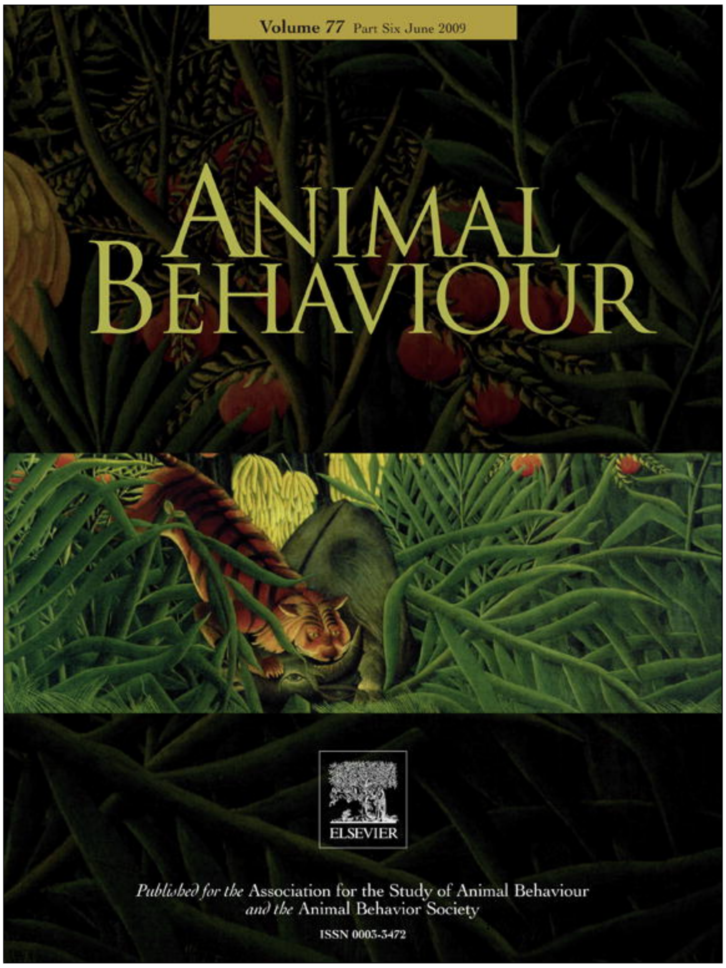
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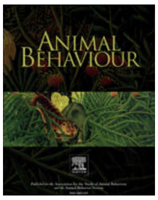

Sex differences in survival costs of homosexual and heterosexual interactions: evidence from a fly and a beetle

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Studies on the costs of sexual reproduction have focused primarily on the costs of heterosexual courtship and mating, whereas the costs of homosexual interactions, such as male–male or female–female displays and mounting, have been relatively neglected. This may reflect an implicit assumption that heterosexual interactions are more costly in most species, but this assumption has never been verified. We tested this assumption experimentally by comparing the effects of hetero- and homosexual interactions on life span in two distantly related insects with contrasting mating systems: the seed beetle *Callosobruchus maculatus*, and the sexually dimorphic carrion fly *Prochyliza xanthostoma*. Despite pronounced behavioural and morphological differences between these species, results were remarkably congruent. Relative to individually housed virgin controls, male life span was reduced to a similar degree in males maintained with other males and males maintained with females. In contrast, female life span was strongly reduced relative to controls when females were kept with males, but was affected very little when females were maintained with other females. Thus, the costs of homosexual and heterosexual interactions are similar for males, but highly dissimilar for females. Our results suggest that the costs of homosexual interactions can be considerable, and may have important consequences for the evolution of mating systems.

