# The mating biology of *Phasmodes ranatriformis* (Orthoptera: Tettigoniidae: Phasmodinae), a mute genus of bushcricket from Western Australia.

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## Abstract

*Phasmodes ranatriformis* Westwood (Orthoptera: Tettigoniidae: Phasmodinae) is an unusual genus where species are both mute and deaf to airborne sound. As its genus name implies, it resembles certain Phasmatodea in being stick-like. The insect is sexually dimorphic in size; males are much smaller than females. The spring-active species is a pollen and nectar feeder. Census data indicate that there is no bias in the sex ratio while males are more vagile than females as the season progresses. Mating occurs during late spring. There is no evidence of inter-sexual signalling. Females are attracted to food sources at which males also feed and at which mating occurs.

Males produce a spermatophore comprising less that 6% of their body weight. Females do not feed on the spermatophore, which is simply held beneath the subgenital plate. Laboratory studies of mating behaviour show male competition for receptive females. Male-male behaviour ranges from complete disinterest to active jousting for mating opportunities. Prior to copulation the male grasps the female with the abdominal cerci at any point on the female's abdomen, eventually making contact with the genitalia by moving the cerci to the female's terminalia. The male then grasps the ovipositor between its mandibles, maintaining a wheel-like position until the spermatophore is transferred. Females may remate within 24 h. There is a correlation between male size and spermatophore size, and a positive correlation between spermatophore size and time since the previous mating. Males may take as long as 7 days for the spermatophore to reach maximum weight. Males attempting to mate with recently mated females transfer a small fraction (< 1.5 %) of their body weight as spermatophore. Females lay eggs into the soil soon after mating.

## Introduction

Males of most tettigoniid insects use acoustic signals to advertise their readiness to mate and receptive females locate calling males by orienting to the source of the sound (Otte 1977; Bailey 1991). The song is also used by males to compete for resources such as calling sites, food or preferred female oviposition sites (Feaver 1983). In those unusual bushcricket species where males are almost deaf, mating strategies have evolved whereby females use spatially discrete food sources as rendezvous sites (Gwynne & Bailey 1988), and males use their calls to solicit matings at these sites (Simmons & Bailey 1990). For example male *Kawanaphila nartee*, a small stick- like species of Zaprochilinae tettigoniid, have significantly reduced hearing function (Bailey & Römer 1991; Bailey & Simmons 1991), and males congregate around flowers rich in pollen and nectar, signalling their willingness to mate to feeding females (Gwynne & Bailey 1988). In *K. nartee*, females, unlike males, are able to detect airborne signals over many meters.

This paper describes the mating behaviour of *Phasmodes ranatriformis*, a nocturnal tettigoniid belonging to the Australian endemic subfamily Phasmodinae (Rentz 1993). The males have no means of sound production, and in both sexes the hearing system is severely reduced. Physiological experiments identified substrate vibration as the most likely means of distance communication in this species (Lakes-Harlen *et al.* 1991), but the sensitivity of the vibration-sensitive subgenual organs was no more developed than in other bushcrickets (*cf* Kalmring & Kuhne 1980). Hence, although substrate-borne vibration may have a role in sexual communication, a more likely way the sexes meet is for males to remain on, and meet with females at feeding sites. Such a system is remarkably similar to that observed for Phasmatodea stick insects (Sivinski 1983).

While plant food may be an important determinant of mating strategy in some bushcrickets, in others the male's donation of a protein-rich spermatophylax is also of importance (Gwynne 1988). The spermatophylax is a glutinous secretion of the male accessory glands and is attached to the externally placed sperm-carrying ampulla. Its size has a profound influence on both male and female mating behaviour (Gwynne 1986, 1988). After copulation females eat the spermatophylax as a nutritious nuptial gift with nutrients contributing directly to the developing eggs (Gwynne 1986). In the absence of the spermatophylax the female will eat the sperm ampula, and so the role of the spermatophylax can also be viewed as a device to protect the male's sperm (Wedell & Arak 1989). A second consequence of the male providing a large and energetically costly spermatophore (Simmons 1990) each time it mates is that the refractory period between successive matings may be over several days, allowing the male to replenish the accessory glands (Davies & Dadour 1989; Simmons & Gwynne 1991).

This paper describes an unusual mating system where the male donates a small spermatophore, which is not fed on directly by the female; the female gains nutrients solely from plants. There is an absence of long distance acoustic communication and mating appears to take place at rendezvous sites. We investigate plant associations of both sexes of *P. ranatriformis* with the hypothesis that mating should occur close to those plants providing most food for the female. If mating is resourced-based then we would expect males to aggregate at and compete for resources used by females, particularly during those periods in the flowering season when the resource is limited. We examine this hypothesis and describe the insect's movement patterns during the season.

