



Experimental quantification of genetic and ontogenetic effects on fighting behavior in the broad-horned flour beetle

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Abstract

Most animal behaviors show large within- and among-individual variation, and this includes competitive male behaviors. With male fighting for example, aggressiveness often correlates with dominance, and contest duration varies with age. However, few studies have directly quantified how mean aggressiveness and contest duration, the variation among individuals in both traits, and the relationship among them, vary with age. Here we address these gaps and examine the effect of male age and genotype on two key aspects of male fighting behavior - aggressiveness (here measured as latency to fight) and contest duration - and the relationship between them. We do this using isogenic lines of the broad-horned flour beetle *Gnatocerus cornutus*. We observed fighting behavior of paired males of similar body size and age. Using uni- and multivariate mixed models, we show that although there was a significant difference between younger and older males in contest duration, mean aggressiveness was not affected by male age. However, the variation in aggression and fight duration varied with age, being greater in younger and older males respectively. Additionally, although there was a positive correlation between aggressiveness and contest duration in younger males, this relationship was not found in older males. Finally, the only significant genetic effect was for aggression in younger males. Our study shows that age differentially shapes key components of male fighting behavior as well as the relationship among them, highlighting the dynamic nature and context-dependence of fighting.

Significance statement

We examined the effect of male age and genotype on two key aspects of male fighting behavior - aggressiveness (here measured as latency to fight) and contest duration - and the relationship between them. Importantly, we provide statistical methods that enable untangling these effects that will be useful to others. We used isogenic lines of the broad-horned flour beetle *Gnatocerus cornutus*, and observed fighting behavior of paired males of similar body size and age. We show that age differentially shapes key components of male fighting behavior as well as the relationship among them, and only find genetic effects for aggression in younger males. These novel results highlight the context dependent nature of fighting.

Keywords Male-male contest · Contest · Aggressiveness · Aging · Genetics · Beetle

Introduction

One behavior frequently correlated with male fitness is fighting (Darwin 1871; Andersson 1994; Emlen 2008; Thornhill and Alcock 2013). In many animals, males fight for access to resources, including females (mating opportunities), and winning contests increases male reproductive success. More aggressive males engage in contests faster or more often (Benus et al. 1991; de Boer et al. 2003), but the duration of each fight will depend on an individual's cost threshold – the point at which costs can no longer be met (Taylor and

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Elwood 2003). Males with lower cost thresholds will fight for less time and are defeated more quickly than males with higher thresholds, who are more persistent in contests (Taylor et al. 2001; Prenter et al. 2006). Aggression and fight duration can also depend on the value of the resource being fought over, with extended and escalated contests more likely with more valuable resources (Batchelor and Briffa 2010). However, because greater aggressiveness and longer contest duration increase the risk of injury, and are costly in time and energetic terms (Glass and Huntingford 1988; Kelly and Godin 2001; Briffa and Elwood 2005), the balance between the benefits of winning and cost of continued fighting should determine optimal male fighting behavior (Smith and Parker 1976; Parker and Smith 1990). In addition to these intrinsic (e.g. cost threshold) and extrinsic (e.g. resource value) individual-level sources of variation in fighting behavior, elements of fighting represent a shared-phenotype, with both fighting behavior and fight outcomes for the focal individual being dependent on the opponent and its behavior (Lane et al. 2020).

Like other behaviors, the costs and benefits of male fighting are expected to vary with age. Hence the shape of the trade-offs between reproduction and survival, and between current and future investment, will vary with age (Rose 1991; Arking 1998; Hillesheim and Stearns 1992; Grotewiel et al. 2005)- and this variation may be adaptive. For example, fighting may be more costly in younger males because of their greater future reproductive potential (a phenomenon also called the “asset protection” principle). Hence, older males may have a higher individual cost threshold than younger males, and as a result, older males could fight for longer or start fights sooner (Kemp 2006), placing them at an advantage when facing younger counterparts.

