



Life history of aggression: effects of age and sexual experience on male aggression towards males and females



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Aggression is a prominent behaviour well studied in a large variety of animals, but it has not been well integrated within life history research. To address this shortcoming, we conducted a series of experiments simultaneously quantifying the effects of age and sexual experience on the use of aggression in male fruit flies. We studied three types of aggression relevant to male fruit flies' natural history: fighting in the context of resource defence, forced copulation with newly eclosed females, and coercion of recently mated females. Young, sexually mature flies were initially reluctant to use aggression towards either males or females. Within a few days, however, their use of aggression increased and then plateaued. While sexual experience caused males to decrease aggression towards females, it did not affect their aggression towards males. It is likely that aggression involves some cost, which leads males to favour peaceful over aggressive pursuit of females. However, sexually experienced males are probably highly motivated to deter other males from their apparently attractive resource. Our results highlight the importance of studying multiple types of aggression and the need for careful assessments of the relative fitness benefits and costs of aggression versus peaceful alternatives in shaping the life history of aggression.

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Life history research has been instrumental in identifying key features characterizing animals as they go through the major life transitions of growth, reproduction and aging (Roff, 2002; Stearns, 1992). The major focus of life history studies has appropriately been on topics such as age and size at sexual maturity, the number and size of offspring, trade-offs between current and future reproduction, and senescence (Stearns, 1992). Although aggression is a prominent and well-studied animal behaviour (Hardy & Briffa, 2013; Nelson, 2005), it has received scant attention in life history research. Notable research on aggression includes extensive work on territorial fights in a variety of spider species (Elwood & Prenter, 2013; Riechert, 1986) and butterflies (Davies, 1978; Kemp, 2013), shell fights in hermit crabs, *Pagurus bernhardus* (Briffa & Elwood, 2001; Elwood & Neil, 1991), contests in red deer, *Cervus elaphus*, and other ungulates (Clutton-Brock, Guinness, & Albon, 1982; Jennings & Gammel, 2013), and violence in humans (Baron & Richardson, 2004; Daly, 2016; Daly & Wilson, 1988; Quetelet, 1833).

The two relevant life history models of aggression predict that younger males should be less willing to fight than older males. This is because younger males have a higher residual reproductive value than older males and can thus lose more from injuries (Kemp, 2006; Parker, 1974). Kemp (2006) noted, however, that young individuals should be more willing to fight under a narrow set of conditions where there is a steep decline in resource-holding potential with age and the benefit from holding a resource is relatively small. While the existing models are insightful, it is not clear how relevant they are to species that lack weapons. In such species, males cannot readily inflict injuries on their opponents, so the costs of fighting are not clear. Another limitation of the current models is that they do not consider a broad range of realistic population dynamics parameters, such as growth rate and density dependence, which strongly affect predictions of life history models (Abrams, 1993; Williams, Day, Fletcher, & Rowe, 2006). Indeed, although both Kemp (2006) and others (Hardy & Briffa, 2013; Huntingford & Turner, 1987) highlighted a general pattern of fighting tending to increase with male age in a variety of species, they also noted many exceptions. Two well-studied species in which peak aggression occurs in young rather than older males are the lizard *Anolis aeneus* (Stamps, 1978) and humans (Farrington, 1986; Reiss & Roth, 1993).

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While many studies reported on variation in aggression with age (reviewed in Hardy & Briffa, 2013; Huntingford & Turner, 1987; Kemp, 2006), most did not carefully account for correlates of age that can affect aggression. Such possible confounds include selective mortality (Huntingford & Turner, 1987), mating experience, as well as subtle effects of social housing conditions prior to tests. For example, if subjects are housed in groups, social interactions within the group might determine subsequent aggression. Another limitation of most studies of aggression is that they focus on a single context, most commonly male fighting associated with access to females. It is widely agreed, however, that aggression is not a unitary phenomenon (Huber & Kravitz, 2010; Moyer, 1968). Hence it is highly appropriate that we incorporate multiple, ecologically relevant types of aggression into routine research protocols.

To broaden our knowledge on the life history of aggression, we have adopted fruit flies (*Drosophila melanogaster*) as a model system and focused on three types of aggression. Several factors make fruit flies an ideal species for examining the life history of aggression. The flies are short-lived and cheap to maintain. Ethical difficulties are limited because the flies do not inflict injuries during fights. There are numerous tools for functional and mechanistic research in this species. Finally, fruit flies have recently been adopted for genetic and neurobiological research on aggression (Anholt & Mackay, 2012; Chen, Lee, Bowens, Huber, & Kravitz, 2002; Dierick & Greenspan, 2006; Edwards et al., 2009; Zhou, Rao, & Rao, 2008), which, combined with our evolutionary ecological approach, can help illuminate general features of aggression and its trajectory throughout life.

