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Prey Recognition and Selection by the Constant Frequency Bat, *Pteronotus p. parnellii*

L.J. Goldman and O.W. Henson, Jr.

Department of Anatomy, University of North Carolina, Chapel Hill, North Carolina 27514, USA

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Summary. In the laboratory the neotropical bat, *Pteronotus p. parnellii* of Jamaica W.I., will readily capture free flying and tethered insects. It will also attack a stationary mechanical insect model when its wing-like parts are rapidly moving. On the basis of our observations we conclude that:

1. *P. parnellii* are attracted to flying insects and recognition of these rather than background objects is dependent on insect wing movements. Insects which are not beating wings are relatively immune from predation.
2. The frequency of the wingbeats of the insects is important in prey recognition. *P. parnellii* are not attracted to insects or to mechanical models of insects when the wing movements are slow.
3. These bats are selective in the acquisition of their prey and not simply opportunistic. They ignore or reject lampyrid beetles, arctiid and ctenuchid moths and the geometrid moth, *Thyrinteina arnobia*. They consume a variety of other Lepidoptera, Coleoptera, and insects from other orders. Their prey consists of both large and small insects.
4. In spite of the emission of intense sonar pulses with a constant frequency component of long duration, they can effectively hunt their prey in relatively confined spaces. They can chase their prey among simple arrays of obstacles and they can pursue insects to within several centimeters of large obstacles.
5. Evidence supports the hypothesis that the basis for insect wingbeat detection is the rapid and repetitive pattern of Doppler-shifts which the beating wings impose on the echoes of the constant frequency component of the bat's pulses.

Introduction

In the bat *Pteronotus parnellii* the emitted biosonar pulses, the structure of the ear, and the sense of hearing differ from other neotropical bats, including other species of *Pteronotus*. The emitted pulses contain brief frequency modulated and long constant frequency components (Novick, 1963; Novick and Vaisnys, 1964). Studies on evoked auditory potentials (Grinnell, 1967, 1970), single units (Suga et al., 1975) and cochlear microphonic potentials (Pollak et al., 1972; Suga et al., 1975) have shown that the ear of *P. parnellii* is sharply tuned to a narrow band of frequencies; when flying, these bats adjust the constant frequency component of their pulses so that the Doppler-shifted echoes returning to their ears fall within or near this frequency band (Pollak et al., 1972). The most remarkable morphological features of the inner ear are its relatively large size and peculiar pattern of nerve fiber distribution in the basal turn (Henson, 1973). The functional significance of these features in relation to the behavior of the bats in their natural environment is not entirely clear. One hypothesis is that the bats can determine their velocity relative to an echo source by assessing the amount of Doppler-shift in echoes. It has also been suggested that the perception of prepetitive Doppler-shifts in the echoes from the beating wings of insects facilitates prey recognition and perhaps permits specific prey identification (Henson et al., 1974; Schnitzler, 1970; Schuller, 1972; Pye, 1967).

Little information exists about the natural history of *P. parnellii* and especially about their hunting behavior. Thus, it is difficult to assess the merit of any hypothesis which purports to explain the significance of the specialized biosonar system that has evolved in this bat. In order to begin to consider hypotheses about prey recognition and identification in their proper context, we need to know more about the foraging behavior, prey selection, and the basis of selectivity of this bat.

Methods

In this study we observed the interactions between hungry bats and their potential prey. The bats, *Pteronotus p. parnellii* (formerly known as *Chilonyceteris p. parnellii*), were caught at the entrance of Mt. Plenty Cave, St. Ann Parish, Jamaica W.I. during a ten day field trip in November, 1975. All tests with Jamaican insects were conducted in Jamaica. Several bats were released at the same time into a large room which was used as the flight chamber (5.4 × 3.3 m with a ceiling height of 2.4 m). The chamber was illuminated by a single light bulb in a wallmounted socket. The rough plaster walls of the chamber were white and provided a background against which the bats and insects could be easily observed. Tests were conducted at night during the normal foraging time of the bats.