Furthermore, resource holding potential (RHP) (the ability to win fights: Parker 1974) or the value of the resource to the individual may increase with age (Harley et al. 1994). In northern elephant seals (*Mirounga angustirostris*), for example, older males have higher win rates in male-male fights than younger males (at least for a period in their mature adulthood), indicating that they have acquired the necessary means for winning contests (i.e., large body size). While this could be part of an overarching life history strategy, it ultimately is age-related variation in RHP that decides contest outcome (Kemp 2000, 2002). Similarly, older male broad-horned flour beetle *Gnathocerus cornutus* win more fights, which suggests resource value or fighting ability increases with age (Okada et al. 2020). Alternatively, older males may have lower resource holding potential as performance declines with age, and hence younger males could be more aggressive (Kemp 2006). It should however be noted that the estimated effect of age will depend on definition of ‘young’ and ‘old’.

Behaviors are often correlated and repeatable within individuals (Sih et al. 2004; Réale et al. 2007). For example, in the wild boar (*Sus scrofa*), more aggressive males more readily engage in a contest and fight more frequently (Bouhuis et al. 2005; Camerlink et al. 2015) and for longer (Camerlink et al. 2015) than less aggressive males. If behaviors vary with age, then the correlations among these behaviors could also vary with age. However, few studies have investigated how correlations among different fighting behaviors, such as the relationship between aggressiveness and contest duration, vary with age.

Here we quantified the effect of age on aggressiveness, defined as the latency to start a fight, and fight duration in *G. cornutus*. These beetles use their enlarged mandibles to engage in fights over access to females and males that win fights secure matings (Okada et al. 2006). When placed in a small container, males use their well-developed mandibles against other males, even in the absence of females (Okada et al. 2006). Typically the larger male wins the fight, and the losing males flees the fighting area and becomes non-aggressive for four days (Okada and Miyatake 2010). Previous work has found that while older males are more likely to win fights, they do not start fights earlier or fight for longer (Okada et al. 2020). However, whether the relationship between latency and duration of male-male fighting varies with age has not been investigated previously, and little is known about the genetic basis of fighting behavior or fight outcome.

Isofemale lines, effectively representing distinct genotypes, are commonly used to investigate the genetic basis of traits (Hoffmann and Parsons 1989; David et al. 2005), especially when avoiding breaking naturally occurring linkage patterns (Hosken and Wilson 2019), and for replicating genotypes to allow for repeated testing without confounding prior experience with the question of interest (e.g., Ingleby et al. 2013). Here we used isolines to test for the role of genetic variation in shaping variation in fight latency and duration, and test for genetic associations between these components of fighting behavior (cf. Matsumura et al. 2020). Additionally, while Okada et al.’s (2020) ‘old’ males were 105 days old, here our ‘old’ males were 50 days old. At this age (50 days) selective disappearance – the loss through death of certain phenotypes which can be problematic in studies of age effects (Bouwhuis and Vedder 2017) is not likely as the maximum lifespan of the beetles is about 140 days in the lab and beetle death rates are low before 50 days old. Hence it is unlikely that the ‘old’ sample in our study contains a subset of only highly performing genotypes (for further discussion of selective disappearance, see Bouwhuis and Vedder 2017). We measured time to contest commencement (fight latency) as aggressiveness (Camerlink et al. 2015) - more aggressive individuals start a fight sooner - and contest duration

as a measure of an individual's cost threshold. We reasoned that older males should invest more in male-male combat than younger males, and hence predicted that older males would show greater aggressiveness and longer contest duration (Kemp 2006). Furthermore, we expected that the relationship among fighting behaviors would vary with age, like many other behaviors (e.g., MacNulty et al. 2009), with young males having a longer latency to fight and shorter fight duration.

