

MOVEMENT IN A ZAPROCHILINE KATYDID (ORTHOPTERA:
TETTIGONIIDAE): SEX-SPECIFIC RESPONSE TO FOOD PLANT
DISTRIBUTION

TODD E. SHELLY¹ AND WINSTON J. BAILEY
Department of Zoology
University of Western Australia
Nedlands, Western Australia 6009
Australia

ABSTRACT

Movement in relation to local food levels was compared between the sexes of the zaprochiline katydid *Kawanaphila narree* Rentz. Adults of both sexes were marked, and their departure rates were estimated (1) early in the season for two plots having high vs. low food density and (2) throughout the season for a single plot with changing food levels. Based on the between-plot comparison, movement of males was independent of food density, whereas females were less likely to leave the rich patch than the poor one. The within-plot comparisons revealed that, despite large changes in food levels, male departure rates did not vary over the season. Females showed increased movement over the season and by the end of the study had a departure rate similar to that of males.

Key Words: Spacing, mate searching, Australia.

RESUMEN

Se comparó el movimiento de los machos y hembras de *Kawanaphila narree* Rentz (Tettigonidae: Zaprochiliinae) en relación con niveles locales de alimento. Adultos de ambos sexos fueron marcados y se calculó la frecuencia de salida (1) en dos parcelas con densidad de alimento alta y baja al comienzo de la temporada y (2) en una sola parcela con niveles de alimento variables a lo largo de la temporada. La comparación entre las parcelas indicó que el movimiento de los machos era independiente de la densidad de alimento mientras que las hembras fueron menos propensas a salir de la parcela con alta densidad. Las comparaciones dentro de cada parcela revelaron que, a pesar de los grandes cambios en los niveles de alimento, la salida de los machos no varió a lo largo de la temporada. Las hembras mostraron incremento de movimiento a lo largo de la temporada y al final del estudio tuvieron una tasa de salida similar a la de los machos.

Males of many insect species encounter and mate with females at resources, such as food or oviposition substrate, that are critical to female reproductive success (Thornhill & Alcock 1983). In many of these species, males aggressively defend territories, and their mating success is directly related to the quality of resources controlled (McLain 1986; Villalobos & Shelly 1991). However, in other species, males do not hold territories and exhibit exploitative (or scramble) competition for mates at re-

¹Present address: Hawaiian Evolutionary Biology Program, University of Hawaii, Honolulu, Hawaii, 96822, USA

source sites (Banks & Thompson 1985; Hafernik & Garrison 1986). Theoretically, these males are expected to have an ideal free distribution (Fretwell 1972), i.e., to space themselves in such a way that each individual has the same probability of encountering females (Parker 1974).

In an earlier article (Shelly & Bailey 1992) on the Australian katydid *Kawanaphila nartee* Rentz, we reported a difference between the sexes in their distribution relative to the local abundance of the primary foodplant. Censuses of nine plots revealed that female abundance increased with increasing foodplant density, whereas male numbers varied independently of foodplant density. Correspondingly, female:male ratios increased with increasing resource richness in the plots. Because males are not territorial (Bailey & Simmons 1991), the resource-dependent increase in female:male ratio suggested that males had more mating opportunities in rich food patches than small ones, i.e., they were not distributed in an ideal free manner.

Focusing on the same katydid species, we here examine movement tendencies of males and females in response to resource abundance. Specifically, we estimated departure rates of the sexes (1) simultaneously for two plots with high vs. low foodplant density and (2) over the adult season for a single plot whose foodplant density showed marked temporal variation.

MATERIALS AND METHODS

Study Site and Species

Field work was conducted during August-November 1990 in Kings Park, a large area of bushland in Perth, Western Australia. The park is largely a shrub-grassland with an open canopy dominated by various species of *Banksia* and *Eucalyptus* trees.