Costs of reproduction are a central tenet of life history theory (Stearns 1992; Roff & Fairbairn 2007). Reproduction is costly because it reduces future prospects of survival or reproduction. The costs of reproduction to females result from mating and offspring production and care. In contrast, male reproductive costs include material and energetic investment in gamete production, courtship, combat and scramble competition, and the costs of mating (Cordts & Partridge 1996; Kotiaho 2001; Martin & Hosken 2004). Most research on the costs of sexual behaviours and interactions has traditionally focused on interactions with members of the opposite sex. However, in many species, males and females may respond aggressively to same-sex individuals and, indeed, may court and attempt to mount them (Aiken 1981; Serrano et al. 1991; Srivastava et al. 1991; Andersson 1994; Vasey 1995; Bagemihl 1999; Fang & Clemens 1999; Harari et al. 2000; Sommer & Vasey 2006; Vasey et al. 2008). Such interactions may function in intrasexual competition, but can also result from perception errors (see below), and it may often be difficult to distinguish these causes in practice. Thus, we refer to all interactions between same-sex individuals as 'homosexual interactions'. The costs of homosexual interactions have been estimated in very few species (especially in females), despite the paramount importance of such costs for models that aim to explain the evolution and maintenance of sexual behaviours.

The costs of homosexual interactions can be substantial. In many species, males compete with rivals for access to females or territories through scramble and/or combat interactions, often expending considerable time and energy, and incurring substantial risk of injury (Thornhill & Alcock 1983; Andersson 1994; Kotiaho 2001). In addition, males often court and mount other males, and the costs of courtship can be very high (Cordts & Partridge 1996). Homosexual mounting has been reported for a wide variety of taxa, including mammals, birds, reptiles and insects (Aiken 1981; Thornhill & Alcock 1983; Bagemihl 1999; Harari et al. 2000; Switzer et al. 2004; Sommer & Vasey 2006). While homosexual interactions in mammals have received a lion's share of research attention, homosexual mounting could be more prevalent in insects, where it sometimes amounts to half of all mating attempts observed (Aiken 1981; Serrano et al. 2000). Although most research has focused on male homosexual interactions, females also show homosexual behaviours in many species (Srivastava et al. 1991; Vasey 1995; Fang & Clemens 1999; Harari et al. 2000; Sommer & Vasey 2006; Gastal et al. 2007).

Homosexual courtship (or courtship-like) behaviours, and homosexual mounting, may serve a variety of sexual functions,

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such as allowing individuals to assert dominance over rivals, or serving as practice for heterosexual encounters (Vasey 1995). However, such behaviours are often hypothesized to result from perception error, or a complete lack of sex recognition (Parker 1968; Aiken 1981; Thornhill & Alcock 1983; Serrano et al. 1991; Harari et al. 2000; Switzer et al. 2004). Thus, a study of homosexual mounting in the flour beetle *Tribolium castaneum* suggests that sex recognition is absent in this species, and frequencies of intra- and intersexual mounting correspond to a random null model (Serrano et al. 2000). In many other species, sex recognition occurs but appears to be poor. In the water bug *Palmacorixa nana*, males preferentially mount individuals that are larger than themselves, probably because females are larger than males (Aiken 1981). Such a mounting strategy unsurprisingly results in a very large percentage of errors (Aiken 1980). Several other studies also support the perception error hypothesis (Savalli & Fox 1999; Harari et al. 2000; Serrano et al. 2000; Switzer et al. 2004; Van Gossum et al. 2005).

Thornhill & Alcock (1983) suggested that homosexual mounting in insects can evolve via selection on males, provided that benefits of increased mating success through rapid but indiscriminate mating attempts outweigh the costs of discrimination. Since only males are likely to gain fitness benefits through increased number of mountings, an explicit prediction from this hypothesis is that males will tolerate higher costs of homosexual mounting. Selection is expected to act against the evolution of costly female–female interactions because females are less likely to benefit from such interactions (but see Harari et al. 2000).

We carried out two experimental studies aimed at comparing the cost of homosexual interactions relative to heterosexual interactions in two very different insects: the carrion fly *Prochyliza xanthostoma* and the seed beetle *Callosobruchus maculatus*. These species have markedly different mating systems. *Callosobruchus maculatus* males mount but do not fight other males. Males chase and climb on females without courtship, transfer very large ejaculates and damage the female reproductive tract with their spiny genitalia (Rup 1986; Fox et al. 1995; Crudgington & Siva-Jothy 2000; Rönn et al. 2007). In contrast, *P. xanthostoma* males fight other males for access to territories and females, court females with an elaborate side-to-side 'waltz', transfer moderately sized ejaculates and lack spines on their genitalia (Bonduriansky 2003; Bonduriansky & Rowe 2003; Bonduriansky et al. 2005).

