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AN OBSERVATION OF APPARENT TEACHING BEHAVIOR IN THE PALLID BAT, ANTROZOUS PALLIDUS

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ABSTRACT.—During a laboratory study of pallid bat (Antrozous pallidus) hunting behavior, we observed an interaction wherein an adult female appeared to aid a juvenile male in learning a novel foraging task. This single observation adheres to the 3 requirements of teaching outlined by Caro and Hauser (1992). A female bat experienced with a hunting task modified her behavior in the presence of a naïve observing male, resulting in a cost of reduced food availability to the female when she was hungry, while directing the male to food resources and accelerating his learning of a foraging task. The experienced female bat altered her behavior in the presence of a naïve male by nonaggressively approaching the perched male several times before flying to a bowl of live mealworms. Within minutes, her behavior led to the initiation of the foraging task by the naïve male. In sharp contrast, 5 other bats took 4–12 nights to learn this foraging task. Audio recordings of contact calls made during the interaction show possible information transfer via acoustic signals. We hope this lone observation will stimulate research on teaching in bats.

RESUMEN.—Durante un estudio de laboratorio sobre el comportamiento de caza del murciélago pálido (Antrozous pallidus), observamos una interacción de una hembra adulta que parecía enseñar una nueva técnica de búsqueda de alimento a un macho joven. Esta sencilla observación cumple con los tres requisitos de aprendizaje descritos por Caro y Hauser (1992). Un murciélago hembra, con experiencia en la caza, modificó su comportamiento en presencia de un murciélago macho inexperto que la observaba, lo que resulta en una menor disponibilidad de alimento para la hambrienta hembra, mientras orienta al macho hacia el recurso y acelera su aprendizaje de búsqueda de alimento. El experimentado murciélago hembra alteró su comportamiento en presencia del macho acercándose varias veces, de manera no agresiva, al macho que estaba colgando y en reposo antes de volar hacia un recipiente con gusanos vivos. En cuestión de minutos, este comportamiento incitó al macho inexperto a su iniciación en la tarea de búsqueda de alimento, en contraste con otros cinco murciélagos que necesitaron entre 4 y 12 noches para aprender esta tarea. Las grabaciones sonoras de los llamados de contacto registrados durante la interacción han mostrado que es posible transferir información a través de señales acústicas. Esperamos que esta observación derive en más investigaciones sobre el aprendizaje de los murciélagos.

Three main criteria characterize teaching behavior (Caro and Hauser 1992). First, an experienced individual, the teacher, must alter its behavior in the presence of a naïve observer. Second, the interaction must not immediately benefit, and may incur a cost to, the teacher. Finally, the observer must gain information from the interaction with the teacher that would have otherwise been difficult to acquire. Behavior meeting these conditions has been documented in only a few species, including meerkats (Suricata suricatta; Thornton and McAuliffe 2006), ants (Temnothorax albipennis; Franks and Richardson 2006), Southern Pied-Babblers (Turdoides bicolor; Rapaport 2006), and Atlantic spotted dolphins (Stenella frontalis; Bender et al. 2009). Here, we report an observation that suggests that pallid bats (Antrozous pallidus) may also be capable of such behavior.

In summer 2012, we captured and housed 7 pallid bats for an experiment investigating the effects of anthropogenic noise on bat foraging behavior. In an anechoic foam-lined flight room (7 \times 5.5 \times 4 m), the bats learned to find a single bowl (10 cm diameter) of live mealworms randomly placed in an array of 30 bowls recessed in a platform. The remaining 29 bowls functioned as controls and contained an equivalent number of freeze-dried mealworms. All bowls were covered with a screen to prevent access to the mealworms and to limit the use of echolocation in the foraging task. A dead mealworm, functioning as a reward, was placed on the screen of the target bowl, and dummy mealworms were placed on the tops of the screened control bowls. This approach allowed the foraging bats to detect sounds produced by the live mealworms in the single baited bowl, while controlling for

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other sensory cues such as olfaction, vision, and echolocation.

Training was required for the bats to hunt in this experimental design. The behavior was typically shaped by first presenting a large, flat bowl of live mealworms on the floor of the flight room. After a bat began to frequent the flat bowl, it was placed on top of the platform. Next, a bowl of live mealworms recessed in the platform was presented. Finally, the recessed bowl was screened (preventing access to the live mealworms within) and a dead mealworm was provided on the screen as a reward. It took 4–12 days of training for bats to learn this behavior.

In one notable instance, an adult female pallid bat, experienced with the hunting task, exhibited apparent teaching behavior when flown with a naïve juvenile male. We caught both bats at the same night roost and, thus, they may have been related or familiar with one another. The male was introduced to the flight room for one night while in the presence of other bats, including the "teaching" bat, but it did not hunt. The following night, the naïve male was released in the flight room with the experienced female. We placed a flat bowl with live mealworms on the floor and a screened, recessed bowl with dead mealworm rewards in the foraging platform. We observed the bats under dim red light, which is visible to humans but less perceptible to bats (Finley 1959).