The life history, feeding biology, and mating system of the species have been described elsewhere (Gwynne & Bailey 1988; Gwynne & Simmons 1990; Simmons & Bailey 1990; Bailey & Simmons 1991; Rentz 1993), and the following summary derives from these earlier studies. The species is univoltine, with adults sexually active between September-November. The adults, which are flightless, feed exclusively on pollen and nectar. A variety of foodplants are utilized, but kangaroo paws (*Anigozanthos manglesii* Endl.), which flowers from August to October (see Results), is the main food source during the early and middle portions of the adult season. As kangaroo paws decline, the zaprochilines switch their feeding to a species of grasstree (*Xanthorrhoea preissei* Endl.), which flowers from August to November. Grasstrees are far less abundant than kangaroo paws and typically occur as isolated individuals separated by distances of 2-10 m. However, each grasstree produces a large stalk bearing thousands of flowers and thus represents a rich, albeit localized, source of pollen and nectar.

Mating behaviour involves the attraction of females to stationary males calling within the vegetation. Males sing throughout the night, but sexual activity is restricted to the 3-h period immediately following sunset (1900-2200 hours). Males are not territorial and are not physically aggressive toward one another. During mating, the male transfers a large, proteinaceous spermatophore to the female, which she then consumes. Both field observations and experiments reveal a seasonal change in sex roles dependent on food availability. Females are apparently food-limited during the kangaroo paws season, and males are the choosy sex at this time. Conversely, flowering grasstrees provide superabundant food resources, and females are then the discriminating sex. Females appear to mate multiply, though field data on remating frequency are inexact.

Zaprochiline Abundance and Movement

During the kangaroo paw season, movement of zaprochilines was studied in 2 plots, each measuring 10 m by 10 m. The main plot (plot A) had a high density of kangaroo paws and was monitored during 3 different periods corresponding to the early (1-22 September), middle (25 September-16 October) and late (20 October-10 November) parts of the kangaroo paws season. The other plot (plot B) had a much lower density of kangaroo paws and was monitored only during the early part of the kangaroo paws season. Counts of flowering kangaroo paws were made approximately one week after the initial zaprochiline census for a given monitoring period. Plots A and B were separated by a distance of approximately 30 m and contained the same sets of plant species.

During a given monitoring period, we censused a plot every 3 days for a period of three weeks. Censuses were performed between 1900-2200 hours, usually under clear skies, but occasionally during light rain (zaprochilines were still active under such conditions). During a census, we slowly and systematically moved through a plot and attempted to locate all *K. nartee* adults. Calling males produce an ultrasonic signal (Gwynne & Bailey 1988) and were located using a "mini bat detector" (QMC Instruments) set at the average dominant frequency of the call (50 kHz). Females and non-calling males were located visually by scanning vegetation with a head lamp.

During the first 3 censuses of a given monitoring period, we marked all individuals with unique color sequences of enamel paint on their abdomen and released them at their original perch. Marking had no apparent effects on the subsequent behaviour of the insects, and individuals typically resumed calling or feeding within minutes of being handled. In the remaining censuses, we simply noted the presence of marked individuals and counted unmarked ones.

Data on the presence or absence of marked individuals were used to calculate emigration rates for both sexes. The numbers of individuals remaining in the plot through time were log transformed to produce decay curves analogous to survivorship curves used in demographic studies. Pairwise slope comparisons followed the method of Zar (1974). Tests significant at $p=0.005$ were also found to be significant using adjusted critical values of the Bonferroni correction (Kleinbaum et al., 1988).

In examining the presence/absence data, we found that some individuals had a "gap" in their record such that they were not observed on a given census date(s) but were observed on the census dates immediately preceding and following the gap. In almost all cases, the gap consisted of only one census date, and we assumed the individual was either missed or was immediately adjacent to the plot and therefore treated the individual as being present throughout (i.e., operationally, we ignored the gap). However, where the gap consisted of 2 or more consecutive census days, we assumed the individual moved away from the plot and considered the first day of absence to be its departure date.