Insects were collected with a black light trap in a pasture approx. 70 m below the entrance of Mt. Plenty Cave and in Shaw Park Gardens in the town of Ocho Rios. Although the composition of the captured insect populations was not identical, many of the same species were caught at both locations. The light trap was turned on at sundown and insects were removed from the trap every few hours. The insects were immubilized with CO_2 and sorted for later release into the flight chamber. After the insects had recovered from the effects of the CO_2, they were released in the chamber along with the bats. Because of the difficulty of handling, observing and recovering small insects, tests were conducted with species having wingspans greater than approx. one cm. Examples of most of these insects were preserved and subsequently identified by the Insect Identification and Beneficial Insect Introduction Institute, Beltsville, Maryland.

The palatability of some insects was tested by hand feeding them to restrained bats which had been in captivity for severa days. These bats were accustomed to being handled and would readily accept mealworm larvae and other palatable insects.

Tethered moths were used to study the importance of insect wing movements for prey detection by the bats. The moths were tethered by passing a fine thread through the tip of the abdomen with a sewing needle. Moths tethered in this manner would beat their wings for considerable periods of time but wing movements could be eliminated by gluing the wings in an extended position. This was done by placing small drops of glue at the points where the wings join the thorax.

Results

1. Behavior of Bats

When released into the flight chamber for the first time, the bats tended to fly in the upper half of the room. After a relatively short period of time they seemed to become accustomed to the chamber and would fly almost anywhere, including under chairs and tables. They generally flew in a circle or figure-eight pattern, utilizing the full expanse of the room. *P. parnellii* are agile, strong fliers with great endurance, and they would often fly for two to three hours without landing; when they did alight, it was only for a few minutes. The bats did not appear to be disturbed or inhibited by the light or by the presence of investigators in the chamber.

After becoming accustomed to the chamber most of the bats would readily hunt the released insects. In most cases the bats appeared to catch the insects with their mouths and only occasionally used their wing membranes to secure their prey. The bats often chased the insects to within a few centimeters of the walls or ceiling. The close proximity of these sound-reflecting surfaces did not seem to limit or interfere with the bats' ability to recognize or capture prey. The bats were only attracted to insects which were beating their wings.

2. Bat-Insect Interactions

The behavior of the released insects varied considerably: Many moths and beetles refused to fly; some were strongly attracted to, and remained close by, the room light; others flew so fast that the bats had no time to react to them. Under natural conditions many of these untestable insects may be suitable prey for *P. parnellii*; however, this could not be verified under our experimental conditions.

In these studies we made no attempt to count the number of times a bat interacted with a given insect. This would have been impossible to do in cases where the bats seemed to ignore an insect since there was no way of distinguishing between the situation where a bat pays no attention to an insect it has detected and the situation in which the insect has not been detected. Another factor which prevented us from quantifying our observations of interactions was that we always had several bats flying which increased the chances of an interaction taking place; at the speeds which bats fly, and with the rapidity and frequency of interactions, there was no way of keeping accurate counts. Thus, we concentrated on observing and describing easily identifiable stereotyped interaction and those which could be repeatedly confirmed through numerous tests with different individuals. The number of individual insects tested is indicated in the text when only one or two insects of a particular species were used; for all other species three or more individuals were tested.

Order Lepidoptera

1. Arctiidae (Utetheisa ornatrix, Ammalo insulata, Halisidota sp.). These three species of moths were often pursued (each of these moths was pursued many times). The bats would usually come within several cm of the moths before turning away and ending the pursuit. On several occasions the moths were caught but they were immediately released without apparent harm. When we attempted to handfeed *U. ornatrix* to a *P. parnellii*, the moths were rejected. When being pursued, all of the arctiids executed evasive maneuvers.