METHODS

Callosobruchus maculatus

This species of seed beetle is a facultative capital breeder (aphagous as adults) and a widespread pest of human grain stores. Because these beetles are well adapted to man-made environments, they are very easy to maintain and have become a popular model system for laboratory research, including studies of mating behaviour (Savalli & Fox 1999; Crudgington & Siva-Jothy 2000; Edvardsson & Tregenza 2005; Fricke & Maklakov 2007). The population used in this study was established in 2003 from 357 adult beetles that hatched from a sample of infested mung beans collected in Kingaroy, Australia. It was propagated at the Department of Primary Industries and Fisheries (DPI) in Queensland, at 250–300 beetles per generation. In 2006, we obtained a sample of inoculated beans from DPI, which produced several hundred beetles. Since then, the beetles have been kept in a Sanyo climate chamber at 30 °C and 14:10 h light:dark cycle. Every generation, approximately 500 beetles have been collected at peak hatching time (approximately 24 days) and transferred to a new jar with 150 g of fresh organic mung beans.

Six experimental treatments were established: virgin males alone, virgin females alone, virgin males in groups, virgin females in groups, males in mixed-sex groups and females in mixed-sex groups. We collected 100 mated females and provided them with 700 g of mung beans (approximately 8400 beans). This quantity of beans per beetle typically results in one egg laid per bean. We then isolated 4500 infested beans and collected virgin beetles over 24 h periods. In all six treatments, beetles were kept in 60 mm petri dishes with 10 g of mung beans regardless of density or mating status. Singly kept males and females were placed individually in 10 blocks of 10 beetles each ($N = 100$ per sex). Males and females in same-sex groups were placed in 10 groups of 20 beetles each. In each 'grouped' petri dish, 10 beetles were marked with white nontoxic face paint. These marked beetles were considered a 'background' against which the death of focal unmarked beetles was scored. As marked beetles died they were replaced from the surplus of the original 4500 isolated beans. Thus at any time during the experiment there were 10 marked beetles in each dish and only the mortality of the unmarked focal ones ($N = 100$ per sex) was scored. 'Mixed-sex groups' for males and females were established and maintained in the same manner, except that instead of marked beetles of the same sex, we had marked beetles of the opposite sex (marked females for the 'male mixed-sex' group and vice versa). Ten dishes of 10 males and 10 females each were created for each of the two 'mixed-sex' treatments. Only male deaths were scored in the 'male mixed-sex' treatment ($N = 100$) while dead females were replaced from the stock. For the 'female mixed-sex' treatment this order was reversed. Deaths were scored twice a day for each treatment.

Prochyliza xanthostoma

Thirty gravid females of *P. xanthostoma* (Walker) were collected from chunks of moose, *Alces alces*, carcasses at the Wildlife Research Station, Algonquin Park, Ontario, Canada, transferred to a controlled temperature (approximately 18 °C) and humidity (approximately 60%) room (16:8 h light:dark cycle) at the University of Toronto, and housed in a 1.5 litre plastic cage with mesh windows. The females were provided with water, sugar cubes and a petri dish with extra-lean 'organic' (nonhormone-treated) ground beef, previously aged for 5 days inside a plastic bag at room temperature, for oviposition. On days 20, 21, 22 and 23 after the start of oviposition, the food substrate was sprayed with water to induce synchronized migrations of final-instar larvae to pupation sites. These larvae were collected and transferred individually or in pairs to glass vials (3 × 9 cm) with mesh lids. After adults emerged inside the vials, some flies were transferred to other vials to adjust treatment sample sizes (see below). Experimental flies were thus laboratory-reared offspring (sired in the wild) of females collected from a wild population. Each vial contained an Eppendorf tube filled with water, with a small piece of filter paper inserted into a slit in the lid, a lidless Eppendorf tube containing ground beef and a small piece of sugar cube. Cages were maintained as above.

