Convergence in foraging strategies by two morphologically and phylogenetically distinct nocturnal aerial insectivores

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(With 4 figures in the text)

We used measurements of morphological parameters of common nighthawks (Chordeiles minor) and big brown bats (Eptesicus fuscus) to derive predictions about foraging behaviour based on the animals foraging at the same site. We tested the predictions using data from direct observation, radio telemetry and diet analysis and found a high degree of convergence in behaviour by these two species.

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Introduction

To further our understanding of foraging, it is important to assess the relative importance of intrinsic (e.g. morphology) and extrinsic (e.g. food availability) factors. For some animals, morphology correlates with foraging ecology, e.g. the relationship between beak size and shape, and the diet of Darwin’s Finches (Grant, 1986). Not surprisingly, studies on these birds and other species illustrate that food availability also influences foraging behaviour (Grant, 1986). Since the morphology of individuals is fixed and, in many cases, prey resources are difficult to manipulate experimentally, one way to assess the relative importance of these two constraints is to compare the behaviour of morphologically different species at the same site where each species should encounter the same prey resources.

There is strong evidence that wing morphology significantly influences flight performance. Associations have been found between morphology and foraging behaviour for both diurnal birds and insectivorous bats (e.g. Feinsinger & Chaplin, 1975; Aldridge & Rautenbach, 1987), but to

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date little work has been undertaken to assess the influence of morphological parameters or the availability of prey on the foraging behaviour of nocturnal insectivorous birds (Norberg, 1986). The Caprimulgidae are a largely insectivorous group whose volant nocturnal habit make an ecologically oriented comparison with insectivorous bats logical.

The purpose of this study was first to generate a series of predictions about foraging behaviour and ecology based on the wing morphology of common nighthawks (Chordeiles minor: Caprimulgidae) and big brown bats (Eptesicus fuscus: Vespertilionidae), and secondly to test the predictions with data collected using radio telemetry, diet analysis and direct observation.

Morphology and prey availability

Methods

The study took place near Okanagan Falls, British Columbia (49° 20' N, 119° 37' W) from May to August 1985–1987. The primary study site was a 300 m stretch along the Okanagan River bordering Okanagan Falls Provincial Park (hereafter 'the Park') (Site 20 of Herd & Fenton, 1983). During the summer, the Okanagan Falls area is hot and dry. The vegetation is characteristically open, grassy patches alternating with stands of trees, Ponderosa pine (Pinus ponderosa) dominates in drier areas, especially between elevations of 500 and 1000 m. Details of climatic conditions and vegetation can be found in Cannings, Cannings & Cannings (1987).

Chordeiles minor were captured at dusk in mist-nets while they foraged over the Okanagan River at the Park. Eptesicus fuscus were captured in mist-nets set in foraging areas, and in harp traps (Tuttle, 1974) and nets placed outside roosts.

(i) We measured body mass (M) to the nearest 0.1 g for each animal on the morning after capture (to ensure that the alimentary tract was empty).

(ii) To estimate wing area (S), we traced the outline of an extended wing, the body between the midline and the wing, and the tail of E. fuscus following the convention of Norberg (1981), and for C. minor followed the convention of Pennycook (1989) and traced the wing and body area only. We measured the area of each tracing with a digital planimeter and doubled the result to derive total wing area.

(iii) The wing span (b) was defined as the distance between the outstretched wingtips of E. fuscus and double the distance between the midline of the body and one outstretched wing for C. minor.

(iv) Wing loading (Mg/S) is calculated as weight (mass times acceleration due to gravity; Mg), divided by the wing area (S) for each species. Since the 2 species in this study are so morphologically different, we used relative wing loading (Mg/(SM²)) which corrects for size-dependent differences assuming geometric similarity in wing loading (Norberg & Fenton, 1988).

(v) Aspect ratio (A), is the square of wing span (b) divided by wing area (S), b²/S.

