

Roost Site Selection and Site Fidelity in the Neotropical Katydid *Docidocercus gigliotosi* (Tettigoniidae)

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ABSTRACT

We investigated the remarkable roosting behavior of *Docidocercus gigliotosi*, an understory pseudophylline katydid in the lowland forests of Panama. The insects used a spiny terrestrial bromeliad, *Aechmea magdalenae*, as a daytime shelter and were significantly more frequently found in those plants, which had been: (1) higher; (2) of better quality; (3) closer to 'night time walkways' into the canopy; and (4) showed a better central tube condition. The katydids demonstrated strong site fidelity, returning to the same plants for up to 3 wk. Such a choice may provide sufficient protection against some predators and serve as a suitable shelter for the offspring.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: bromeliad; Panama; predation; pseudophyllinae.

THE IMPORTANCE OF KATYDIDS AS MEMBERS OF ECOSYSTEMS, their roles as herbivores and predators, and as a primary protein source for many vertebrates and invertebrates, is only beginning to be fully appreciated (Nickle 1992, Nickle & Heymann 1996, Martins & Setz 2000, Naskrecki 2000). The primary defense strategy of katydids in response to diurnal predators is crypsis by general appearance and behavior (Belwood 1988, 1989; Castner & Nickle 1995; Nickle & Castner 1995). Neotropical katydids also use curled leaves in the forest understory and on the ground, or plant structures such as unfolded leaves as daytime shelters (*e.g.*, Belwood 1988). At least 11 species of birds in Bolivia and Peru hunt for insects in understory leaf litter (Remsen & Parker 1984). Checker-throated antwrens (*Myrmotherula fulviventris*) in Panama are specialized in searching and handling curled dry leaves looking for katydids and other arthropods (Gradwohl & Greenberg 1980). The effect of bird predation on foliage or leaf litter-dwelling insect populations can be severe, reducing the number of insects up to almost 50 percent within a few weeks (Holmes *et al.* 1979, Gradwohl & Greenberg 1982). The abundance and degree of activity of katydids has also been shown to depend strongly on the ambient light level, with highest levels during new moon conditions (Lang *et al.* 2005), indicating the influence of visually hunting predators on the ecology of these insects.

Katydid also constitute a major food source for nocturnal predators, such as Neotropical bats (Belwood 1988, 1989; Kalko *et al.* 1999), some of which (*e.g.*, *Micronycteris hirsuta*, *Lophostoma silvicolum*) are attracted by the calling songs or other noises created by phonotactic activities of their prey (Belwood & Morris 1987). Forest-living katydids exhibit a range of behaviors and signal characteristics which appear to be adaptations to predation pressure from bats, one of which is the partial or complete replacement of airborne sound signals by tremulation, the production of substrate vibration

(Morris *et al.* 1994). Tremulation signals represent a 'private' mode of communication; eavesdropping is only possible for those predatory receivers equipped with sensitive vibration receptors and when attached to the vibrating structure. Thus, bats passively listening to airborne sound signals have no access to tremulation signals. Belwood and Morris (1987) reported an exception to the 'rule' of low duty cycle acoustic signaling for the pseudophylline katydid *Ischnomela pulchripennis*, where males call at night from the top of a spiny terrestrial bromeliad. They suggested that these plants represent an effective protection against passively listening bats, reducing predation pressure for the katydids within these plants. Here, we report about the use of these bromeliads as roosts of the katydid *Docidocercus gigliotosi*, and its strong site fidelity within the plants. We suggest that the observed preference may be adaptive in the context of high predation.

METHODS

STUDY SITE AND ORGANISMS.—The study was conducted on Barro Colorado Island (BCI), in central Panama (0°09' N, 79°51' W) within Gatún Lake, part of the Panama Canal. BCI is almost entirely covered with secondary and primary semi-deciduous lowland tropical forest (Foster & Brokaw 1982). Observations and data collection took place in February/March and June/July 2002.

We focused on *D. gigliotosi*, a pseudophylline katydid which is one of the most common katydids on the island (Belwood 1988). From reconstruction of thousands of insect remains in roosts of *M. hirsuta* and *M. megalotis*, two gleaning insectivorous bats (Kalko *et al.* 1996), it is known that both species feed on *D. gigliotosi*, which constitutes about 20 percent of the diet of *M. hirsuta* (Belwood 1988, 1989). Male *D. gigliotosi* signal their presence and location by airborne sound and tremulation signals, which are transmitted through the plant as substrate vibrations (Morris *et al.* 1994).