We established treatments similar to those in the beetle experiment, but with pairs instead of groups: virgin males alone ($N = 122$), virgin females alone ($N = 120$), virgin males in pairs ($N = 85$ pairs), virgin females in pairs ($N = 57$ pairs), female–male pairs ($N = 81$ pairs). All pairs remaining at 28 days of age in the female–female, male–male and female–male treatments were separated into individual cages to examine both immediate (preseparation) and overall (pre- and postseparation) effects of treatment on survival. Each cage was checked every 7 days for mortality until all flies had died. Pairs were separated at 28 days because, based on a pilot study, a substantial proportion of flies was expected to survive to that age.

Data Analysis

We used survival analysis to test for differences in life span between treatments. For treatments with grouped animals, analysis was carried out using block-mean life span as the unit of replication (i.e. one datum for each dish of 10 beetles or vial of two flies of the same sex). However, results were qualitatively identical when each individual's life span was used as a unit of replication (not shown). Because paired flies that were both still alive at 28 days of age were separated into individual vials for the remainder of their lives, we also tested for differences in life span between treatments during the first 28 days of life by censoring data for individuals surviving beyond 28 days (without blocking, which would introduce a bias in relation to pairs with one surviving individual). Survival analysis was carried out in Statistica 7.0 (StatSoft, Tulsa, OK, U.S.A.). Corrections for multiple testing were not appropriate for this analysis because each test evaluated a distinct hypothesis, and the overall pattern observed was consistent with a priori expectations (Perneger 1998).

RESULTS AND DISCUSSION

Despite significant differences between these taxa in biology and mating behaviour, costs of interactions for males in homosexual groups equalled the costs of interactions for males in heterosexual groups in both beetles and flies (Figs 1, 2, Table 1). The survival curves of males kept with females and those kept with other males were similar, and median life span in both treatments was lower than that of virgin males kept alone. This result suggests that costs of courtship and mounting (beetles) and courtship and combat (flies) directed towards other males are not only substantial but comparable to the overall costs of courtship and copulation with females. We note that same-sex courtship and mounting attempts are likely to impose costs on the recipient as well as on the performer.

In *C. maculatus*, males actively chase and mount other males (A. Maklakov, personal observations), and the main costs of these behaviours are likely to be loss of energy and water in these capital breeders. Additionally, a mounting male's genitalia occasionally get stuck under the elytra of another male, leading to injury and rapid death of one or both males (A. Maklakov, personal observations). However, *C. maculatus* males do not engage in combat. In *P. xanthostoma*, the main costs of homosexual interactions for males probably reflect energy investment in the side-to-side 'waltz' display that males use both to court females and to challenge rival males (Bonduriansky 2003). Males in both homosexual and heterosexual pairs spend much of their time displaying to their partner (R. Bonduriansky, personal observations). Males also engage in combat (Bonduriansky & Rowe 2003). However, paired males establish a dominance hierarchy via escalated bouts of combat (lasting up to 2 min) within the first few minutes, after which combat bouts become very brief (approximately 1 s duration) and infrequent (R. Bonduriansky, unpublished data). Males housed in homosexual pairs spend little time fighting, but perform the 'waltz' display relentlessly throughout their lives (R. Bonduriansky, personal observations).

Our principal conclusion, that costs of homosexual and heterosexual interactions were similar for males but not females, is reinforced by the qualitative similarity between results for flies and beetles, as well as the differences in experimental design applied to these organisms. First, flies were combined in pairs, whereas beetles were combined in groups of 10. Second, paired flies were separated after 28 days if both individuals were still alive, whereas grouped beetles were never separated, and dead individuals were replaced. Yet, similar patterns still emerged for both species, suggesting that our findings are robust to variation in population density and duration of social interaction. Male flies in male–male pairs had significantly reduced survival overall as well as during the first 28 days of life compared with single males. In contrast, males in male–female pairs showed a significant reduction in survival relative to single males only during the first 28 days. This tentatively suggests that heterosexual interactions may have weaker latent effects than homosexual interactions in this species, perhaps as a result of somatic damage associated with combat (flies). In contrast, for females in female–male pairs, the reduction in survival relative to single females was less clear over the first 28 days ($P = 0.088$) than overall ($P = 0.029$). A conclusive test for differential latent effects of homosexual versus heterosexual interactions would require larger sample sizes to augment power at late ages.