Materials and methods

Insects and culture

The stock population of *G. cornutus* used in this study has been maintained in the laboratory for over 50 years. Animals were reared in incubators under 16 L:8D light conditions (7:00 light on, 23:00 light off) at 25°C. We used a mixture of whole grain flour and beer yeast (19:1) as food. Last instar larvae were collected from laying pots and placed individually into 24-well plates to allow pupation. When the pupae hatched, we fed the adult beetles and reared them as described above until the start of the experiment. In this study, we used 18 iso-female lines established from the stock population (Matsumura et al. 2020). Initially, 18

males and 18 females were selected at random and paired. Subsequently, full-sib matings within each family were used to propagate each line for over 40 generations until the present study was conducted. Isolines represent distinct genotypes, and the variation among isolines can therefore provide insight into the genetic variation underlying various characters among individuals in the base population that these lines were derived from (Hoffmann and Parsons 1989). Previous work has shown these isolines capture significant genetic variation (e.g. Matsumura et al. 2020).

As a measure of body size, we used mid-prothorax width (± 0.01 mm) of males using the dissecting microscope monitoring system (see Fig. 1, in Okada and Miyatake 2009). To remove the confounding effect of body size (Okada et al. 2006), opponents' body sizes were matched. In this study, we used 10-day old ('young') and 50-day old ('old') males. We chose 50 days to minimize problems associated with selective disappearance that can significantly impact studies of aging effects (e.g., Curio 1983; Bouwhuis and Vedder 2017). Our beetles live on average about 110 days, and 50 days represents about half their average lifespan (see Methods). Most individuals (> 97%) survive to this age (S. Nishitani personal observation; and see Okada et al. 2020). Thus, although strictly 50 days should be referred to as middle-aged, here we will refer to them as 'old' to distinguish them from the 10-day old 'young' males.

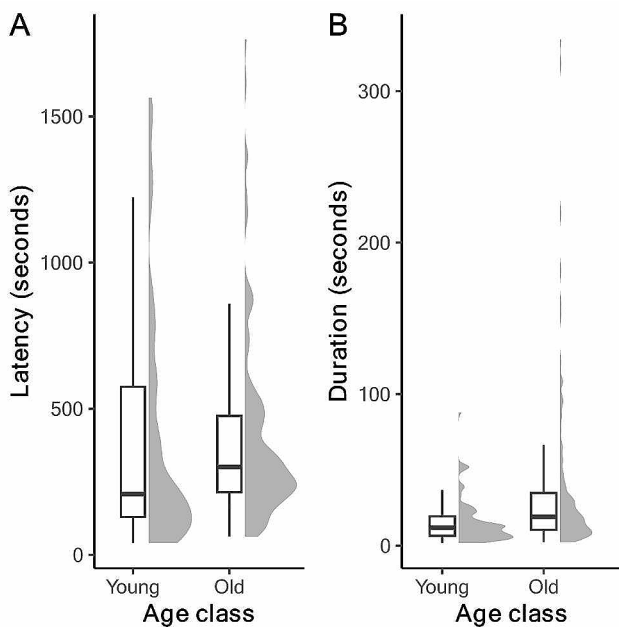


Fig. 1 Effects of male age on the latency (A) and duration (B) of fighting in *G. cornutus*. While male age did not affect how long it took for fights to begin, it did affect the duration of fights, with older males fighting for longer. Furthermore, the variance in latency was smaller in older males, whereas the variance in duration was larger among older males

Fighting behavior

Only males with no fighting experience were used in the experiment. An individual's fighting ability depends on the phenotype of its opponent (Lane et al. 2020), and experimentally there is no perfect solution to this dependency – neither random opponent allocation nor the use of standardized opponents are perfect solutions to this social-environment effect, especially when fighting outcomes are non-transitive. Here we chose to fight males against opponents from the same age and isoline as themselves. That is, each male fought against a genetically identical opponent of the same age. To control for the effect of body size on fighting success, males were paired so that the difference in body size between contestants was less than 0.01 mm (Okada and Miyatake 2010). Thus, males were both phenotypically and genetically matched.