As the preceding paragraph indicates, we assume that the disappearance of marked individuals from our study plots resulted primarily from emigration and that mortality was of secondary importance. This assumption appears valid, because (1) individuals typically live for several weeks in the laboratory (Simmons & Gwynne 1993), yet the numbers of marked individuals decreased markedly over just a few days (see Results) and (2) compared to the relatively straightforward explanation involving variable food abundance, unusual (and therefore unlikely) patterns in predation intensity would be required to account for the spatial and sexual differences observed in population decay curves (see Results). In addition, because of the rapid disappearance of marked individuals, successive censuses in a plot were not simply repeated estimates for the same local population of insects. Though census data from

different dates were not completely independent (since some individuals were counted on two or more censuses), the high turnover of individuals lessened this statistical problem, and hence inter- and intra-plot comparisons of abundance were considered valid.

During censuses in the early part of the kangaroo paws season, we also marked the position of each individual in plots A and B, respectively, by placing a numbered tag immediately adjacent to the perch. On the day following a census, we recorded the coordinates of these tags (to the nearest 0.1 m) on gridded maps of the study plots. These data were used to investigate spacing patterns of both sexes via analysis of nearest neighbor distances (Clark & Evans 1954).

RESULTS

Early season censuses in plots A and B revealed a differential effect of kangaroo paws density on the local abundances of male and female zaprochilines. Presumably owing to increased food levels, female abundance in plot A during the early season was approximately 50% higher than that recorded in plot B (Mann-Whitney test; $U=58$; $P < 0.01$; Table 1). In contrast, male abundance was, on average, not significantly different between plots A and B (Mann-Whitney test; $U=22$; $P > 0.05$; Table 1).

An intersexual difference in response to changing food levels was also apparent when seasonal trends in abundance were examined for plot A (Table 1). Female abundance varied significantly among monitoring periods (Kruskal-Wallis test; $H=15.3$; $P < 0.001$). Corresponding to an increase in flowering kangaroo paws, female numbers increased significantly between the early and middle monitoring periods (nonparametric multiple comparisons test; Zar, 1974; $q=4.6$; $P < 0.005$), whereas male abundance was similar between these 2 periods ($q=1.8$; $P > 0.05$). The number of flowering kangaroo paws declined dramatically by late season, and both male ($q=4.2$) and female ($q=5.6$) abundance decreased significantly from their mid-season levels (non-parametric multiple comparisons test; Zar, 1974; $P < 0.01$ in both tests).

Differences in male and female emigration rates for plots A and B were consistent with the inter-plot differences in abundance. In the early part of the kangaroo paws season, females emigrated from plot B at a greater rate than from plot A (Fig. 1; Table 2). For example, 36% of the females marked in plot A remained there for at least 9 days compared to only 9% of the females in plot B. Average residency of females was approximately 7 days for plot A but only 4 days for plot B. In contrast, no inter-plot difference in departure rates was noted for males (Fig. 1; Table 2), and approximately 15% of the males in both plots remained for at least 9 days. Average male residency

TABLE 1. ABUNDANCE OF MALE AND FEMALE *K. NARTEE* [MEAN (SD); N=8] AND FLOWERING KANGAROO PAWS (N=1) IN PLOTS A AND B.

| | Males | Females | Kangaroo Paws |
|--------|--------|---------|---------------|
| Plot A | | | |
| Early | 27 (7) | 25 (5) | 146 |
| Middle | 25 (6) | 31 (5) | 307 |
| Late | 16 (7) | 14 (5) | 93 |
| Plot B | | | |
| Early | 25 (5) | 16 (4) | 50 |

