Courting strategies and conflicts in a monogamous, biparental termite

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In species where parental investment is extensive for both sexes, both males and females are predicted to exhibit choosiness when seeking their lifetime partners. Evidence is presented that both courting males and females are choosy in the wood-dwelling, biparental termite *Zootermopsis nevadensis*. There are, however, sex differences both in the method of mate rejection and in the mate-choice criteria. In particular, females are more likely than males to invite an extra suitor into the nest, whereas males are more likely than females to leave their nest and partner and seek a replacement elsewhere. Correlational analyses of adults show that head width is a mate-choice criterion used by females, whereas body mass and fat mass are used by males. Among males and females that sought replacement mates, those that had been rejected previously were more likely to end up paired with an adult that also had been rejected, compared with adults that had not been rejected. Additional findings reveal a rich repertoire of courting behaviours characterized by extensive intra- and intersexual conflict, including mate rejection, intrasexual combat, and even intrapair aggression.

Keywords: mate choice; sexual selection; parental investment; cooperation; punishment; Isoptera

1. INTRODUCTION

A key prediction of theories of parental investment and sexual selection (Trivers 1972; Williams 1966) is that when both parents provide extensive parental investment, both sexes should exhibit choosiness in finding their mates (Trivers 1972; Thornhill 1976; Gwynne 1981; Parker 1983; Real 1990; Crowley *et al.* 1991), especially when pairing for life. Studies of monogamy and biparental care in some vertebrates, including humans, reveal that both males and females engage in mate choice, sexual competition, mate rejection (divorce), and even intrapair aggression (Buss 1994; Andersson 1994; Gowaty 1996; Mock *et al.* 1996; in Rubenstein & Wrangham 1986; Black 1996).

By contrast, the classical picture of the termite mating system is that of a peaceful, monogamous partnership enduring the lifetime of a nest-founding pair (Grassé 1984; Nalepa & Jones 1991), this being four to five years in many wood-dwelling termites, and up to 20 years in other species (Watson & Abbey 1989; Shellman-Reeve 1997a). Anecdotal observations of courtship in diverse termite species have prompted some researchers to conclude that mate choice is not likely to occur in termites (reviewed by Grassé 1984; Nalepa & Jones 1991). However, as noted by several investigators of mating systems (Thornhill & Alcock 1983; Eberhard 1985; Alexander *et al.* 1997), quantitative study of the courtship activities of termites has been conspicuously absent. This absence is surprising, given that all of the over 2200 species of termite probably exhibit some monogamous biparental care in young colonies (Shellman-Reeve 1997a; Thorne 1997), including species that also show facultative polygyny and polyandry, i.e. multiple reproductive males and females. Compared

with vertebrates and other invertebrates (Clutton-Brock 1991; Blumer 1982; Eickwort 1981), termites represent the second largest animal taxon (next to birds) to exhibit monogamous biparental care, and will probably be a key taxon for comparative studies of mate choice and conflict among socially monogamous organisms.

Parental investment is extensive for both male and female nest-founding adults of the termite *Zootermopsis nevadensis* (Shellman-Reeve 1990, 1994a,b, 1996, 1997b), as in most termites (Grassé 1984; Nalepa & Jones 1991; Lenz 1994; Shellman-Reeve 1997a; Thorne 1997). Unlike many species of birds, in which offspring care is completed within a single breeding season (Rubenstein & Wrangham 1986; Black 1996), juveniles of this wood-dwelling termite develop very slowly, serving as workers for three to four years before developing into winged adults. As in many vertebrates and invertebrates in which males and females face similar selective pressures (see Andersson 1994), *Zootermopsis* males and females are roughly monomorphic (Shellman-Reeve 1994b). At least through the first year of colony life, both nest-founding partners participate extensively in nest construction, excavation, defence, and nutritional care of young (Shellman-Reeve 1990, 1994a, 1997b). A mate-removal study of *Z. nevadensis* showed that one-year-old colonies headed by single parents (male or female) suffered a mortality rate twice that of two-parent colonies of the same age, indicating that biparental care greatly improves offspring survival (Shellman-Reeve 1997b). In such circumstances of high parental investment, both sexes should be similar in their degree of mate choosiness, provided that there is opportunity for choice. At new settlement sites that attract high numbers of