Finally, metabolic costs to male tettigoniids of mating are both calling (Bailey *et al.* 1993) and the production of the nutrient rich spermatophore (Simmons 1990). We predict that in mating systems where males are silent and provide very small spermatophores both sexes will re-mate over a relatively short time interval (hours), and competition between males for access to females will be low compared with species where male mating costs are high.

## Material and Methods

### Field Site

Field studies were conducted during the spring (August - October) of 1992 after preliminary studies during 1990-1991. The study site was an area of 5 hectares in the south-western part of King's Park (Perth), a large city reserve of near natural bush-land. The woodland is dominated by an upper story of *Acacia*, *Banksia* and eucalypts and has a diverse herbaceous layer. The plant community consisted of grass, sedges and herbs (Table 1), which for most of this study contained species in flower. Sources of pollen and nectar from these flowers became less abundant as the season developed (Simmons & Bailey 1990; Gwynne & Simmons 1990).

**Table 1**

Insect plant association of *Phasmodes rantriformis* in Kings Park ranked by total and for each sex for spring season 1992.

| Plant Species Perennials | Association males | females | total |
|---|---|---|---|
| *Anigozanthos manglesii* | 59 | 44 | 103 |
| *Mesomelaena stygia* | 14 | 8 | 22 |
| *Daviesia* sp | 12 | 8 | 20 |
| *Xanthorrhoea preissii* | 9 | 7 | 16 |
| *Jacksonia sternbergiana* | 8 | 7 | 15 |
| *Gompholobium tomentosum* | 5 | 6 | 11 |
| Grasses | 6 | 4 | 10 |
| *Sowerbaea laxiflora* | 2 | 7 | 9 |
| *Haemodorum* sp | 1 | 1 | 2 |
| *Burchardia umbellata* | 2 | 0 | 2 |
| *Gladiolus caryophyllaceus* | 0 | 2 | 2 |
| *Banksia attenuata* | 2 | 0 | 2 |
| *Casuarina* sp | 1 | 1 | 2 |
| *Jacksonia furcellata* | 1 | 0 | 1 |
| *Conostylis aculeata* | 0 | 1 | 1 |
| *Hibbertia huegelii* | 1 | 0 | 1 |
| *Acacia pulchella* | 1 | 0 | 1 |

The study area selected was known from earlier surveys to have a significant population of *P. ranatriformis* and, during late August to mid-September, is dominated by stands of kangaroo paws (*Anigozanthos manglesii*). This plant provides an abundant source of pollen on which *P. ranatriformis* and *K. nartee* feed (Gwynne & Bailey 1988).

### The bushcricket *Phasmodes ranatriformis*

The subfamily Phasmodinae is a sister group to the Zaprochilinae, which have recently been considered a separate subfamily (Gorochov 1988: Rentz 1993). From its highly modified body form and extreme reduction in the acoustic / vibratory mechanism of communication, the insect appears to have evolved independently of other tettigoniid groups, and so the traits that make it so distinctive may be considered derived. Species of this genus, as well as exhibiting the elongate appearance of Phasmatodea stick insects (length 100-200 mm, width 5-10 mm), also show extreme size dimorphism with adult males one third to half the body mass of females.

*P. ranatriformis* (Fig 1) is entirely phytophagous and as a juvenile will feed on a range of grasses and herbs, but in its pre-adult and adult stages it feeds more exclusively on pollen and nectar. Its appetite for pollen leads to the unusual behaviour of feeding on the perianths of immature, unopened kangaroo paws (*Anigozanthos manglesii*) to attack the newly developed anthers within (Hopper 1993).

Oviposition was observed in sandy soil close to plants and occurred throughout the observation period. Oviposition was twice seen to follow mating, while on another occasion a female was found ovipositing at 1935 h and then with a spermatophore at 2100 h.

### Population census

Insects were located by flash-light during the first four hours after sunset by walking randomly through the study area. Searches were repeated every 2-4 days throughout the season. Once found, insects were marked by a numbered tag (3M™ high density reflecting tape - grade 7810). The small, self adhesive tag was fixed to the hind femur. Subsequent re-captures were made easy by this light-reflecting strip, which could be seen over distances exceeding 20 m. The location of each insect was marked with a coloured flagging tape tied to the closest plant, and the distance moved by each insect from its previous site was measured on the following day. Plant associations and the insect's behaviour were noted at the time of capture.

