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Directionality of drinking passes by bats at water holes: is there cooperation?

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In 2000 and 2001, we used an infrared imaging system to film the drinking behaviors of bats at high-use water holes outside Boulder, Colorado. We recorded for two hours on each of four nights at two water hole sites, Stockton Cabin (SC) and Bear Creek (BC), known to be high in bat visitation and small enough to allow filming of the entire hole from a single position. A total of 855 drinking passes was observed: 417 and 438 in SC and BC, respectively. Of these, 814, or 95.2%, of all drinking passes occurred from a particular directional pathway (dominant approach pathway) at each site, with a mere 1.3% occurring from the immediately opposite direction, and 3.5% occurring from a direction convergent with, but not opposite to, the dominant approach path. At both sites, the direction of the dominant approach path was against stream-flow. The strict directionality of drinking passes portrayed at the water's surface was in stark contrast to activity above the water hole where no directionality of flight could be discerned, even when dozens of bats were circling together. We hypothesize that bats use unidirectional coordination of drinking passes to lessen the chance of collisions and/or to avoid the energetic expense of collision avoidance.

Key words: bats, behavior, cooperation, water resources, Colorado

INTRODUCTION

Throughout the literature there is little consideration or documentation of how interspecific cooperation may be important to species coexistence. Three types of cooperation have been observed: 1) mutually facultative, a rather loose form of cooperation leading to coexistence, 2) mutually obligate, the tightest cooperation, leading to coexistence or extinction relative to the relationships strength, and 3) nonmutually facultative, obligate for one, but facultative for the other, an extension of parasitism, that would predictably lead to either coexistence of

both or extinction of the obligate (Tokeshi, 1999).

For bats, cooperative interactions such as eavesdropping (Fenton and Morris, 1976; Bell, 1980; Barak and Yom-Tov, 1989), following behavior (Wilkinson, 1992), and imitative learning (Gaudet and Fenton, 1984) occur within and among species. Group foraging is also commonly found in several species (e.g., Dwyer, 1970; Bradbury and Vehrencamp, 1976; Sazima and Sazima, 1977; Howell, 1979; Barak and Yom-Tov, 1989) that exhibited co-ordinated flight; presumably an advantageous behavior that effects efficient foraging (Wilkinson, 1995).

Cooperation among females using allomaternal care has been documented in several species of bats (see Jones, 2000 for review).

In this paper we report on drinking behaviors among bats utilizing high-use water holes located outside Boulder, Colorado. Although for some bat species foraging over water may provide an acoustic advantage (Siemers *et al.*, 2001), behaviors associated with drinking at water holes has received little attention. We find that bats organize around distinctive approach pathways during drinking passes. The cues bats use to organize the patterns documented at our study sites has yet to be determined, however, future investigations into drinking behaviors are planned.

MATERIALS AND METHODS

We focused this study on two water holes known to be the highest in bats activity and species diversity in the area based upon six years of mist net data. These two sites are referred to as Shadow Canyon (SC) and Bear Canyon (BC) and are small water holes (< 3 m in diameter) that allowed for our camera's lenses to cover the entire site from a single position during filming. On the nights of 4 and 5 July 2000, and 22 and 23 July 2001, we used an Indigo Systems 'Merlin' midrange cooled, infrared imaging system with a SONY video walkman 8-mm VCR, to film the drinking behaviors of bats at two high-use water holes in Colorado. The camera was position at

approximately 1.5 m from the edge of each water hole on a tripod approximately 1.0 m in height. We began filming a few minutes before bats began arriving and continued filming for 1.5 hours on each of the four nights.

We played back videos using a General Electric VG4261 VCR attached to a Sony Trinitron Monitor. On the screen of the monitor we placed a transparent diagram of compass directions positioned relative to true north at each site. In order to calculate approach angle of individuals to each water hole, a compass diagram was partitioned into 45° portions (Fig. 1). This produced eight categories, each encompassing a range of degrees as follows: 1: 0–45, 2: 46–90, 3: 91–135, 4: 136–180, 5: 181–225, 6: 226–270, 7: 271–315, and 8: 316–360. Because filming was conducted from a position lateral to and slightly above each water hole, we determined, conservatively, that our best resolution on approach angles was in increments of 45°. Data on the position of each individual during its drinking pass relative to the eight directional categories was recorded. A drinking pass was tallied only when the individual's face made contact with the water's surface. From these data we calculated the angle of approach for each pass relative to our eight categories, the frequency of drinking passes per category, and the relative frequency of drinking passes per category. Raw pass data from each category recorded from each water hole were analyzed with χ^2 -analyses using NCSS 6.1 (Number Crunching Statistical Systems, Kaysville, UT).

RESULTS

Six years of trapping data show that SC averaged 12.34 bats per net per night (bnn)

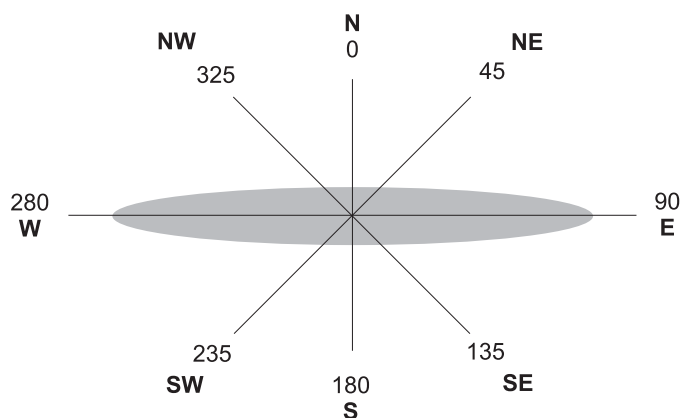


FIG. 1. Schematic to show placement of compass settings relative to calculating approach pathways of passes at each site. Gray area depicts water hole

among nine species ($n = 396$) and BC that averaged 10.52 bnn among eight species ($n = 400$) attracted the highest levels of visitation by bats and supported the highest diversity of bat species in the area. On highly active nights, capturing 50–70 individuals in two 7 m mist nets over a two-hour period was usual.

