

## OBSERVATION OF MOVEMENT AND ACTIVITY VIA RADIO-TELEMETRY REVEALS DIURNAL BEHAVIOR OF THE NEOTROPICAL KATYDID *PHILOPHYLLIA INGENS* (ORTHOPTERA: TETTIGONIIDAE)

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**Abstract.** Detailed knowledge of species' and individual behaviour is important for the understanding of ecological processes, but relevant data, particularly on small animals like insects are still widely lacking. Using newly available miniaturized technology, we radio-tracked movement and activity of ten male individuals of the Neotropical katydid *Philophyllia ingens* (Tettigoniidae: Phaneropterinae) in its natural rainforest habitat during  $3.1 \pm 1.8$  days. Although most katydids are assumed to be predominantly nocturnal our results revealed peaks of activity during the day, probably feeding and/or stridulating activity, while long distance movements of  $\geq 100$  m were only observed at night. Home range size was  $1139 \pm 555$  m<sup>2</sup>. Onset, but not drop-off of activity was correlated with peaks in wind speed and temperature. In addition, we observed a daily concerted downward movement from the canopy that may be a behaviour to avoid predation, while the earlier upward movement might be connected with temperature and food availability.

**Key words:** Barro Colorado Island, home range, movement, bushcrickets, predation.

### INTRODUCTION

Understanding the behavior of individual organisms is key to analyzing large-scale ecological processes such as predator-prey cycles or plant-animal interactions (Odum *et al.* 1971). However, detailed behavioral data on small, cryptic species from tropical forests remain scarce, particularly where insects are concerned. New monitoring and tracking technologies have already provided unexpected and important knowledge for the understanding and protection of small animals and their ecosystems. For example GPS-tracking of oilbirds (Steatornithidae) revealed that they are not seed predators, as had been assumed, but important long-distance seed dispersers (Holland *et al.* 2009). Radio-tracking of groups of bats specialized on swarming insects showed that they increase foraging efficiency through group hunting (Dechmann *et al.* 2009, 2010), and the same method revealed mechanisms important for migratory behavior in crickets and dragonflies (Wikelski *et al.* 2006, Sword *et al.* 2008) or dispersal in beetles (Hedin & Ranius 2002, Hedin *et al.* 2008).

Here we apply these technology-aided observation methods to tropical katydids (Orthoptera: Tettigoniidae, subfam. Phaneropterinae), a group of large canopy-living and cryptic insects, that play an important role in tropical rainforest ecosystems on several levels. On the one hand they interact with plants in their environment as important herbivores (Nickle & Castner 1995), and on the other hand they are an important food source for a wide variety of predators including monkeys, bats, birds, lizards, snakes, toads, frogs, mantids, amblypygids, and spiders (Belwood & Morris 1987, Belwood 1990, Martins & Setz 2000, Naskrecki 2000, Nickle 1992).

The commonest known predation-avoidance strategy of katydids is their cryptic appearance, mimicking leaves and lichens to hide from diurnal predators. In fact 71.4% of all rainforest katydids in Peru have no specialized morphological adaptations against predation other than color. They remain exposed but motionless to be inconspicuous, during the day on the leaves where they chose to stay just prior to sunrise (Nickle & Castner 1995). Only when disturbed do they fly and/or jump repeatedly until safe. However, color does not protect katydids from nocturnal

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predators such as bats. Here, behavioral adaptations, for example altered calling behavior, are more useful strategies (Belwood & Morris 1987, Belwood 1990). Katydids call predominantly at night, calling rates during moonlit nights being much lower than during dark nights when they are less visible to predators, indicating that this may be a widely applied strategy (Lang *et al.* 2006). However, not only species which have the potential to call but also vocally silent katydids are preyed upon at night (Kalka & Kalko 2006, Dechmann *et al.* unpubl. data), indicating that knowledge about patterns of movement and activity is important to understanding when and which predators are able to detect and prey on katydids, but published information on this has been almost completely lacking (Nickle & Castner 1995).

In the first detailed movement study on Neotropical katydids, we tracked the movements of *Philophyllia ingens* Hebard 1933, one of the most commonly encountered species of the tropical lowland forest in Panama, with miniaturized radio transmitters in combination with automated 24-h monitoring of activity. Even though males of this species are known to sing during both day and night (Piotr Naskrecki, pers. comm.), we expected to find activity and movement occurring mostly during the night, anticipating predominantly diurnal inactivity as well as small home ranges (Nickle & Castner 1995, Lang 2008; but see Heller & von Helversen 1993).