We estimated the abundance of flying insects using a whirligig or rotary trap (Holroyd, 1983; Kunz, 1988) mounted on a small island of rock 2 m from the shore of the Okanagan River, or on the river bank at the site where both species regularly foraged. The trap held 2 isokinetic nets attached to collecting bottles containing 70% ethanol, one at 1 m and one at 4.5 m above the ground or water, which were swept through a 4.2 m diameter circle. Each net had a mouth area of 0.1431 m² and at 20 rpm sampled 2329 m³/h.

In 1986, we operated the trap at dusk on 16 evenings, usually for 2 hours beginning 30 minutes before C. minor started foraging. In 1987, we ran the trap on 30 different dates for 10 min each hour from 20:00 to 23:00 h. Due to the different sampling schedules, insect catches were standardized by converting to density.

For each trap sample we counted the number of insects from each taxonomic order and measured the body length of 10 individuals from each net sample (or as many as were captured if less than 10) to the nearest 0.1 mm. The insects were air dried and weighed to the nearest 0.1 mg using a Mettler AE100 electronic
balance. We subdivided the caddisflies (Trichoptera) into 2 groups; 'small' caddisflies (family Hydroptilidae) had body lengths less than 5 mm and 'large' caddisflies were 5 mm or longer (families Hydropsychidae and Leptoceridae). Diptera were subdivided into the Chironomidae and 'other' Diptera.

Results

Morphology

Chordeiles minor, with a body mass of about 80 g, and a large gape, characteristic of the family Caprimulgidae, uses vision to detect flying insect prey (Gross, 1940; Caccamise, 1974). This species has relatively long narrow wings with a high aspect ratio but a rather low relative wing loading in comparison with other birds (Norberg, 1989; Table I). Eptesicus fuscus averages 18 g in body mass and uses broad-band frequency-modulated (FM) search phase echolocation calls to detect prey (Knick, 1982). The relatively short narrow wings of this species results in about average relative wing loading and aspect ratio compared with other bats (Norberg & Rayner, 1987). Chordeiles minor has a significantly larger aspect ratio than E. fuscus suggesting relatively longer, narrower wings (Table I), but there is no difference in relative wing loading between the two species.

Prey abundance

We identified 118,000 insects from whirligig trap samples in 1986 and 63,000 in 1987 (Fig. 1). The relative abundance of the different insect types between years was significantly different ($\chi^2 = 18.3$, d.f. = 6, $P < 0.01$). This difference was largely attributable to the increase in the number of dipterans in 1987. Numerically, chironomids made up the majority of insects in both years. Large caddisflies constituted 13.5% of the insects in 1986, but only 3.9% in 1987. After 1 June, when both E. fuscus and C. minor foraged in large numbers, the minimum insect density was 130

<table>
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<tr>
<th>Parameter</th>
<th>E. fuscus</th>
<th>C. minor</th>
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<tbody>
<tr>
<td>Mass M (kg)</td>
<td>$0.0186 \pm 0.0027$</td>
<td>$0.0793 \pm 0.0083$</td>
</tr>
<tr>
<td>Span b (m)</td>
<td>$0.33 \pm 0.12$</td>
<td>$0.60 \pm 0.16$</td>
</tr>
<tr>
<td>Wing area S ($m^2$)</td>
<td>$0.0162 \pm 0.0014$</td>
<td>$0.0402 \pm 0.0031$</td>
</tr>
<tr>
<td>Wing loading Mg/S (N m$^{-2}$)</td>
<td>$11.9 \pm 1.6$</td>
<td>$19.5 \pm 2.6$</td>
</tr>
<tr>
<td>Relative wing loading (Mg/SM$^{1/2}$)</td>
<td>$44.5 \pm 0.9$</td>
<td>$45.3 \pm 0.7$</td>
</tr>
<tr>
<td>Aspect ratio A (b$^2$/S)</td>
<td>$7.1 \pm 0.6$</td>
<td>$8.9 \pm 0.6$</td>
</tr>
<tr>
<td>Measured flight speed (m/s)</td>
<td>$3.5 \pm 0.4$</td>
<td>$5.3 \pm 0.2$</td>
</tr>
<tr>
<td>$V_{mp}$ (m/s)</td>
<td>$3.8$</td>
<td>$5.6$ (36; Rayner, 1979)</td>
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** One-tailed t-test, $P < 0.01$
per 1000 m$^3$ of air sampled (6 July 1987) and the minimum caddisfly density was 3.7 per 1000 m$^3$ (12 June 1987). By way of comparison, in two other studies where the same whirligig trap was used to sample insects, insect densities were much lower. Maximum insect densities of 28 g/10$^3$ m$^{-3}$ were measured near Long Point, Ontario (Holroyd, 1983) which represents only 10% of our maximum value (5000 per 1000 m$^3$) when converted to the same units. Near Milk River, Alberta, Saunders (1989) took 48 nightly samples and never recorded a density greater than 100 insects per 1000 m$^3$.