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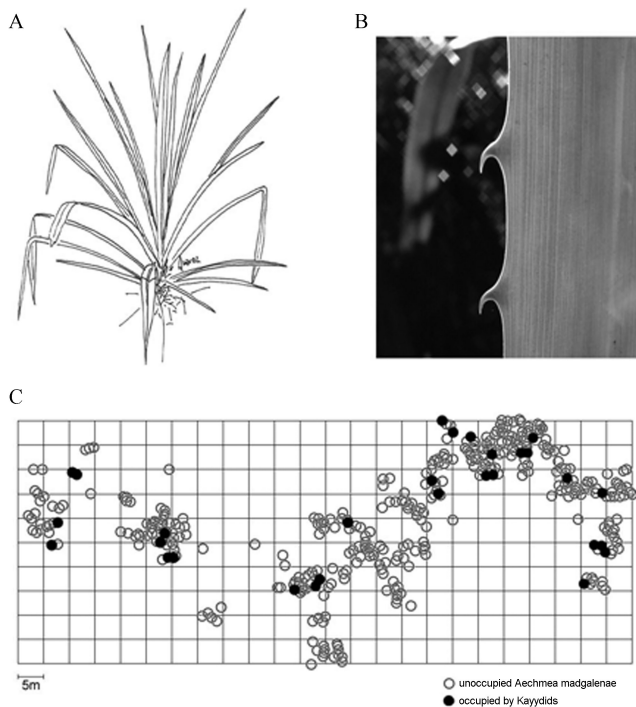


FIGURE 1. (A) *Aechmea magdalenae* plant; (B) close up of the 2 cm leaf edge spines; (C) Location of *A. magdalenae* plants in part of stand 'Zetek 15' on BCI, Panama, mapped with a geographical information system. Each plant is marked with a circle; those occupied with one or more *D. gigliotosi* katydids are shown with filled circles.

During the day, *D. gigliotosi* was found roosting in *Aechmea magdalenae* (André), a terrestrial bromeliad in the pineapple family which can grow *ca* 2.5 m (Fig. 1A). A striking characteristic of this plant is the presence of numerous, inch-long spines along the leaves (Fig. 1B). These plants are abundant throughout the Barro Colorado Nature Monument, sometimes forming dense stands with more than 1000 individuals (0.2–0.4 bromeliads/m²). Such large stands are separated on average by more than 1000 m on BCI. The leaves of the plant form a long tube in the center, where most insects were found roosting. The stand 'Zetek 15' (Croat 1978) includes about 1300 individual plants in total and is located within primary forest.

SITE MAPPING AND CENSUSING.—A census plot (120 × 50 m, area 3000 m²) including 471 *A. magdalenae* plants was laid through the western part of Zetek 15 (Fig. 1C). In contrast to the eastern part, where bromeliads are too dense to enable us to control all of them for insects, our census plot allowed access to every single bromeliad. The position of each plant within the plot was determined and plotted onto a GIS-map (ArcView, Environmental Systems Research Institute, Inc.). In addition, we took standardized photographs of each 5 × 5 m² in our plot for later identification of a particular site (always from the southwest corner of the 5 × 5 m² with a single-lens reflex camera covering the whole square with an 115° wide angle

lens) and to compare the state of individual plants, which were marked with numbers, throughout the duration of the study.

At intervals of 2–4 d, each plant was carefully searched for katydids, especially the tube formed by the central leaves, where most insects were found during the day. Adult katydids were marked with consecutive numbers on both fore wings, using waterproof permanent markers. Nymphs at various stages of larval development remained unmarked, but their presence was recorded. The individual numbers of the host plant and the katydid as well as additional parameters were noted. A census was typically conducted from 0900 h to 1200 h during February/March and June/July 2002.