## METHODS

Our study site was on Barro Colorado Island (BCI), Republic of Panama ( $9^{\circ}09'N$ ,  $79^{\circ}50'W$ ), a field station of the Smithsonian Tropical Research Institute (STRI). BCI is covered by semi-deciduous tropical lowland rainforest (Leigh 1999). Our exact study area, the forest immediately surrounding the Lutz tower, a 48-m canopy tower, was located in a small v-shaped valley created by a stream. All data for wind and temperature were taken at the Lutz tower ([http://striweb.si.edu/esp/physical\\_monitoring/download\\_bci.htm](http://striweb.si.edu/esp/physical_monitoring/download_bci.htm)). The study was carried out during the dry season from 26 February to 7 March 2008.

We caught *Philophyllia ingens*, a species that was very common on BCI during our study period (1–5 individuals/night), with hand nets or by hand at lights of the station at night. Only one female was found at the lights, thus we decided to use only male katydids. Katydid identification to the level of species using the Orthoptera Species File (<http://orthoptera.speciesfile.org>) was later confirmed by Piotr

Naskrecki. Captured individuals were kept in inflated plastic bags and fed *ad libitum* with cucumbers for a maximum of 15 h until we equipped them with transmitters. We attached radio transmitters (see below) to the pronotum with a combination of eyelash adhesive (Andrea glue, American International Industries, Commerce, CA) aided by a minute application of superglue (Krazy glue, Elmers, OH). Fixing the transmitter to the pronotum minimized interference with flight and movement while providing a flat and smooth surface. To ensure that transmitters did not interfere with wing movement, test flights were performed with each individual after tagging. We equipped 11 and successfully radio-tracked ten male katydids. We weighed 13 additional individuals to the nearest 0.1 g (laboratory scale: GX-200, A&D Company, Japan) to get a measure of species mean body mass and to determine the percentage of body mass added by the transmitters. The mean ( $\pm$  SD) weight of *P. ingens* in our study was  $3.53\text{ g} \pm 0.64$ .

We used two types of VHF radio transmitters: katydids ID1 and ID2 received a pulsing TP-4 (Sparrow Systems, Fisher, IL), which produced a 1-Hz pulsed radio signal. On the remaining nine katydids we used the model TR-2, which produced a continuous radio signal. Both types of transmitters weighed 300–350 mg each. Consequently, with the transmitters we added *ca.* 8.5% of the insect's mean body mass. Katydids were released onto trees at an average distance of 3 m from the Lutz tower within one hour of tagging as follows: 26 February, three individuals; 27 February, three; 28 February, two; 1 March, one; and 4 March, two. They all started crawling at the moment of release. See Fig. 1 for a description of the setup of the study.

**Movement data.** In order to record large-scale movements of katydids (i.e. translocations of the insect from one observation to the next), we used radio-telemetry with human trackers. Five shift-working teams of two radio-trackers each collected the movement data. From 26 February 22:00 h until 29 February 21:00 h all katydids that had been released were localized every two hours. During the subsequent four days we focussed on four main times: sunrise (06:00 h), noon (12:00 h), sunset (18:00 h), and midnight (00:00 h). From 4 March 14:00 h until 5 March 12:00 h we concluded the observation period with one additional 22-hour period with two-hourly tracking. We triangulated the positions of released katydids by determining the direction of the

strongest signal of the transmitters with a pair of hand-held radio receivers (AR8200, AOR Inc., Torrance, CA) attached to three-element YAGI-antennas or a highly directional multi-harmonic 605 Mhz 12-element YAGI-antenna (Sparrow Systems, Fisher, IL; Cochran & Pater 2001). We marked the place of the strongest vertical incoming signal ("R<sub>h</sub>" in Fig. 1) with flagging tape labeled with the time and the katydid identification number. We then took the compass bearing and distance of the marked place, usually trees, from the base of the canopy tower. These data provided the basis for a coordinate map of all vegetation occupied by the individual katydids. The accuracy of our telemetry measurements was 4.1 ± 5.6 m, computed from data gathered during four days with a hidden transmitter. To measure how high in the trees the katydids were we located the height at which the 605 Mhz 12-element YAGI-antenna provided the strongest horizontal incoming signal ("R<sub>v</sub>" in Fig. 1) while climbing up the canopy tower (for precision, see Cochran & Pater 2001).