Two males were simultaneously placed on a sheet of filter paper in a well (17 mm diameter, 20 mm high) of 48-well plate (Cell Star, Greiner Bio-One, Kremsmünster, Austria). Trials were then continuously monitored until fight outcomes could be scored. In the present study, we defined the winner and loser following methods described in Okada and Miyatake (2009); the winner was the male that pushed his opponent out of the fight site and chased him. The loser

was the male that retreated from the fight site (Okada et al. 2006). We analysed the latency of the contest (i.e., how long it took before the two males initiated a fight: aggression) and the contest durations (i.e., time from first attack to the end of fighting). Trials lasted up to 30 min. We observed 3–10 pairs from each isoline (total; 10 days old: $n=87$ pairs, 50 days old: $n=128$; see supplementary Table 1). All observations were conducted in a room maintained at 25 °C between 12:00 to 19:00.

Statistical analyses

We tested for differences in mean latency and duration between young and old males in separate univariate generalised linear mixed models. Latency and duration measure the time elapsed until the start and the end of a fight, respectively, and are positive non-integer values that show a right-skewed distribution (Fig. 1). We therefore assumed a Gamma distribution and used a log link function using the `glmer` function in the R package `lme4` 1.1–31 (Bates et al. 2015) in R 4.2.2 (R Core Team 2017). Separate models with age as a categorical fixed effect and isoline as a random effect were fitted to both latency and duration. The statistical significance of the fixed effect of age class on both traits was based on a likelihood-ratio test.

Second, we fitted four separate trait- and age-specific models to obtain trait and age-specific estimates of the variance among versus within isolines, again using generalised linear mixed models with isoline as a random effect. The proportion of variance explained by isoline in each of the four ‘traits’ (latency and duration at young and old age) was calculated following Nakagawa et al. (2017): The variance explained by isoline was divided by the sum of the variance explained by isoline and the residual (or observation-level) variance, and the latter was obtained using the `trigamma` function. P -values for the variances explained by isoline were based on likelihood ratio tests and halved following Self and Liang (1987).

Third, we tested if the variance components estimated by these univariate models differed significantly between age classes using two bivariate mixed models in ASReml-R v 4.1.0.176 (Butler 2022), with either the latency for young and old males, or the duration for young and old males, as the two response variables. We used likelihood-ratio tests to compare models that estimate age-specific variances to models in which these have been constrained to be identical. At this stage, we did not model any correlations among traits. Because at the time of writing ASReml-R cannot fit multivariate models with more than one non-Gaussian trait (Salvador Gezan, VSN Support, pers. comm.), we used log-transformed traits and Gaussian error families for these models. Although we can therefore not directly compare the

multivariate variance components to those estimated above, they were found to be qualitatively similar to those provided by the univariate Gamma models.

Fourth, we estimated the correlations between latency and duration in both age classes, again within and across isolines, within a single multivariate model. To test if each correlation was significantly different from zero, we compared this unconstrained model to a model in which the correlation was constrained to zero. This was complemented by a test if these correlations differed from each other (i.e., among age classes), by comparing the full model to a model in which correlations were constrained to be identical. Because for each male we have a measurement of latency and duration only for a single age class, the within-line correlations between age classes (e.g., latency young versus old) are not estimable and were therefore always constrained to zero.

Ethical note

For the experiments on fighting behavior, the insects were reared and tested in a manner that did not stress them according to Guidelines for the ethical treatment of nonhuman animals in behavioral research and teaching. The experimental animals used were bred in captivity. The rearing cages were managed in the same manner as in previous studies, and we did not induce any pain.

Results

The mean latencies to engage in a fight (i.e., aggressiveness) for young and old males were 399 s and 395 s, respectively, and were not significantly different from each other ($b \pm \text{s.e.} = 0.038 \pm 0.108$, $\chi^2_1 = 0.13$, $P = 0.72$; Fig. 1A). However, on average fights between young males were significantly shorter than fights between old males (15.8 and 36.7 s, respectively; $b \pm \text{s.e.} = 0.81 \pm 0.13$, $\chi^2_1 = 35.6$, $P < 0.001$; Fig. 1B). Note that model estimates are on the log-link scale.