adults, several pairs often initiate colonies within 3–6 cm of their nearest neighbour (Shellman-Reeve 1994a,b), suggesting ample opportunity for mate choosiness. Moreover, cohabiting pairs compete strongly for critical, limiting nutrients, such as a log's nitrogen-rich cambium layer (Shellman-Reeve 1994a, 1997b). Competition for nest sites on the cambium layer probably explains why adults form partnerships immediately after dispersal to the log. New pairs fight against neighbouring adults at nest boundaries, and against wandering intruders. Single individuals that engage in aggressive interactions spend less time holding nest sites than single individuals that do not engage in aggression. In contrast, a pair spends a similarly high percentage of time holding a nest site during aggression and in the absence of aggression, indicating that cooperative nest defence is one driving force favouring monogamous, biparental care (Shellman-Reeve 1994a). Under such conditions that demand nest defence, adults should seek attributes in a mate that will increase a pair's competitiveness. Current mathematical models of mate choice (Parker 1983; Real 1990; Crowley *et al.* 1991) predict that choosiness by both sexes will result in positive assortment with respect to overall mate quality.

I observed the courtship activities of *Z. nevadensis* adults under natural field conditions to test the above predictions. This study provides the first quantitative field data on courtship strategies, mate choice and courting conflicts in termites.

2. MATERIALS AND METHODS

(a) *Behavioural trials*

In eight courtship trials conducted on *Z. nevadensis* subsp. *nuttingi*, detailed observations were recorded of five to ten newly dispersed adults of each sex as each adult sought a 'mate' (i.e. its potential lifetime partner). Newly dispersed adults collected from six new settlement logs were the sources of adults used in courtship trials, with approximately 50–100 adults being captured at each settlement log just seconds after they landed on the log and before their disappearance beneath the bark (Shellman-Reeve 1994a, 1996). Only adults collected from a single log were used in any given trial; thus, adults that interacted within a trial would also probably have interacted with each other in nature. All newly captured adults were marked with enamel paint on the head, thorax, or abdomen, and kept in individual containers provided with food and water. Captivity did not appear to alter the adults' willingness to seek and find mates. Within an average of two days from their initial collection, ten healthy females and ten healthy males were selected and placed in a 20 cm × 30 cm observation area on a 'cambium-rich' region of a log (Shellman-Reeve 1994a) that was covered with plastic wrap stapled to the wood xylem. The log had previously been cleared of all newly established pairs (i.e. pairs that had recently settled at the log and the presence of which indicated that the wood was suitable for nesting). Marked adults placed onto observation areas were free to move out of these areas, and thus not all adults were observed in the trials. A total of 14 females and 19 males did not participate in courtship activities (four were seriously injured). A total of 66 females and 61 males were observed in the eight trials (figure 1). No adult was used in more than one courtship trial.

In each trial, a log was placed in an opaque tent to create dim lighting for facilitation of pairing behaviour. Immediately

after placing the last termite in the observation area, I started recording the behaviours of all individuals for 1.5 h. This time period approximates the maximum 2 h period (between 16.00 and 18.00 PST) that *Z. nevadensis* has to form pairs before its sister species, *Z. angusticollis*, disperses to the same log and engages in nest settlement and nest defence (Shellman-Reeve 1994a,b). Since there are immediate conspecific and hetero-specific pressures favouring joint nest defence (Shellman-Reeve 1994a,b), it is probable that the 1.5 h observation period is sufficient for some stable pairs to form within *Z. nevadensis*.

Audiotape records of pairing activities were augmented with visual records from a Sony Hi 8 mm camcorder. Thus, I obtained both focal and instantaneous records of behavioural activities. Non-aggressive behaviours included standing or turning in parallel with another adult, allogrooming, mutual antennation, proctodeal palpation of another adult, digging in the cambium, collecting water, abdominal smearing (apparently to mark a nest site), mate inviting (i.e. raising the abdomen in a 45° angle or performing an arched or stilt-like walk that typically attracted the opposite sex), wandering and walking within and outside a nest area, and leaving or following extra-pair adults. Aggressive (intolerant) behaviours included restraining an adult (such as by standing on their backs), pushing, bumping, lunging, biting, and physical dragging.