**Activity data.** In order to determine whether the animals were active or not (this includes activity such as feeding or stridulation, which does not necessarily involve changing location) we used automated determination of changes in signal strength caused by the relative position of the animal to the tracking unit (Kays *et al.* 2011). We installed an automated receiving unit (ARU: Sparrow Systems) on the fifth level of the canopy tower, *ca.* 11 m from the ground, to monitor katydid activity between 26 February 21:00 h and 3 March 16:00 h around the clock ("A" in Fig. 1; Lambert *et al.* 2009). The ARU recorded the signal strength of all radio transmitters within its reception range every 12 seconds in logarithmic units (i.e. dBm). We computed average activity (Avg\_acti) in dBm per hour and transmitter, based on the changes in signal strength or absence thereof (Kjos & Cochran 1970). Following Bisson *et al.* (2009) we considered an approximate doubling of signal strength, in our case a change in signal strength by 1.5 dBm, between subsequent measurements of

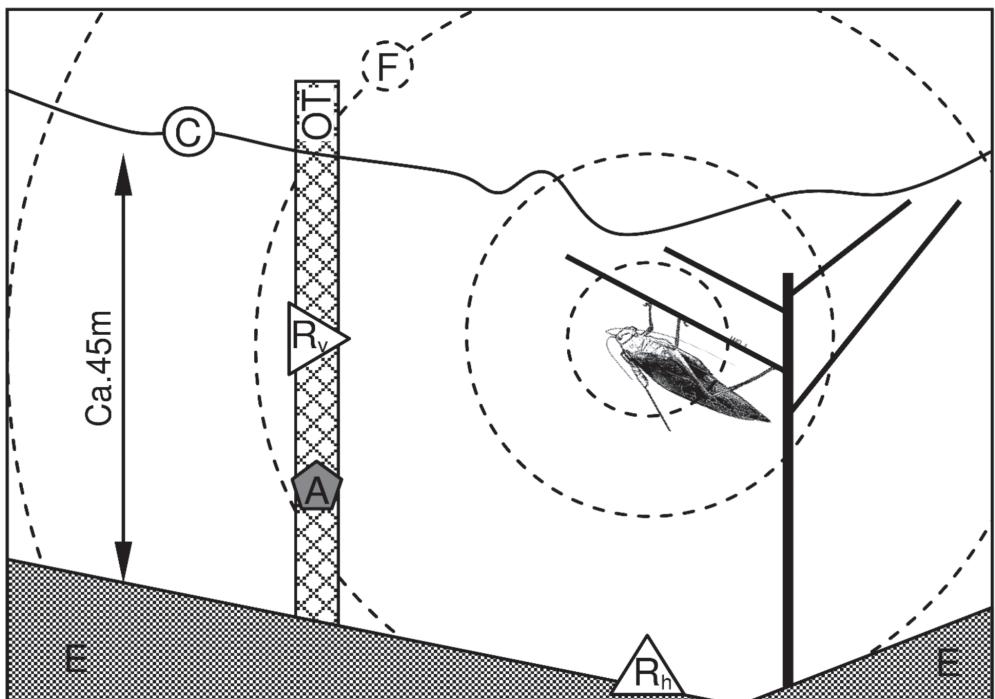


FIG. 1. Experimental set up. Katydid with transmitter on a stylized tree in the middle of stacked cycles (F) representing transmitter radio-waves. E) Shape of the ground at the observation site; C) stylized edge of the top of the canopy *ca.* 45m from ground; OT) observation tower with (A) automated receiving unit and (R<sub>v</sub>) exemplary mobile vertical receiver; R<sub>h</sub>) exemplary mobile horizontal receiver.

continuous radio signals from an individual to determine whether the animal had been active in the preceding 12 s. This threshold was confirmed by behavioral observations of three captive katydids for 15 min each in the laboratory before release (total of 270 independent observations with matched behavioral and radio-determined activity/inactivity).

**Data analysis.** We used SPSS 16.0 (SPSS Inc., Chicago, IL) for all statistical tests. Mean values from all study animals are reported as means  $\pm$  SE unless otherwise noted.