As illustrated in Fig. 1, there is a large amount of variation in both latency and duration within both age classes, and the variance in (log-transformed) fight latency and duration differs significantly between both age classes. Whereas the variance in log-transformed latency measured in seconds is significantly higher among young males (1.00) than among old males (0.46; $\chi^2_1 = 15.8$, $P < 0.001$), the variance in fight duration is significantly lower among young males (0.68) compared to old males (1.05; $\chi^2_1 = 4.6$, $P = 0.032$).

Of the variance in latency among young males, a statistically significant 18% was attributable to isoline ($\chi^2_{0/1} = 8.5$, $P = 0.002$). In contrast, the variance explained by isoline was much smaller and non-significant for the latency of

old males (3%; $\chi^2_{0/1}=0$, $P=1$), and the duration of fights between either young (5%, $\chi^2_{0/1}=0$, $P=1$) or old males (7%, $\chi^2_{0/1}=2.7$, $P=0.051$).

As there is only evidence for variation among isolines for fight-latency in young males, and maybe duration in old males, among-line correlations (genetic correlations) between (log-transformed) age-specific latency and duration are not estimable. Looking within lines (testing for phenotypic correlations), there was a statistically significant positive correlation between log-transformed latency and duration in young males (Fig. 2A: $r \pm \text{s.e.} = 0.32 \pm 0.10$, $\chi^2_1=8.9$, $P=0.003$). The correlation was much weaker and non-significant in older males (Fig. 2B: $r \pm \text{s.e.} = 0.025 \pm 0.089$, $\chi^2_1=0.08$, $P=0.78$), and significantly weaker than the correlation in young males (Fig. 2B: $\chi^2_1=4.7$, $P=0.031$).

Discussion

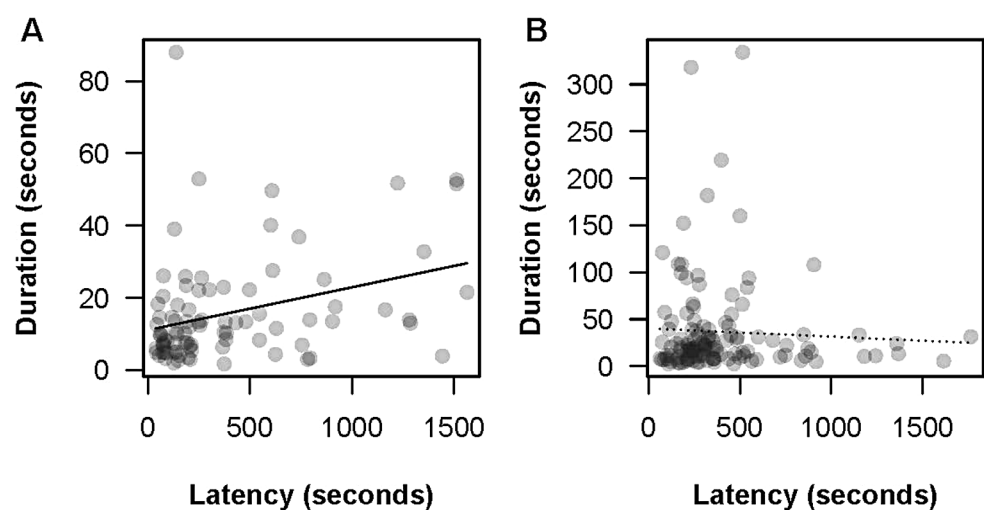
There have been few investigations into the impact of age on fighting behaviors and the within-individual associations between fighting behaviors. We tested for such effects here using horned flour-beetle isolines. Our main findings were that age affected contest duration, with older males fighting for longer, but there were no effects of age on aggression - the time it took for individuals to engage in a fight (fight-latency). We also found limited effects of genotype, with fight latency at young age being the only trait with substantial genetic variation, and it was only at young age that we saw phenotypic correlations between fight latency and duration. We discuss these findings in turn.