**Predictions**

Based on the morphological differences between *E. fuscus* and *C. minor*, we formulated three predictions to assess the impact of morphology on foraging behaviour.

**Flight speed**

Flight speed is positively correlated with wing loading and body mass in both birds (Pennycuick, 1975) and bats (Norberg & Rayner, 1987). On the basis of the large difference in size, we expected that *C. minor* should fly faster than *E. fuscus*. We calculated the minimum power speed (*V_{mp}* of *C. minor*) to be almost 2 m/s faster than that of *E. fuscus* (Table I). Predicted flight speeds were estimated from morphological measurements using the calculations of Pennycuick (1989) for *C. minor* and Norberg & Rayner (1987) for *E. fuscus* (Table I). *V_{mp}* is the speed requiring the lowest power output for an animal to remain in flight. Although animals may not necessarily fly at this speed while foraging, it allows for a comparison of flight abilities.

**Attack rates**

If *C. minor* flies faster than *E. fuscus* and forages at the same place and time, the birds should encounter more insects per unit time than *E. fuscus*. This should translate into higher attack rates,
assuming that the prey detection abilities of the two species are roughly equal in spite of the different means of perception. Echolocation as a prey detection system has been well studied for *E. fuscus* (e.g. Kick, 1982), while for *C. minor* there are no published data on visual acuity except to record the presence of *Tapeta lucida* which should enhance perceptual abilities under conditions of low light (Nicol & Arnott, 1974).

Foraging duration

We used Nagy’s (1987) equation for desert birds to estimate a daily energy expenditure (DEE) of 88.8 kJ/day for *C. minor*, and data from Bell, Bartholomew & Nagy (1986), to estimate a DEE value of 32.9 kJ/day for *E. fuscus*. Cummins & Wuycheck (1971) report that most insects have a similar energetic content. Therefore, *C. minor* should require more than twice as much food in absolute terms as *E. fuscus* on a daily basis. To meet this energetic demand, we predict that *C. minor* will need to forage for significantly longer periods of time than *E. fuscus*, all else being equal.

Foraging behaviour

Methods

Marking

Individual *C. minor* were sexed by throat colour and tail pattern (Sclander, 1954): all captured individuals were classified as adults based on plumage and banded using numbered aluminium Canadian Wildlfe Service bands. We affixed radio transmitters to nighthawks in the manner described by Brigham (1989). The transmitter package caused some birds to fly unnaturally for several minutes, probably until they adjusted to a new centre of gravity.

We banded bats on the forearm with plastic split rings or numbered aluminium bands (National Band and Tag Co., Newport, Kentucky). Juveniles were distinguished from adults by the degree of ossification of the third-digit metacarpal-phalangeal joint (Racey, 1974). Pregnancy was assessed by palpation and lactating females were recognized when gentle pressure yielded milk from a nipple. We glued transmitters (0.8–1.0 g) to bats (Brigham & Fenton, 1986) with body masses greater than 15.0 g, making the maximum transmitter load 6.7% of body mass. For 23 of 33 animals the transmitter load was less than 5% of body mass as suggested by Aldridge & Brigham (1988).

