



Male same-sex pairing as an adaptive strategy for future reproduction in termites



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A wide variety of animals display same-sex behaviours, including courtship, copulation and pairing. However, these behaviours create a paradox, as selection seemingly acts on maladaptive traits, and they have often been regarded as cases of mistaken identity, especially in invertebrates. We show that termite males show nest establishment and pairing formation that usually occur in monogamous colony foundation and demonstrate how this contributes to their fitness. We found that pairs of male dealates stopped searching for females and established nests without females, although single males rarely ceased searching for mates. Males in these male–male pairings had much higher survival than single males. Our colony fusion experiment showed that a male in a surviving same-sex pair can replace a male in an incipient colony and produce offspring. A mathematical model demonstrated that the observed strategy of establishing a male–male pairing instead of searching for females is advantageous when the risk of predation is high, even when colony fusion is very rare. These results indicate that, under certain ecological conditions, a cooperative same-sex pairing with a potential rival for reproduction can be adaptive. Our study implies the existence of various possibilities for explaining the adaptive significance of same-sex sexual behaviours.

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From insects to primates, various animal species show same-sex behaviours such as courtship, copulation and pairing (Bagemihl, 1999; Bailey & Zuk, 2009; Poiani, 2010; Sommer & Vasey, 2006). The persistence of this behaviour represents an evolutionary paradox, because it cannot directly result in reproduction. In mammals and birds, various possible benefits of same-sex behaviours have been suggested (Bailey & Zuk, 2009; Sommer & Vasey, 2006; Vasey, 1995). In addition, the adaptive value of same-sex pairing has been demonstrated in a wild population of Laysan albatross, *Phoebastria immutabilis*, in which a female in a female–female pair can reproduce by mating with a male in another monogamous pair (Young & VanderWerf, 2014; Young, Zaun, & Vanderwerf, 2008). Conversely, although same-sex behaviours occur in more than 100 species of insects and arachnids (Bagemihl, 1999; Scharf & Martin, 2013), their adaptive significance is not well understood.

In insects, the occurrence of same-sex behaviour is often explained by the nonadaptive mistaken identity of individuals

(Burgevin, Friberg, & Maklakov, 2013; Caballero-Mendieta & Cordero, 2012; Han & Brooks, 2015; Harari, Brockmann, & Landolt, 2000; Logue, Mishra, McCaffrey, Ball, & Cade, 2009; Scharf & Martin, 2013; Serrano, Castro, Toro, & López-Fanjul, 2000). Several hypotheses of adaptive significance of same-sex behaviour have been suggested, such as sperm transfer to a female through another male, harming other males, or learning how to court females (Levan, Fedina, & Lewis, 2009; Scharf & Martin, 2013). Some studies have tried to test these hypotheses in insects (Bailey & French, 2012; Dukas, 2010; Levan et al., 2009; Shimomura, Mimura, Ishikawa, Yajima, & Ohsawa, 2010), but these have not strongly supported reasons other than mistaken identity (Bailey & French, 2012; Scharf & Martin, 2013). A recent study has revealed that same-sex sexual behaviour between males is the by-product of an adaptive discrimination strategy to avoid rejection errors (Engel, Männer, Ayasse, & Steiger, 2015). That is, when the cost of accepting males is smaller than that of rejecting females, it is advantageous to accept other individuals without careful discrimination. This is a reasonable explanation for same-sex interactions, especially in polygamous and promiscuous mating systems. However, in monogamous species, in which one male mates with one female, the acceptance error of pairing with another male is critical for both

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males involved. In such a mating system, there must be some adaptive significance to this same-sex behaviour.

Termite colonies are typically founded by a monogamous pair of reproductive adults. In a certain season, alates (winged adults) fly off in large swarms and disperse. After dispersing, individuals shed their wings and run for a few days until they encounter a dealate of the other sex (Vargo & Husseneder, 2009). The pair then searches for a suitable nesting site in tandem, with the male following the female (Vargo & Husseneder, 2009). In *Reticulitermes* termites, males sometimes display same-sex tandem running, much like heterosexual pairs (Li, Liu, Lei, & Huang, 2015; Li, Zou, Lei, & Huang, 2013; Matsuura, Kuno, & Nishida, 2002). This cannot be attributed to a lack of sexual recognition ability because the responses of a male to other males differ from those to females (males compete for the following position when they encounter each other), and if a male–male tandem encounters a female, two males struggle for a female and the back male is likely to win the female (Matsuura, Kuno, et al., 2002). The adaptive explanation for this same-sex pairing is the dilution of predation risk, similar to a ‘selfish herd’ (Hamilton, 1971). Matsuura, Kuno, et al. (2002) showed that when single or tandem dealates encountered a predator ant *Pachycondyla chinensis*, the escape rate of dealates forming a tandem becomes at least 0.5 because an individual ant cannot capture two dealates. Thus, a male same-sex pair is expected to search not for a nesting site but for females, without which they cannot reproduce. However, nests consisting of two males have been observed in the field at the frequency of one in 57 (Kitade, Hayashi, Kikuchi, & Kawarasaki, 2004). This male–male pairing may indicate the existence of novel and long-term same-sex sexual interactions in termites.