Initially, the male bat was reluctant to fly and perched on the wall while the female bat began flying and hunting from the flat bowl. She landed on the flat bowl several times and took live mealworms. The sounds of prey consumption might have alerted the male to the presence of food, which has been observed in other studies (Gaudet and Fenton 1984, Page and Ryan 2006). After landing on the flat bowl several times, the female then altered her behavior and flew within several centimeters of the perched male. When the female approached the male, she did not produce squabble or irritation vocalizations (Brown 1976), indicating that the interaction likely was not threatening or aggressive. After this first approach, she flew away from the male, and then returned and flew within several centimeters of him a second time. After the second approach, the female bat landed on the flat bowl and began to eat. When the female took flight from the bowl, the male bat left his perch and began following her; they circled the room together several times. The male then landed on the flat bowl and ate at least one mealworm. He subsequently flew and began to land on the flat bowl repeatedly. Several times, both bats were observed eating from the open bowl together. When all the live mealworms from the open bowl were consumed, the female started taking dead mealworms from the top of the screen of the recessed bowl. After the female landed on the screened bowl several times, the male landed next to her on the bowl and ate a dead mealworm, thus performing the desired hunting task. He continued to land on the recessed bowl until all of the dead mealworms were consumed. The male learned to hunt in the experimental design in a single training session with the experienced female and a total of 2 nights of exposure to the flight room, which is faster than when bats learn via observational learning (Gaudet and Fenton 1984).

During the interaction, ultrasonic microphones were used to monitor acoustic communication. The female bat produced broadband, multiharmonic, low-frequency calls, particularly when taking off from a bowl. These acoustic signals match what Arnold and Wilkinson (2011) report as individually specific contact calls in pallid bats and potentially functioned as a stimulus enhancement (Heyes 1994). A spectrogram of a series of these calls (Fig. 1) illustrates the calls' spectral characteristics, and average spectral and temporal parameters of the calls were identified (Table 1). Arnold and Wilkinson hypothesized that contact calls might facilitate cooperative behavior between individuals (Arnold and Wilkinson 2011), as might be the case here.

Social learning has been documented in several bat species and in a range of contexts, including information transfer about roost sites in female Bechstein's bats (Myotis bechsteinii; Kerth and Reckardt 2003); the transmission of novel foraging behaviors and acoustic cue association with prey in fringe-lipped bats (Trachops cirrhousus; Page and Ryan 2006); and the use of social calls by female greater spearnosed bats (Phyllostomus hastatus) to coordinate foraging and defend feeding sites (Wilkinson and Boughman 1998). Observational learning has also been reported in big brown (Eptesicus fuscus; Gaudet and Fenton 1984, Wright et al. 2011), little brown (Myotis lucifugus; Gaudet and Fenton 1984), pallid

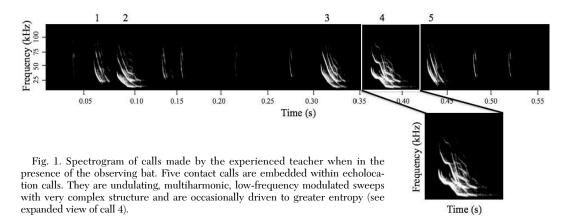


TABLE 1. Means of time and frequency parameters of the 5 calls shown in Fig. 1. Standard deviations are in parentheses. Parameters were assessed using a Hanning window with an FFT of 1024.

Parameter	Mean	SD
Call duration (ms)	24.92	6.6
Bandwidth (kHz) ± 15 dB	124.76	0.26
Dominant frequency (kHz)	25.02	3.09
Frequency (kHz) at +15 dB	54.04	13.12
Frequency (kHz) at –15 dB	14.96	5.06

(Gaudet and Fenton 1984), fringe-lipped (Page and Ryan 2006), and mouse-eared bats (*Myotis myotis*; Clarin et al. 2014). Furthermore, in fringe-lipped bats, the presence of a tutor for captive foraging animals facilitated the tendency for bats to investigate novel acoustic cues (Jones et al. 2013), and in mouse-eared bats, information transfer was increased when an observer interacted with a demonstrator (Clarin et al. 2014).

The unique feature of our observation is the modification of behavior by the female bat in the presence of the naïve observer bat. which indicates that this behavior lies within the framework of teaching and not observational or social learning. The observed interaction exhibits the 3 criteria of teaching outlined by Caro and Hauser (1992). First, the female bat changed her behavior in the presence of the naïve male bat by interrupting her foraging activities to approach the male multiple times. Second, the female exhibited behaviors (e.g., gaining the attention of the male and demonstrating the hunting task) that cost her access to additional food resources. Bats had access to food only during the hunting task, so any food the female forfeited in the flight room was not compensated with

additional feeding. Bats were provided enough food to maintain body weight, but they would continue to eat if given the opportunity. Finally, the male bat gained information about foraging in a novel environment that would have otherwise required several additional days to attain, had the interaction not occurred.

This observation is, to our knowledge, the first example of potential teaching behavior in bats. Although observed by chance, the behavior raises important questions about teaching and learning in bats, and we hope it will stimulate future experimental studies designed specifically to examine teaching behaviors in bats.

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