We attached radio-transmitters to 27 *C. minor* (15 females and 12 males) and collected data for 935 contact days. We radio-tagged 33 *E. fuscus* (2 adult males, 16 pregnant females, 6 lactating females, 4 post-lactating females and 5 juvenile females) and recorded data for 288 contact days. Neither species consistently foraged in any discrete area except the Park.

Flight speed

We measured the flight speed of foraging *C. minor* and *E. fuscus* on 6 evenings in 1987 using a Panasonic Digital 5000 video camera and a Panasonic portable AG-2000 video cassette recorder (VCR). Both bats and birds were filmed at dusk as they foraged parallel to a rope calibrated in 0.1 m intervals and stretched 3 m above the ground between 2 poles. The camera was operated continuously while an observer judged when individuals flew within 1 m of the rope, along a 5 m course. Flights were analysed using the stop action mode of the VCR to determine speed in m/s.
Foraging attack rate

We defined an attack by either C. minor or E. fuscus as a deviation from straight line flight during feeding periods (equivalent to the feeding ‘dips’ of Griffin (1958), the ‘erratic diving movements’ of Buchler & Childs (1981) and the ‘sideways displacements’ of Møller (1987)). The small size of prey precluded determination of both prey identity and the outcome of attacks. On 2 occasions we monitored the foraging behaviour of E. fuscus for 5 minutes with a QMC mini-bat detector (QMC Instruments, 23 Aberdeen Rd., London N5 2UG) and both times we found an exact correspondence between the occurrence of feeding buzzes (Griffin, Webster & Michael, 1960) and flight deviations. These data strongly suggest that for E. fuscus, deviations are indicative of attacks (see also Buchler & Childs, 1981). Measurements of attack rates by both species were made at the Park during the dawn and dusk feeding periods in 1986 and 1987. Data from an attack sequence were included if a single individual made 3 or more attacks or if observation continued uninterrupted for at least 10 seconds.

Foraging duration

For each day that an animal carried an active radio transmitter, we determined the duration of foraging bouts. The duration of bouts included the time spent commuting between roost or nest sites and the foraging area. In 1986 and 1987, we monitored the foraging behaviour of C. minor and E. fuscus during the entire night, at least once per week. We followed individuals using 2 Merlin 12 receivers (Custom Electronics, Urbana, Illinois); one receiver was operated from a height of land near the Park and the other was operated from a vehicle. When possible, the observers maintained radio contact and triangulated signals to establish animal positions.

Some adult female bats undoubtedly gave birth to or weaned offspring during the period they carried active transmitters. However, since we did not recapture individuals often enough to assess the timing of changes in reproductive condition, nor could we confidently determine a change in condition by a change in behaviour, we used the reproductive condition at the time of capture as the classification for all data collected for an individual. On average, individuals carried transmitters for 9 days, which is much shorter than the gestation and lactation periods.

Diet analysis

For both species, diet samples were collected from individuals captured at the Park. We analysed 10 E. fuscus faecal pellets for each individual captured, unless fewer were produced. The minimum number of insects consumed was estimated by counting eyes, legs or antennae as suggested by Kunz & Whitaker (1983). We could consistently count the number of individual trichopterans and dipterans consumed, but not the number of coleopterans or lepidopterans. When the number of individual insects could not be counted, we assumed a minimum of one individual consumed for each pellet in which the order was present (Coutts, Fenton & Glen, 1973).

The diet of C. minor was determined by identifying insect parts in faecal samples, regurgitated pellets, and stomach contents of birds who accidentally died. The minimum number of lepidopterans was often difficult to determine and we assumed a minimum of one individual per sample.