Behavioural observations in the field were made under dim red light. Where interactions occurred with other conspecifics the behaviour was aurally recorded on a cassette recorder and later transcribed. Individuals were allowed to complete their behaviour until the observer was satisfied that any interaction, mating or oviposition behaviour had concluded. Unmarked individuals involved in such an interaction were then caught, marked and released close to the point of capture.

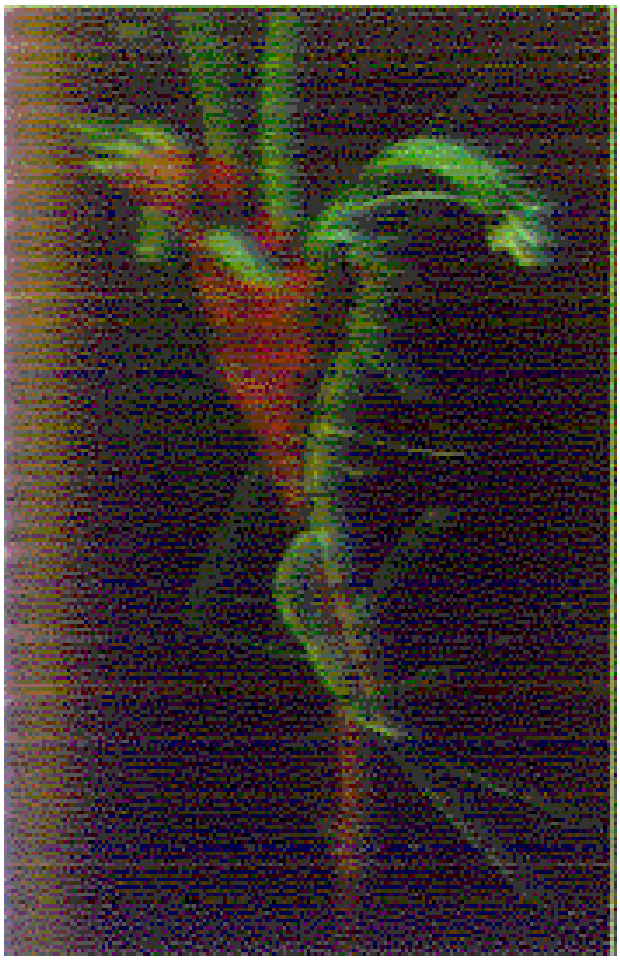

**Figure 1**. *Phasmodes ranatriformis* mating on a kangaroo paw in Kings Park (photograph by DT Gwynne).

The area of more-or-less homogeneous bushland was bounded by paths, which conveniently delineated our study site. However, once each week we would survey an area 50 m outside this defined site, searching for reflecting tags and so recording the number of emigres.

### Laboratory observations of mating behaviour

Males and females were collected during the early adult season (August to early September) as final instar nymphs or recently emerged adults. Field sites used to collect insects for the laboratory were from areas in Kings Park more than 100 m beyond the boundary of the field site described above. Once in the laboratory, insects were housed in a light-reversed regime maintained at 20 ± 2 °C. All individuals were uniquely marked with white liquid correction fluid and placed in large mesh cages with flowers, herbs and pollen *ad libitum*. The weights of each individual were recorded, and for males, weights were taken before and after mating, so giving the weight of the spermatophore passed.

We observed mating in two ways. First, we released two females with a single male (preliminary observations showed that two females placed with a single male increased mating frequency) in a wire-mesh cage (30 $cm^3$) in which there was fresh vegetation and pollen bearing flowers. Each cage of three insects was observed over the first three hours after darkness. When a female mated she was replaced with another un-mated female. Times to the commencement of mating from the start of the dark period, copulation duration and the number of mating attempts were observed on each occasion. Interactions, whether they resulted in mating or rejection, were noted.

The second approach was to release 8 to 10 males with a similar number of females into larger wire-mesh cages (60 $cm^3$). This high density arrangement allowed females to exert a choice between males, and for males to compete for mating opportunities. As indicated above, aggregations of both sexes occur in the field, and although not to the same extent as this laboratory manipulation, the situation could have similarities to that found in nature. Again, at the end of each mating, males were temporarily removed and weighed and females, once mated, were allowed to oviposit in sand trays from which eggs were removed.

## Results and Discussion

### Field Observations

**Plant association.** During the day *P. ranatriformis* is extremely cryptic, resting along the length of thin leaved plants such as sedges, grasses and the spiny forms of *Jacksonia.* At night the insect may be seen moving over vegetation or feeding on pollen rich flowers. Both sexes are opportunistic feeders, moving from one plant to another as each senesces. In early spring kangaroo paws (*Anigozanthos manglesii)* are a rich source of nutrients and there appears to be a distinct association between these plants and the distribution of *P. ranatriformis* (Table 1). Later in the season, when grass trees (*Xanthorrhoea preissii)* produce their pungently rich nectar, *P. ranatriformis* may be found feeding on flower spikes along with other tettigoniids such as *Kawanaphila nartee* (Simmons & Bailey 1990).