(b) *Characteristics of nest-founding adults and operation definitions for analysis*

(i) *Interaction behaviours and pairing criteria*

Allogrooming, mutual antennations and proctodeal palpations are probably important behaviours for assessing the quality and sex of a prospective mate. Because assessment behaviours and the responses that followed usually occurred within seconds, an interval of 1 min was arbitrarily selected as a reasonable period for mate assessment between any two adults. In other words, two adults were considered 'paired' if they were stationary or active less than 2.5 cm apart and engaged in non-aggressive interactions (see §2a above) for more than 1 min. This pairing criterion was chosen before statistical analysis and was also used in a previous study of cooperative nest defence between newly paired adults (Shellman-Reeve 1994a). Individuals that formed pairs continued to contact and interact with wandering adults. Adults were considered no longer paired if they ceased sharing a nest site together after 1 min (see also the definition of 'rejection', below).

(ii) *Nesting characteristics*

'Nest', 'nest site' and 'nest territory' are terms used interchangeably to describe the area defended by an adult. At high-density nest sites, pairs settle directly on the cambium layer (Shellman-Reeve 1994a), i.e. the area covered by plastic sheeting in this study. Nest-founding adults separate themselves from other pairs by actively defending a nest territory, an area *ca.* 2–5 cm in diameter (see Shellman-Reeve (1994a) for additional nesting descriptions). Adults delay their first copulatory encounter until the pair has established a secured or partly secured nest. Copulation may be delayed by up to two weeks in *Zootermopsis* (in Nalepa & Jones 1991) and was not observed during this study.

(iii) *Outcomes of mate choosiness*

'Mates' and 'partners' are terms used interchangeably to describe any member of a pair; an 'extra-pair' adult is any adult in a nest with a pair. 'Rejection' and 'desertion' are used interchangeably. A rejection (desertion) occurred when one

Figure 1. (a) The proportions of keepers, non-rejected choosers, rejects, or loners within each sex per trial. (For definitions of each, see § 2b(iii).) (b) Overall percentage of sex similarity in these proportions of keepers, non-rejected choosers and loners. Statistical comparisons for each of eight trials showed no overall sex differences in the proportions of males versus females that were classified as keepers, non-rejected choosers, rejects or loners (paired *t*-test, d.f. 7; $p > 0.48$ or greater for each of the four comparisons; statistics conducted on the arcsin, square-root transformation of all proportions; untransformed proportions are displayed). (c) Overall percentage of sex difference in the methods used by males and females to replace a mate. Females and males differed significantly in the way in which replacement mates were chosen. More females (78%) than males (22%) invited an additional mate into the nest. These invitations usually resulted in an intrasexual contest, after which a mate was chosen or was ousted by the competitor. More males (67%) than females (33%) wandered the log for a replacement mate (some following extra-pair adults that passed by) (Fisher exact test, two-tailed, d.f. 1, $p < 0.05$).

adult left its partner and nest and did not return to re-pair with that partner (the departing adult being the 'rejecter' and the partner being the 'rejected'). Rejection (desertion) also occurred when one adult was ousted from the nest by a same-sex competitor or by both members of a new pair, and the adult did not return to re-pair with its former partner. Adults fell into four mutually exclusive categories based on their pairing history by the end of observations: they were 'keepers' if they found and kept only one mate until the end of the trial (i.e. were non-rejecting and non-rejected), 'non-rejected choosers' if they left or ousted (with a new partner) at least one mate but were themselves never rejected, 'rejects' if they were left by their partner or were ousted by a same-sexed competitor (with its former mate)

at least once in a trial period (even if they behaved like non-rejected choosers before or after rejection), or 'loners' if they had not paired by the end of the observations.

(c) Phenotypic analyses

Head width, body mass and lipid mass were chosen as characters potentially used in the assessment of mate quality. Head width was measured as the maximum distance between the compound eyes, with a micrometer at $\times 40$ power in an Olympus dissecting scope (precision ± 0.01 mm). Body mass was determined from adults that were oven-dried at 70°C for 24 h, cooled in a desiccator for 24 h, then weighed on a Mettler semi-micro balance (precision ± 0.05 mg). Lipid mass was

determined as the difference between total body mass and lean body mass, the latter being obtained after lipids were extracted from adults that incubated at room temperature for 48 h in 25 ml of petroleum ether (b.p. 30–60 °C) (modified from Shellman-Reeve 1996). Mean ($\pm$ s.d.) head width (mm) of males and females was 2.03 ± 0.03 and 2.07 ± 0.03 , respectively. Mean ($\pm$ s.d.) body mass (mg) of males and females was 8.6 ± 0.7 and 9.3 ± 0.6 , respectively. Mean ($\pm$ s.d.) lipid mass (mg) of males and females was 3.13 ± 0.3 and 3.53 ± 0.4 , respectively (calculations within each trial, $N=8$ trials, $n=66$ females, 61 males).