We analysed 83 C. minor diet samples, including: 59 faecal pellets, 9 regurgitated pellets and the contents of 15 stomachs. We identified 3674 prey items from these samples. For E. fuscus we analysed 395 faecal pellets and identified 1086 prey items.
Statistical analysis

We used a rejection level of 0.05 for both one- and two-tailed tests and present means ± 1 standard error (S.E.). Where multiple sample tests showed significant differences between means, we used a least significant difference test (LSD) to identify significant differences between individual means (Sokal & Rohl, 1981).

Results

By 1 June of each year, we estimated that 200–300 nighthawks foraged over the 300 m stretch of river during both dusk and dawn bouts. The number of birds declined through late July and August, but by mid August as many as 50 birds still foraged at the Park each night. In all three years, E. fuscus were seen foraging when we arrived at the study area (earliest was 8 May 1987) and when we left (latest was 18 August 1987). We estimated that on warm summer nights at least 200 E. fuscus foraged over the river.

During 147 dusk and dawn observation periods totalling over 300 hours in duration, C. minor always began foraging bouts above tree top height (> 30 m) over the river. During both dusk and dawn bouts, the birds gradually foraged at lower altitudes, eventually flying less than 0.5 m above the surface of the river before departing. This was reflected in that we only captured C. minor near the end of foraging bouts when the birds flew low over the river. Epistesicus fuscus consistently foraged 5–10 m above the surface of the river, rarely flying below an altitude of 5 m. At the Park, E. fuscus were only captured in mist-nets hung between 9 m towers placed parallel to the river on the dike, and never in nets strung 0–3 m above the surface of the water.

There was considerable temporal overlap in the dusk and dawn foraging periods of the two species. On average, C. minor were first observed foraging 28.3 ± 4.2 min before sunset and 54.0 ± 6.3 min before sunrise. The last foraging individual was observed 68.2 ± 3.7 min after sunset and 15.3 ± 8.7 min after sunrise. The first E. fuscus arrived at the Park 35.4 ± 2.9 min after sunset and the last individual observed foraging departed 48.6 ± 7.1 min before sunrise.

Flight speed

Both species foraged at speeds not significantly different from V_{mp} (one sample t-tests; t = 0.2, d.f. = 35, P > 0.05; t = 0.3, d.f. = 9, P > 0.05 for C. minor and E. fuscus, respectively). However, the ‘right’ minimum power speed may be difficult to estimate; Rayner's (1979) equation gives V_{mp} = 3.6 for a bird the size of Chordeiles which is much lower than the value of 5.6 obtained from Pennycook's equation. We suggest that both species are probably flying near V_{mp}.

The mean flight speed of C. minor was significantly faster than that of E. fuscus (5.3 ± 0.2 m/s, n = 36 versus 3.5 ± 0.4 m/s, n = 10, respectively; P < 0.05) as expected on the basis of the difference in size between the two species. Although flight speed may vary during actual insect pursuit (Kalko & Schnitzler, 1989), our data highlight the different capabilities of the two animals.

Foraging attack rate

Attack rates did not differ between years or between dusk and dawn foraging bouts for either C. minor or E. fuscus (ANOVA F = 3.5, P > 0.05, n = 52 dates and F = 2.1, P > 0.05, n = 41 dates, respectively) and therefore the dusk and dawn data for both years were pooled for each species.
There was no significant difference in the mean attack rate between the two species (C. minor \( \bar{x} = 18.4 \pm 0.7 \) attacks/min, \( n = 3487 \) attacks, E. fuscus \( \bar{x} = 18.0 \pm 1.2 \) attacks/min, \( n = 2855 \) attacks; one-tailed \( t = 0.31, d.f. = 91, P > 0.05 \)).

Foraging attack rate was not correlated with insect density for E. fuscus or for C. minor \( (r^2 = 0.06, P < 0.05, n = 13 \) dates; and \( r^2 = 0.11, P < 0.05, n = 19 \) dates, respectively). This suggests that insect prey were sufficiently abundant to allow both species to maintain maximal attack rates.