**Individual movement**. Fig 2 shows the mean distance

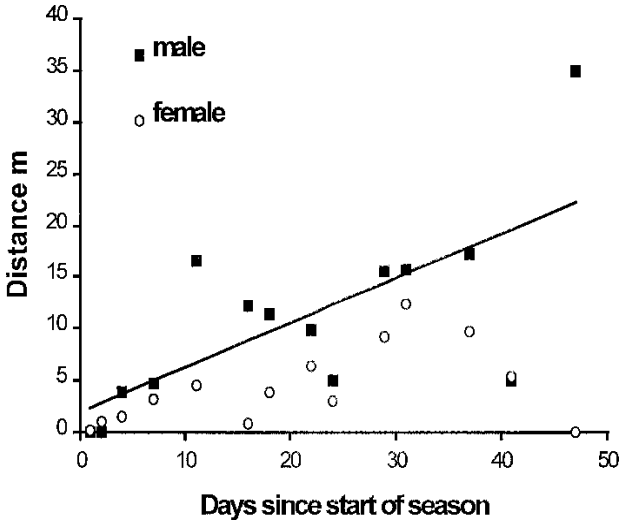


**Figure 2**. Mean distance moved by both sexes between successive captures over the entire season.

moved by both sexes between successive captures in the field over the entire sampling period. Males increase the distance over which they move as the season progresses ($r^2$ = 0.49; $F_{1,12}$ = 11.5; P = 0.005), while females showed no significant change in distance moved over the same period ($r^2$ = 0.21; $F_{1,12}$ = 3.2; P > 0.05). Although most animals moved less than 10 m from the site at which they were first collected, 9 individuals moved over 20 m, and this number included two males moving over 40 m.

Shelly & Bailey (1992) found that female abundance of *Kawanaphilla nartee* was more sensitive to the availability of pollen bearing flowers than male abundance. As flowers senesced females moved out of the sampling area at a great rate than males, presumably because females required higher levels of nutrients to nurture their developing eggs. By contrast, *P. ranatriformis* males rather than females emigrated from sampling areas at a faster rate than males. Increased male movement with the decline in flower availability in *P. ranatriformis*, which is a different measure to emigration, may be related to a reduction in pollen availability and quality. Alternatively, females, once mated, may have been less inclined to mate again and so males would have to move further to find receptive females.

A weekly census of a 20 m strip surrounding the study site showed a low recapture rate (4 males from 117 marked insects of both sexes). We conclude that few animals had emigrated from the study site. An indirect measure of predation was the presence of tags on the ground, which, because of their reflecting quality, could be found at night. These tags could have signified death by predation, the shedding of a limb or merely that the tag fell off. There was no indication of sex biased mortality; 24 tags were recovered of which 11 were from males and 13 from females.

**Mating and oviposition**. We observed only 7 copulations in the field, and an additional 3 cases where the female was carrying a spermatophore. Nine of these 10 observations occurred before mid-October, and 9 of the 10 after 2000 h. If mating takes place at a rendezvous site then we would expect more than one insect to be present at these sites and, if there was competition for females at the mating site, then a male-biased sex ratio. Two or more individuals were found within 1 m of each other during the time when most matings occurred (Fig 3) but the sex ratio of these small groups of three or more individuals was no different from 1:1.

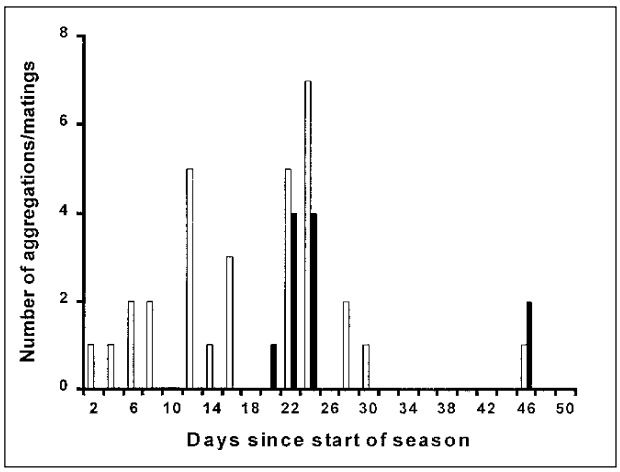


**Figure 3**. Frequency of aggregations (open) formed from two or more *P. ranatriformis* and number of matings (solid) observed in the field throughout one season.