Older males fought for longer than younger males and there was more variation in the duration of their contests. This is broadly consistent with theoretical predictions that a “late-hawk” strategy (act more aggressively at old age)

is common across broad contest-model parameter space (Kemp 2006). A possible reason for the mean duration increasing with age is that the threshold at which an individual stops competing – the individual cost threshold – of older males is higher as they will have fewer opportunities to engage in future reproductive competitions (and beetles fight for access to females). That is, the opportunity costs of fighting are lower for older males, and they hence value winning current fights more than younger males. Life history theory predicts increased investment in current activities as future investment opportunities decline (Stearns 1992), and this prediction has empirical support (Magnhagen and Vestergaard 1991; Candolin 1998; Poizat et al. 1999; Kemp 2002). Our results are broadly consistent with this fundamental conjecture, and with findings for female wasps (*Goniozus nephantidis*). In this species, older females win fights over prey-items, presumably because they value winning more (Humphries et al. 2006).

Not all studies find age effects on contest duration (e.g., Lee et al. 2014). For example, previous work with *G. cornutus* did not find a difference between young and old male fight durations, although it did find that older males win more fights (Okada et al. 2020). Okada et al. (2020) however used males that were significantly older than the old males we used here, and opponents were selected at random and not from the same isoline as in the present study (also see Brandt 1999). If there was selective disappearance during aging (Bouwhuis and Vedder 2017), the former could account for differences between the two studies, with for example only superior genotypes living to very advanced age and winning more fights without having to fight for longer (Okada et al. 2020). Alternatively, our male-matching protocol (males fought with related same-age and -sized males (i.e. from the same isoline) may have impeded detection of age effects because males probably had very similar resource holding potential. Investigating the importance

Fig. 2 Relationship between latency and duration of fighting in *G. cornutus* in young (A) and old (B) males. Note that for illustrational purposes, each point shows an individual, but all statistical analyses account (control) for any variation among lines



of asymmetric resource holding potential is something for future consideration. Close ability matches often leads to longer fights (Austad 1983, Jonart et al. 2007), and there is a positive relationship between relatedness and fight duration in anemones (Lane et al. 2020). This, coupled with age differences in future opportunities/value of winning (Stearns 1992), probably explains why we revealed a difference not previously detected (Okada et al. 2020).

It is not entirely clear why there was greater variation in fight duration in older males. If older males had experienced (more) previous fights, this would provide one explanation for the difference, but the beetles used here had no previous exposure to fighting. It may be that within-individual variation generally increases over time because of stochastic environmental or mutational effects and that explains the increased variance in older males. Be that as it may, this would not explain the opposite effect noted for aggressiveness (latency to fight), which did not vary with age, but the variance in aggression was greater in younger males. This average effect is consistent with previous work on *G. cornutus* that found that the likelihood of fight initiation did not vary with age (Okada et al. 2020; also see Okada et al. 2019), but deviates from our *a priori* expectations – we expected aggression to also increase with age for the reasons outlined above with respect to fight duration (and see e.g., predictions from Kemp 2006). One possibility is that aggressiveness is independent of resource holding potential and/or resource value. In wild boar, aggressiveness does not affect the outcome of a contest (Camerlink et al. 2015), which is consistent with the absence of an association between the value of aggression and/or fighting ability. However, other studies have shown that measures of aggression are correlated with estimated resource holding potential and other factors, like stage of the breeding cycle (e.g., Jonart et al. 2007). In any case, we see no effect of age on aggression, mirroring work with burying beetles *Nicrophorus vespilloides* (Lee et al. 2013). Whether this is a general pattern and precisely why there was no effect remains to be established. Additionally, the greater variation in aggression in younger males may reflect variation in how well they had been able to accrue and assimilate resources, with older males all having had sufficient time to accumulate what they need, resulting in lower variation in aggression. It is worth noting that our methods mean selective disappearance (Bouwhuis and Vedder 2017) is unlikely to explain the reduction in variation we see at older age. In the present study, no individuals were assayed as both young and old males, and so age-associated changes in contest behavior were not explicitly measured. This would be an interesting area for future study.

