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SHORT COMMUNICATION

The early bat catches the fly: Daylight foraging in soprano pipistrelles

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The timing of evening emergence in insectivorous bats is probably a trade-off between the advantage of emerging earlier (access to small insect prey, peaking in abundance before dark), and the lower risk of falling victim to diurnal predators relying on vision, associated with late emergence (Fenton et al. 1994; Jones and Rydell 1994; Rydell and Speakman 1995; Rydell et al. 1996; Duvergé et al. 2000).

Closed habitats surrounding roosts offer protection from predators, thus making earlier emergence less risky to bats (Duvergé et al. 2000; Russo et al. 2007). Generally speaking, species with higher wing loadings (i.e. faster flyers) may emerge earlier because they may be more likely to escape aerial attacks by predators than are those species with low wing loadings – which are more manoeuvrable but inevitably slower (Norberg and Rayner 1987). However, at sites sheltered from diurnal avian predators small bats manoeuvrable enough to hunt in clutter may also start foraging earlier. Over the course of the night, small dipterans are most abundant at dusk, and so bats feeding mainly on these prey items tend to forage earlier than those whose favoured food is

available in abundance throughout the night (Jones and Rydell 1994).

As typically nocturnal mammals, bats very rarely exhibit daylight activity, i.e. flight activity occurring more than one hour after sunrise or before sunset. Its main function is feeding (Speakman 1990, 1991); therefore daylight activity occurs sporadically, when bats become more risk-prone (i.e. when the risk of starvation is severe). In the absence of diurnal avian predators, *Nyctalus azoreum*, a bat endemic to the Azorean archipelago, is a well-known exception among bats because it exhibits a high frequency of daylight flights (Moore 1975; Speakman and Webb 1993; Speakman 1995).

Our study was set in a beech forest of Central Italy, where flights before sunset by non-identified bats had been previously observed (D. Russo unpublished data). Our aim was to identify the species involved and describe its activity, as well as the habitat where pre-sunset flights occurred.

Our observations took place in June and July 2007–08 in a mountain canyon (1203 to 1700 m a.s.l.) near the village of Villavallelonga (central Italy), in the Abruzzo, Lazio and Molise National Park. The site is extensively covered with beech (*Fagus sylvatica*) forest. Surrounding areas also include oak coppice, pastures and meadows. On the basis of terrain morphology, we surveyed two forest micro-habitats within the canyon: (1) the

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beech forest covering the slopes (hereafter termed “forest” for simplicity), and (2) the 2.5-km long canyon bottom, bordered with beech trees, and mostly beneath canopy. Its floor was covered with large stones, ferns, moss, grass, shrubs, a thick leaf litter and coarse organic debris.

To identify which species foraged before sunset and relate this behaviour to habitat structure, we carried out acoustic surveys of bat activity taking place before sunset both in the canyon bottom and the forest. On two successive days, we surveyed with a bat detector two 1.2 km transects walked in 40 min, starting 60 min before sunset. One was walked along the canyon bottom, the other along an almost parallel forest trail ca. 80 m higher up. We applied the same sampling design to open areas (forest-pasture ecotone): because no bats were recorded there, we excluded them from final analyses. To compare bat activity before and after sunset, we also surveyed the return route in 40 min, beginning 15 min after sunset. Environmental variables (ambient temperature taken with a 0.1 °C resolution digital thermometer, wind speed expressed as Beaufort scale and cloud cover estimated on a 0–8 scale) showed negligible differences between days.

Transects walked before sunset allowed us to locate the main foraging sites – i.e. where most foraging attempts occurred, as shown by the high feeding buzz rates recorded (Griffin et al. 1960). Such sites were then visited repeatedly in the two years of study to (1) confirm that the phenomenon was not occasional (2) ascertain its onset time precisely, and (3) carry out behavioural observations of foraging. In some cases we also assessed foraging attempt rates by counting feeding buzzes from the detector’s heterodyne channel.

At both transects and sampling points, we took real time ultrasound recordings with a Pettersson D1000X bat detector (sampling rate 350 kHz). They were saved as wave files onto a flashcard storage device. The bat detector was kept in the heterodyne mode and tuned continuously between 20 and 60 kHz to cover frequency ranges of all bats foraging in the area (D. Russo unpublished data). When a bat pass (i.e. a series of clicks heard in frequency division as a bat flew within range; Fenton 1970) was heard in the heterodyne mode, we recorded it in real time. Sound analysis was performed with BatSound 3.31. Call identification was carried out with the discriminant functions developed by Russo and Jones (2002). Species whose likelihood of correct identification was <80% were classified to genus. When present, social calls were also used for identification (Barlow and Jones 1997).