As expected, the relative cost of homosexual interactions was much lower for females. In *P. xanthostoma*, virgin females kept alone lived only 3% longer than females in same-sex pairs (Fig. 1, Table 1). Females of this species do not normally engage in combat, nor do they perform a courtship dance (Bonduriansky 2003). However, when kept for extended periods of time in all-female groups, some females show male-like behaviours, including the side-to-side 'waltz' display and brief combat-like interactions with other females (R. Bonduriansky, personal observations). These female–female interactions may function in competition among females for control of high-quality oviposition sites, where females are often observed to jostle and push one another in the wild (R. Bonduriansky, personal observations). Such interactions could perhaps result in somatic damage, particularly at high population

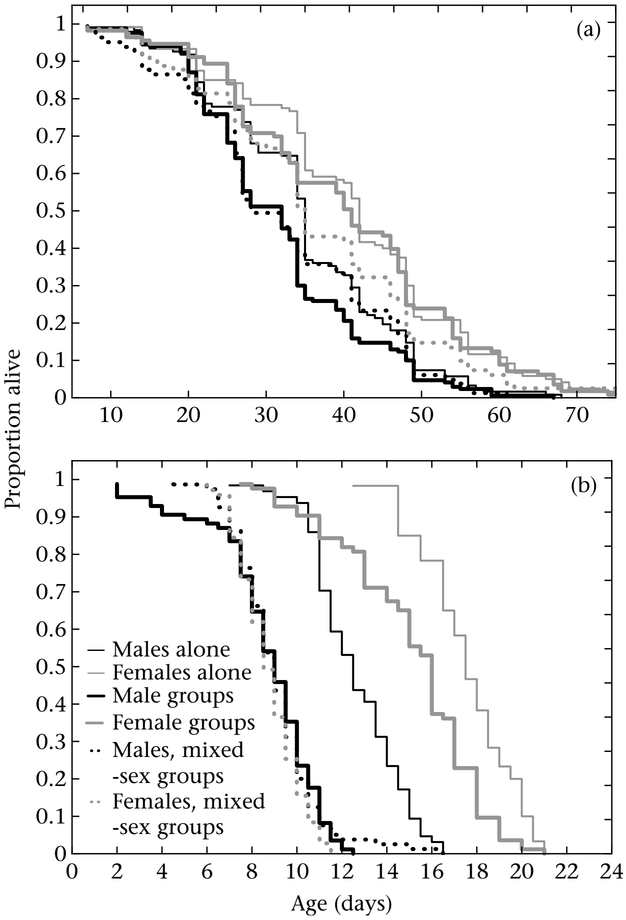

Figure 1. Survival curves for (a) *P. xanthostoma* and (b) *C. maculatus* in different experimental treatments.

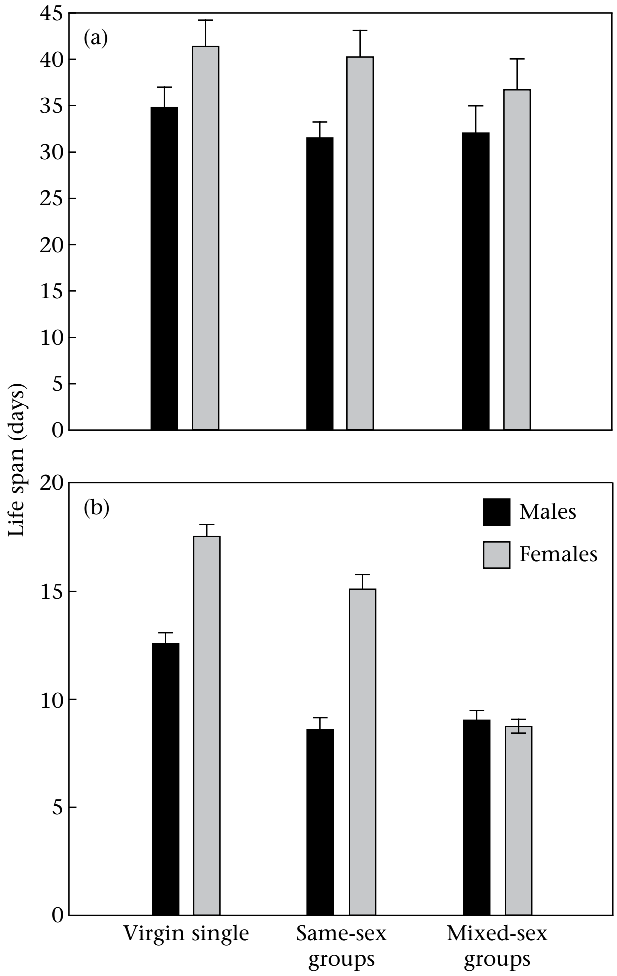

Figure 2. Mean life span + SE in (a) *P. xanthostoma* and (b) *C. maculatus* in different experimental treatments.

