppy, *Poecilia reticulata*, old males produce slower-swimming sperm than younger males, but these differences do not translate into a fertilizing advantage for younger males under sperm competition [28]. Similarly, sperm motile performance declines in old male barn swallows, *Hirundo rustica*, but increases when exposed to a medium derived from the female oviduct [27]. Finally, mating with old males has negative consequences for female reproductive success in the hide beetle, *Dermestes maculatus* [29, 30], but not in the seed beetle, *Callosobruchus maculatus* [31].

Variation in reproductive success is often caused by multiple male traits, particularly in species where females mate multiply and paternity is determined by both pre- and postinsemination episodes of sexual selection. Because previous studies have often focused on individual reproductive traits, it is difficult to establish whether such patterns generate a biologically relevant source of variation in male reproductive success. The present results show that male reproductive function declines at multiple stages, from mating performance to sperm competitive quality, indicating that studies focusing on individual traits are unlikely to fully capture the magnitude of reproductive senescence and its fitness implications. Importantly, we show that different male traits senesce at different rates, and this has critical implications for sexual selection and sexual conflict. Under a female-biased sex ratio, which is common in this species [11], male social status is not affected by male age, which means that aging males are able to achieve dominant status. Indeed, because they can only achieve reproductive success through social dominance, aging males are strongly sexually selected to monopolize sexual access to females. When this happens, however, females pay a substantial fertility cost and are naturally selected to avoid this costly monopoly.

These antagonistic payoffs create the potential for sexual conflict over mating between aging males and their prospective partners. Whether females benefit or lose by mating with old males has long been debated. On the one hand, variation in longevity might represent the ultimate honest signal of heritable viability, suggesting that females mating preferentially with old males might obtain genetic benefits for their offspring [33, 34]. On the other hand, it has been argued that old males might not necessarily have high breeding values for fitness [35], thus questioning genetic benefits. Our study contributes to this discussion by demonstrating that mating with an old male is also associated with drastic direct fertility costs. In addition, increasing evidence indicates that offspring viability might also be severely compromised by paternal age [17, 18]. Potential genetic benefits of mating with old males appear therefore unlikely to offset such costs. The fitness payoffs that females obtain by mating with socially dominant males are similarly contentious [36]. In the fowl, mating with dominant males has the potential to convey genetic benefits because social status conveys reproductive benefits in both males and females [37, 38], and competitive behavior associated with status is partly heritable [39]. However, males that are able to monopolize access to females, such as dominant males, might be unable to fertilize all of the eggs available, creating conflict over mating decisions [40, 41]. The results of our study reconcile these scenarios by showing that the intensity of sexual conflict is modulated by an interaction between male age, male status, and the social environment. In other words, social status might represent a reliable signal of male quality in male-biased populations but—as a result of male reproductive senescence—might be associated with net fertility costs to females in female-biased populations. Although recent studies have shown that sexual conflict can lead to female infertility and accelerate female senescence [42], our study identifies a novel link between senescence and sexual conflict by showing that the reproductive senescence suffered by males can strongly reduce the fertility of their partners.

In addition, with few exceptions [22, 23], most studies have failed to distinguish between individual senescence and population-level trends. Our study indicates that age-dependent declines in reproductive performance are largely explained by population-level trends. A possible explanation for these population-level trends, which requires further investigation, might be the selective disappearance of males that invest highly in reproduction. Male reproductive investment is notoriously costly in the fowl [43], and it is likely that males with high reproductive investment early in life might suffer a higher risk of mortality associated with the cost of increased reproductive investment. However, we also detected high variability in the reproductive performance trajectories of individual males, and after controlling for population-level trends, we could not exclude the possibility that the performance of individual males also declines with age in two interrelated reproductive traits, the probability of semen transfer and the number of sperm inseminated. This indicates that individual senescence might have a subtle but potentially important influence on age-dependent declines, revealing the importance of disentangling population-level processes from individual-level processes when studying the causes and consequences of senescence.

In short, we have shown that age-dependent declines in multiple aspects of male reproductive function can account for a considerable proportion of variance in male reproductive success, particularly under intense competition over mating and fertilization. This highlights the need to measure male reproductive performance across episodes of pre- and postinsemination sexual selection to better understand the significance of male senescence.