A significant positive non-genetic association (i.e., within lines) between aggression and duration of fighting was found in younger, but not older males. Thus, at young age, fighting behavior is phenotypically integrated to an extent – and could be thought of as a young-male behavioral syndrome (Briffa et al. 2015) – but the association breaks down at older age. This pattern mirrors that seen in hermit crabs *Pagurus bernhardus* where aggression correlates with other behaviors in some (environmental) conditions, but not others (Mowles et al. 2012). Similarly, in fallow deer (*Dama dama*) individuals vary in the consistency of their fighting behaviors (Jennings et al. 2013). The lack of an association between aggressiveness and contest duration in older males also reflects findings in wild boar (Camerlink et al. 2015). There it was assumed that because aggressive males fight more frequently (Bolhuis et al. 2005; Camerlink et al. 2015), they decrease investment in any single contest to avoid risks and contest costs. Thus, aggressive males may abandon a contest quickly even if they initiate them more frequently. Importantly and as noted above, aggressiveness does not predict fight outcomes in boar (Camerlink et al. 2015). The difference between young and old males is a clear indication that behavioral associations can change over time and context (cf. Briffa et al. 2015). However, relatively few studies have reported the disappearance of a behavioral correlation with age, so the generality (or not) of this pattern, is not clear.

There is more clarity on the effects of age on the likelihood of winning fights. In the brown butterfly *Melanitis leda*, male winning rates decrease with age (Kemp 2003), suggesting resource holding potential decreases with age in this species. On the other hand, in the northern elephant seal, older males win more contests, indicating that male resource holding potential increased with age (Haley et al. 1994), possibly due to positive effects of accumulated contest experience with aging. Indeed, many previous studies could not separate the effects of experience from aging per se (see Kemp 2002). Previous work on flour beetles (Okada et al. 2020), however, found older naive males with no previous fighting experience won more fights. Similarly, as males in our study had not engaged in fighting before, the age effects we find are not confounded by experience. Further studies are needed to disentangle experience and age effects on fighting behavior, and their role in shaping variation in age effects among species.

We found effects of genotype on aggression (fight latency) at young age, with genotype explaining about a fifth of the variation in aggression in young males. Other studies have also found direct and indirect genetic effects on elements of fighting behavior (e.g., Lane et al. 2020).

However, the genetic effect we documented was not evident at older age, and in neither age classes was there a genetic effect on fight duration. Again, this reflects findings reported elsewhere (e.g., Simon et al. 2006; Shefferson et al. 2017; Lane et al. 2020), and studies in many systems find changes in genetic contributions to phenotypic variation with age (e.g., Coulson et al. 2006; Nussey et al. 2008). It is interesting that in an experimental evolution study of loser effects, fighting success did not evolve (Okada et al. 2019), which is consistent with our finding of limited genetic variation in fighting behavior. Additionally, the lack of genetic variation in fight duration at all ages means that the two behaviors we measure here (duration and latency) are not genetically correlated (or only very weakly so). Finally, we found no evidence for genetic trade-offs between early- and late-age performance, which again, is not without precedent (Nussey et al. 2008), but we note again there was a phenotypic association between aggression and fight duration at young age.

In summary, we find limited genetic variation for fighting behavior, and the significant genetic effect we did detect disappeared with age. Additionally, there were only effects of age on the duration of fighting, with male aggression being similar in young and old males. These findings are not in line with general theoretical predictions (e.g., Kemp 2006) of significant general effects of age coupled with specific effects of age on other male sexually-selected characters (e.g., Tidière et al. 2017). Future work should focus on disentangling the effects of aging and experience, to gain a more general view of the effects of age on fighting behavior in this and other species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-024-03451-w>.

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Author contributions KM, MD and TM conceived and designed the study. TN and KM performed the experiment and KM, EP and DJH data analyses. KM, TM, EP and DJH contributed to the interpretation of data, and drafted the manuscript. All authors approved the final version and agree to be accountable for the content therein.

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Data availability All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declarations

Competing interests We declare that we have no competing interests.

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