densities. None the less, the costs of female–female interactions appear to be negligible compared with the costs of heterosexual courtship and mating. In *C. maculatus*, females kept in groups suffered an 11.2% reduction in life span compared with females kept alone (Fig. 2, Table 1), suggesting that there is some cost to female–female interactions in this species. This may be because, while *C. maculatus* females do not perform agonistic interactions such as fighting, they do engage in female–female mounting (A. Maklakov, personal observations). However, homosexual interactions had a much smaller effect on female survival than on male survival in *C. maculatus* (Fig. 2).

We have shown that male homosexual interactions substantially reduce survival, and the magnitude of this reduction is comparable with the full costs of reproduction in two very different species of insects. In contrast, the costs of female homosexual interactions are negligible (*P. xanthostoma*) or small (*C. maculatus*) compared with the costs of heterosexual interactions. Despite a long-standing interest in the evolution of homosexual interactions in animals, the costs associated with homosexual interactions are almost never quantified and are generally assumed to be low (Aiken 1981). These results strongly suggest a need to quantify the costs of homosexual interactions in the same way that researchers routinely quantify costs of reproduction when studying the evolution of mating strategies. Our findings are also consistent with the expectation that expression of costly homosexual behaviour is reduced in females, compared with males.

Table 1

Survival analysis results for beetles (*Callosobruchus maculatus*) and flies (*Prochyliza xanthostoma*) under contrasting social conditions

Comparison	Beetles		Flies (all data)		Flies (to 28 days)	
	TS	*P*	TS	*P*	TS	*P*
M versus M-M	4.67	**<0.0001**	2.81	**0.005**	2.74	**0.006**
M versus M(F)	4.67	**<0.0001**	1.45	0.15	2.68	**0.007**
M-M versus M(F)	−0.15	0.88	−1.45	0.15	0.31	0.76
F versus F-F	3.21	**0.001**	1.02	0.31	1.23	0.22
F versus F(M)	4.52	**<0.0001**	2.19	**0.029**	1.70	0.088
F-F versus F(M)	4.52	**<0.0001**	0.85	0.39	0.56	0.57
M versus F	−10.37	**<0.0001**	−4.088	**<0.0001**	−4.088	**<0.0001**
M-M versus F-F	−4.67	**<0.0001**	−4.97	**<0.0001**	−3.26	**0.001**
M(F) versus F(M)	1.58	0.11	−2.23	**0.026**	−2.24	**0.025**

M = single, virgin males; M–M = virgin males in pairs/groups; M(F) = males housed with females; F = single females; F–F = virgin females in pairs/groups; F(M) = females housed with males. Cox–Mantel test statistics (TS) are shown, with corresponding *P* values. For flies, results are shown for both the entire range of life spans, and for the first 28 days (i.e. prior to separation of paired individuals). Significant results are shown in bold.

Conclusions

Our results reinforce the need to study behavioural and life history traits in the context of the environment in which they evolve. Whereas the costs of sexual behaviours such as courtship and mounting are typically quantified in heterosexual interactions, our results suggest that the actual costs of these behaviours will vary depending on social and ecological conditions such as the adult sex ratio, because a substantial fraction of the net cost may reflect behaviours directed at same-sex individuals. Although some behaviours directed at same-sex individuals (such as combat in *P. xanthostoma*) may function in sexual competition, other behaviours (such as homosexual mounting in *C. maculatus* and homosexual courtship in *P. xanthostoma*) appear to be nonadaptive consequences of relatively indiscriminate responses by males. Thus, the net costs and benefits of such behaviours may depend on the relative frequencies of heterosexual and homosexual encounters, and these costs may influence the evolution of male behaviours.