3. RESULTS

(a) *Mate choosiness: similarities and differences*

Males and females varied in the time taken to pair with a partner, and in the propensity to keep a partner within the 1.5 h observation period. Some individuals of both sexes found and paired with a partner within minutes of the onset of the trial, whereas others waited much longer before pairing with their first mate; a few individuals, called loners, never paired within the trial period. By the end of the observations, 40 males and 40 females had paired, 8 males and 9 females had formed clusters containing more than two adults (typically three adults or two pairs whose specific partners could not be discerned) and 13 males and 17 females were single, of which four males and four females, respectively, were loners.

Females and males showed no overall differences in the percentage that became keepers, non-rejected choosers, rejects, and loners (described in figure 1a). By the end of observations, the mean ($\pm$ s.d.) number of partners of an adult was 1.48 ± 0.71 ($N=8$ trials, $n=66$) and 1.66 ± 0.81 ($N=8$, $n=61$) for all females and all males, respectively (all adults included). Among the adults that sought replacement mates, the mean ($\pm$ s.d.) number of partners of an adult was 1.97 ± 0.68 ($N=8$, $n=36$) and 2.13 ± 0.53 ($N=8$, $n=36$) for females and males, respectively.

Non-rejected choosers, i.e. those adults that chose to replace at least one mate but were themselves never rejected, sought a replacement mate in one of two ways: an adult could (i) reject his (her) mate by leaving the nest and his (her) partner, either by wandering away or by following another adult in search of a replacement mate (called the 'leave-and-search' strategy), or (ii) actively invite or allow an extra-pair individual in the nest territory, which typically resulted in the unwanted mate being ousted either by the same-sex competitor or by both members of the new pair (called the 'stay-and-invite' strategy). Males and females exhibited significant differences in their preferred method of mate rejection. A male was more likely than a female to exhibit the leave-and-search strategy. By contrast, a female was more likely than a male to exhibit the stay-and-invite strategy (figure 1b). The active solicitation of a potential partner, which arrived within one or two minutes, involved waving the abdominal tip in the air or walking in a stilted, frenzied manner. These calling behaviours are consistent with the notion that inviting adults are using pheromonal cues. One sex-attractant gland, located beneath sterna IV, is active in both sexes of *Z. nevadensis* (Pasteels 1972). The findings reported here suggest that such attractants may provide a mechanism for attracting multiple suitors,

thereby enhancing the prospects for mate choice, without leaving a nest site. Adults that were invited or allowed into the nest territory by one member of the pair subsequently engaged in combat with the same-sexed member of the pair in all but one case.

(b) *The operational sex ratio (OSR), mate choosiness, and intrapair aggression*

The relative choosiness of the sexes, as measured by the propensity to reject partners, was significantly positively correlated with the female:male operational sex ratio (OSR) across behavioural trials (figure 2a), the OSR being defined as the ratio of fertilizable females to sexually active males at any given time (Emlen & Oring 1977). The difference in the fractions of rejected males and rejected females also was significantly negatively correlated with the female:male OSR (see figure 2a).

Rejections were often associated with aggression between a male and female pair. Of all adults that sought replacement partners (36 males and 36 females rejected by or rejecting their mates), 44% were involved in some form of intrapair aggression with their previous partners. Females and males actively restrained, bumped, pushed, lunged, dragged, or bit their partners before pair dissolution or within minutes after (when the two former mates met again as one or both sought a replacement mate).

The proportion of initiators of intrapair aggression that were male compared with female was correlated positively with the difference in the proportion of rejects between the sexes across behavioural trials (figure 2b). These data show that intrapair aggression was usually initiated by the more frequently rejected sex. Most intrapair aggressions appeared to be catalysed by the presence of one or more wandering adults. Although not all intrapair fights led to break ups, most (67% of 18 fighting pairs) did so.

(c) *Phenotypic correlates of mate choosiness*

An adult that lost its mate owing to rejection by that mate was more likely to be single at the end of a trial than was an adult that rejected its mate, but had itself never been rejected (figure 3a). Rejected adults that did pair again were more likely to end up paired with adults that had also been rejected (figure 3b). Moreover, comparisons of paired adults revealed that males with large head widths significantly tended to end up paired with females of large body mass and large lipid amounts, whereas males with small head widths significantly tended to end up paired with females of small body mass or of smaller lipid amounts, or both (figure 4).