A total of 855 passes was recorded at the two sites (SC: $n = 417$; BC: $n = 438$). Of these, 814, or 95.2%, of all drinking passes occurred from a particular pathway (dominant approach path) at each site, with a mere 4.8% occurring from other compass directions. Although the compass angle of the dominant approach path differed between sites, the pattern of an established drinking pathway was consistent. At SC, 396 of 417 drinking passes were between 46° and 90° (Table 1) and at BC, 418 of 438 drinking passes were between 0° and 45° . The χ^2 -analyses show these patterns to be significantly different from an equal distribution of passes across all angle classes (SC: $\chi^2 = 834$, $d.f. = 7$, $P < 0.001$; BC: $\chi^2 = 876$, $d.f. = 7$, $P < 0.001$). At highest activity, time between drinking passes was approximately 0.5–2.0 seconds. We note that number of drinking passes recorded may not equal number of individuals using the site, as each bat may pass to drink more than once per sample.

On 4 and 5 July 2000, 91.2% and 92.6% of the drinking passes at SC and BC respectively adhered to a dominant flight path, whereas in 2001, filming on 23 and 24 July showed 97.7% and 97.6% of drinking passes, respectively adhered to the dominant flight path. The angle of the dominant flight path did not vary between years. At both sites, the direction of the dominant approach path was against a mild stream-flow. The strict directionality of drinking passes portrayed at the water's surface was in stark contrast to activity above the water hole where bats entered the camera lense field

TABLE 1. Frequency data of drinking passes at Shadow Canyon (SC) and Bear Canyon (BC) water holes. $a_i(\text{deg})$ — range of compass degrees; f_i — number of passes; relative f_i — relative frequency

$a_i(\text{deg})$	f_i		Relative f_i	
	SC	BC	SC	BC
0–45	12	418	0.028	0.954
46–90	396	9	0.949	0.020
91–135	0	0	0.000	0.000
136–180	9	0	0.021	0.000
181–225	0	11	0.000	0.025
226–270	0	0	0.000	0.000
271–315	0	0	0.000	0.000
316–360	0	0	0.000	0.000

from variable directions, with at times dozens of individuals circling the water hole.

DISCUSSION

The drinking patterns of bats visiting water holes described herein, indicate that bats establish a consistent approach pathway for drinking at water holes. Individuals observed in flight above the water hole showed no apparent directionality relative to the distinct flight paths used when approaching to drink. In fact, drinking approaches mimicked a landing strip at an airport involving, in some instances, individuals approaching single-file as if descending to land. Moreover, on several occasions, individuals approaching the site from above and in the opposite direction of the drinking pathway were observed orchestrating u-turns that entered them into the dominant drinking pathway. The only consistent parameter observed was that the dominant approach path was more or less in the opposite direction of stream flow, which at these sites was minimal. Other parameters, however, such as surface airflow and shadows from vegetation at the site may be used by bats to coordinate drinking behaviors. Curiously, our data show that in early July bats conformed to the set pathways less so

than later in July. These data suggest that there may be a learning curve for juveniles as they become volant. At our field sites, newly volant young begin to be captured in mid-June, with older juveniles and subadults captured mid-July through August. It seems reasonable to surmise that newly volant juveniles would learn water hole etiquette from mimicking adults and older juveniles and therefore later in July many juveniles have learned the approach paths making for less confusion at water holes. Moreover, because individuals, adults included, would likely drink at several different water holes nightly, or over the course of the summer, presumably they would need to learn the predesignated approach path at each site by watching other bats drinking.

The most obvious reason for orchestrating drinking paths at water holes is to lessen the risk of aerial collisions as the bats approach the site, drink, and exit. On several instances during peak activity, individuals attempted to drink from a convergent or opposite angle and near collisions were observed. Because their mouths are full of water after drinking, detection of other bats in their flight path by using sonar may be affected; although eavesdropping on the calls of other bats should still be possible (M. B. Fenton, pers. comm.). That individuals would have difficulty emitting echolocation pulses due to oral cavity obstruction is supported by studies showing that the duration of 'post-buzz pause' was significantly longer after successful prey capture. For some species increased pause-length was correlated with prey size and apparently handling time (Acharya and Fenton, 1992; Britton and Jones, 1999). Another possible adaptive pressure for defined drinking pathways at water holes would be averting the energetic expense associated with collision avoidance.

The data presented herein adds to the few studies concerning cooperation in bats, and, to our knowledge is the first to quantifying cooperative, coordinated behaviors at the interspecific level, in this case, involving up to nine species. Intraspecific cooperation among bats is known to occur while foraging as well as among individuals in maternity roosts (e.g., Gaudet and Fenton, 1984; Wilkinson, 1985, 1987, 1995; Galef, 1988; Kerth and König, 1999). The fact that in early July, when newly volant juveniles are active, adherence to the prescribed flight path is less, suggests that this cooperation is a form of imitative learning. Moreover, these behaviors may be mutually obligate, the tightest form of cooperation (Tokeshi, 1999). Further investigations into these behavioral patterns are planned.

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