**Movement data.** We used Biotas 1.03 (Ecological Software Solutions LLC, Hegymagas, Hungary) to calculate home range sizes via minimum convex polygons. For calculation of home ranges we only used data of katydids tracked for three days or more ( $N = 6$ , tracked 72–182 h). We termed large movements beyond 100 m “dispersal” and did not include them in the home range calculations, even if we do not know the adaptive value of this behavior for the animals. To describe altitudinal movements we treated each measurement as an individual data point and grouped them in sets of four hours (00:00–04:00 h; 04:00–08:00 h; 08:00–12:00 h, etc.). The mean of every time-slot was compared using one-way ANOVA, correcting for individuals to account for different numbers of data points. We used circular statistics, Rayleigh’s test, integrated in Biotas, to examine whether there was directionality in the movement data. We tested whether the distance of horizontal movements was larger during daytime (06:00–18:00 h) or nighttime (18:00–6:00 h). We summed all distances moved within each time-slot for each katydid and treated them as individual data points. Comparisons were performed using the non-parametric Kruskal-Wallis test.

**Activity data:** We calculated the “total hourly activity” of all tracked katydids from the mean hourly activity of all individuals (Avg\_acti) and tested for significant changes with another one-way ANOVA.

## RESULTS

During the ten days of observation, we kept on catching, tagging and releasing new katydids with transmitters at the observation site, while others disappeared from the range of the automated receiver (ARU) as well as from the human observers during the same time period. Thus not all individuals were monitored for the same total amount of time (Table 1). One individual left the range of our receivers within two hours of release and was only relocated once at the end of the study (ID 4; Table 1). We excluded this animal from our data analysis. The remaining ten male katydids were monitored on average for  $3.1 \pm 1.8$  d for activity and localized 50  $\pm 40$  (SD) times.

**Movement data.** Five katydids left the study area (henceforth called “dispersal” even if the exact purpose of the behavior is unknown) after less than three days. All of these dispersal events (100–430 m,  $N = 5$ ) took place between 23:00 h and 01:00 h. Mean home range size of the remaining six individuals was  $1139 \pm 555$  m<sup>2</sup> (see examples in Fig. 2). We could not detect any directional pattern in the short distance movement data (Rayleigh’s test for all individuals tested,  $P >> 0.05$ ). Mean distance moved was  $32 \pm 26$  m (day) and  $40 \pm 31$  m (night) for each katydid, and no statistical difference was found (Kruskal-Wallis,  $\chi^2 = 1.04$ ,  $df = 1$ ,  $P >> 0.05$ ).

We collected a total of 202 data points on altitude of the katydids above ground, which were randomly distributed throughout the tracking period. Katydids remained more or less stationary from 20:00 h to 08:00 h at an average of 10 m above ground. They performed an upward movement starting at sunrise followed by a distinct downward movement (ANOVA;  $N = 202$ ,  $df = 5$ ,  $F = 4.991$ ;  $P < 0.001$ ) beginning at noon (Fig. 3).

**Activity data.** The daily curve of mean ambient temperature varied between a minimum of 23°C at 07:00 h

TABLE 1. Monitoring summary. ID: individual number (ID 7 missing due to different species); movement n: number of movement data points per katydid; movement t(h): number of hours each katydid was tracked; activity t(h): number of units of hourly activity recorded by the ARU.

ID	1	2	3	4	5	6	8	9	10	11	12
Number of movement data points	127	99	28	2	59	75	37	7	19	24	22
Recording time of movement (h)	182	161	225	214	148	164	95	9	70	12	12
Recording time of activity (h)	139	53	26	0	139	75	74	10	74	74	64