**Foraging duration**

Chordeiles minor carrying radio-transmitters made two foraging bouts daily, a 'dusk bout' and a 'dawn bout'. Birds observed flying in the daytime were not considered to be foraging based on the complete lack of deviations in flight path.

Individual E. fuscus made from zero to five foraging flights per night. The bats invariably foraged at dusk ('dusk bout') when the temperature was above 12 °C (Audet & Fenton, 1988). Other foraging periods during the night were termed 'subsequent bouts'. When the temperature was above 12 °C at sunset, bats made an average of 1.7 subsequent flights per night.

Dusk foraging bouts by C. minor were of a significantly longer duration than dawn bouts (two-tailed \( t = 10.8, d.f. = 431, P < 0.001; \bar{x} = 47.7 \pm 0.8 \) and 27.0 \( \pm 1.8 \) min, respectively). There were no significant differences in the duration of dawn bouts due to sex or year effects (ANOVA, \( F = 0.8, P > 0.05, n = 78 \) bouts). There was a significant difference in dusk bout duration between the three years and the sexes (one-way ANOVA, \( F = 8.0, P < 0.01, n = 362 \) bouts), which the LSD test showed could be attributed to the two male birds carrying transmitters in 1986. These individuals foraged for a significantly shorter time than males or females in the other years. Since both males roosted less than 1.0 km from the Park while the mean commuting distance was 2.67 ± 0.11 km (\( n = 284 \)), and there was a significant positive correlation between the duration of dusk feeding bouts and
commuting distance \( (r^2 = 0.30, \ P < 0.05, \ n = 284) \), we pooled the foraging bout duration data for year and sex.

Although we undoubtedly misclassified some foraging bout durations relative to our age and sex categories, bout lengths by *E. fuscus* depended on sex and age class for dusk (ANOVA, \( F = 7.37, \ P < 0.001 \)) and subsequent bouts, respectively (\( F = 3.27, \ P < 0.05 \); Fig. 2). Therefore, during any 24-hour period, individual *C. minor* foraged for the same length of time as pregnant *E. fuscus*, but for significantly less time than the other three sex and age classes of *E. fuscus* (ANOVA, \( F = 21.1, \ P < 0.05 \), LSD test; Fig. 2).

**Fig. 3.** Percentage distribution of the major insect taxa available (a), in the diet of *Epitesicus fuscus* (b), and in the diet of *Chordeiles minor* (c) for (a) 1986 and (b) 1987. Abbreviations for insect groups are as follows: Chr—Chironomidae, Dip—Diptera excluding Chironomidae, Col—Coleoptera, Eph—Ephemeroptera, Hym—Hymenoptera, Lep—Lepidoptera, Tch—large Trichoptera and Oth—other.
Diet analysis

The proportion of prey types eaten were not significantly different between years for *C. minor* ($\chi^2 = 11.1, d.f. = 5, P > 0.05$) or *E. fuscus* ($\chi^2 = 8.5, d.f. = 5, P > 0.05$) so the diet data were pooled for the two years. Large trichopterans constituted the highest frequency of occurrence in the diets of both species (Fig. 3).

The large trichopterans ($n = 77$), dipterans (5) and coleopterans (14), recovered intact from *C. minor* stomach and regurgitated samples, were significantly larger than the average size available (two-tailed $t = 4.66, P < 0.001$; $t = 8.68, P < 0.001$; $t = 13.98, P < 0.001$, respectively; Fig. 4). Lepidopterans ($n = 6$) and ephemeropterans (7) recovered intact from *C. minor* were not significantly longer (two-tailed $t = 0.35, P > 0.05$; $t = 1.90, P > 0.05$, respectively).

Although we could not measure the size of prey items consumed by *E. fuscus*, the size of intact eye capsules passing through the digestive system indicated that only large caddisflies and non-chironomid dipterans were consumed.