Here, we show that termite males show nest establishment and pairing formation just like those in monogamous colony foundation and how male–male pairing can contribute to their fitness. We hypothesized that colony fusion with an incipient colony can provide an opportunity of reproduction to a male in a male–male pair. Colony fusion is relatively common in *Reticulitermes* termites: field studies have estimated that fusion occurs in 2.3–31% of mature colonies of *Reticulitermes flavipes* (DeHeer & Vargo, 2004; DeHeer & Vargo, 2008; Perdureau, Bagnères, Dupont, & Dedeine, 2010). In the case of incipient colonies, colony fusion can occur more frequently because they are often nesting in the same branch or log (Kitade et al., 2004), and in other termite species, incipient colonies that are in the same piece of wood are known to often interact and merge (Shellman-Reeve, 1994; Thorne, Breisch, & Muscedere, 2003). In this study, we first examined whether male–male pairs stop searching for females and initiate nest establishment without females. Second, we examined the survival benefits gained by a male same-sex pairing. Third, we performed a colony fusion experiment between a male–male pairing and an incipient colony founded by a male–female pair to identify the adaptive significance of same-sex pairing between termite males. Finally, we developed a mathematical model to examine whether such a male–male pairing is actually more adaptive than continuing to search for females under some ecological conditions.

EXPERIMENTAL METHODS

We collected alates of the termite *Reticulitermes speratus*, together with a piece of nesting wood, just before the swarming season. Seven colonies were collected from pine or Japanese cedar forests in Kyoto, Japan between 2013 and 2015 (2015: A, B, C and D; 2014: E and F; 2013: G). The colonies were maintained at 20 °C in

the laboratory until the experiments to control flight timing. Just before each experiment, we transferred the plastic boxes into a room at 25 °C and prompted alates to emerge and fly by cutting the wood. Alates were then separated by sex and maintained with nestmates in petri dishes containing moist unwoven cloth. Alates were used for the experiments within a day of flight.

Experiment 1: Nest Establishment by Male–Male Pairs

To examine whether male–male pairs initiate nest establishment without females, we compared the time until nest establishment among three types of units: single males (M), male–male pairs (MM) and male–female pairs (MF). All males were obtained from three colonies (A, B and C), whereas females were from colony D. Thus, there were three types of unit for single males (M_A , M_B and M_C). Male–male pairs were prepared using two males from different original colonies ($M_A M_B$, $M_A M_C$ and $M_B M_C$). Male–female pairs were constructed by allocating one female to a male from each colony ($M_A F_D$, $M_B F_D$ or $M_C F_D$). All males were marked individually to allow them to be distinguished. We made five replicates for three combinations of original colonies and thus 15 replicates per unit type. As a site for nest establishment, we prepared a petri dish (diameter = 40 mm), which was stuffed with mixed sawdust and had a small opening (diameter = 3 mm) on its side for termites to excavate and enter. The mixed sawdust was made of brown rotten pinewood and cellulose powder at a ratio of 5:1 by volume. We placed a petri dish and each respective unit of dealates in an arena (petri dish: diameter = 90 mm) and observed them every 6 h for 120 h to determine how long it took each unit to initiate nest establishment by entering the nest site. We defined the time until nest establishment for MM and MF as the time it took both dealates to enter the nest site completely and plugged the opening of the nest site by building a wall from the mixed sawdust. Similarly, we defined the time until nest establishment for M as the time it took the single male to do so. Thus, the data for single males could not be compared directly with those for MM and MF because the data for MM and MF are for two individuals but the data for M is for one individual. To control for this, we prepared another experimental set of single males and the data for single males were paired for all combinations of MM, and then the data for each combination were used for analysis (Matsuura & Nishida, 2001).

We analysed the frequency of nest establishment after 120 h by using a chi-square test. We also analysed the time until nest establishment by generating Kaplan–Meier survival curves, using both log-rank tests and Wilcoxon tests to check for an overall difference between units. Post hoc pairwise comparisons between all units comprised Bonferroni-corrected log-rank tests and Wilcoxon tests (adjusted α value: 0.016). Results of both tests were similar, so we report only the P values given by the log-rank tests. We checked the effect of combination type on time elapsed for each unit type and found a significant difference between combinations only for MM pairs (log-rank test: $\chi^2_2 = 8.6$, $P = 0.013$). As the kinds of combination differed between unit types, we pooled the data for different combinations within each unit type to compare the time elapsed between them. Units not showing nest establishment by 120 h were right-censored. All analyses were conducted using the ‘survival’ and ‘MASS’ packages in R v3.1.3 software (R Core Team, 2015).

Experiment 2: Survival Advantage of MM Pairing

We compared the survival rates between single males and males of male–male pairs to investigate the survival benefits of a

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