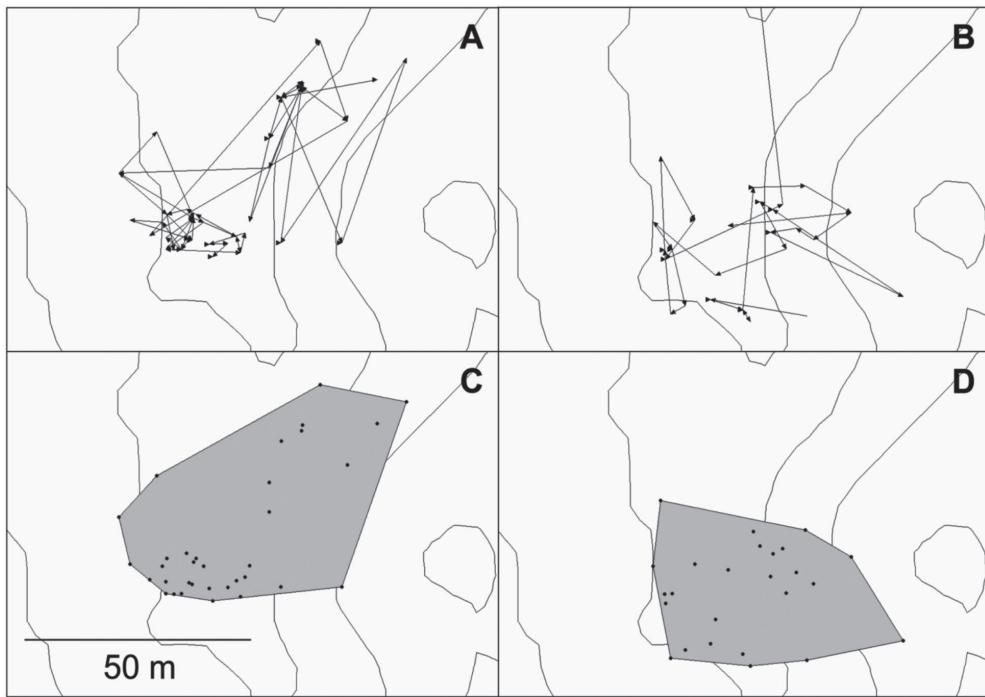


FIG. 2. Examples of movement data. A) movements of katydid ID 1 tracked during eight days; B) movements of ID 5 tracked during three days; C) mean home range of ID 1 ( $1992 \text{ m}^2$ ); D) mean home range of ID 5 ( $1403 \text{ m}^2$ ), arrows show the direction of movement (time overlay possible).

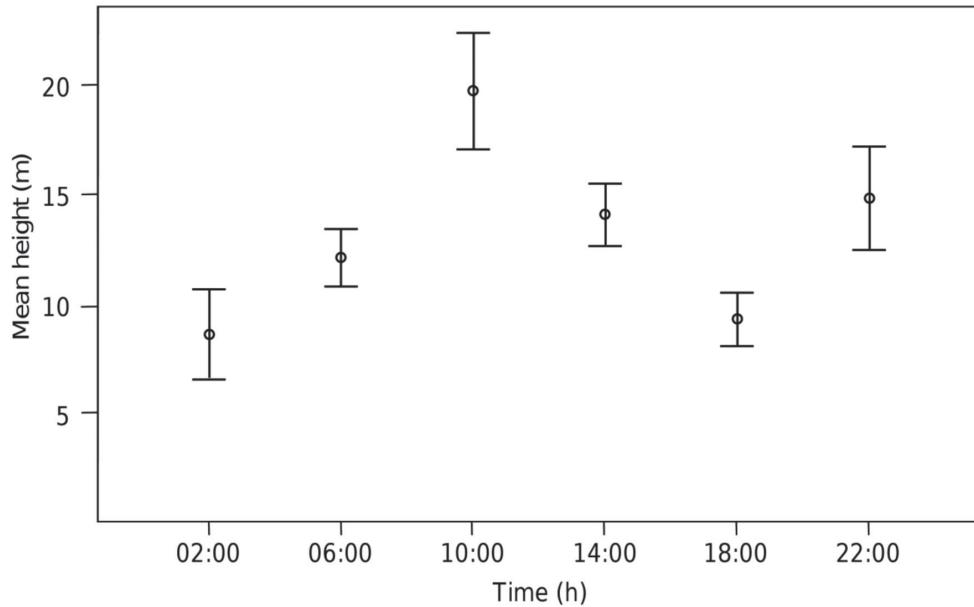


FIG. 3. Altitude above ground averaged in 4-hour batches (see text) of all katydids.