We focused on three realistic types of male aggression, fighting in the context of resource defence, forced copulation with recently eclosed (teneral) females, and coercion of recently mated females. In settings with small, dispersed fruit and low fly density, capable male fruit flies use aggression to monopolize the attractive patches that females seek for feeding and egg laying (Dow & Schilcher, 1975; Hoffmann, 1987; Markow, 1988). Resource-holding males also rely on aggression to guard females they have recently mated with (Baxter, Barnett, & Dukas, 2015a). By far, fighting in the context of resource defence has dominated the mechanistic literature on fruit fly aggression, although most papers refer to it as territorial aggression (Chen et al., 2002; Edwards, Rollmann, Morgan, & Mackay, 2006; Hoffmann, 1987).

In addition to the male–male aggression protocol, we also examined two types of male aggression towards females. Forced copulation with teneral females has been well characterized in the field and laboratory. Such forced copulation occurs primarily within 2 h post eclosion. During this short period, the vaginal plates of teneral females are still soft. Hence the females cannot physically resist intercourse by males that succeed in mounting them in spite of the females' persistent efforts to dislodge the males. We chose this type of aggression because it occurs at a sufficiently high frequency and thus can have significant effects on both male and female fitness (Dukas & Jongsma, 2012a, 2012b; Markow, 2000; Seeley & Dukas, 2011). While the role of coercion in the remating of recently mated females has not been well addressed, there is ample evidence that such rematings are more likely to occur at high male-to-female ratios, after long periods of persistent male mating attempts, and when females have no refuge from males (Byrne, Rice, & Rice, 2008; Gromko, Gilbert, & Richmond, 1984; Wigby & Chapman, 2004). These features are typically associated with convenience polyandry (Arnqvist & Rowe, 2005; Thornhill & Alcock, 1983), where females give in to males' persistent harassment and remate. We should note that aggression and forced copulation are typically discussed in distinct bodies of literature, so one might question whether it is appropriate to call forced copulation aggression. We feel, however, that when physical force is used by

one actor (the aggressor), which the other actor (the victim) attempts to evade, and when the aggressor inflicts injuries that reduce the expected life span of the victim (Dukas & Jongsma, 2012b), the term aggression is appropriate.

Overall then, we tested the effects of male age and mating experience on three types of aggression. The theoretical models suggest that, generally, male aggression should increase with age (Kemp, 2006; Parker, 1974). Furthermore, we have previously documented that sexually mature, 1-day-old males spent less time than did 4-day-old males courting recently mated females that were unlikely to remate. Males' mate choosiness decreased with age and reached asymptote by age 7 days (Baxter, Barnett, & Dukas, 2015b; Dukas & Baxter, 2014). This suggests that young males are less willing to incur costs associated with access to females than are mature males. We thus predicted that, as with our mate choosiness data (Baxter et al., 2015b), both male–male and male–female aggression would initially increase and then asymptote with male age. Our predictions for the effects of sexual experience were more complex. Previous data indicated a higher mate choosiness in previously mated than in virgin males (Baxter et al., 2015b; Byrne & Rice, 2006). Hence we predicted that, compared to virgin males, sexually experienced males would show less coercion of teneral and recently mated females because such females clearly reject pursuing males. As for male–male aggression in the context of resource defence, we predicted no effect of sexual experience owing to the operation of two opposing factors. On the one hand, we expected sexual deprivation to increase males' motivation to use aggression in order to secure access to females. On the other hand, because encountering and mating with females informs males that they occupy an attractive resource, we expected previously mated males to show a higher motivation to use aggression for resource defence than males that had not encountered females previously.

METHODS

General

We used descendants of wild-caught *D. melanogaster* collected in several southern Ontario localities in August 2014. We housed the flies in population cages containing several hundred flies per cage. We kept the cages in an environmental chamber at 25 °C and 60% relative humidity with a 12:12 h light:dark cycle, with the lights turning on at 1000 hours. We reared the experimental flies at a low density of about 300 eggs per 240 ml bottle containing 50 ml of standard fly medium made of water, sucrose, cornmeal, yeast, agar and methyl paraben. We sexed flies within 4 h of eclosion to ensure virginity and minimal experience with other flies. We used gentle aspiration to sex and transfer males into individual 40 ml vials each containing 5 ml of medium, and CO₂ to sex and place females in groups of 20 per vial, which also contained 5 ml of medium and a dash of live yeast.

We conducted all tests in cylindrical arenas made of Plexiglas (3 cm in diameter and 2.5 cm high). To deter flies from climbing on the arenas' walls and ceilings, we coated the walls with Insect-a-Slip (Fluon, BioQuip, Gardena, CA, U.S.A.) and the ceilings with Surfasil (Sigma Aldrich, Oakville, ON, Canada). We covered the floor of each arena with filter paper, and placed at its centre a circular food patch (1.3 cm in diameter, 1.5 mm high) coated with a suspension made of 3 g of live yeast in 100 ml of grapefruit juice. Throughout the study, we provided flies with ad libitum food optimized for fruit flies' preferences and needs, kept flies at low densities and kept to a minimum the duration of aggressive encounters.

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