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Male–male courtship behaviour, not relatedness, affects the intensity of contest competition in the field cricket

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Males often compete intensely against rival males because access to females is a major factor contributing to their reproductive success. However, there is controversy over whether male–male competition is weakened when rival males are related, with reduced aggressiveness leading to inclusive fitness benefits. Furthermore, same-sex sexual behaviour is also expected to mitigate male–male contests. Here, I examined how relatedness, developmental familiarity (i.e. males reared in the same container or not) and same sex sexual behaviour affect the intensity of male–male competition in wild-caught field crickets, *Teleogryllus occipitalis*. Relatedness and familiarity had no significant effect on the intensity of male–male contest behaviour. However, same-sex sexual behaviour did weaken male–male competition. In conclusion, my results indicate that same-sex sexual behaviour in this cricket has adaptive significance by mitigating risky male–male contest behaviour.

In parallel to female mate choice, male–male competition is a major force driving the evolution of sexual dimorphism (Andersson, 1994). In many populations, males intensively compete against their rivals for access to females and/or to inseminate eggs. Such aggressive behaviour expends large amounts of energy, with a high risk of injury (e.g. Eurasian lynx, *Lynx lynx*: Mattisson et al., 2013; nematode *Steinernema longicaudum*: Zenner, O'Callaghan, & Griffin, 2014).

However, it might be possible to mitigate intrasexual aggression and conflict by engaging in same-sex sexual behaviour (Bailey & Zuk, 2009). Indeed, same-sex sexual behaviour allows males to resolve dominance hierarchies without escalating to an injurious fight in the broad-horned flour beetle, *Gnatocerus cornutus* (Lane, Haughan, Evans, Tregenza, & House, 2016). The evolutionary significance of same-sex sexual behaviour has been explored (reviewed by Bailey & Zuk, 2009; Scharf & Martin, 2013). For example, sexual behaviour between females helps to establish social dominance in American bison, *Bison bison* (Vervaecke & Roden, 2006). Same-sex sexual behaviour also allows males to transfer their sperm indirectly to females through a male intermediary in the flour beetle *Tribolium castaneum*, although the effect on male reproductive success is small (Levan, Fedina, & Lewis, 2009). Other authors argue that same-sex sexual behaviour is nonadaptive and occurs because males are not able to discriminate between the sexes (e.g. common toad, *Bufo bufo* Marco & Lizana, 2002).

Field crickets often exhibit extreme aggression, with males fighting to defend the territories that they use to call and attract females. Aggressive male–male contests in field crickets are considered to be risky, because the mouth parts of male *Gryllus pennsylvanicus* are subject to more damage than those of females (Judge & Bonanno, 2008). Same-sex sexual behaviour has been reported for *Teleogryllus occipitalis* by Honda-Sumi (2002). Therefore, same-sex sexual behaviour might mitigate the risk of contests between male crickets.

In addition, kinship between males might also mitigate intrasexual competition (Díaz-Muñoz, DuVal, Krakauer, & Lacey, 2014; Hamilton, 1964; Kokko & Ots, 2006; Pizzari, Biernaskie, & Carazo, 2015). For instance, the increased fitness of relatives might provide indirect benefits to individuals through the increased transmission of genes that are identical by descent, i.e. representing another component of kin selection. Theoretical models suggest that the intensity of competition depends on the relatedness between males only when male–male competition leads to females being harmed (Faria, Varela & Gardner, 2015; Pizzari et al., 2015; Rankin, 2011). This is because the inclusive fitness of males is decreased when females

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are harmed through male–male competition. If male–male competition does not lead to females being harmed, its intensity should not be affected by the relatedness between males (Pizzari et al., 2015). Another required condition for male–male competition to depend on kinship is a structured population, because males make up a significant fraction of the smaller population, and thus a single male's competitiveness can have a larger negative effect on his own fitness when females are harmed (Pizzari et al., 2015).

In some mammals and birds, preferential cooperation among relatives has often been observed during reproduction (reviewed by Pizzari et al., 2015). Furthermore, relatedness has been found to weaken male–male competition in asocial insects. For instance, Carazo, Tan, Allen, Wigby, and Pizzari (2014) empirically showed that high relatedness among males reduces pre- and postcopulatory male–male competition in *Drosophila melanogaster*. Fighting behaviour between full-sib brothers before copulation was lower than that between unrelated males. The seminal fluid of male *D. melanogaster* inhibits the rate of remating by females, but also facilitates oviposition, while decreasing female longevity (probably a by-product; Holland & Rice, 1999). However, these deleterious effects increase the insemination success of males (Holland & Rice, 1999). Carazo et al. (2014) observed that females were harmed less when they cohabited with three brothers than when they cohabited with groups of three unrelated males. Thus, it was hypothesized that *D. melanogaster* males behave less selfishly towards relatives to gain indirect fitness benefits. However, additional tests on *D. melanogaster* proved controversial. Studies of some populations of *D. melanogaster* have found evidence that male–male postcopulatory competition is modulated by kin selection (Carazo, Perry, Johnson, Pizzari, & Wigby, 2015; Hollis, Kawecki, & Keller, 2015), but others have not (Chippindale, Berggren, Alpern, & Montgomerie, 2015; Martin & Long, 2015), posing questions about the generality of the phenomenon in *D. melanogaster*, and about its underlying proximate mechanisms.