Furthermore, our results have interesting implications for the evolution of sex differences in life span. Sexual dimorphism in life span is widespread, and is often suggested to result from differential costs of reproduction between the sexes (Trivers 1972; Liker & Szekely 2005). In this study, we experimentally manipulated reproductive opportunities in *C. maculatus*, where sexual dimorphism in life span is commonly observed (Fox et al. 2003, 2004; Maklakov et al. 2007), as well as in *P. xanthostoma*. In *C. maculatus*, virgin males' life spans were 28% shorter than virgin females' life spans and the difference increased to 42% when animals were kept in homosexual cohorts. In contrast, we found no evidence for sexual dimorphism in life span when males and females were provided with the opportunity to reproduce (i.e. kept in mixed-sex groups).

Thus, in both species, sexual dimorphism in life span was strongly dependent on social conditions: isolated virgin females lived much longer than males, and dimorphism was even greater when flies were maintained in same-sex groups. However, dimorphism all but disappeared when the sexes could interact and reproduce. This suggests that, despite the potential to live longer, females actually have similar mortality rates to males under normal reproductive conditions, and selection acts similarly on survival (and, perhaps, ageing rate) in the sexes. Thus, sexual dimorphism in life span commonly observed in studies of virgin cohorts may be an indirect by-product of sex differences in other life history traits (e.g. resource acquisition), as well as in sexual behaviour, rooted in sex-specific reproductive strategies (Bilde et al. 2009).

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References

Aiken, R. B. 1980. The role of acoustic signalling in the aggregating and mating behaviour of *Palmacorixa nana* Walley (Heteroptera: Corixidae). Ph.D. thesis, University of Toronto.

Aiken, R. B. 1981. The relationship between body-weight and homosexual mounting in *Palmacorixa nana* Walley (Heteroptera, Corixidae). *Florida Entomologist*, **64**, 267–271.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Bagemihl, B. 1999. *Biological Exuberance: Animal Homosexuality and Natural Diversity*. New York: St Martin's Press.

Bilde, T., Maklakov, A. A., Meisner, K., la Guardia, L. & Friberg, U. 2009. Sex differences in the genetic architecture of lifespan in a seed beetle: extreme inbreeding extends male lifespan. *BMC Evolutionary Biology*, **9**, 33.

Bonduriansky, R. 2003. Layered sexual selection: a comparative analysis of sexual behaviour within an assemblage of piophilid flies. *Canadian Journal of Zoology*, **81**, 479–491.

Bonduriansky, R. & Rowe, L. 2003. Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. *Evolution*, **57**, 2046–2053.

Bonduriansky, R., Wheeler, J. & Rowe, L. 2005. Ejaculate feeding and female fitness in the sexually dimorphic fly *Prochyliza xanthostoma* (Diptera: Piophilidae). *Animal Behaviour*, **69**, 489–497.

Cordts, R. & Partridge, L. 1996. Courtship reduces longevity of male *Drosophila melanogaster*. *Animal Behaviour*, **52**, 269–278.

Crudgington, H. S. & Siva-Jothy, M. T. 2000. Genital damage, kicking and early death: the battle of the sexes takes a sinister turn in the bean weevil. *Nature*, **407**, 855–856.

Edvardsson, M. & Tregenza, T. 2005. Why do male *Callosobruchus maculatus* harm their mates? *Behavioral Ecology*, **16**, 788–793.

Fang, J. M. & Clemens, L. G. 1999. Contextual determinants of female-female mounting in laboratory rats. *Animal Behaviour*, **57**, 545–555.

Fox, C. W., Hickman, D. L., Raleigh, E. L. & Mousseau, T. A. 1995. Paternal investment in a seed beetle (Coleoptera: Bruchidae): influence of male size, age, and mating history. *Annals of the Entomological Society of America*, **88**, 100–103.

Fox, C. W., Dublin, L. & Pollitt, S. J. 2003. Gender differences in lifespan and mortality rates in two seed beetle species. *Functional Ecology*, **17**, 619–626.