ROOST SITE SELECTION.—To determine a nonrandom distribution of the katydids towards particular plants, different parameters were noted for each plant within the stand. These included: height (in 25-cm intervals); number of fallen leaves in the central tube (0, 1, 2, or more); number of leaves forming the central tube; number of damaged leaves forming the central tube; total number of leaves; number of damaged leaves of the whole plant and the general quality of the plant. The quality was a subjective scale with four categories, ranging from bad to excellent: category 0 (bad quality): > 60 percent of leaves damaged, < 10 percent of leaves fresh, plant appears strongly desiccated; category 1 (medium): 40–60 percent of leaves damaged, > 10 percent of leaves fresh, plant starting to desiccate; category 2 (good): 20–40 percent of leaves damaged, > 10 percent of leaves fresh, additional fresh, fleshy leaves in the center; category 3 (excellent): < 20 percent of leaves damaged, only a few peripheral (older) leaves damaged; > 20 percent of leaves fresh, additional fresh, fleshy leaves in the center. To prevent a subjective bias in the scaling based on the occupation status of the plant, the markings on the plants were removed before scaling, and the measurer had no *a priori* knowledge about its status. All plants were measured within 2 d in the first week of March for the first time. In a second, similar census conducted within 2 d in the third week of July 2002, the distance to the nearest tree or liana was recorded (contact = 0, < 1, 1–2, and > 2 m) in addition to most other parameters from March.

ROOST SITE FIDELITY AND MIGRATORY BEHAVIOR.—To monitor nocturnal insect behavior in the forest, we conducted a census in the morning and marked the captured males and females (in addition to their numbers on the fore wings) either with small (2 × 2 mm) pieces of 3M reflecting tape on both fore wings or with yellow fluorescent powder. At about 1700 h the same day, we checked all plants within the plot containing marked animals. From 1800 h until midnight, or 0600 h the next morning, respectively, we observed marked individuals with two infrared video cameras (Sony MiniDV PC100 Camcorder with a HVL-IRH2 infrared emission light) or a five seconds on-interval of a flashlight, covered with a red light filter. Each observer (five in total) was only able to follow one individual each evening. In total, we observed 18 individual *D. gigliotosi* in 12 nights of field observations. Records of all activities were taken with their timestamp, and individual insects were observed migrating into the canopy, until they disappeared. Six activity categories were used: 'no activity,' 'cleaning,' 'tremulating,' 'calling,'

TABLE 1. Univariate analysis of the bromeliad's parameters (Contingency tables, χ^2 -test of independence). P-values show the results of a chi-square test of independence to test the hypothesis if there is any association of each covariate and the outcome (katydid within the bromeliad). P-values in bold type mark associations which are considered significant. Condition categories ranged from poor (0) to excellent (3); # represents the counted number of leaf litter and (un-)damaged leaves. Adult katydids and nymphs were analyzed separately for both surveys in March and July, respectively.

Covariates	Unoccupied		Occupied by katydids			Occupied by nymphs		
	Median	1st & 3rd quartile	Median	1st & 3rd quartile	P (χ^2 test)	Median	1st & 3rd quartile	P (χ^2 test)
March								
Plant height (in 25-cm steps)	125	100/150	175	150/175	< 0.001	175	150/175	0.14
Condition category of plant (excluding dead plants)	Good	Medium/excellent	Good	Good/excellent	0.064	Excellent	Good/excellent	0.26
Type of central tube (tight, open)	Open	Open/tight	Tight	Open/tight	0.159	Open	Open/tight	0.62
# leaf litter leaves in the central tube	3	0/3	0	0/1	0.003	0	0/0	0.001
# leaves (tube), damaged	0	0/1	0	0/1	0.350	1	0/1	0.091
# leaves (tube), not damaged	3	3/3	3	3/3	0.943	3	2.5/3	0.98
# leaves (rest), damaged	3	2/5	4	2/6	0.573	3	2.5/5	0.14
# leaves (rest), not damaged	11	10/14	14.5	12/18	0.011	16	14.5/18	0.55
July								
Plant height (in 25-cm steps)	125	100/150	150	125/175	0.008	150	125/175	0.028
Condition category of plant (excluding dead plants)	Good	Medium/excellent	Excellent	Good/excellent	< 0.001	Excellent	Good/excellent	< 0.001
# leaf litter leaves in the central tube	0	0/3	0	0/0	0.006	0	0/0	0.009
Distance to nearest tree (m)	< 1	< 1/1–2	< 1	< 1/1–2	0.179	< 1	In contact/1–2	0.099

'moving,' and 'jumping.' The originally occupied plants and the immediate neighboring plants were then searched for the marked katydids every 30 min until they returned before sunrise.

