Remaining cryptic during motion — behavioral synchrony in the proboscis bat (*Rhynchonycteris naso*)

MIRJAM KNÖRNSCHILD[1, 4], CHRISTINA HARVIEW[2], RACHEL MOSELEY[3], and OTTO VON HELVERSEN[1]

[1]*Department of Zoology, University Erlangen-Nürnberg, Staudtstrasse 5, D-91058 Erlangen, Germany*
[2]*Department of Biology, Bryn Mawr College, 101 N. Merion Avenue, Bryn Mawr, PA 19010, USA*
[3]*Department of Biology, Bucknell University, 701 Moore Avenue, Lewisburg, PA 17837, USA*
[4]*Corresponding author: E-mail: mknoerns@biologie.uni-erlangen.de*

INTRODUCTION

Most bat species inhabit roosting sites in which they are well concealed during the day, such as caves or tree holes, whereas others roost in exposed locations on tree trunks or branches (Kunz and Lumsden, 2003). For the latter, it is essential to appear cryptic in order to avoid predation or disturbance at the day-roost. Several traits have evolved to enhance the bats' cryptic appearance, including cryptic coloration (e.g., the greenish wings of the foliage-roosting bat *Paranyctimene raptor* — Bonaccorso, 1998) or disruptive markings (e.g., the contrasting metacarpals and phalanges of the tent-roosting flying fox *Cynopterus brachyotis* — Kunz and Lumsden, 2003). Behavioral habits may also aid in camouflaging roosting bats. One remarkable example is the 'leaf wrapping behavior' exhibited by the Australian flute-nosed bat *Murina florium*, which conceals these foliage-roosting bats effectively from visually oriented predators (Schulz, 1999). In general, there are many more known examples of morphological adaptations for cryptic roosting than there are of behavioral adaptations (Kunz, 1982; Kunz and Lumsden, 2003). Remaining completely motionless during the day is a behavioral habit that obviously assists in camouflage, but it conflicts with the bats' need for comfort behavior, such as grooming or stretching.

We studied the cryptic roosting habits of the proboscis bat, *Rhynchonycteris naso*. This neo-tropical member of the emballonurid family roosts in very exposed areas on tree trunks, branches, vines or man-made structures which are in close proximity to running water (Bradbury and Emmons, 1974). Group size is intermediate, and ranges from 5 to 50 individuals of both sexes (Bradbury and Vehrencamp, 1976). Individuals of small groups normally roost in a vertical line, whereas larger groups tend to form ovals (Bradbury and Emmons, 1974). Independent of group size, a vertical line is always formed when individuals roost on structures with a small diameter, such as thin trunks, branches and vines (authors' personal observation). Despite its exposed day-roosts, *R. naso* is physically very cryptic due to the woolly and mottled pelage with two wavy pale lines on the back and tufts of pale hair on the forearms (Dalquest, 1957; Bradbury and Vehrencamp, 1976). This protective camouflage allows the roosting bats to resemble a patch of lichen or moss (Hill and Smith, 1984). Bradbury and Emmons (1974) first reported a 'synchrony in grooming periods by group members' and 'frequent periods of gentle rocking', a stereotypic behavior in which the bats sway rapidly from side to side while both feet and wrists remain attached to the surface of the roost. This peculiar behavior occurs frequently during the day and is often exhibited synchronously by many or all group members, but it is not triggered by disturbance. When startled or approached, the bats do not rock, but instead remain motionless before they fly off together. Therefore, the functional significance of rocking has remained unclear (Bradbury and Emmons, 1974), but a somewhat related behavior in arachnids, termed whirling or bobbing, is proposed to provide a camouflage defence against predators (Jackson, 1990; Heuts *et al*., 2001; Grether and Donaldson, 2007). Group members of *R. naso* not only synchronize rocking and grooming but also urinating (authors' personal observation), but the benefit, if any, of this behavioral synchrony is unknown.