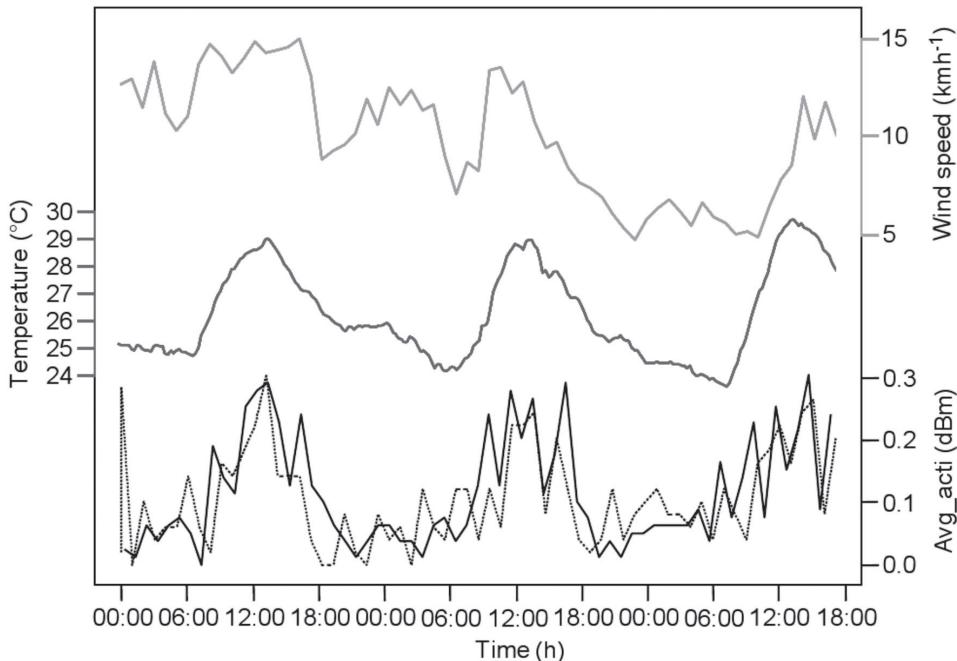


FIG. 4. Wind speed at 48 m above ground in  $\text{km h}^{-1}$  (upper line), temperature at 48 m above ground in  $^{\circ}\text{C}$  (middle line) and katydid average activity (Avg\_acti; lower solid line: ID11, lower dashed line: ID5) in standardized decibel values (dBm) at the observation site during three continuous days (1 to 3 March 2008).

and a maximum of  $28^{\circ}\text{C}$  at noon, typically a few degrees higher at 48 m (Fig. 4) than at 1 m above ground. Mean wind speed peaks slightly later than mean temperature, but otherwise follows a similar daily pattern. The activity data indicate that *P. ingens* is diurnal and that at least the onset of main activity is correlated with changes in environmental parameters, e.g. daily high temperatures and/or daily high wind speeds (Fig. 4). Activity starts to increase around 10:00 h and peaks between 11:00 h and 14:00 h. Katydid activity then decreases sharply towards 16:00 h until reaching the nightly low level at 21:00 h. Mean activity of all katydids around noon (11:00–14:00 h) is significantly higher than during the other three time slots (ANOVA;  $N = 10$  katydids;  $\text{df} = 23$ ;  $F = 4.729$ ;  $P < 0.001$ ). Katydids were most active at temperatures of about  $26^{\circ}\text{C}$ . Importantly, katydid activity started to decrease 20 min after the hottest time of the day (between 14:00 h and 15:00 h; Fig. 4). Mean observed katydid activity was strongest when wind at 48 m above ground reached the  $10 \text{ km h}^{-1}$  mark but then dropped while the wind speed was still higher than  $10 \text{ km h}^{-1}$ .

## DISCUSSION

Here we present the first in-depth radio-tracking study on tropical katydids showing that continuous behavioural observations on individual insects in the field can yield surprising results. We fitted the insects with miniaturized transmitters to follow movement (i.e. changes of their location) as well as activity (distinguishing between the resting, inactive animal and the active animal, even if it does not change location). The majority of rainforest katydids are thought to be predominantly nocturnal, shown by a study on understory katydids (Nickle & Castner 1995). However, our data indicate that *Philophyllia ingens* is most active during the day, even if not changing location.

The automated receiving units registered differences in the signal strength of the transmitters, caused even by very small-scale movements of the animals. The observed activity was not caused by wind moving leaves on which the katydids were sitting, as mean daily activity levels dropped earlier than mean wind speeds. Katydids are ectotherms and generally perform better at high ambient temperatures (Huey & Kingsolver 1989). The activity peak of our study

species coincided with the onset of the warmest time of the day, which may simply be when performance of individuals is best, perhaps either to increase foraging efficiency or predation avoidance, or both. However we do not know how close the high temperatures during the day are to the critical thermal maximum of katydids (Huey & Kingsolver 1989).