**Laboratory Observations**

**Male agonistic behaviour.** Aggression is a typical part of male behaviour in bushcrickets, particularly where males compete for territory or for mating opportunities (e.g. Feaver 1983). Although we saw no evidence of male agonistic behaviour in the field, in the laboratory males were observed to interact (i) without the presence of a female, (ii) over the possession of females, and (iii) with other males involved in copulation. The frequency and stereotypy of this behaviour suggests that it is part of the male's normal behavioural repertoire and not an artefact of caged insects.

*Courtship and copulation.* We observed over 50 interactions within both the smaller cages containing 3 individuals (1 male and 2 females), and in larger cages housing 8 to 10 individuals of each sex. Twelve from the 19 copulations took place within 1 hour of scotophase.

Males appeared to detect females when they were within 15-20 cm and walked towards them, occasionally stopping and re-orienting toward her. However, during these occasions there was no evidence of signalling, either by posture or by rhythmic movements of the body or body parts. Once antennal contact was established, the female would either remain passive or walk away. We observed on 8 occasions males and females walking over each other with no apparent indication of their detecting either's presence.

By contrast, males intent on copulation, and once within contact of the female, moved rapidly toward the female with abdomen curved and genitalia open. Successful mating was always preceded by the male grasping the female's long ovipositor with the mandibles, while at the same time curling the abdomen to clasp the female's abdomen. The shortest pre-copulation period saw a male link directly with the female genitalia within 3 s of antennal contact. More usually the male clasped the female's abdomen, and whilst holding on to the ovipositor, could be seen sliding the genitalia toward the genital plate, releasing and re-clasping the abdomen without losing hold of the ovipositor. Once in contact with the female genitalia, the male manoeuvred the female's sub-genital plate before producing a spermatophore. Males remained looped for 5-10 minutes before changing grip on the ovipositor, moving their hold towards its tip. In the field both sexes walked during copulation, often covering distances exceeding 1 m. Once disengaged they broke up with kicking from both sexes.

On no occasion did we observe females feeding on the spermatophore, which was almost entirely hidden by the sub-genital plate. The spermatophore remained visible under the sub-genital plate for approximately 3 h after which time it was absorbed by the female.

Female rejection is a distinct behaviour. After the male makes contact with the female, and begins to loop the

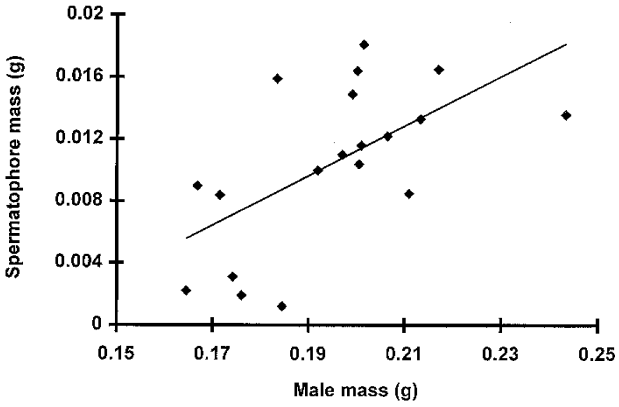


**Figure 4**. Relationship between spermatophore mass and male body weight.

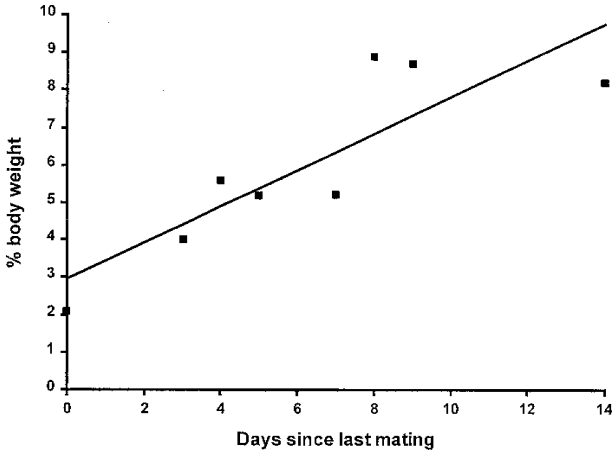


**Figure 5**. Variation in spermatophore weight, expressed as a percent of male body weight with the time since males last mated.

abdomen towards the wheel position, the female may struggle and kick the male away. On occasions the female lets go of the substrate, dropping to the ground. If the male manages to grasp the female near the genital plate the female will loop around and bite the male until he releases her. Where the female is entirely passive, the male may grasp the female's head, thorax or legs in its unsuccessful attempt at copulation.