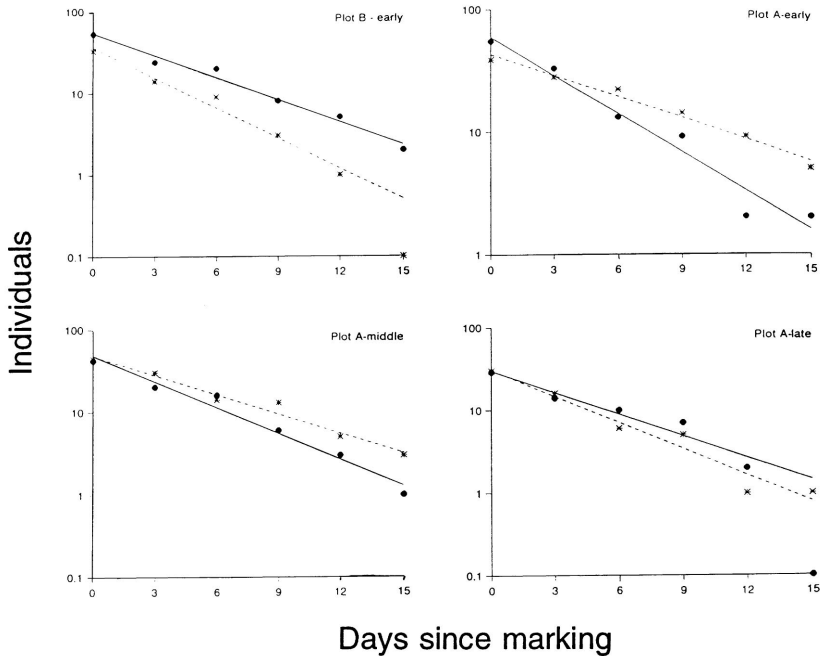


Fig. 1. Survivorship data for marked males (solid circles/lines) and females (open circles/dashed lines) in the two study plots. Numbers of individuals (log scale) remaining in the plot are graphed against days since marking. Linear regressions: Males (solid lines) - (a) $Y=1.72-0.08X$; $r^2=0.93$ (b) $Y=1.73-0.09X$; $r^2=0.94$ (c) $Y=1.67-0.09X$; $r^2=0.98$ (d) $Y=1.54-0.09X$; $r^2=0.95$. Females (dashed lines) - (a) $Y=1.53-0.10X$; $r^2=0.98$ (b) $Y=1.63-0.055X$; $r^2=0.97$; (c) $Y=1.66-0.07X$; $r^2=0.97$ (d) $Y=1.45-0.08X$; $r^2=0.95$.

was about 5 days in both plots A and B. As this result suggests, during the early season males left plot A at a greater rate than did females (Fig. 1; Table 2).

The degree to which emigration rates varied over the season also differed between the sexes. In plot A, female emigration rates showed a consistent increase through time: rates increased 30% between the early and middle period and 20% between the middle and late periods, though the latter difference was not statistically significant (Fig. 1; Table 2). Correspondingly, average female residency in plot A declined from 7 days in the early season to approximately 4 days by late season. In contrast, male emigration rates from plot A were similar between all monitoring periods (Fig. 1; Table 2). Owing to this difference, male and female emigration rates became more similar through time, with middle season values differing marginally and late season values not differing at all (Table 2).

Early season mapping of the positions of individual zaprochilines revealed that on most dates both males and females were randomly distributed in both Plots A and B. Males in plot A and females in plot B were randomly distributed on all 8 dates ($P=.05$ in these and all subsequent tests; t-test following Clark & Evans, 1954). Female distribution in plot A was random on 6 dates, aggregated on one date, and regular on one date. Male distribution on plot B was aggregated on one date and random on all others.

