Great tits search for, capture, kill and eat hibernating bats

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Ecological pressure paired with opportunism can lead to surprising innovations in animal behaviour. Here, we report predation of great tits (Parus major) on hibernating pipistrelle bats (Pipistrellus pipistrellus) at a Hungarian cave. Over two winters, we directly observed 18 predation events. The tits specifically and systematically searched for and killed bats for food. A substantial decrease in predation on bats after experimental provisioning of food to the tits further supports the hypothesis that bat-killing serves a foraging purpose in times of food scarcity. We finally conducted a playback experiment to test whether tits would eavesdrop on calls of awakening bats to find them in rock crevices. The tits could clearly hear the calls and were attracted to the loudspeaker. Records for tit predation on bats at this cave now span more than ten years and thus raise the question of whether cultural transmission plays a role for the spread of this foraging innovation.

Keywords: foraging innovation; novel food source; hibernation; torpor; prey detection; sensory ecology

1. INTRODUCTION
Ecological pressure paired with opportunism can lead to surprising innovations in animal behaviour, such as chimpanzee tool use (Goodall 1964), raiding of fox food caches by ravens (Careau et al. 2007), capture of emerging bats by raptors (Fenton et al. 1994) and problem solving in foraging guppies (Laland & Reader 1999). A recently discovered case is the predation of a large aerial hawking bat on night migrating songbirds (Popa-Lisseanu et al. 2002). Conversely, here we present evidence for opportunistic predation of a songbird, the great tit (Parus major), on bats. Four anecdotal reports have suggested that tits might prey on hibernating bats as an additional food source in winter. Ryberg (1947) described dead bats in front of hibernacula in Sweden with ‘injury, caused e.g. by timtice (possibly also bigger birds)’ (p. 31). Sachanowicz & Krasnodebski (1996) saw a great tit feeding on a dead bat at a cave in Poland. At the same place, Radzicki et al. (1999) found one dead and two live bats with injuries presumably from tit beaks. It was unclear in all


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remotely via a 20 m cable. The sound level of playback calls was about 40–46 dBA at 1 m (Voltcraft SL-400 sound level meter) and sounded realistic to the human ear.

3. RESULTS

(a) Foraging and feeding behaviour
We observed a total of 16 predation events of great tits on pipistrelle bats in the winter 2004/2005 and two events in 2005/2006. The tits flew into the cave, flew slowly at close distance to cave walls and ceiling and repeatedly landed and sometimes vanished into crevices for few seconds (electronic supplementary material, video S1). We then saw them pecking the captured bats on rocks inside the cave (electronic supplementary material, videos S2 and S3) or on the cave floor. Typically 5–15 min would elapse from the time a tit entered the cave until we observed it with a captured bat. For transport, they took the bats into their beaks and sometimes carried them out of the cave to feed in nearby trees (electronic supplementary material, videos S4 and S5). The tits started eating the bats from either the head (figure 1a, b), back or abdomen. In addition to the direct observations, we found five pipistrelle carcasses in 2004/2005 and three in 2005/2006. All eight showed obvious traces of bird pecks, but no signs of chewing by a mammalian predator. Considerable parts of muscle mass had been pecked off these carcasses; on one, only skin and bones remained (figure 1c). The highest predation rates we observed were three predation events within 35 min on 8 February 2005 and five events within 1 h 40 min on 15 February 2005.

(b) Provisioning experiment
We observed 17 events of a tit preying on a bat on 10 days without food provisioning, but only one predation event when the birds had access to experimentally provisioned, abundant food. Predation in non-provisioning times was significantly more common than expected by an even distribution of predation over observation time (see §2; binomial test, $p = 0.0113$). The number of bat carcasses with signs of bird feeding that we found upon arrival to the cave provided additional support to the hypothesis that the intensity of the predation on the bats was inversely correlated with availability of other food to the tits. On 10 visits to the cave without prior food provisioning, we found six carcasses, while on 12 visits with food provisioning we found only two, but this difference was not statistically significant (binomial test, $p = 0.0927$).

(c) Bat calls and playback experiment
The vocalizations of awakening bats were noisy multi-harmonic sounds of about 0.8 s (examples in figure 2; summary statistics of call parameters in table 1). Often, they were followed by one or several tonal, mostly downward frequency modulated calls.