*Spermatophore size.* Spermatophore mass ranged from 0.65-8.98 percent of the male's body weight ($\bar{x}$ = 5.24 ± se 0.58; n = 19) and had a linear relationship with male weight (Figure 4; $r^2 = 0.37$; $F_{1,18} = 9.8$; P = 0.0062). There was no significant relationship between spermatophore size and copulation duration. Some males (n = 4) mated more than once within 24 h but there was no evidence of any relationship between male weight and the number of times the male mated. The replenishment of the spermatophore, expressed by spermatophore mass donated at the next copulation was positively related with the number of days since the previous mating (Fig 5; $r^2 = 0.73$; $F_{1,7} = 16.0$; P = 0.007). It would appear that males mated with less than the maximum spermatophore size. Such a finding is consistent with other studies on variation in spermatophore weight with the length of time since the previous mating (Simmons *et al.* 1994).

**Repeated mating and male size advantage.** Females are polyandrous, and in 4 of 6 cases where a female re-mated within 24 hours, in 3 cases the second male transferred a relatively small portion of the spermatophore amounting to less than < 1.5 % body weight. The fourth case, where the second male's spermatophore was more than 1.5 % of body weight, the first male's spermatophore was close to the mean size. In one case, a recently-mated female allowed a second male to couple, but within a few seconds the second male withdrew and walked away. The minimum time between copulations by a female was 150 mins. Data on repeated copulations (Fig 6), although derived from a small sample size (n = 6) indicate that the second male may be able to detect the presence of the first male's spermatophore, so providing a small spermatophore. In 5 of the 6 occasions where different males mated with an already mated female within 24 hours the second male's spermatophore was smaller and on three occasions was minute.

Of the 49 encounters where both sexes were present *ad libitum* in each cage, larger males gained more mates than smaller males ($t_{45} = 1.78$; n = 49; P < 0.05). Thirteen of the 17 males mated and 2 of the rejected males that encountered other females were rejected, each on 6 occasions. These males never mated.

**Duration of copulation and refractory period**

For many insects, longer copulation confers an advantage to the male, particularly where females are able to re-mate with competing males (Thornhill & Alcock 1983), a case clearly demonstrated by phasmids (Sivinski 1983). But, any adaptive advantage of protracted copulation is more difficult to argue where the male delivers a spermatophore from which the sperm migrate to the spermatheca at a later stage. In most Ensifera, sperm transfer takes place after spermatophore attachment. In this case, increased duration of copulation can only be seen to be an advantage if the presence of the

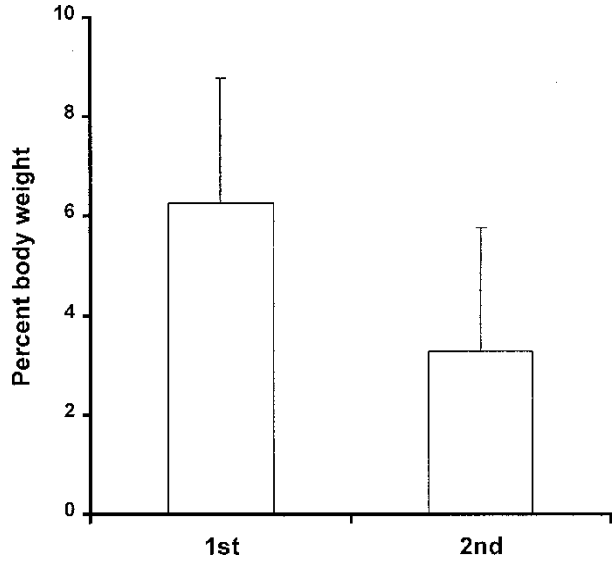


**Figure 6**. Mean spermatophore mass (± sd) as percent of body weight delivered to the female within 24 hrs after first and second matings (n= 6).

male prevents the female from feeding on the ejaculate. Indeed in some species of tettigoniids females are subject to a male-induced refractory period by the inclusion of chemicals in the spermatophylax (Gwynne 1990; Simmons & Gwynne 1991). The spermatophore is small in *P. ranatriformis* and the period of time between female mating attempts appears to be far shorter than that observed for other bushcrickets (e.g. *R. verticalis*, 3-4 days; Davies & Dadour 1989). We conclude that as females may remate within 1 day of the previous mating, the male does not deliver any material that will induce a postmating refractory period. Indeed, given the size of the spermatophore it may be advantageous to females to remate, so increasing the opportunity to sample more males and for males to control the size of the ejaculate (sperm number) if the female has recently mated.