STATISTICAL ANALYSIS.—Statistical analyses were performed using SPSS for Windows 11.0 and Instat (Graphpad Software, Inc.). As a response variable, we were interested in the probability of the animals being present in the plants of the stand. As possible covariates which could influence the presence probabilities, we investigated parameters which were collected during the two surveys in March and June. Bivariate associations between each covariate and the probability of the presence of adult katydids/nymphs were tested with contingency tables; a chi-square test of independence was performed. A P -value ≤ 0.05 was considered significant.

We used the McNemar's test, a nonparametric method used on nominal data to determine whether the datasets from March and July are comparable. Using logistic regression analysis, we tested multivariate associations between the covariates and the presence probability. To build the final model, we used a stepwise strategy beginning with a model containing all variables which were significant in the univariate analysis. As criterion to include or exclude additional variables, the P of the likelihood ratio test was used. $P \leq 0.05$ was considered significant in the multivariate analysis.

RESULTS

ROOST SITE SELECTION.—Sixty-eight adult *D. gigliotosi* were found roosting in the bromeliads during the study period. The overall

presence probability for adult katydids was 6.8 percent (32 adult katydids in 471 plants) in February, and 7.6 percent (36/472) in June. In addition, 2.8 percent (13/471) of the bromeliads were occupied by nymphs in February, and 12.3 percent (58/472) in June. The probability of finding an adult katydid in a bromeliad is equal in March and July (P of McNemar-test if probability is different between the two surveys = 0.69). The adult sex ratio was 17 males to 15 females (1.13:1) in the first survey, and 21 males to 15 females (1.4:1) in June.

In the monitored stand of *A. magdalenae* plants, *D. gigliotosi* were not randomly distributed, but were found to be highly selective in choosing a roost site with respect to: (1) height; (2) quality; (3) central tube condition; and (4) the neighborhood of 'night time walkways' to the canopy. Figure 1C shows a GPS-derived plot of the stand, in which plants occupied by one or more individuals are marked with dark spots.

Table 1 shows the univariate correlation analysis of all measured parameters and the presence or absence of katydids in the bromeliad. For adult katydids, the height of the plant, as well as the quality and the number of rotten leaves inside the central tube (central tube condition) were significant in both surveys, as was the number of undamaged leaves within the central tube. The central tube condition was also significant for nymphs in March and July, while the height and overall quality of the bromeliad was significant only in July.

Table 2 shows the results for the chi-square tests to survey for an association between each covariate (measured parameter). The correlation between the height of the bromeliad and plant quality is highly significant. In addition, higher bromeliads had tighter

TABLE 2. Bivariate correlation analysis of the bromeliad's parameters (Contingency tables, χ^2 -test of independence). Numbers show P-values of tests of association between the different covariates. P-values in bold type mark associations which are considered significant.

Covariates	Plant quality	Type centr. tube	No. of leaf litter in the tube	No. of leaves (tube), damaged	No. of leaves (tube), not damaged	No. of leaves (rest), damaged	No. of leaves (rest), not damaged
Plant height	< 0.001	< 0.001	0.15	0.33	0.34	< 0.001	< 0.001
Plant quality	–	< 0.001	0.14	< 0.001	0.041	< 0.001	< 0.001
Type of central tube	–	–	< 0.001	< 0.001	0.96	0.28	< 0.001
No. of leaf litter in the tube	–	–	–	0.62	0.052	0.35	0.050
No. of leaves (tube), damaged	–	–	–	–	0.030	0.001	0.80
No. of leaves (tube), not damaged	–	–	–	–	–	0.14	0.060
No. of leaves (rest), damaged	–	–	–	–	–	–	< 0.001

central tubes, more undamaged and less damaged leaves. *Aechmea magdalenae* of better quality had tight central tubes, less damaged leaves in the tube and, in general, less leaf litter in the central tube. Further correlations are found between the opening of the central tube and the number of leaf litter inside, and the number of damaged and undamaged leaves of a bromeliad. A significant *P*-value in Table 2 could be interpreted as a bivariate association between the covariate and the probability of finding a katydid within the plant.