Male Phaneropterinae can sing during the day, and the observed diurnal sedentary activity may thus also be connected to display behavior, e.g. stridulating and continuous movement to attract females, thus avoiding acoustically oriented nocturnal predators like bats (Heller & von Helversen 1993). All long-distance movements we observed happened at night and similar behavior may have led to the impression that the Phaneropterinae are nocturnal.

Nocturnal predators have a significantly stronger impact on the abundance of arthropods on plants than diurnal predators (Kalka *et al.* 2008). By being diurnally active while remaining in the same spot, *P. ingens* might avoid attracting these more efficient nocturnal predators. However katydids have to be inconspicuous also during the day. When we threw two katydids into midair in a clearing during daytime to measure how far they would be able to fly (unpubl. data), both were caught by birds before reaching the shelter of the vegetation. In addition, we found the transmitters of two tracked katydids along with various body parts, indicating predation by a small bird or rodent. Although we cannot exclude an influence of the transmitters, predation on our katydids was high. Therefore behavior leading to predation avoidance should be valuable and avoidance of long-distance movements during the daytime could be adaptive.

The time of highest activity – around noon – coincided with the time when the katydids were situated highest in the trees. Katydids stayed at a height of approximately 10 m above ground throughout most of the day. This foliage-rich layer of the lower-canopy harbors a high diversity of plant species, which might provide good feeding habitat as well as opportunities for camouflage. The observed upward movement to the higher canopy in the morning might then be induced by temperature gradients or the presence of sun-exposed substrates. The reason for the significant downwards movement in the evening remains unclear, but moving to places with lower light levels might be a reaction to increased predator activity in the evening (Lang *et al.* 2006). We wish to avoid any strong adaptive interpretations of the diurnal al-

titudinal movements because our height measurements were difficult to conduct and probably represent underestimates due to the v-shape of the valley.

We do not know in detail what our katydids did when they moved position and whether this was correlated with feeding, finding mates, or other potential behaviors. Therefore we employ commonly used terms from the radio-telemetry literature to describe our data, even though future studies might allow more accurate definitions of the behaviors in question. The “home range” of our *P. ingens* was about 1100 m<sup>2</sup> and thus they clearly move frequently between trees and branches, even if without detectable daily directional patterns. More interestingly, there is also no difference between day and night in the mean distance covered, once “dispersal” events are excluded. In contrast, all five katydids which disappeared from our reception range did so between 23:00 and 01:00 h. We conclude that male katydids stay in a certain area, making short-distance movements to search for food or as a consequence of display behavior. But from time to time long distance movements are undertaken for unknown reason.

Radio-telemetry with miniaturized transmitters enabled us to study the individual large-scale movements and small-scale activity of katydids in environments such as the canopy of tropical rainforests, which are hard for scientists to reach. Data from four similarly-sized katydid species indicate that the transmitters’ effect on mortality and flight capability is negligible (H. Grimm unpubl. data). Previous studies on other insects used transmitters of much higher relative mass: 35%-50%, 20%-25%, and 34% of insect body mass instead of the 8.5% in our study (Riecken & Raths 1996, Hedin & Ranius 2002, Wikelski *et al.* 2006, Sword *et al.* 2008), so our results provide valuable new insights and reliable information on behavior.