We investigated whether rocking could play a role in the bats' cryptic roosting habits. We firstly hypothesized that bats engage in rocking behavior to resemble patches of vegetation swaying in the wind and, hence, that rocking is triggered by gusts of wind. We tested this hypothesis by relating the occurrence of rocking to simultaneous wind velocity at the roosting sites. We secondly hypothesized that synchronous rocking by many individuals is used to actively disguise other behaviors, such as grooming or urinating, and tested this hypothesis by conducting behavioral observations during rocking periods.

MATERIALS AND METHODS

Observations and measurements were carried out at the Biological Station La Selva in Costa Rica (10°25'N, 84°00'W) in two consecutive years (July 2007, June 2008). The five social groups of *R. naso* that were used for this study occupied day-roosts under the roofs of both abandoned and inhabited buildings throughout the station property. These 'artificial' day-roosts were comparable to 'natural' day-roosts (e.g., on tree trunks) with regard to their exposure to general weather conditions like heat and wind. Group size ranged between 8 and 35 bats. Bats of all groups were habituated to the presence of human observers, which made it possible to gather data without causing noticeable disturbance.

Each group was observed ten times for a minimum of 30 minutes per observation session (total observation time: 37.4 hours). During each observation session, we recorded the occurrence of rocking and the associated behaviors grooming and urinating. We estimated the total number of bats rocking by assigning one of five categories (0, 25, 50, 75, and 100% of the group). This estimation was conducted at the end of each rocking bout because usually one or few individuals started rocking and then others progressively joined in. When a single bat rocked for only a few seconds and ceased without others joining in, we assigned the 0% category because we interpreted it as an unsuccessful attempt of one individual to engage other group members in rocking behaviour. We also noted whether rocking was accompanied by either grooming (i.e., licking and/or scratching of pelage and wing membranes) or urinating (i.e., lifting the body away from the surface with both forearms and feet while excreting clearly visible droplets of urine) or both. In addition, wind velocity measurements were conducted every two minutes and whenever rocking occurred. We used a Kestrel® 1000 Pocket Wind Meter (Nielsen-Kellerman Co., Boothwyn, PA 19061, USA; range: 0.1–60.0 m/s; resolution: 0.1 m/s) that was placed in close vicinity to the roosting bats (maximum distance of two meters).

Since multiple rocking periods could occur during an observation session, the data was averaged per category (0, 25, 50, 75, and 100% of the group) for each session. The occurrence of grooming and urinating was scored with values of 0 or 1 for each rocking bout, added for all the rocking bouts within an observation session and then averaged over all observation sessions per group (always separately for each rocking category). We used General Linear Mixed Models (GLMM) to test for relations between wind velocity, rocking, and associate behaviors. Multiple measurements per group were controlled for by adding group identity as a random factor in the GLMM. All statistical tests were conducted using SPSS version 11.5 (SPSS Inc., Chicago, IL, USA).

RESULTS

Rocking occurred significantly more often during a gust of wind than during a calm (repeated measures ANOVA: $F_{1, 4} = 238.61$, $P < 0.001$; mean occurrence of rocking during gusts and calms for every observation session; five groups with 10 repeated measures each). Nonetheless, the relation between the occurrence of rocking and wind velocity was not mandatory: not every gust of wind was accompanied by rocking (143, i.e. 34.6% of the 413 gusts measured were not followed by rocking; wind velocity: 0.1–0.5 m/s) and, likewise, single bats sometimes rocked briefly despite a complete calm (53, i.e. 11.4% of the 466 rocking occurrences observed). We found a significant positive relation between the wind velocity and the percentage of rocking bats per group (GLMM with wind velocity as independent and % of rocking bats as dependent variable: $F_{1, 19} = 521.00$, $P < 0.001$). An increase in wind velocity by 0.2 m/s caused an approximate 25% increase in the amount of rocking bats per group (fixed effect: wind velocity; estimate = 0.246, $T_{19} = 22.83$, $P < 0.001$; see Fig. 1A).