Finally, we tested with a logistic regression model for March and July whether the significant bivariate associations were multivariately significant (Table 3). The association between plant height and quality was so high that the parameter 'quality' was completely excluded in the logistic regression analysis.

The results for the March survey indicate that the probability of finding an adult katydid within an *A. magdalenae* correlates significantly with the height of the bromeliad ($P < 0.001$) and less than three leaves of leaf litter present in the central tube ($P = 0.013$). The estimated odds ratio (estimator of relative risk) of 1.73 for the height of the plant means that the odds (ratio of present to absent katydid) are 1.73 times higher if the plant itself is one step (25 cm) higher. There was no significant correlation for the probability of finding a katydid nymph and any covariate.

For July, Table 3 shows the results of the logistic regression models for adult katydids and nymphs. As in March, the chance of discovering an adult *D. gigliotosi* within a bromeliad in July became significantly higher with increasing height of the plant (Table 3A). The distance to the nearest tree was measured and introduced into the model in July as a new parameter. Katydid preferred *A. magdalenae* plants next to trees, which represent pathways up to the canopy. A similar model was found for nymphs in July (Table 3B). As for adults, we found nymphs with a significantly higher probability in higher plants, with less leaf litter in the central tube and close to trees.

Figure 2 shows the distributions of height of occupied and unoccupied *A. magdalenae* within our study plot. While, overall, the plants were distributed over all height classes, katydids were found preferentially in the higher plants. Over the whole study

period, we found no *D. gigliotosi* roosting in a bromeliad <100 cm high.

ROOST SITE FIDELITY AND MIGRATORY BEHAVIOR.—In a mark-and-recapture-study we demonstrated high roost site fidelity. Sixty-five adult katydids were found and marked during one period. We recaptured 35 up to a maximum of 17 d (Fig. 3). Only three were found >2 m from the initial marking site; the maximum recapture distance was 10 m. Sixty-six percent of recaptured katydids were recovered in the same plant. Some individuals were found in the same *A. magdalenae* over a period of >2 wk. In no case did we find marked individuals in stands outside the original stand where individuals were first marked. There was no significant sex difference in the probability of recapturing or the site dependency.

Nymphs remained unmarked, but there was evidence that nymphs returned to the same *A. magdalenae* in the morning. Of the 58 plants, in which we found nymphs in July, 48 percent were also used by adults. In 65 percent of these plants, nymphs were seen in every census for up to 14 d. In addition, our nighttime observations showed that most of the nymphs fed only on nearby plants in the understory, making a return to the host plant likely.

During the day, all observed katydids ($N = 83$) roosted motionless within the central tube of the bromeliads, formed by the central leaves. Four males, three females, and eleven nymphs were observed individually for several hours at night. After sunset at 1830 h, adults became active at 1900–1930 h. For grooming activity, the katydids stayed in the plant and three males tremulated within that period. One insect left the bromeliad at 1935 h, the others shortly after 2000 h. They used nearby lianas or trees to climb up to the lower canopy within the next hour, where they could no longer be observed. One male climbed to the top of the highest leaf of his roost plant and started calling and tremulating after 20 min. This male continued calling and tremulating until 0400 h in the morning. The other individuals returned to their host plants around 0400 h in the morning, climbed back into the central tube within the next 30 min, and ended their nocturnal activity about an hour before sunrise. In addition, the roost site of another nine adult *D. gigliotosi* was surveyed in regular intervals in the evening. All had

TABLE 3. Results of multivariate analysis of bromeliad parameters in association to the probability of finding katydids within *A. magdalenae* bromeliads (logistic regression) in July 2002. (A) Adult katydids (N = 285; 33 present, 252 absent) and (B) Nymphs (N = 285; 58 present, 227 absent). P-values (Wald test) in bold type mark associations which are considered significant. For a detailed description of the covariates see text. – coeff: regression coefficient (parameter estimator); exp(coeff): odds ratio (estimator of relative risk); 95% CI: confidence interval of the odds ratio; P: result of the Wald test to test the hypotheses if the parameter estimator was significantly different from zero.