2. Ctenuchidae (Empyreuma anassa, Cosmosoma auge, Cosmosoma achemon, Lymire melanocephala, Nyridela chalciope). These moths would fly for long periods of time in the presence of the bats. In spite of numerous opportunities, the moths were never pursued or captured and only once with *L. melanocephala*, was a bat observed to begin a pursuit. At no time did the moths exhibit evasive behavior.

3. Geometridae (Thyrinteina arnobia). The bats pursued these moths but always terminated the pursuit before making physical contact. The moths always executed evasive flight patterns while being pursued. It was our impression that, in spite of these evasive maneuvers, the bats could have captured these insects if they had been suitable prey. The avoidance maneuvers of *T. arnobia* did not appear significantly different from those of other moths which were easily captured by *P. parnellii.*

4. Noctuidae (Nymbis garnoti, Bendis formularis, Zale sp.). These common moths were vigorously pursued and eaten by the bats. They all took evasive action, some more successfully than others. In some cases, were it not for our repeated launching of the moths, they would undoubtedly have escaped predation by quickly landing and remaining inactive.

Order Coleoptera

1. Scarabaeidae (Bothynus sp., Cyclocephala sp., Diplotaxis sp., Phyllophaga sp.). These beetles, which were common in our collection, had to be tossed into the air before they would fly. Once in flight, they were immediately pursued and captured and all were consumed with the exception of one *Bothynus* which was apparently too hard to be successfully chewed. This mutilated beetle was later handfed to another bat which was also unable to consume it. None of the beetles exhibited evasive behavior. Beetles that were tossed into the air but did not open their wings were not pursued by the bats.

2. Lampyridae (Photinus sp.). These insects were completely immune to predation. The bats ignored these slow-flying beetles which, in turn, never exhibited evasive flight patterns. When these beetles were handfed to restrained bats, they would sometimes be seized, but were immediately rejected.

Miscellaneous

In some cases only one or two specimens of a particular species of insect were collected. In the course of testing, these were often mutilated or eaten before they could be properly identified beyond the familial level.

1. Hemiptera—Pentatomidae, Unidentified Green Stink Bug. A single specimen was pursued, captured and eaten as soon as it was released. Its flight path was straight, with no signs of evasive maneuvers.

2. Orthoptera—Tettigoniidae. One katydid and one long-horned grasshopper were repeatedly released in the chamber. Both flew rapidly and directly to one of the walls of the room every time they were released. We were never convinced that the bats really had time or the proper opportunity to detect or pursue these insects. It should be noted, however, that in our laboratory *P. parnellii* would attack and eat tethered, flying, long-horned grasshoppers which were collected in North Carolina.

3. Lepidoptera. Butterflies (Nyphalidae) were captured with a hand net late in the afternoon; they would readily fly among the circling bats, but the bats paid no attention to them. One skipper (Hesperiidae) was captured and eaten on its first flight across the room. Also one unidentified, large moth with a 7 cm wingspan was quickly caught and eaten.

3. Experiments with Tethered Moths

Our observations on tethered insects were based on interactions between *P. parnellii* and native North Carolina noctuids (*Pseudaletia unipuncta, Hyphantria cunea, Feltia sp., Mamestra sp.*). When these moths were released untethered, they were readily pursued and eaten by the bats. Pairs of bats were released in the presence of one flying and one nonflying (wings glued) tethered moth. The insects were suspended approx. one m from the ceiling and approx. one m apart. Four pairs of bats were used for nine five-minute trials. The flight patterns of the bats brought them within a few m of the moths approx. 15 times in a typical one-minute interval. All nine of the flying, tethered insects were caught and eaten within four minutes. The first attack on the flying moths usually occurred within 20 s, but the bats were not always successful in securing them due to interference from the thread used to tether the insect. Only two of the nine moths which could not beat their wings were attacked and eaten.

Another nonflying moth, which had remained suspended for more than five minutes without being attacked, became unglued and was captured and eaten within 10 s of the time it started to beat its wings.