Discussion

To summarize, we found that *C. minor* foraged over the Okanagan River at 5-3 m/s, a speed probably close to $V_{mp}$, and made 18-3 attacks/min. Both sexes foraged for an average of 45 minutes at dusk and 25 minutes at dawn, feeding on large caddisflies and flying ants. *Eptesicus fuscus* foraged at a mean speed of 3.5 m/s, which is also probably near $V_{mp}$ in the same habitats as *C. minor*, making 18-0 capture attempts/min. The duration of foraging by *E. fuscus* was dependent on the sex and age class of the individual, ranging from about 85 minutes nightly for pregnant females to 163 minutes for lactating females. Large caddisflies and flies other than midges
constituted the majority of the diet. Taken as a whole, our data illustrate a striking similarity in foraging behaviour by two taxonomically and morphologically distinct animals.

The observation of large numbers of *C. minor*, *E. fuscus*, swifts, swallows, kingbirds and *Myotis* bats (Fenton et al., 1980; Herd & Fenton, 1983; Brigham, 1988) regularly foraging at the Park throughout the summer reinforces our insect sampling results which show that flying insect prey were predictably abundant at this site. However, it is unlikely that the abundant prey resource at this site is unique. Perry, Perry & Stanford (1986) showed that the emergence period of ephemeropterans and caddisflies is extended in regulated rivers. Further, caddisflies and other aquatic insects are often abundant at the outlet of lakes where nutrients are abundant (G. B. Wiggins and J. M. Culp, pers. comm.). This suggests that many sites may support similarly high insect densities.

**Flight speed**

As we predicted on the basis of morphology, foraging *C. minor* flew faster than foraging *E. fuscus*. That both species foraged at speeds near *V_{mp}* suggests that the animals are minimizing the cost of flight while foraging on the same prey resource.

**Attack rate**

Since *C. minor* and *E. fuscus* both concentrated their foraging activity at the Park, they should have encountered similar distributions and densities of flying insects. The faster flying *C. minor* should have encountered prey at a higher rate, potentially enabling this species to attack prey more often, although the increased efficiency of the bat due to its lower flight speed and higher maneuverability could influence this. There was no significant difference in attack rates, however, suggesting that insect densities were so high that both species attacked prey at a maximum rate. Support for this contention is the fact that the highest attack rate reported in the literature for insectivorous bats is 10 per min by *Pipistrellus pipistrellus* (Swift, 1980), about half the rate we measured for *E. fuscus* and *C. minor*. Møller (1987) reported that, under some circumstances, attack rates by swallows (*Hirundo rustica*) can reach 20 per minute but only for short periods of time. Brigham (1988) found *H. rustica* could maintain an attack rate of above 15 per minute at the Park. Shields & Bildstein (1979) observed *C. minor* make only two attacks/min while foraging in the light of a search. The high attack rates we observed are even more noteworthy in the light of the fact that our method underestimates the actual attack rate because: 1) we could only detect attacks accompanied by a deviation in flight path and; 2) our data include sequences of juvenile bats, who attack prey significantly less often than adults (Racey & Swift, 1985). Although evidence from other studies shows that the feeding rates of aerial insectivores are affected by prey density (Shields & Bildstein, 1979; Anthony, Stack & Kunz, 1981; Racey & Swift, 1985; Rydell, 1989), we found no correlation between the attack rate of either *C. minor* or *E. fuscus* and insect density or caddisfly density. Racey & Swift (1985) observed aggressive interactions between *P. pipistrellus* below a prey density of 1250 insects per 1000 m$^3$; we observed no conspecific or heterospecific aggressive interactions at any insect density. We therefore conclude that the high insect density at the Park represents an abundant food resource, resulting in attack rates which are probably close to the maximum attainable by either species.
Foraging duration