4. DISCUSSION

(a) *Mate choosiness: similarities and differences*

As predicted in a species where high investment is provided by both sexes, males and females were similar in the degree of mate choosiness. Only 41% of all females and 34% of all males maintained a stable partnership with their first mate up to the end of observations. The remaining adults that had paired at least once (54% of all females, 59% of all males) ended up seeking a replacement mate, either because they rejected (deserted) their

Figure 2. (a) Relationship between the female:male operational sex ratio (OSR) and the relative choosiness of the sexes. The female:male OSR correlated significantly with the relative choosiness of the sexes across trials (the fraction of non-rejected chooser males minus the fraction of non-rejected chooser females) (product moment correlation coefficient, $r=0.82$; $p<0.014$, d.f. 7, simple regression on arcsin, square-root transformed proportions (plots show untransformed data)). Because the relation between OSR and relative choosiness of the sexes may be confounded by variation in mate quality (Owens & Thompson 1994), a partial correlation analysis was conducted to examine how variation in mate quality influenced the correlation between mate choosiness and OSR. Sample variance (S^2) of each sex's head width, body mass, or fat mass (calculated from all same-sexed adults per trial) was used as the measure of variance in mate quality. Partial correlational analysis confirmed the significant relation between OSR and relative sex choosiness, controlling for each sex's S^2 for each phenotypic character (partial r values between 0.875 and 0.810, d.f. 5, $p<0.05$, six tests conducted). By contrast, this analysis showed no significant relation between each sex's S^2 of phenotypes and the relative choosiness of a sex, controlling for the OSR (partial r values between -0.53 and $+0.12$, d.f. 5, $p>0.10$). Thus, differences in the variance in quality of potential mates does not account for the association across trials between relative choosiness of the sexes and OSR. As predicted by the sexual selection theory, the regression line crosses the x -axis at a sex ratio of unity, i.e. the levels of

first partner, or because they themselves were rejected (deserted). Females and males did not statistically differ in their propensity to keep or switch mates, nor did they differ in the likelihood of being rejected by their mates (figure 1b).

The sexes, however, exhibited strikingly different methods of mate choice. Among non-rejected choosers, i.e. those adults that preferentially sought a replacement partner but were themselves never rejected, a male was twice as likely as a female to exhibit the leave-and-search strategy (figure 1c). Such an adult left his (her) partner, either to wander singly over the log area, or to follow another adult in search of a replacement mate. By contrast, a female was 3.5 times as likely as a male to exhibit the stay-and-invite strategy (figure 1c). Entry of extra-pair adults resulted in intrasexual combat in 90% of all cases. Thus, contrary to Nalepa & Jones's (1991, p. 90) hypothesis that little male courtship aggression is expected in termites, aggression among courting males (and females) in *Zootermopsis nevadensis* is frequent and intense.

In cases where an extra-pair mate was invited, the same-sexed adults (either two females or two males) sparred with each other, often face to face, while the other adult stood near to or groomed each combatant in alternation, seemingly to incite their mutual antagonism. Indeed, in one such case, fighting between two males persisted for 25 min, with the female alternating her groomings of each combatant. Incitation reported in other animals has been suggested to enhance a provocateur's chances of acquiring a better mate. For example, in polygynous elephant seals, the female is hypothesized to enhance her prospects for a mate through her advertisement vocalizations, thereby provoking suitors into combat, and afterwards, mating with the winner of such contests (Cox & Le Boeuf 1977). Not all cases of termite intrasexual combat arise from soliciting (calling in) extra-pair adults. In such cases, a female does not alternate her attentions between both suitors. Future studies that compare invited and uninvited nest entries will help to determine whether the inviting (calling) sex incites aggression between same-sexed suitors, or whether a courted adult's alternation of attentiveness between two suitors provokes intrasexual combat, for example by prolonging the duration of intrasexual combat.

Figure 2. (Cont.) choosiness are similar between the sexes when the OSR is 1.0. Additional analysis (not shown) revealed that the fraction of male rejects minus the fraction of female rejects was significantly negatively correlated with the female:male OSR (product moment correlation coefficient, two-tailed test, $r=-0.73$; $p<0.042$, d.f. 7, proportions arcsin, square-root transformed). (b) Relationship between the sex ratio of initiators of intrapair aggression and the relative propensity of the sexes to be rejected. The proportion of initiators of intrapair aggression that were male versus female (no. of male initiators/(no. of male + no. of female initiators)) was significantly positively correlated with the fraction of male rejects minus the fraction of female rejects; $r=+0.74$; $p<0.035$, d.f. 7, simple regression on arcsin, square-root transformed proportions (plots show untransformed data). These findings show that intrapair aggression was usually initiated by the more rejected sex.