To provide a picture of prey available to foraging bats, we also assessed insect abundance by sampling insects with sticky traps and hand-net sweeps in both micro-habitats. Four sticky traps were set along a 400-m transect in both habitats, one every 100 m, and kept in

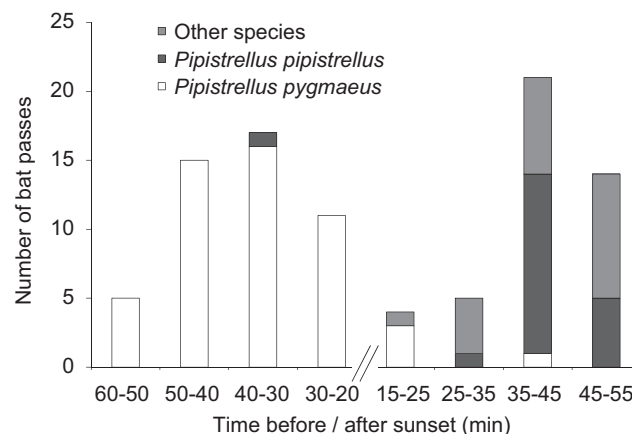


Fig. 1. Numbers of passes (pre-sunset, $n=48$; post-sunset, $n=44$) recorded in 40 minutes, respectively, before and after sunset along a 1.2 km transect walked in the canyon bottom. Pre-sunset observation started 60 minutes before sunset; post-sunset 15 minutes after sunset.

place for 48 h starting one hour before sunset. Moreover, on the days we set and removed such traps, at each trapping site we also collected insects by 20 hand-net sweeps/site/day, totalling 160 sweeps/micro-habitat ca. one hour before sunset. We pooled all insects sampled in each micro-habitat for analysis and classified them by main taxonomic group. Insects swarming away from trapping sites were unrepresented in these samples. Therefore, we also handnetted them opportunistically for species identification.

We grouped numbers of passes recorded in transects in 10-min intervals and compared them between micro-habitats with a sign test. Samples taken at corresponding times in the two micro-habitats were paired for analysis. A two-way analysis of variance followed by a Tukey’s post-hoc test for pairwise comparisons was used to compare insect catches (main factors habitat and taxon). Normality of residuals was tested with a Ryan Joyner test. Statistical significance was set at $P < 0.05$. All analyses were performed with Minitab rel. 13.1.

Acoustic surveys showed that the early forager was the smallest aerial hawkler occurring in the study area specialised in dipteran food, i.e. *P. pygmaeus* (Fig. 1); only one pass was attributed to another species (*P. pipistrellus*). After sunset, *P. pygmaeus* activity decreased in the canyon bottom: it ranked third in activity ($n=4$), after *P. pipistrellus* ($n=19$) and “other species” (including four *Myotis* sp., three *Barbastella barbastellus*, 9 *Hypsugo savii* and 5 undetermined passes). In the forest, activity was absent before sunset, sporadic after it: two passes from *Myotis* sp., one from *B. barbastellus* (sign test for difference between micro-habitats: median = 13.0; $P < 0.005$). Further observations made on different days from recording points in this micro-habitat confirmed the absence of bat activity before sunset.

We observed foraging in the canyon during two years in June and July at feeding sites identified in preliminary transect work. Foraging was always observed well before sunset. In eight instances we could precisely determine the first appearance of a foraging bat, which occurred 61.7 ± 11.3 min (range 41 – 78 min) before sunset. As seen in transects, foraging was almost exclusively exhibited by *P. pygmaeus*: practically no other species was detected except, sporadically, *P. pipistrellus*. We confirmed that bats were actually foraging because we recorded numerous feeding buzzes. For instance, in three five-minute foraging bouts by a single bat we recorded 18.0 ± 5.8 buzzes/min. After the bats' first appearance, foraging remained significant practically during the whole time preceding sunset. In one case, a single bat started to forage 61 min before sunset and did so uninterruptedly for 58.5 min in the same feeding site. This was in a 41×19 m approximately elliptical spot, delimited by trees apparently used as landmarks, corresponding to a surface of 405 m^2 .

Bats only foraged at closed canopy sites. Foraging took place both beneath the canopy, i.e. ca 10 m above ground, and at lower heights (1–4 m above ground). Bats foraging high up commonly also exhibited dives toward the ground. When insect swarms were present, bats foraged on them. Up to four bats were observed hunting in the same foraging area, but generally only a single bat was recorded. Activity was often observed simultaneously at several foraging sites in the canyon, so it was not restricted to few aberrant bats.