Experimental Procedures

This study was conducted on a feral population of domestic fowl, *Gallus gallus domesticus*, at Tovetorp Zoological Research Station, Stockholm University, Sweden during the months of May through August between 2002 and 2009. Within this period, the population ranged from 37 to 76 females and from 44 to 77 males, with males living up to 8 years. The study comprised four experiments. Experiment 1 investigated the relationship between male age and social status under different sex ratios. Experiment 2 explored the relationship between male age and different aspects of reproductive performance, both across cohorts and longitudinally within individual males. Experiment 3 quantified the impact of male age on fertilization success under sperm competition via an artificial insemination approach. Finally, experiment 4 measured male and female reproductive success in relation to male age and social status in seminatural groups. The experimental methodology, including molecular parentage analysis and statistical analysis, is detailed in Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes nine tables and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.04.059.

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References

1. Medawar, P. (1952). An Unsolved Problem in Biology (London: Lewis).
2. Williams, G.C. (1957). Pleiotropy, natural-selection, and the evolution of senescence. Evolution *11*, 398–411.
3. Hamilton, W.D. (1966). The moulding of senescence by natural selection. J. Theor. Biol. *12*, 12–45.
4. Rose, M.R. (1991). Evolutionary Biology of Aging (New York: Oxford University Press).
5. Jones, O.R., Gaillard, J.M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H., Bize, P., Brommer, J., Charmantier, A., Charpentier, M., et al. (2008). Senescence rates are determined by ranking on the fast-slow life-history continuum. Ecol. Lett. *11*, 664–673.
6. Nussey, D.H., Coulson, T., Festa-Bianchet, M., and Gaillard, J.M. (2008). Measuring senescence in wild animal populations: Towards a longitudinal approach. Funct. Ecol. *22*, 393–406.
7. Pizzari, T., Froman, D.P., and Birkhead, T.R. (2002). Pre- and post-insemination episodes of sexual selection in the fowl, Gallus g. domesticus. Heredity *88*, 112–116.
8. Parker, G.A. (2006). Sexual conflict over mating and fertilization: An overview. Philos. Trans. R. Soc. Lond. B Biol. Sci. *361*, 235–259.
9. Birkhead, T.R., and Pizzari, T. (2002). Postcopulatory sexual selection. Nat. Rev. Genet. *3*, 262–273.
10. Collias, N.E., and Collias, E.C. (1996). Social organization of a red junglefowl, Gallus gallus, population related to evolutionary theory. Anim. Behav. *51*, 1337–1354.
11. Pizzari, T., and Birkhead, T.R. (2000). Female feral fowl eject sperm of subdominant males. Nature *405*, 787–789.
12. Pizzari, T. (2001). Indirect partner choice through manipulation of male behaviour by female fowl, Gallus gallus domesticus. Proc. Biol. Sci. *268*, 181–186.