Figure 3. (a) Pairing history of all adults that sought a replacement mate and their final pairing status by the end of the observations. *Rejects and non-rejected choosers differed significantly in their final pairing status (2×3 contingency analysis, χ^2 , $p < 0.0002$, d.f. 2). In particular, the percentage of rejected adults that remained single was significantly higher than was the percentage of non-rejected choosers that remained single (2×2 analysis excluding clustered adults, Fisher exact, two-tailed, $p < 0.0001$). (b) Percentage (and number) of rejects versus non-rejected choosers whose final mate had been a rejected adult, a non-rejected chooser, or a keeper. †Rejects and non-rejected choosers differed significantly in the types of final mates (2×3 contingency analysis, χ^2 , $p < 0.023$, d.f. 2). A similar percentage of rejects and non-rejected choosers found and paired with keepers, these being adults that had not been previously paired. However, a higher percentage of rejects paired with other rejected adults than with non-rejected choosers, whereas a higher percentage of non-rejected choosers paired with other non-rejected choosers than with rejected adults (2×2 analysis excluding keepers, Fisher exact, two-tailed, $p < 0.020$).

(b) *The OSR and intrapair aggression*

As predicted by sexual selection theory (Emlen & Oring 1977; Parker 1983; Gwynne 1990; Real 1990; Crowley *et al.* 1991), courting adults of *Zootermopsis nevadensis* were choosier in the sex that enjoyed a greater availability of mates (figure 2a). In addition, males and females were more likely to be rejected by the sex that had fewer same-sex competitors. These findings indicate that courting males and females are capable of assessing their mating opportunities, perhaps by assessing visitation rates of wandering adults or total concentration of pheromones of calling adults. Variation of the OSR, which under natural field conditions deviates widely around a 1:1 sex ratio in *Z. nevadensis* (Shellman-Reeve 1996), probably affects the level of mate choosiness by affecting the mate-search costs for both sexes (Emlen & Oring 1977; Parker 1983; Reeve 1989; Real 1990; Crowley *et al.* 1991).

Intrapair aggression was coupled to a surprisingly high percentage (44%) of rejections. Various aggressive behaviours were initiated by adults toward their mates, either within their nest or shortly after rejection of the mate. The threat of being rejected or deserted, particularly for the sex with more limited opportunities for pairing, may partly explain the high levels of intrapair aggression in *Zootermopsis nevadensis*. A higher proportion of males than females initiated intrapair aggression when there was a higher proportion of male rejects in a trial, and a higher proportion of females than males did so when

there was a higher proportion of female rejects per trial (figure 2b). Indeed, most intrapair aggressions were catalysed by the presence of one or more wandering adults near the vicinity of the nest, and most (67% of 18 fighting pairs) resulted in the break up of the partnership. These findings indicate that such aggressions are mediated by the threat of losing one's mate. One seemingly paradoxical question still looms: because the initiator of the aggression is of the sex that is most likely to be rejected, what benefit does an initiator obtain by being aggressive toward its mate? It would seem that he or she should be conciliatory, rather than aggressive, toward its mate, especially if the aggression hastens the rejection (aggression is often reciprocated and sometimes escalates).

Clutton-Brock & Parker's (1995) model of punishment tactics may apply to this situation. Among the evolutionarily stable strategies (ESSs), a partner (typically the dominant) may inflict aggression, as an act of punishment, to coerce (suppress) a partner to refrain from future behaviours that are likely to reduce the fitness of the aggressor. For example, in some species of monogamous birds, the dominant partner may retaliate against his mate for attempting (or attaining) an extra-pair copulation (Clutton-Brock & Parker 1995), thereby decreasing the likelihood that the subordinate mate will repeat any behaviour that will lower the dominant's fitness. In the context of termite courtship, it is possible that even a low-quality mate will use aggression to coerce (suppress) his or her mate if aggression reduces his or her partner's