	Coeff	Exp(coeff)	95% CI	P
(A) Adults				
Plant height (in 25-cm steps)	0.394	1.484	1.101–1.998	0.009
No. of leaf litter leaves in central tube (0 leaves)				0.028
1 leaf	–	–	–	–
2 leaves	–0.761	0.467	0.128–1.708	0.250
3+ leaves	–2.579	0.076	0.010–0.578	0.013
No. of distance to nearest tree (0 m)				0.037
<1 m	1.409	4.092	1.446–11.576	0.008
1–2 m	1.187	3.276	1.108–9.687	0.032
>2 m	0.176	1.193	0.214–6.648	0.841
(B) Nymphs				
Plant height (in 25-cm steps)	0.218	1.244	0.997–1.552	0.053
No. of leaf litter leaves in central tube (0 leaves)				–
1 leaf	–0.786	0.456	0.163–1.278	0.135
2 leaves	–1.308	0.27	0.108–0.678	0.005
3 + leaves				0.050
No. of distance to nearest tree (0 m)	0.902	2.465	1.161–5.236	0.019
<1 m	0.792	2.207	1.000–4.872	0.050
1–2 m	–0.241	0.786	0.200–3.086	0.730
>2 m	0.218	1.244	0.997–1.552	0.053

left their host plants by 2045 h, and returned about an hour before sunrise.

DISCUSSION

The katydid *D. gigliotisi* is strongly associated with the bromeliad plant, *A. magdalenae*. However, in a stand of 471 individual plants, only a fraction is occupied by one or more adults, and our survey indicates that the distribution of katydids is not random. The insects are more prevalent in some plants with respect to: (1) height; (2) quality; (3) condition of the tube formed by the central leaves; and (4) the neighborhood of ‘nighttime walkways’ to the canopy. The first three of these are related to the protective function for an insect roosting in the central tube. Tall bromeliads offer a long, tight

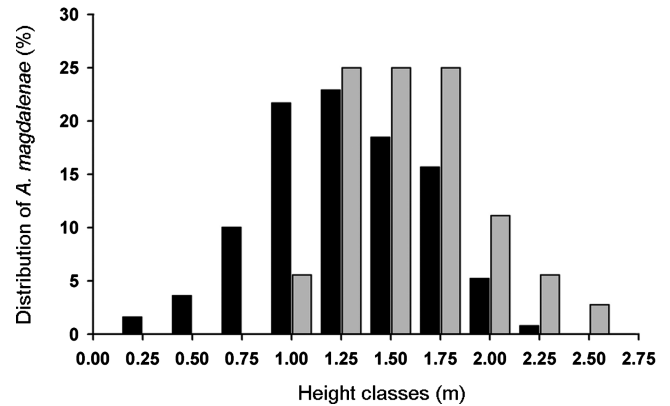


FIGURE 2. Height classes in *A. magdalenae*. Gray bars: plants occupied by katydids; dark bars: unoccupied plants. Note that katydids occupied primarily higher plants.

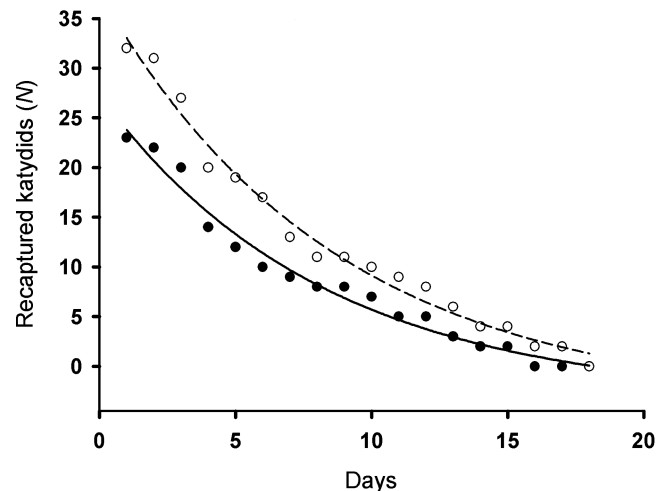


FIGURE 3. Recapture rates over time for the adult katydids following their marking on day 0. Filled circles: katydids recaptured exclusively in the same bromeliad they were originally captured. Open circles: data including insects, which were not only recaptured in the same bromeliad of initial marking, but also in neighboring plants. A nonlinear, single exponential decay model with three parameters was used to fit in the curves.

central tube, which, in combination with the long, sharp spines makes it almost impossible for predators such as mammals or birds to catch insects hidden deep in the tube. Smaller plants, even those with a tight central tube and of excellent quality, would allow access for small mammals and birds to catch katydids inside, as the spines on the leaves of short plants are probably too small and the central tube too short to serve as a protective shelter.