13. Ligon, J.D., and Zwartjes, P.W. (1995). Female red junglefowl choose to mate with multiple males. Anim. Behav. *49*, 127–135.
14. Løvlie, H., and Pizzari, T. (2007). Sex in the morning or in the evening? Females adjust daily mating patterns to the intensity of sexual harassment. Am. Nat. *170*, E1–E13.
15. van de Pol, M., and Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. Anim. Behav. *77*, 753–758.
16. van de Pol, M., and Verhulst, S. (2006). Age-dependent traits: A new statistical model to separate within- and between-individual effects. Am. Nat. *167*, 766–773.
17. Radwan, J. (2003). Male age, germline mutations and the benefits of polyandry. Ecol. Lett. *6*, 581–586.
18. Pizzari, T., Dean, R., Pacey, A., Moore, H., and Bonsall, M.B. (2008). The evolutionary ecology of pre- and post-meiotic sperm senescence. Trends Ecol. Evol. *23*, 131–140.
19. Kirkwood, T.B.L., and Austad, S.N. (2000). Why do we age? Nature *408*, 233–238.
20. Holmes, D.J., Thomson, S.L., Wu, J., and Ottinger, M.A. (2003). Reproductive aging in female birds. Exp. Gerontol. *38*, 751–756.
21. Bouwhuis, S., Sheldon, B.C., Verhulst, S., and Charmantier, A. (2009). Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proc. Biol. Sci. *276*, 2769–2777.
22. Nussey, D.H., Kruuk, L.E.B., Morris, A., Clements, M.N., Pemberton, J.M., and Clutton-Brock, T.H. (2009). Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. Am. Nat. *174*, 342–357.
23. McCleery, R.H., Perrins, C.M., Sheldon, B.C., and Charmantier, A. (2008). Age-specific reproduction in a long-lived species: The combined effects of senescence and individual quality. Proc. Biol. Sci. *275*, 963–970.
24. Fumihito, A., Miyake, T., Takada, M., Shingu, R., Endo, T., Gojobori, T., Kondo, N., and Ohno, S. (1996). Monophyletic origin and unique dispersal patterns of domestic fowls. Proc. Natl. Acad. Sci. USA *93*, 6792–6795.
25. Mitchell, P.C. (1911). On longevity and relative viability in mammals and birds, with a note on the theory of longevity. Proc. Zool. Soc. Lond. *1*, 425–548.
26. Ray, J. (1678). The Ornithology of Francis Willoughby (London: John Martyn).
27. Møller, A.P., Mousseau, T.A., Rudolfsen, G., Balbontín, J., Marzal, A., Hermosell, I., and De Lope, F. (2009). Senescent sperm performance in old male birds. J. Evol. Biol. *22*, 334–344.
28. Gasparini, C., Marino, I.A.M., Boschetto, C., and Pilastro, A. (2010). Effect of male age on sperm traits and sperm competition success in the guppy (*Poecilia reticulata*). J. Evol. Biol. *23*, 124–135.
29. Jones, T.M., Featherston, R., Paris, D.B.B.P., and Elgar, M.A. (2007). Age-related sperm transfer and sperm competitive ability in the male hide beetle. Behav. Ecol. *18*, 251–258.
30. Hale, J.M., Elgar, M.A., and Jones, T.M. (2008). Sperm quantity explains age-related variation in fertilization success in the hide beetle. Ethology *114*, 797–807.
31. Fricke, C., and Maklakov, A.A. (2007). Male age does not affect female fitness in a polyandrous beetle, *Callosobruchus maculatus*. Anim. Behav. *74*, 541–548.
32. Radwan, J., Michalczyk, L., and Prokop, Z. (2005). Age dependence of male mating ability and sperm competition success in the bulb mite. Anim. Behav. *69*, 1101–1105.
33. Kokko, H., and Lindström, J. (1996). Evolution of female preference for old mates. Proc. Biol. Sci. *263*, 1533–1538.
34. Kokko, H. (1997). Evolutionarily stable strategies of age-dependent sexual advertisement. Behav. Ecol. Sociobiol. *41*, 99–107.
35. Hansen, T.F., and Price, D.K. (1995). Good genes and old age: Do old mates provide superior genes? J. Evol. Biol. *8*, 759–778.
36. Qvarnström, A., and Forsgren, E. (1998). Should females prefer dominant males? Trends Ecol. Evol. *13*, 498–501.
37. Jones, M.E.J., and Mench, J.A. (1991). Behavioral correlates of male mating success in a multisire flock as determined by DNA fingerprinting. Poult. Sci. *70*, 1493–1498.
38. Collias, N., Collias, E., and Jennrich, R.I. (1994). Dominant red junglefowl (*Gallus gallus*) hens in an unconfined flock rear the most young over their lifetime. Auk *111*, 863–872.
39. Craig, J.V., Ortman, L.L., and Guhl, A.M. (1965). Genetic selection for social dominance ability in chickens. Anim. Behav. *13*, 114–131.
40. Warner, R.R., Shapiro, D.Y., Marcanato, A., and Petersen, C.W. (1995). Sexual conflict: Males with highest mating success convey the lowest fertilization benefits to females. Proc. Biol. Sci. *262*, 135–139.
41. Harris, W.E., and Moore, P.J. (2005). Female mate preference and sexual conflict: Females prefer males that have had fewer consorts. Am. Nat. *165* (*Suppl 5*), S64–S71.
42. Bonduriansky, R., Maklakov, A., Zajitschek, F., and Brooks, R. (2008). Sexual selection, sexual conflict and the evolution of ageing and life span. Funct. Ecol. *22*, 443–453.
43. Cornwallis, C.K., and Birkhead, T.R. (2008). Plasticity in reproductive phenotypes reveals status-specific correlations between behavioral, morphological, and physiological sexual traits. Evolution *62*, 1149–1161.