We found a significant positive relation between the percentage of rocking bats per group and the occurrence of both grooming and urinating (GLMM with % of rocking bats as independent variable and (a) occurrence of grooming as dependent variable: $F_{1, 23} = 20.37$, $P < 0.001$; and (b) occurrence of urinating as dependent variable: $F_{1, 23} = 23.93$, $P < 0.001$). Synchronous grooming increased constantly as the percentage of rocking bats per group increased, whereas synchronous urinating occurred only when at least 75% of all group members exhibited rocking behavior (Fig. 1B). In the majority of cases, rocking was accompanied by either grooming or urinating (rocking with associate behaviors = 56%; rocking without associate behaviors = 38%; grooming without rocking = 6%). This suggests that synchronous rocking is used to conceal other behaviors which, undisguised, might undermine the cryptic roosting habits of *R. naso*.

DISCUSSION

Our study shows that proboscis bats are more likely to rock during gusts of wind than during calms, and that the proportion of rocking group members increases with increasing wind velocity.

Synchronous grooming and urinating often accompanied rocking, especially when many group members were participating. These findings provide evidence that rocking is a behavioral adaptation for the bats' cryptic roosting habits. Rocking during gusts of wind could aid in camouflaging the bats because roosting *R. naso* resemble patches of vegetation that might have to sway in a breeze in order to appear persuasive (Emmons, 1990). However, rocking did not occur during all gusts of wind, at least not when the wind velocity was low. This could imply that rocking for camouflage is only obligatory during higher wind velocities and merely optional during lower wind velocities. The fact that rocking was often accompanied by synchronous grooming and urinating suggests that individual bats might perceive gusts of wind as convenient occasions to engage in comfort behaviors which are well disguised by the
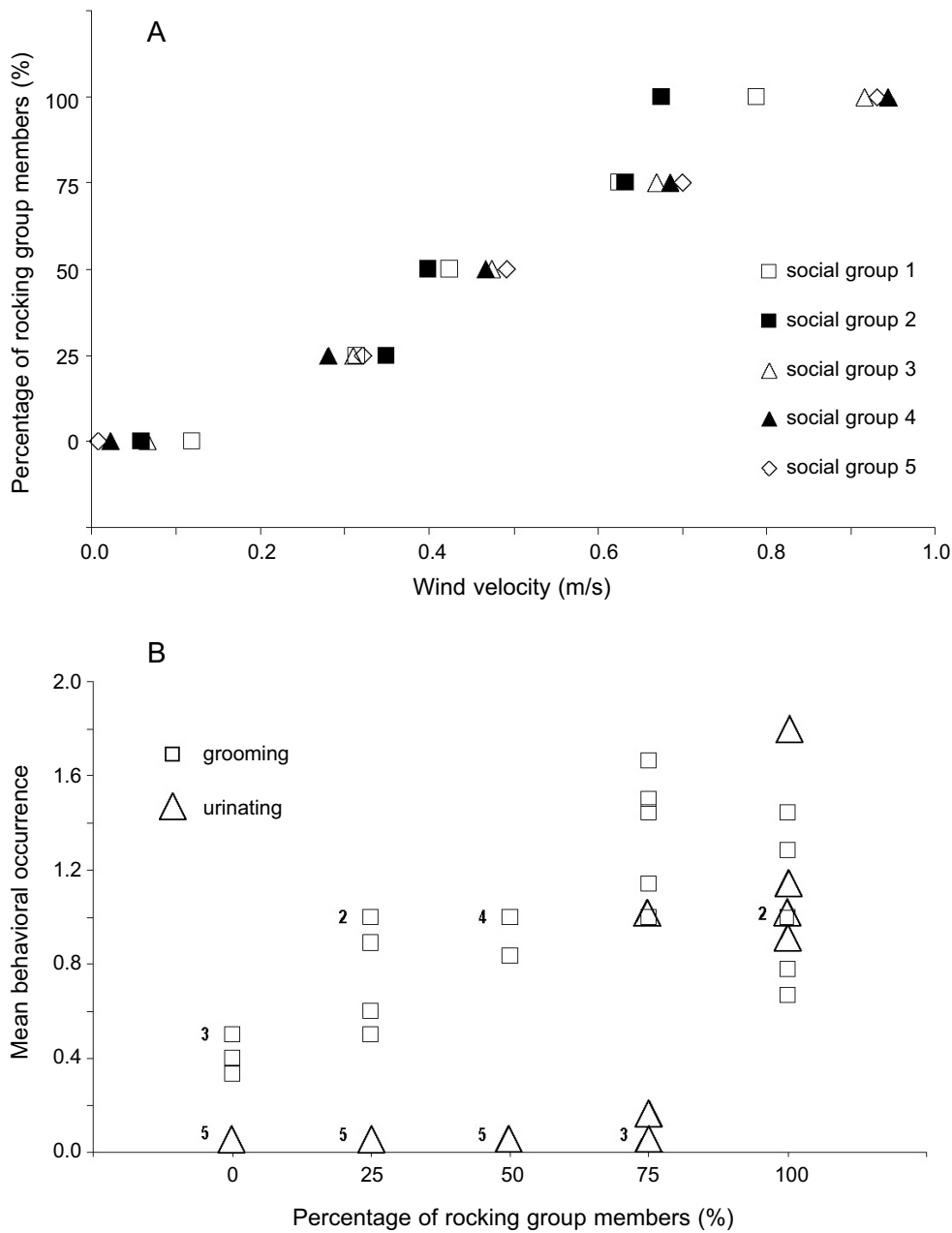