Figure 4. Correlations between mates with respect to phenotypic quality (head width, body mass and lipid mass). Head width, body mass and lipid mass were chosen as characters potentially used in assessment of mate quality. Mean correlations of male head width with female mate's body mass (a) and female mate's lipid mass (b) were significant (one-sample t -test, two-tailed, with an expected mean correlation coefficient of zero, $n=8$ trials, 40 pairs). By contrast, correlations of female head width with male mate's body mass (mean $r=0.11$, $n=8$ trials, 40 pairs) and female head width with male mate's lipid mass (mean $r=0.11$, $n=8$ trials, 40 pairs) were not significant ($p=0.55$ and 0.56 , respectively). Additional correlational analyses conducted on male and female mate's head widths (mean $r=0.30$, $n=8$ trials, 40 pairs) and on male with female mate's body masses (mean $r=0.22$, $n=8$ trials, 40 pairs) were not significant ($p=0.12$ and 0.19 , respectively), and confirm prior correlational findings of 158 newly paired mates on 14 logs in the field (Shellman-Reeve 1994a).

ability to effectively assess potentially better partners. By doing so, the aggressor may reduce his or her overall probability of being rejected via mate choice. Indeed, the intent to suppress mate assessment of other potential suitors by the aggression may also shed light on Heath's (1903, p. 51) observations of newly formed pairs of *Zootermopsis* 2–3 days after the initial pairing. Heath observed that one member of a pair would sometimes chew off the tips of his mate's antennae (the primary chemosensory organ). Such an act of aggression (also reported in other termite species (LaFage & Nutting 1978)) often led to a reciprocal act of antenna-mutilation by its mate.

(c) Phenotypic correlates of mate choosiness

Why do the sexes differ in their method of mate choice? Throughout the courtship period, adults exhibited various tactile behaviours (see §2) that suggest chemical and morphological assessment of mates. Sharing of proctodeally derived nutrients is common

between males and females of *Zootermopsis nevadensis* in early colonies (Shellman-Reeve 1990). Palpation of the proctodeum, for example while tandemly following a potential mate, frequently occurred for both sexes, as in many termite species (Grassé 1984; Nalepa & Jones 1991). However, no nutritional exchanges were observed during the courtship phase, indicating that nutritional gifts, important in some insects (see, for example, Gwynne 1981; Thornhill 1976; Thornhill & Alcock 1983) are not important enticements for courting termites, perhaps because partners delay copulating for several days (Nalepa & Jones 1991). However, pairing was not random with respect to phenotype. Adults that lost their mate owing to rejection by that mate were more likely to be single at the end of a trial than were adults that rejected their mates (figure 3a). Rejected adults that did pair again were especially likely to end up paired with adults that had also been rejected (figure 3b). Furthermore, males with large head widths tended to end up paired with females of large body mass and large lipid amounts, whereas males with small head widths tended to end up paired with females of small body mass or of smaller lipid amounts, or both. A male's head width and his final mate's body mass and lipid mass showed a significant mean positive correlation over the eight trials (figure 4). These findings indicate that both sexes assort positively with respect to quality, because adult head width and body mass are strong indicators of a male's or a female's ability to win fights in mate competition in *Z. nevadensis* (Shellman-Reeve 1994b). In addition, fat reserves are thought to be important for early offspring production in many termites (Lenz 1987, 1994; Nalepa & Jones 1991; Shellman-Reeve 1997a).

Sex-specific preferences for these different attributes might explain why more females than males replace mates with the stay-and-invite strategy whereas more males than females replace mates with the leave-and-search strategy. Females, which emphasize head width in mate choice, may allow or perhaps even incite fights between two suitors to directly assess fighting skill or willingness to cooperatively defend a nest (Wilson & Dugatkin 1997). These features are especially likely to be important on logs attracting high densities of competing, nest-founding adults (Shellman-Reeve 1996, 1997b). In contrast, a male may be assessing female body mass and lipid reserves because they are reliable indicators of future fecundity, as they are for many other insects. If so, a male may gain less by allowing or inciting fights between females, even when having a cooperative defender is important (Shellman-Reeve 1994a).

In conclusion, mate-choice strategies of males and females strongly reflect the extensive maternal and paternal care in these dampwood termites, as is expected under theories of parental investment and sexual selection. For both sexes, courtship is fraught with conflict, including intrapair antagonism, possible incitement of combat, and partner rejection. In sum, these data emphasize the pervasiveness of mate choosiness and courting conflicts in socially monogamous vertebrates and invertebrates.

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