That males attempt to interrupt other copulating pairs may provide evidence of positive selection on males to remain in copulation, at least until they have secured the spermatophore. If mate guarding occurs, even if only to prevent interruption and perhaps spermatophore displacement, then we may predict that copulation duration should increase in the presence of other males. Such a behaviour should be influenced by male density, however, we found no relationship in either of two series of trials which examined if male density influenced copulation duration between first and second mating.

For the first series, where males were allowed 2 females, copulation duration was 66.4 mins (± sd 63.1 mins; n = 19). However, copulation duration was longer, 101.7 mins (± 96.5 mins; n = 10), where males were exposed to females in the presence of other males. This difference between mean copulation duration, although in the expected direction, was not significant.

**Agonistic behaviour.** On no occasion did we observed male encounters in the field that could be classed as aggressive. However, although interactions were rare in the laboratory we twice observed males engaged in jousting by forcing the legs of the opponent from the substrate with the loser moving away from the winner. There were no females close by, and unlike male behaviour in the presence of a female, they did not curl their abdomen into a coupling position. Males were observed to compete for access to females by similar pushing behaviour with males trying to maintain contact with the female. On three occasions jousting over possession of the female resulted in the female moving away, and in one of these interactions the second male moved away once the first male had secured a grasp of the female. Males sometimes interrupted a second male's copulation by forcing the first male away from the female (n = 3). On 2 of these occasions the first male was successful, but in neither case did the intruding male attempt to copulate with the female. In two other instances the second male grasped the first male's abdomen, moving its claspers along the abdomen, but was unable to induce the first male to release the female. One male remained in this pseudocopulation position for 27 minutes. Although agonistic behaviour over territory may be weakly developed in this species, jousting behaviour should be considered part of the insect's normal behavioural repertoire.

**Mating system**

Mating in this species appears to be on or close to rendezvous plants where females remain feeding while males search between plants for both food and mates. There is no indication of any long range communication process, either by sound or chemical means. Substrate vibration, as incidental movement, could be expected to play a part in bringing the sexes together but there appears to be no rhythmic or patterned signalling. Where substrate vibration is important, morphological changes may be expected to enhance the detection of contact signals and the extreme body length, although undoubtedly having a cryptic function may, as in the phasmids, be advantageous in collecting vibratory information over a larger area of the plant.

Do males search for females? Our data on adult distribution indicate that males are more vagile than females, particularly as the season develops. That males were found close to a mating pairs suggests that males search for females, but the absence of any consistent male biased sex ratio in the "aggregations" indicates the need for more careful scrutiny of the encounter between the sexes in the field. It is possible that females remain at feeding sites and in the vicinity of competing males.

As with many polygamous species, where females remate within hours of the first copulation, the post-copulatory refractory period increases the likelihood that the first eggs laid by the female are fertilised by the most recently mated male's sperm (Thornhill & Alcock 1983). In bushcrickets the refractory period between repeated matings is dependent on the time of sperm ampulla attachment (Gwynne 1986; Weddel & Arak 1989; Simmons & Gwynne 1991) For example, in *Decticus verrucivorus* the refractory period is from 2 days when the ampulla is removed immediately after copulation, to 6 days when the ampulla remains attached for 3 hours (Weddel & Arak 1989). In *Requena verticalis* and *K. nartee* the spermatophylax is large, being > 20 % of the male body weight in the latter species (Gwynne, 1986; Gwynne & Bailey 1988) and in both these species nutrients from the associated spermatophylax contribute to the developing oocytes (Gwynne 1988; Simmons 1990). Spermatophore mass of *D. verrucivorus* constitutes less than 15 % of the males body weight with a mean of 9.45 % (Wedell & Arak 1989), and in this case it is just sufficiently large to prevent the female from consuming the sperm.

In *P. ranatriformis* the spermatophore is small, representing 10 % or less of the male's body weight and the spermatophylax is insignificant compared to the sperm ampulla. The spermatophore is not fed on by the female. As attachment time of the ampulla is critical for the release of any chemical that may induce a refractory period (see above) a female would have to remove the ampulla to decrease mating intervals. That female *P. ranatriformis* remate within 24 h suggests that no refractory period inducing -chemical is transferred in the ampulla. Further, that males can recognise prior mating during this period suggests that the spermatophore is acting as a sperm plug.

It is difficult to see any advantage for males to release a small ejaculate. Presumably, as there appears to be no

mechanism of sperm displacement, or of sperm feeding by the female, the cavity under the subgenital plate would be filled. The most reasonable explanation for the small size of the second ejaculate in 3 of the 4 cases is that a male, once in copulation releases sufficient ejaculate to fill the sub-genital area. He stops because there is no more room.

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## References

Bailey WJ 1991 Acoustic Behaviour of Insects: An Evolutionary Approach. Chapman & Hall London.