Although we predicted that the larger sized C. minor would forage for longer than E. fuscus for energetic reasons, our results show that the birds spent the same or a smaller proportion of every 24-hour period feeding. We hypothesize that C. minor cannot benefit energetically by extending foraging into the day because of lower insect abundance at these times, and the fact that Tapeta lucida are a disadvantage in bright light due to the bleaching of visual pigments (Lythgoe, 1979). Chordeiles minor foraged only at dusk and dawn when insect abundance has been shown to peak (Lewis & Taylor, 1965; Hespenheide, 1975; Buchler, 1976; Anthony & Kunz, 1977; Racey & Swift, 1985), which is consistent with the hypothesis that prey density and distribution influence temporal aspects of foraging behaviour (e.g. Sjöberg, 1985; Ferguson, Galpin & de Wet, 1988). We conclude from the foraging duration results that C. minor must either require less energy than predicted by Nagy’s (1987) allometric equation or have a significantly greater capture success rate than E. fuscus.

Prey size and type

Large trichopterans made up the majority of the diet of both species. Despite the statistical differences in the size of prey eaten by C. minor relative to that available, the actual difference in size between those trichopterans eaten and those available was less than 1 mm and probably not biologically significant. A body length of about 5 mm represents the minimum size of prey eaten by C. minor. Whether this is due to active selection by the birds or an inability to detect or react to smaller prey is unknown (e.g. Barclay, 1985). Eptesicus fuscus should be able to detect chironomids, the most abundant insects at the Park, at a distance of about 1 m (Kic, 1982), yet they were not present in the diet. This suggests active prey selection or insufficient time to react to and capture these insects. The diet analysis shows that both C. minor and E. fuscus ate the same types of prey in similar proportions, except for the consumption of flying ants by C. minor. The similarity in diet is consistent with the fact that both species exploited the same prey resource.

Conclusions

As well as obvious size differences between C. minor and E. fuscus, the two species differ in their means of orientation and prey perception. For bats, several authors have proposed an association between the design of echolocation calls and foraging strategy (Barclay, 1985, 1986; Fenton, 1986; Schmitzler et al., 1987; Neuweiler, 1989). Since there are no published data on the visual acuity of C. minor, making specific predictions on the basis of perceptual abilities is not possible. On a general level, however, the similarity in foraging behaviour by E. fuscus and C. minor, despite differing means of perception, is noteworthy. Chordeiles minor made attacks at the same rate as E. fuscus, despite flying faster and presumably encountering prey at a higher rate. This implies that the visually orienting birds may not detect flying insect prey as well as acoustically orienting bats. Further research is needed to test this hypothesis directly.

We conclude that C. minor and E. fuscus are capable of using the abundant insect resources in a very similar manner despite morphological differences. The equivalent attack rates and equivalent or shorter foraging duration by C. minor are not consistent with the predictions generated by morphology, suggesting that in situations with abundant prey, morphological constraints on foraging are less important. However, it remains to test these predictions at a site where prey are
less abundant and potentially a limited resource. In these situations, the constraints imposed by morphology should be much more evident.

Summary

We measured the morphological parameters, flight speed, attack rate, foraging duration and diet of Chordeiles minor (Aves: Caprimulgidae) and Eptesicus fuscus (Mammalia: Vespertilionidae), two sympatric nocturnal aerial insectivores. In spite of vastly different body sizes and perceptual systems, both species foraged in a similar manner over the Okanagan River near Okanagan Falls, British Columbia, Canada. Chordeiles minor flew at 5-3 m/s during dusk and dawn foraging bouts for an average of 70 min nightly. The birds foraged in open habitats and low over the Okanagan River making 18-4 attacks/min, eating primarily large caddisflies and flying ants. Eptesicus fuscus flew at 3-5 m/s and foraged for a total nightly duration of 85-160 min on average, during one dusk and 1-7 subsequent bouts. The bats also flew in open habitats making an average of 18-0 attacks/min, eating primarily large caddisflies. We conclude that the predictably abundant prey resource available over the Okanagan River is responsible for the similarity in the foraging strategies of these two species.

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REFERENCES


FORAGING CONVERGENCE IN NOCTURNAL AERIAL INSECTIVORES