TABLE 2. MATRIX SUMMARIZING STATISTICAL COMPARISONS OF SLOPES OF THE SURVIVORSHIP CURVES (I.E., EMIGRATION RATES) SHOWN IN FIG. 1.

| | | Be ¹ | Ae | Am | Al | |
|---------|----|-----------------|----|----|----|-------|
| Females | Be | * | ns | ns | ns | |
| | Ae | *** | ** | ns | ns | Males |
| | Am | *** | * | ms | ns | |
| | Al | ns | * | ns | ns | |

¹On the matrix borders, upper case letters (A,B) designate plot; lower case letters (e,m,l) designate early, middle, and late monitoring periods, respectively. Within the matrix, elements above the diagonal represent comparisons between male populations, and elements below the diagonal represent comparisons between female populations. Elements on the diagonal represent comparisons between male and female populations. ns - not significant; ms - marginally significant ($P < 0.1$); * - $P < 0.05$; ** - $P < 0.005$; *** - $P < 0.001$.

DISCUSSION

Consistent with our previous study (Shelly & Bailey 1992), male and female *K. nartee* exhibited different spatial distributions relative to food resources: in the early season comparison of the two plots, male abundance was similar between rich and poor food patches, whereas females were more numerous in the rich patch. Previously, we suggested that this difference might have reflected a sampling bias. Females were perhaps most conspicuous in dense patches of kangaroo paws, where they were often feeding on exposed flowers well above the ground. In contrast, males usually perched close to the ground regardless of the vegetation, and therefore our ability to locate males was, more or less, independent of the density of kangaroo paws. Although this possibility cannot be dismissed completely, the intersexual difference in movement described here is strong corroborative evidence that the intersexual difference in spacing was real and was not simply a sampling artifact.

It appears unlikely that predation (rather than emigration) accounted for the decay curves observed for marked individuals. If, as seems likely, predators (e.g., spiders, mantids) displayed an "aggregative response" (Hassell et al. 1976) to the zaprochilines (i.e., settled preferentially in areas of higher prey abundance), then we might have expected decay curves to be steeper in plot A (where zaprochiline abundance was higher) than in plot B. Yet, the opposite trend was observed for females, and decay curves for males were similar in the two areas. In addition, and independent of an aggregative response by predators, it remains difficult to explain why predation would have a differential sex-bias in the 2 study plots, i.e., why (in the early season) females would be more vulnerable to predation than males in plot B but less vulnerable in plot A?

The "uncoupled" spatial distributions of males and females observed during the kangaroo paws season contrasts dramatically with the situation described for the katydid *Orchelimum nigripes* Scudder (Feaver 1983). In this species, males initially established territories in areas of high female eclosion. However, females later moved to preferred oviposition sites, inducing males to relocate as well and establish new territories at the oviposition area. Moreover, males typically perched along the borders of the oviposition areas, where they had a higher chance of intercepting females. Based on these observations, Feaver (1983) concluded that males assessed territory locations, not on the basis of the resources present (otherwise males would have settled within oviposition areas independently of females), but by directly monitoring female abundance.

At present, it is not known what strategy male *K. nartee* use to maximize encounters with potential mates. Based on the present results, it appears unlikely that males use food resources or conspecific calling as a cue to female abundance (see also Bailey & Simmons 1991). It is possible that movement by females may have greatly reduced spatial variation in male mating opportunities. Despite their lowered emigration from rich food patches, females still displayed a relatively high level of movement: even when flowering kangaroo paws were abundant, 40%-50% of the females moved out of plot A within 3 days of being marked. Consequently, males in poor food patches may have encountered females travelling to new feeding or oviposition sites. If female traffic were sufficiently high over the entire habitat, the ability of males to differentiate areas of high and low female abundance may have been limited, leading to the even distribution of males over the habitat.

However, this explanation simply raises another unanswered question, i.e., why do female *K. nartee* move so frequently? The observation that female emigration from plot A increased between early and mid season (despite an increase in flowering kangaroo paws) suggests an age effect, perhaps related to increased searching for oviposition sites. Any tendency to disperse eggs, and thereby spread mortality risks, would further contribute to frequent movement by females. In short, it appears that understanding the movement and distributional patterns of females (and thus males) may require information on the oviposition behavior, particularly the identification of preferred egg-laying sites.

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