Because the presence of female harm and the population structure have not been examined yet in the field cricket *T. occipitalis*, rigorous tests of the theory cannot be conducted. However, it is important to investigate this phenomenon in other taxa and strains that have not been reared in the laboratory. Furthermore, to my knowledge, whether relatedness between males affects the occurrence of same-sex sexual behaviour has not been examined in asocial animals. If same-sex sexual behaviour mitigates male–male competition, it may be more common among related than among unrelated males. I examined the effects of same-sex sexual behaviour and relatedness on the intensity of male–male contest competition. Developmental familiarity is considered to be one of the cues used for kin recognition. Alternatively, individuals may bias cooperative and tolerant behaviours to familiar individuals if they lead to direct fitness benefits (Chapais, 2001). Therefore, I also investigated the intensity of contest behaviour among males of different familiarity. I conducted an experiment using three treatments: unrelated–unfamiliar males, related–unfamiliar males and related–familiar males. Furthermore, I measured the frequency of male–male courtship behaviour, and tested whether it mitigated the intensity of male–male contest behaviour.

METHODS

Ethical Note

All experimental procedures in this study were conducted in accordance with the guidelines for the use of animals in research in Kagoshima University.

Cricket Collection and Rearing

Teleogryllus occipitalis (Orthoptera: Gryllidae) is widely distributed in low grasslands and farmlands of southwest Japan, China, Taiwan and Southeast Asia (Honda-Sumi, 2005; Orthopterological Society of Japan, 2006). All individuals used in this experiment were first-generation progeny of crickets collected from Amami Oshima Island in Japan (28°19′N, 129°22′E) in July to August 2015 and May 2016. Collected nymphs were reared to adulthood in a container (58.0 × 38.5 cm and 31.5 cm high) under a 16:8 h light: dark photoperiod (light cycle: 0300–1900) at 24–26 °C. The crickets were supplied with egg-cartons for shelter, cotton-plugged vials as a water source, and an excess of rabbit food (Marukan, Osaka, Japan) and cat chow (Purina, Kobe, Japan) for food. Newly emerged adults were collected within 24 h, and each cricket was maintained in a separate plastic cup (diameter = 10.5 cm; height = 5.0 cm) until the experiments.

Manipulation of Relatedness and Familiarity

Single virgin adult male crickets aged 7–10 days were randomly paired with single virgin females aged 7–14 days. The pairs were transferred to containers (diameter = 9 cm; height = 10 cm) with food, egg-carton shelter and soil in a 50 ml beaker. The soil was sprinkled with water every 2–3 days to provide a water source and to make the soil a suitable oviposition site. The crickets were allowed to mate and oviposit for approximately 14 days, after which they were removed. The same conditions were maintained in the containers until the eggs hatched. Hatched nymphs were collected within 48 h, and then 20–25 full-sib nymphs were placed in a container (29.9 × 19.2 cm and 20.1 cm high; two or three containers for each full-sib family). I obtained the progeny from 29 full-sib families for this study. Related males were full-sib brothers. ‘Familiarity’ was defined as individuals that were reared in the same container from the first to the last instar. Last-instar nymphs were individually placed in separate containers (diameter = 10.5 cm; height = 5.0 cm) with excess food, filter paper for shelter and cotton-plugged water vials. Three treatments were set up: related–unfamiliar, related–familiar, unrelated–unfamiliar. An unrelated–familiar treatment was not set up for logistical reasons.

Measurement of Male–Male Contest and Courtship Behaviour

An adult male aged 10–12 days was paired with a rival male. The males were marked on the pronotum with a dot of white paint (Magic Opaque Colour, Teranishi, Japan) 10–30 min before the experiment, for identification. Each male was tested only once. All observations were conducted 10–90 min before the dark cycle. The pair of males was introduced to a plastic arena (18.5 × 10.5 cm and 15 cm high). Crickets were transferred as gently as possible to minimize handling disturbance. Field crickets that win competitions stridulate and often chase the loser (Alexander, 1961; Hofmann & Schildberger, 2001). The intensity of contest behaviour was recorded using a categorical scale of aggression (modified from Hofmann & Schildberger, 2001), where 0 = mutual avoidance, 1 = antenna fencing and aggressive song, 2 = bilateral maxillae/mandible spreading, 3 = maxillae/mandible engagement and 4 = grappling. When focal crickets produced courtship song to rival males, the behaviour was recorded as same-sex sexual behaviour. Cricket body weight (to the nearest 0.1 mg) was measured with an electronic balance (Mettler AE50 balance Mettler-Toledo, Greifensee, Switzerland) immediately after observation.