In all, 1139 insects were sampled by sticky traps and handnets at trapping sites (Fig. 2). Trapping showed that most insect groups were more abundant in the canyon bottom than in forest. The two-way ANOVA showed significant effects of both micro-habitat ($F_{1,55} = 6.60$; $P < 0.05$) and taxonomical category ($F_{7,55} = 23.50$; $P < 0.005$) but the interaction between such factors was not significant. Tukey's post-hoc tests demonstrated that the groups which stood out significantly in terms of abundance were hemipterans (more abundant than all taxa except brachycerans and hymenopterans), brachycerans (more abundant than all except hemipterans and hymenopterans), and hymenopterans (superseding lepidopterans, nematocerans, neuropterans and thrips). In the canyon we also noticed small insect swarms at ca. 3 m above ground on which bats clearly foraged (as shown by the emission of numerous feeding buzzes). Sampling showed swarms to be made of small nematocerans, namely fungus gnats (Mycetophilidae) *Coelosia truncata* Lundstroem, 1909. Samples were handnetted very close (< 1 m) to foraging bats, so we were sure that sampled insects were preyed upon by bats. At the same time, we also inspected the forest trail, where no swarms were noticed. For comparison, an equal number of hand-net sweeps were performed at corresponding sites

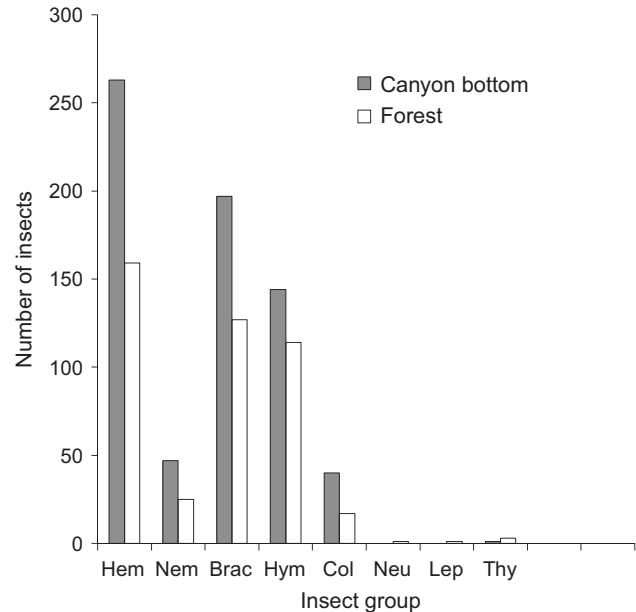


Fig. 2. Insects caught by sticky traps set along a 400-m transect in forest and canyon bottom micro-habitats (one every 100 m, kept in place for 48 hours starting one hour before sunset) and by 160 sweeps/micro-habitat done ca. one hour before sunset. Insects are lumped together by main taxonomical group. Hem: Hemiptera; Nem: Nematocera; Brac: Brachycera; Hym: Hymenoptera; Col: Coleoptera; Neu: Neuroptera; Lep: Lepidoptera; Thy: Thysanoptera.

on forest trail, but only three insects (two nematocerans, one brachyceran) were caught.

The early foraging we observed matches the temporal definition of “daylight” activity given by [Speakman \(1990\)](#), who defines the occurrence of daylight flight “so sporadic that a single researcher could not monitor its occurrence adequately for any meaningful analysis”. Although occasional observations of daylight activity are not rare (e.g. [Hirakawa 2006](#); [Ciechanowski and Anikowska 2007](#)), the situation we describe here was different: at least in the months when we did our investigation, activity was commonly recorded and we verified its occurrence across years. Hence, this appears to be a local adaptation in the species' behavioural repertoire. Apart from the case of *Nyctalus azoreum* ([Moore 1975](#); [Speakman and Webb 1993](#); [Speakman 1995](#)), and locally *Nyctalus noctula* ([Urban and Zieja 2003](#)), to our best knowledge the situation described in our study is novel among echolocating bats.

Daylight foraging was restricted to a specific habitat structure where two conditions were met, i.e. (1) presence of forest cover, and (2) abundant insect prey. Small nematoceran swarms may represent profitable prey, as suggested by the high rates of feeding buzzes recorded and direct observation of insect capture events. Moreover, brachycerans were still active at the time bats were foraging before sunset, so may have been caught too. In

agreement with Barlow (1997), Bartonička et al. (2008) observed the occurrence of Muscidae (active in daylight) in the species' diet. According to the latter authors, this would reopen the question of foliage gleaning in *P. pygmaeus* but, as they pointed out, some flies have crepuscular activity (Peng et al. 1992) so may be caught on the wing. In our opinion, the occurrence of Muscidae in diet may also be explained by the habit of *P. pygmaeus* of foraging before sunset, when flies are still active.

In riparian habitats, typical feeding habitats of *P. pygmaeus*, Nicholls and Racey (2006) reported that the species leaves roost soon after dusk. Likewise, Davidson-Watts and Jones (2006) found that bats emerged 33.5 ± 21.5 min after sunset: the ones we studied started to forage over one and a half hours earlier. This plasticity in activity time is probably linked with the different habitats used: early foraging must be prohibitive in open space such as riparian habitats, where the risk of falling victim of diurnal aerial predators is much greater.

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