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## REFERENCES

- Belwood, J.J. 1990. Anti-predator defenses and ecology of neotropical forest katydids, especially the Pseudophyllinae. Pp. 8-26 in Bailey, W.J. & D.C.F. Rentz (eds.). The Tettigoniidae: Biology, Systematics and Evolution. Springer Verlag, Bathurst, Australia.
- Belwood, J.J. & G.K. Morris. 1987. Bat predation and its influence on calling behavior in Neotropical katydids. *Science* 238: 64-67.
- Bisson, I.A., Butler, L.K., Hayden, T.J., Romero, L.M. & M.C. Wikelski. 2009. No energetic cost of anthropogenic disturbance in a songbird. *Proceedings of the Royal Society (B)* 276: 961-969.
- Cochran, W.W. & L.L. Pater. 2001. Direction finding at ultra high frequencies (UHF): improved accuracy. *Wildlife Society Bulletin* 29: 594-599.
- Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C. & M. Wikelski. 2009. Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proceedings of the Royal Society (B)* 276: 2721-2728.
- Dechmann, D.K.N., Kranstauber, B., Gibbs, D. & M. Wikelski. 2010. Group hunting—A reason for sociality in molossid bats? *PLoS ONE* 5(2): e9012
- Hebard, M. 1933. Notes on Panamanian Dermaptera and Orthoptera. *Transactions of the American Entomological Society* 59: 103-144.
- Hedin, J. & T. Ranius. 2002. Using radio telemetry to study dispersal of the beetle *Osmoderma eremita*, an inhabitant of tree hollows. *Computers and Electronics in Agriculture* 35: 171-180.
- Hedin, J., Ranius, T., Nilsson, S.G. & H.G. Smith. 2008. Restricted dispersal in a flying beetle assessed by telemetry. *Biodiversity and Conservation* 17: 675-684.
- Heller, K.G.. & D. von Helversen. 1993. Calling behavior in bushcrickets of the genus *Poecilimon* with differing communication systems (Orthoptera: Tettigoniidae, Phaneropteridae). *Journal of Insect Behavior* 6: 361-377
- Holland, R.A., Wikelski, M., Kummeth F. & C. Bosque. 2009. The secret life of oilbirds: new insights into the movement ecology of a unique avian frugivore. *PLoS ONE* 4(12): e8264
- Huey, R.B. & J.G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution* 4: 131-135.
- Kalka M.B. & E.K.V. Kalko. 2006. Gleaning bats as underestimated predators of herbivorous insects: diet of *Micronycteris microtis* (Phyllostomidae) in Panama. *Journal of Tropical Ecology* 22: 1-10.
- Kalka, M.B., Smith, A.R. & E.K.V. Kalko. 2008. Bats limit arthropods and herbivory in a tropical forest. *Science* 320: 71.
- Kays, R., Tilak, S., Crofoot, M., Fountain, T., Obando, D., Ortega, A., Kuemmeth, F., Mandel, J., Swenson, G., Lambert, T., Hirsch, B. & M. Wikelski. 2011. Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *Computer Journal* 54: 1931-1948.
- Kjos, C.G. & W.A. Cochran. 1970. Activity of migrant thrushes as determined by radio-telemetry. *Wilson Bulletin* 82: 225-226.
- Lambert, T.D., Kays, R.W., Jansen, P.A., Aliaga-Rossel, E., & M. Wikelski. 2009. Nocturnal activity by the primarily diurnal Central American agouti (*Dasyprocta punctata*) in relation to environmental conditions, resource abundance and predation risk. *Journal of Tropical Ecology* 25: 211-215.
- Lang, A.B. 2008. Roost site selection and site fidelity in the neotropical katydid *Docidocercus gigliotosi* (Tettigoniidae). *Biotropica* 40: 183-189.
- Lang, A.B., Kalko, E.K.V., Römer, H., Bockholdt, C. & D.K.N. Dechmann. 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146: 659-666.
- Leigh, E.G. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, New York.
- Martins, M.M. & E.Z.F. Setz. 2000. Diet of buffy tufted-eared marmosets (*Callithrix aurita*) in a forest fragment in southeastern Brazil. *International Journal of Primatology* 21: 467-476.
- Naskrecki, P. 2000. Katydids of Costa Rica. Volume 1. Systematics and bioacoustics of the cone-head katydids. The Orthopterists' Society at the Academy of Natural Sciences of Philadelphia, Philadelphia.
- Nickle, D.A. 1992. Katydids of Panama (Orthoptera: Tettigoniidae). Pp. 142-184 in Quintero D. & A. Aiello (eds.). *Insects of Panama and Mesoamerica, Selected Studies*. Oxford University Press, New York.
- Nickle, D.A. & J.L. Castner. 1995. Strategies utilized by katydids (Orthoptera: Tettigoniidae) against diurnal predators in rainforests of northeastern Peru. *Journal of Orthoptera Research* 4: 75-88.
- Odum, E.P., Barrett, G.W. & R. Brewer. 1971. *Fundamentals of ecology*. W.B. Saunders, Philadelphia.
- Riecken, U. & U. Rath. 1996. Use of radio telemetry for studying dispersal and habitat use of *Carabus coriaceus* L. *Annales Zoologici Fennici* 33: 109-116.
- Sword, G.A., Lorch, P.D. & D.T. Gwynne. 2008. Radiotelemetric analysis of the effects of prevailing wind direction on Mormon cricket migratory band movement. *Environmental Entomology* 37: 889-896.
- Wikelski, M., Moskowitz, D., Adelman, J.S., Cochran, J. & D. Wilcove. 2006. Simple rules guide dragonfly migration. *Biology Letters* 2: 325-329.