Discussion

Our observations of the bat-insect interactions provide at least partial answers to questions about the hunting behavior and prey selectivity of *P. parnellii.*

1. In what type of environment does *P. parnelli* hunt? Observations of *P. parnellii* chasing insects within a few cm of sound-reflecting surfaces or obstacles suggest that these bats are capable of hunting in complicated environments where the vegetation is relatively dense. This is substantiated by the observation that in the laboratory they will capture tethered insects flying in the midst of an array of vertically oriented strings with separations of approximately 50 cm (Goldman, unpublished). Bateman and Vaughan (1974) observed a closely related subspecies of *P. parnellii* in Mexico, hunting insects among the chairs and tables at their campsite. Thus, *P. parnellii* seems to be able to detect, follow and capture prey against what must be a cluttered background of echoes.

2. What does *P. parnellii* eat? The Mexican subspecies, presumably *P.p. rubiginosa*, is said to consume mostly microlepidopterans, small beetles and small dipterans (Bateman and Vaughan, 1974). Our studies on the smaller Jamaican subspecies of *P. parnellii* indicate that they readily capture and consume medium to large-sized insects. The size range of insects known to be captured and eaten extends from those as small as fruit flies (Novick and Vaisnys, 1964) to moths with a wingspan of 7 cm.

3. Are *P. parnellii* opportunistic or selective in the acquisition of prey? Our observations demonstrate that *P. parnellii* does select its prey. The most striking examples of this selectivity were the consistent avoidance of certain moths (Arctiidae, Ctenuchidae, and the geometrid, *T. arnobia*) and the ravenous consumption of others (Noctuidae). Similarly, the bats avoided fireflies (Lampyridae) but readily consumed other beetles (*Scarabaeidae*). The consistent rejection of *T. arnobia* was unexpected since Dunning's (1968) studies on the prey preferences of several caged *P. parnellii* indicate that these bats eat geometrids. Our observations of the avoidance of arctiids and ctenuchids was consistent with Dunning's report. The status of arctiids and ctenuchids as prey for other bats is uncertain due to the techniques used in previous studies of bat prey preferences. These techniques (stomach content and fecal pellet analysis) do not allow the taxonomic identification of Lepidoptera below the ordinal level. There are, however, reports of arctiids having been consumed by the pallid bat, *Antrozous* (Ross, 1967) and *Myotis lucifugus* (Dunning, 1968). Reports of bats capturing fireflies are cited by Lloyd (1973). Neither the fireflies nor the bats were identified in the cases he reported.

4. What is the basis for selectivity? Dunning (1968) has suggested that *P. parnellii* can sense aposematic odors emitted by some ctenuchid and arctiid moths and in so doing avoid preying on these presumably distasteful insects.

In view of the physical complexity of the hunting environment of *P. parnellii* and the unpredictable nature of wind and eddy currents, the bats probably cannot rely on olfaction as a reliable means of prey identification over distances greater than several centimeters. Over short distances, however, the emission of an aposematic odor by an insect might be effective in alerting a pursuing bat about the distastefulness of its intended prey. This sort of interaction may explain the observed termination of the pursuit of the geometrid, *T. arnobia*, and perhaps some of the arctiids as well.

Because all of our tests were carried out in an illuminated room, one may question the use of vision in prey selection. The visual capacities of *P. parnellii* are not known, but there is strong circumstantial evidence that vision was not the basis for the prey selectivity that we observed. In the laboratory, *P. parnellii* often crash into brightly colored, smooth surfaces. These mirror-like surfaces would not return strong echoes unless the bat approached them at right angles, but if vision were used the bats would have been able to avoid these obstacles regardless of the angle of approach. An additional fact that strongly indicates that vision is not utilized is that in our laboratory *P. parnellii* have vigorously and repeatedly attacked a stationary mechanical prey model which resembled a real insect only in that it had moving wing-like parts. This model consisted of a 2 × 5 cm white paper rectangle attached to the end of the shaft of a variable speed motor. When these artificial "wings" rotated at speeds roughly equivalent to moth wingbeat frequencies, the bats attacked the model as if it were an insect. The model was never attacked when the motor rotated slowly. The attack on this model consisted of the bat swooping down and making contact with the paper "wings." In some cases the bats wrapped their wings around the model (Goldman and Henson, unpublished).