FIG. 1. Relationship between A — the wind velocity and the percentage of rocking group members and B — the percentage of rocking group members and the mean occurrence of the associated comfort behaviors grooming and urinating. Means of 10 observation sessions per social group are shown. In Fig. 1B some symbols fully overlap to an extend indicated by the numbers next to the respective symbols

simultaneous rocking of group members. In our belief, rocking of *R. naso* is one of the few examples of behavioral adaptations for cryptic roosting. In contrast to previous findings in different species (Kunz, 1982; Schulz, 1999; Kunz and Lumsden, 2003), the behavioral adaptation for cryptic roosting exhibited by *R. naso* consists not of passive motionlessness but of active movement. Together with its morphological adaptations (Dalquest, 1957; Bradbury and Vehrencamp, 1976), rocking allows *R. naso* to remain cryptic during motion.

LITERATURE CITED

BONACCORSO, F. J. 1998. Bats of Papua New Guinea. Conservation International, Washington, D.C., 496 pp.

BRADBURY, J. W., and L. H. EMMONS. 1974. Social organization of some Trinidad bats. I. Emballonuridae. Zeitschrift für Tierpsychologie, 36: 137–183.

BRADBURY, J. W., and S. L. VEHRENCAMP. 1976. Social organization and foraging in emballonurid bats. I. Field studies. Behavioral Ecology and Sociobiology, 1: 337–381.

DALQUEST, W. W. 1957. Observations on the sharp-nosed bats, *Rhynchiscus naso*. Texas Journal of Science, 9: 219–226.

EMMONS, L. H. 1990. Neotropical rainforest mammals — a field guide. University of Chicago Press, Chicago, 307 pp.

GRETHER, G. F., and Z. R. DONALDSON. 2007. Communal roost site selection in a neotropical harvestman: habitat limitation vs. tradition. Ethology, 113: 290–300.

HEUTS, B. A., M. WITTEVELDT, L. M. DIONISIO PIRES, and F. VAN WAGENINGEN. 2001. Long-duration whirling of *Pholcus phalangioides* (Araneae, Pholcidae) is specifically elicited by salticid spiders. Behavioural Processes, 55: 27–34.

HILL, J. E., and J. D. SMITH. 1984. Bats — a natural history. University of Texas Press, Austin, 243 pp.

JACKSON, R. R. 1990. Predator-prey interactions between jumping spiders (Salticidae) and *Pholcus phalangioides* (Pholcidae). Journal of Zoology (London), 220: 553–559.

KUNZ, T. H. 1982. Roosting ecology of bats. Pp. 1–55, *in* Ecology of bats (T. H. KUNZ, ed.). Plenum Press, New York, 450 pp.

KUNZ, T. H., and L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–89, *in* Bat ecology (T. H. KUNZ and M. B. FENTON, eds.). University of Chicago Press, Chicago, 798 pp.

SCHULZ, M. 1999. Leaf wrapping behavior in the flute-nosed bat *Murina florium*. Bat Research News, 40: 6–8.