Fox, C. W., Bush, M. L., Roff, D. A. & Wallin, W. G. 2004. Evolutionary genetics of lifespan and mortality rates in two populations of the seed beetle, *Callosobruchus maculatus*. *Heredity*, **92**, 170–181.

Fricke, C. & Maklakov, A. A. 2007. Male age does not affect female fitness in a polyandrous beetle, *Callosobruchus maculatus*. *Animal Behaviour*, **74**, 541–548.

Gastal, M. O., Gastal, E. L., Beg, M. A. & Ginther, O. J. 2007. Elevated plasma testosterone concentrations during stallion-like sexual behavior in mares (*Equus caballus*). *Hormones and Behavior*, **52**, 205–210.

Harari, A. R., Brockmann, H. J. & Landolt, P. J. 2000. Intrasexual mounting in the beetle *Diaprepes abbreviatus* (L.). *Proceedings of the Royal Society of London, Series B*, **267**, 2071–2079.

Kotiaho, J. S. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews*, **76**, 365–376.

Liker, A. & Szekely, T. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution*, **59**, 890–897.

Maklakov, A. A., Fricke, C. & Arnqvist, G. 2007. Sexual selection affects lifespan and aging in the seed beetle. *Aging Cell*, **6**, 739–744.

Martin, O. Y. & Hosken, D. J. 2004. Copulation reduces male but not female longevity in *Saltella sphondylli* (Diptera: Sepsidae). *Journal of Evolutionary Biology*, **17**, 357–362.

Parker, G. A. 1968. Sexual behaviour of blowfly *Protophormia terrae-novae* R-D. *Behaviour*, **32**, 291–308.

Perneger, T. V. 1998. What's wrong with Bonferroni adjustments? *British Medical Journal*, **316**, 1236–1238.

Roff, D. A. & Fairbairn, D. J. 2007. The evolution of trade-offs: where are we? *Journal of Evolutionary Biology*, **20**, 433–447.

Rönn, J., Katvala, M. & Arnqvist, G. 2007. Coevolution between harmful male genitalia and female resistance in seed beetles. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 10921–10925.

Rup, P. J. 1986. Mating and its attendant behaviour in *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). *Journal of Stored Products Research*, **22**, 77–79.

Savalli, U. M. & Fox, C. W. 1999. The effect of male mating history on paternal investment, fecundity and female remating in the seed beetle *Callosobruchus maculatus*. *Functional Ecology*, **13**, 169–177.

Serrano, J. M., Castro, L., Toro, M. A. & Lopez-Fanjul, C. 1991. The genetic properties of homosexual copulation behavior in *Tribolium castaneum*: diallel analysis. *Behavior Genetics*, **21**, 547–558.

Serrano, J. M., Castro, L., Toro, M. A. & Lopez-Fanjul, C. 2000. Inter- and intraspecific sexual discrimination in the flour beetles *Tribolium castaneum* and *Tribolium confusum*. *Heredity*, **85**, 142–146.

Sommer, V. & Vasey, P. L. 2006. *Homosexual Behaviour in Animals: an Evolutionary Perspective*. Cambridge: Cambridge University Press.

Srivastava, A., Borries, C. & Sommer, V. 1991. Homosexual mounting in free-ranging female Hanuman langurs (*Presbytis entellus*). *Archives of Sexual Behavior*, **20**, 487–512.

Stearns, S. C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.

Switzer, P. V., Forsythe, P. S., Escajeda, K. & Kruse, K. C. 2004. Effects of environmental and social conditions on homosexual pairing in the Japanese beetle (*Popillia japonica newman*). *Journal of Insect Behavior*, **17**, 1–16.

Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.

Trivers, R. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Van Gossum, H., De Bruyn, L. & Stoks, R. 2005. Reversible switches between male-male and male–female mating behaviour by male damselflies. *Biology Letters*, **1**, 268–270.

Vasey, P. L. 1995. Homosexual behavior in primates: a review of evidence and theory. *International Journal of Primatology*, **16**, 173–204.

Vasey, P. L., VanderLaan, D. P., Rains, D., Duckworth, N. & Kovacovsky, S. D. 2008. Inter-mount social interactions during heterosexual and homosexual consortships in Japanese macaques. *Ethology*, **114**, 564–574.