When stimulated by the orientation pulses of bats, many arctiid and ctenuchid moths emit bursts of ultrasonic pulses (Dunning and Roeder, 1965; Sales and Pye, 1974). These sounds presumably serve to warn the bats that these moths are unpalatable. When Dunning and Roeder played back recordings of arctiid sounds, hunting bats turned away from potential prey. In a later study with *P. parnellii*, Dunning (1968) found that arctiids and ctenuchids were rejected even when they did not produce warning sounds. In our experiments we did not monitor sound production, and we do not know if the rejection of the arctiids and ctenuchids was a result of their emission of aposematic sounds or was based upon the bats' analysis of the echoes from these moths.

We did not monitor sound production by the bats during our field tests in Jamaica. In the laboratory, however, we have monitored the pulses of *P. parnellii* during their pursuit of tethered insects and during their attacks on our mechanical prey model. In all cases it was clear that the bats were utilizing their sonar to locate these objects. Although it is well known that bats use echolocation for the detection of obstacles and prey, it is not clear that echolocation provides a basis for prey versus obstacle discrimination or for prey selection. If insect wingbeats could be detected by a bat, they would provide a reliable means of distinguishing a flying insect from an obstacle. There are two types of acoustic signals that *P. parnellii* might utilize for this: 1) insect wingbeat-generated sound; and, 2) echoes of the bats' own pulses which are rapidly and repetitively Doppler-shifted by the insects' beating wings. Insect wingbeat-generated sounds would be expected to have the same or some harmonic multiple of the wingbeat frequency. The low frequency hearing capacities of *P. parnellii* have not been investigated, but if they are as insensitive to low frequencies as other bats (Henson, 1970), it is unlikely that wingbeat-generated sounds could be detected. On the other hand, the ear of *P. parnellii* is highly sensitive to minor changes in frequency, and there is every indication that wingbeat-induced Doppler-shifts in the echoes of the constant frequency component of the pulse can be readily and accurately assessed. Suga et al. (1975) have noted that changing the stimulus frequency a few percent can cause threshold changes of 50 dB in single unit responses. Also, Pollak et al. (1972) have shown that changes of a few hundred Hz markedly change the amplitude of cochlear microphonic potentials in *P. parnellii.* Our preliminary studies of the Doppler-shifts in the echoes from tethered flying insects have shown that the beating wings can cause rapid Doppler-shifts as great as 800 Hz (Henson and Goldman, 1976). Frequency shifts of this magnitude cause marked amplitude modulations of the cochlear potentials in *P. parnellii* (Pollak et al., 1972) and they should certainly be detectable. We must conclude that the rapid wingbeats of most insects can provide these bats and possibly other constant frequency bats (Schuller, 1972) with a basis for distinguishing insects from other objects. Insects with low wingbeat frequencies may have some immunity from predation by *P. parnellii* because the echoes would be difficult to distinguish from background echoes. This is supported by the failure of *P. parnellii* to attack our mechanical insect model when the motor was rotating slowly. Also, it will be recalled that butterflies which generally have wingbeat frequency around 15 Hz were completely ignored. It has been hinted by Pye (1967) and Schnitzler (1970) that the analysis of the Doppler-shift patterns caused by insect wingbeats might provide a basis for the recognition of specific insect species. It must be pointed out, however, that wingbeat frequency is not species specific and that even within a given species it is at least partially dependent on age, sex, ambient temperature, and activity. Furthermore, preliminary studies in our laboratory have clearly shown that the amount and rate of Doppler-shifting due to insect wingbeats is highly variable and dependent upon the orientation of the insect with respect to the sound source and the receiver (Goldman and Henson, in preparation). Thus, while the detection of insect wingbeats may facilitate the recognition of prey, there is no experimental evidence to support the hypothesis that the analysis of insect wingbeat patterns enables bats to identify specific kinds of insects. This does not, however, preclude the possibility that some insects have evolved mechanisms for imposing a characteristic aposematic signature upon the echoes of the pulses of bats. The fireflies, which in our studies were totally ignored by *P. parnellii*, may possess this sort of defence mechanism.