Alternative daytime roost sites for insects are curled dead leaves, which are abundant in dense foliage in the forest understory (e.g., Gradwohl & Greenberg 1980). Indeed, *D. gigliotisi* has also occasionally been found in curled leaves during the daytime, and anecdotal evidence suggests the katydid may return to the same leaf

after nighttime activity (Belwood 1990). However, curled leaves are potentially dangerous, since some bird species have developed specialized searching strategies for katydids and other arthropods in them (Gradwohl & Greenberg 1980, Remsen and Parker 1984). These specialized bird species have never been observed searching on, or within, *A. magdalenae* plants.

A second argument for the choice of *D. gigliotosi* for *A. magdalenae* due to a protective function from predators is the onset of their nighttime activity. They are not active when gleaning bats show most flight activity (which is likely to be related to foraging activity). Although we were only able to observe the nocturnal behavior of seven adult individuals and 11 nymphs during this study, the results are corroborated by another study on the nocturnal communication activity of 42 male *D. gigliotosi* (Lang *et al.* 2005). As in this study, all males became active more than 1 h after sunset and inactive shortly after midnight. *Lophostoma silvicolium*, an understory gleaning insectivorous bat has a peak in flight activity about 1 h after sunset, when it flies to its hanging perch (Lang *et al.* 2005), and 1 h before sunrise, when it flies back. Radiotelemetry showed a similar pattern of activity in *M. hirsuta* (S. Spehn, unpublished data). This correlates with our finding that *D. gigliotosi*, one of the bat's common prey species, does not exhibit nocturnal activity until major bat flight activity is over, and they also return to their bromeliad roost right before the bats return to their roosts.

The hypothesis that *A. magdalenae* provides an appropriate protective roost site is further supported by the finding that, in the census performed in March and July, *D. gigliotosi* were found primarily in higher bromeliads and those of better overall quality. Yet, the quality of individual bromeliads changed significantly between March and July; some plants which had been considered of excellent quality in March had most of their leaves damaged in July (probably as a result of desiccation) and/or the central tube was covered by leaf litter. In both censuses, significantly more katydids were found using the plants of excellent quality as roost sites. Thus, new generations of katydids cannot simply remain in the plant where they have spent their larval life, but have to find their own suitable roost.

Docidocercus gigliotosi also preferred plants in the vicinity of nearby trees or lianas which could be used as walkways to the canopy. Like most pseudophylline katydids, *D. gigliotosi* is a poor flier and does not perform continuous flight for more than 3–4 s (pers. obs.). Thus, the insects approach the canopy at night by walking and occasional jumping, where the nearest route can be an important parameter. Night time observations of individual insects and the mark and recapture study both indicate that they use the same route to return to their previous roost site. The site fidelity is remarkable given the fact that the insects leave their roost at night and walk considerable distances in the vertical direction, yet more than 90 percent of all recaptured individuals were found either within the same or neighbor plant, or at a distance no more than 2 m away during the following days. Some individuals were found in the same *A. magdalenae* for a period of more than 2 wk. However, 30 marked animals were never recaptured after being marked and released. We favor two explanations for these results: (1) our studied area covered only about a third of the entire bromeliad stand on Zetek 15, thus it is likely that the marked animals occupied

bromeliads in the uncontrolled part of the stand in the following days; (2) the life span of adult katydids is believed to be only several weeks long in the wild, so that it is possible that a reasonable part of the marked animals was subject to predation the days following the marking.

We do not know what kind of activity the insects perform during their time in the canopy, and, in particular, whether mating occurs between individuals which are separated by some distance in the understory. If this does not happen, the data of the mark-and-recapture study would indicate that there is very little horizontal movement of males and females in a population. In conjunction with a reduced active space of acoustic and vibration signaling, and reduced flight capability this situation may strongly reduce the chances of mating with individuals of neighbor populations, or even between more distant individuals of a population within the same stand of bromeliads.

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