We broadcast the vocalizations of awakening bats to one or several tits (maximum eight) that were present close to our loudspeaker for a total of 27 times. Forty-five out of 56 tits showed a clear response to the playback, 11 did not. A reaction consisted of orienting in the direction of the hidden speaker and approaching

Figure 1. (a) Freshly killed pipistrelle bat ($P. pipistrellus$), where a tit pecked off parts of snout and face. (b) Freshly killed pipistrelle, where a tit pecked off parts of head and ventral musculature. (c) Skin and skeleton of a dead pipistrelle found just below trees outside the cave in which tits had been observed feeding on bats. Inner organs, brain and flesh were missing; skin bore clear signs of bird beak pecks. (d) Great tit ($P. major$) looking at and approaching a hidden loudspeaker (arrow) that broadcast calls of an awakening pipistrelle bat.
the speaker in flight or on foot (figure 1d). As the tits might observe and copy each other’s behaviour, we did not regard the reaction of birds that were simultaneously present at the speaker as independent. Indeed, all tits present simultaneously always showed the same response; either all or none reacted to the playback. Overall, 18 playbacks elicited a response, while nine did not.

4. DISCUSSION
The slow flights along and frequent landings on the cave walls and the direct observation of 18 predation events over 22 days with only 45 h of time at the cave indicates that the tits specifically and systematically searched for and killed bats. Extended pecking on the bats and substantial removal and ingestion of flesh, brain and other organs suggest that the birds were killing the bats for food and were not, for example, in competition for nest holes in the cave. The substantial decrease of the observed killing of bats by tits after experimental provisioning of energy-rich food further supports that bat-killing served a foraging purpose. Tits were also observed to kill other songbirds in competition for nest holes in summer (Merilä & Wiggins 1995) and for food in winter (Caris 1958). Our data support a trend found for non-migrating birds, such as tits, to rely more on innovative feeding behaviours in winter than in other seasons (Sol et al. 2005).

Upon playbacks of calls from awakening bats, many tits approached and inspected the loudspeaker. This is evidence that they were able to hear and localize the bat calls, even though the frequency with maximum energy (table 1) was above their upper hearing limit (Langemann et al. 1998). Thus, tits could eavesdrop on awakening calls to find bats in crevices. Interestingly, similar calls of awakening bats in Canada were found to repel mammalian predators (Martin & Fenton 1978). It therefore is even conjecturable that bats vocalize in an attempt to defend themselves against predation (pursuit-deterrence; see Caro 1995). If calling indeed reveals the bats’ location to opportunistic birds, the tits’ foraging innovation may change the direction of selection on the use of this call.

The first observation of a tit preying on a bat at Istállos-kő cave was in winter 1995/1996 (Estók 1996), 10 years before our present observations and thus clearly exceeding the typical lifespan for a wild tit (0.1% survival probability from egg to 8 years of age (Tinbergen & Daan 1990). The tits in our study were not marked; however, we are certain that several, if not many, individuals foraged for bats. This raises the question of whether cultural transmission plays a

Figure 2. Examples of vocalizations from awakening pipistrelle bats. Sonagram representation (FFT 512); oscillogram below, 70 dB dynamic range. (a) Typical example that closely corresponds to the average call parameters listed in table 1. (b) Example with especially prominent tonal components and long, trailing downward frequency modulated call. Scale bar, 100 ms.
role for the spread of this foraging innovation, as was the case for the famous blue tits (Cyanistes caeruleus) in the British Isles that learned to open milk bottles (Fisher & Hinde 1949). If so, it raises another question to be addressed in future studies: does cultural transmission link the Hungarian bat-eating tits to the Polish ones (see §1) or did this behavioural innovation arise independently at the two sites, as a consequence of similar opportunities present?

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Table 1. Sound parameters of vocalizations from awakening pipistrelle bats (second order means ± s.d.).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean ± s.d. (sound files)</th>
<th>n (vocalizations)</th>
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<tbody>
<tr>
<td>highest frequency</td>
<td>29.8 ± 3.9 kHz</td>
<td>8 51</td>
</tr>
<tr>
<td>frequency with maximum amplitude</td>
<td>15.1 ± 2.6 kHz</td>
<td>8 51</td>
</tr>
<tr>
<td>lowest frequency</td>
<td>3.9 ± 1.6 kHz</td>
<td>8 51</td>
</tr>
<tr>
<td>duration (onset to onset)</td>
<td>0.78 ± 0.24 s</td>
<td>10 61</td>
</tr>
<tr>
<td>interval (onset to onset)</td>
<td>2.25 ± 0.54 s</td>
<td>9 60</td>
</tr>
<tr>
<td>trailing tonal calls</td>
<td>1.9 ± 0.6</td>
<td>7 50</td>
</tr>
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