Bailey WJ & Römer H 1991 Sexual differences in auditory sensitivity: mismatch of hearing threshold and call frequency in a tettigoniid (Orthoptera: Tettigononiidae: Zaprochilinae). Journal of Comparative Physiology A 169:349-353.

Bailey WJ & Simmons LW 1991 Male-male behavior and sexual dimorphism of the ear of a zaprochiline tettigoniid (Orthoptera: Tettigoniidae). Journal of Insect Behavior 4:51-65.

Bailey WJ, Withers PC, Endersby M & Gaull K 1993 The energetic costs of calling in the bushcricket *Requena verticalis* (Orthoptera: Tettigoniidae: Listroscelidinae). Journal of Experimental Biology 178:21-37.

Davies PM & Dadour IR 1989 A cost of mating by *Requena verticalis* (Orthoptera: Tettigoniidae). Ecological Entomology 14:497-469.

Feaver MN 1983 Pair formation in the katydid *Orchelimum nigripes* (Orthoptera: Tettigoniidae). In: Orthopteran Mating Systems: Sexual Selection in a Diverse Group of Insects (eds DT Gwynne & GK Morris). Westview Press, Colorado, 209-239.

Gorochov AV 1988 [*In Russian*] 4. The classification and phylogeny of grasshoppers (Gryllida-Orthoptera, Tettigonioidea). In: The Cretaceous Biocoenotic Crisis and the Evolution of Insects (ed A Pomerenko). "Hayka", Moscow, 145-190.

Gwynne DT 1986 Courtship feeding in katydids (Orthoptera: Tettigoniidae): Investment in offspring or in obtaining fertilisations? American Naturalist 128:342-352.

Gwynne DT 1988 Courtship feeding and the fitness of female katydids (Orthoptera: Tettigoniidae). Evolution 42:545-555.

Gwynne DT 1990 Testing parental investment and the control of sexual selection in katydids: the operational sex ratio. American Naturalist 136:474-484.

Gwynne DT & Bailey WJ 1988 Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae). Behaviour 105:202-223.

Gwynne DT & Simmons LW 1990 Experimental reversal of courtship roles in an insect. Nature 346:172-174.

Hopper SD 1993 Kangaroo Paws and Catspaws: A Natural History and Field Guide. Department of Conservation and Land Management, Perth.

Kalmring K & Kuhne R 1980 The coding of airborne-sound and vibration signals in bimodal ventral-nerve cord neurons of the grasshopper *Tettigonia cantans*. Journal of Comparative Physiology 139:267-275.

Lakes-Harlan R, Bailey WJ & Schikorski T 1991 The auditory system of an atympanate bushcricket *Phasmodes ranatriformes* (Westwood) (Tettigoniidae: Orthoptera). Journal of Experimental Biology 158:307-324.

Otte D 1977 Communication in Orthoptera. In: How Animals Communicate (ed T Sebeok) Indiana, Bloomington, 334-361.

Rentz DCF. 1993 Tettigoniidae of Australia. Vol 2. The Austrosaginae, Zaprochilinae and Phasmodinae. CSIRO, Canberra.

Shelly T & Bailey WJ 1992 Experimental manipulation of mate choice by male katydids: the effect of female encounter rate. Behavioural Ecology and Sociobiology 30:177-182

Simmons LW 1990 Nuptial feeding in tettigoniids: male costs and the rates of fecundity increase. Behavioural Ecology and Sociobiology 27:43-47.

Simmons LW & Bailey WJ 1990 Resource influenced sex roles of zaprochiline tettigoniids (Orthoptera: Tettigoniidae). Evolution 44:1853-1868.

Simmons LW & Gwynne DT 1991 The refractory period of female katydids (Orthoptera: Tettigoniidae): sexual conflict over the remating interval? Behavioural Ecology 2:276-282.

Simmons LW, Llorens T, Schinzig M, Hosken D & Craig M 1994 Sperm competition selects for male mate choice and protandry in the bushcricket, *Requena verticalis* (Orthoptera: Tettigoniidae). Animal Behaviour 47:117-122.

Sivinski J 1983 Predation and sperm competition in the evolution of coupling durations, particularly in the stick insect *Diapheromera veliei*. In: Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects (eds D T Gwynne & G K Morris). Westview Press, Boulder, 147-163

Thornhill R & Alcock J 1983 The evolution of insect mating systems. Harvard University Press, Cambridge.

Wedell N & Arak A 1989 The wartbiter spermatophore and its effect on female reproductive output (Orthoptera: Tettigoniidae, *Decticus verrucivorous*). Behavioural Ecology and Sociobiology 24:117-125.