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References

Bateman, G.C., Vaughan, T.A.: Nightly activities of mormoopid bats. J. Mammal. **55**, 45–65 (1974)

Dunning, D.C.: Warning sounds of moths. Z. Tierpsychol. **25**, 129–138 (1968)

Dunning, D.C., Roeder, K.D.: Moth sounds and the insect-catching behavior of bats. Science **147**, 173–174 (1965)

Grinnell, A.D.: Mechanisms of overcoming interference in echolocating animals. In: Animal sonar systems, biology and bionics, Vol. 1 (ed. R.-G. Busnel), pp. 451–481. Jouy-en-Josas 78, France: Lab. Physiol. Acoust., INRA-CNRZ 1967

Grinnell, A.D.: Comparative auditory neurophysiology of neotropical bats employing different echolocation signals. Z. vergl. Physiol. **68**, 117–153 (1970)

Henson, M.M.: Unusual nerve-fiber distribution in the cochlea of the bat *Pteronotus p. parnellii.* J. acoust. Soc. Amer. **53**, 1739–1740 (1973)

Henson, O.W., Jr.: The ear and audition. In: Biology of bats, Vol. II (ed. W.A. Wimsatt), pp. 181–262. New York: Academic Press 1970

Henson, O.W., Jr., Goldman, L.J.: Prey detection and physiological aspects of the cochlea in the bat, *Pteronotus p. parnellii.* Anat. Rec. **184**, 425 (1976)

Henson, O.W. Jr., Pollak, G.D., Johson, R.A., Goldman, L.J.: Specialized properties of the auditory system in the bat *Pteronotus p. parnellii.* Anat. Rec. **107**, 373 (1974)

Lloyd, J.E.: Firefly parasites and predators. Coleopterists Bull. **27**, 91–106 (1973)

Novick, A.: Orientation in neotropical bats. II. Phyllostomatidae and Desmodontidae. J. Mammal. **44**, 44–56 (1963)

Novick, A., Vaisnys, I.R.: Echolocation of flying insects by the bat *Chilonycteris parnellii.* Biol. Bull. **127**, 478–488 (1964)

Pollak, G.D., Henson, O.W., Jr., Novick, A.: Cochlear microphonic audiograms in the "pure tone" bat, *Chilonycteris parnellii parnellii.* Science **176**, 66–68 (1972)

Pye, J.D.: Discussion of paper by J.W.R. Griffiths: Theories of sonar systems in relation to biological organisms. In: Animal sonar systems, biology and bionics, Vol. I (ed. R.-G. Busnel), p. 1133. Jouy-en-Josas 78, France: Lab. Physiol. Acoust. INRA-CNRZ 1967

Ross, A.: Ecological aspects of the food habits of insectivorous bats. Proc. West. Found. Vert. Zoologists. **1**, 205–263 (1967)

Sales, G., Pye, J.D.: Ultrasonic communication by animals. London: Chapman and Hall 1974

Schnitzler, H.U.: Comparison of the echolocation behavior in *Rhinolophus ferrumequinum* and *Chilonycteris rubiginosa.* Bijdr. Dierk. **40**, 77–80 (1970)

Schuller, G.: Echoortung bei *Rhinolophus ferrumequinum* mit frequenzmodulierten Lauten. J. comp. Physiol. **77**, 306–331 (1972)

Suga, N., Simmons, J.A., Jen, P.H.S.: Peripheral specialization for fine analysis of Doppler-shifted echoes in the auditory system of the CF-FM bat *Pteronotus parnellii.* J. exp. Biol. **63**, 161–192 (1975)