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Does a live barn owl (*Tyto alba*) affect emergence behavior of serotine bats (*Eptesicus serotinus*)?

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We studied the impact of predation risk on emergence behavior of a maternity colony of *Eptesicus serotinus*. Observations were made during sets of three consecutive nights — control, treatment and post-treatment. On treatment nights, a trained individual of barn owl (*Tyto alba*) was displayed during the emergence of the colony. Presence of the owl did not induce any significant change in the emergence parameters with exception of the degree of clustering. In pregnancy bats increased their clustering during treatment and post-treatment nights. The presence of the owl induced changes in relationships among emergence parameters. If bats emerged earlier when predation risk supposed to be higher, they increased their degree of clustering to decrease the individuals’ probability of being attacked. We conclude that clustering in emergence is an important anti-predation strategy.

Key words: *Eptesicus serotinus*, *Tyto alba*, emergence, predation risk, reproduction

INTRODUCTION

A bat colony represents a large potential food source concentrated in a small area, and thus may attract predators. Although bats are known to fall prey to a large diversity of predators (Gillette and Kimbourgh, 1970), much reported predation appears to be opportunistic. Only for *Macieiaramphus alcinnus*, *Falco rufignularis* and *Strix nigrolineata* are bats a major component of the diet (Cade, 1987; Gerhardt, 1994). However, some individuals of other avian predators can specialize in preying on bats, e.g., *Tyto alba* (Bauer, 1956; Romano et al., 1999; authors’ unpublished data), *Strix aluco* (Obuch, 1992; 1998) or *Falco tinnunculus* (Negro et al., 1992; Lee and Kuo, 2001). Speakman (1991) estimated that predation by avian predators accounts for about 11% of the annual mortality of British bats despite the apparent low representation of bats in the diets of predatory birds.

Bats seem to be most vulnerable to predation during their predictable evening emergence and morning return, when they are concentrated near their roost from which they must emerge/enter through sites with limited access (Barclay et al., 1982; Erkert, 1982; Negro et al., 1992; Roberts et al., 1997; Lee and Kuo, 2001). The factors regulating the timing of nocturnal activity are of endogenous (hormonal) as well as exogenous (light, temperature, etc.) origin (reviewed by Erkert, 1982). Colony size, reproductive status and level of predation risk can also contribute to variation in timing of emergence (Jones and Rydell,
Emergence consists of groups of bats leaving the roost together, interspersed with periods when few or no individuals leave. This behavior has been called ‘outburst activity’ or ‘clustering’ (Speakman et al., 1992). Two hypotheses concerning the functional significance of clustering are considered (Speakman et al., 1999). It may be an anti-predator behavior (Hamilton, 1971) or bats may emerge together to coordinate their foraging behavior (Wilkinson, 1992; Wilkinson and Boughman, 1998). The idea that clustering simply reflected an artefact of the movement of a large number of animals through a restricted hole (bottleneck effect — Bullock et al., 1987) was rejected by Speakman et al. (1999), who showed that bottlenecks disrupted clustering rather than promoted it.

Although many aspects of bat behavior are supposed to be affected by predation risk, there have been few attempts to demonstrate the influence of predation risk on emergence behavior. Speakman et al. (1992), Kalcounis and Brigham (1994) and Petřželková and Zukal (2001) used a predator model associated with or without recorded calls, to study the response to predation risk on emergence behavior. Effective anti-predator defense mechanisms depend on efficient recognition of potential predators. In all the above mentioned studies the potential perceived threat to bats of owl models/playbacks was discussed. To our knowledge only Fenton et al. (1994) observed anti-predator behavior of bat colonies to a real predator pressure.

In the present study, we studied the impact of the presence of a barn owl (Tyto alba) on the emergence behavior of a maternity colony of serotine bats (Eptesicus serotinus). Unlike comparable previous studies we used a live trained animal. Our aim was to investigate the responses of bats to a live moving animal rather than to a stuffed model associated with recorded calls (Petřželková and Zukal, 2001).

Materials and Methods

Study Colony

Field work was carried out from the beginning of May to the end of June in 2000 at a maternity colony of E. serotinus in Střelice (49°09’N, 16°30’E), a small village near Brno, Czech Republic. Bats roosted in the attic of a family house at the periphery of the village and emerged from up to five exit holes (crevices between roof tiles or between the roof molding and tiles). One exit hole was used more frequently (> 80% of colony members) than the others. The front part of the house faced a street (southwest) and the rear of the house, with exit holes, to a complex of gardens (northeast). The rear of the house was covered by walnut (Juglans regia) branches. Střelice is surrounded mainly by agricultural land with patches of woodland.

Bats usually start to establish a colony at this site at the end of April or beginning of May and leave the roost during July/August. However, in the year of this study the first bats appeared at the roost in the mid-April and departed at the end of June. Experiments began in the mid-May and last until beginning of July.

Data Collecting

Emergence activity was monitored every week, on three consecutive nights. The first night served as a control, with emergence activity recorded without the presence of the owl. During the second night, a trained owl was displayed during the emergence period. On the third night changes in emergence after the night when the predator was presented were recorded. Each observation started approximately 30 minutes before the expected onset of emergence period according to the time of sunset and lasted until no bat had emerged for 15 minutes. The barn owl used for the predator treatment was a 1-year male, which was always handled by a falconer. We chose a barn owl, because it preys on bats, including Eptesicus serotinus (Obuch, 1998), and because this species had been recorded at the locality (J. Vačkař, pers. com.). A stuffed specimen of barn owl was used in a previous study (Petřželková and Zukal, 2001). During predator treatment the falconer with the owl stood on the flat roof beneath the roost exit. The owl was flown tethered on a 60 cm long belt or sat on the falconer’s raised hand, occasionally flapping its wings. When
flown the owl was at the same height or just beneath
the stream of emerging bats. The emergence behavior
of bats was recorded from the roof of an adjacent
garage or, on the first and third nights when the
falconer was absent on the same roof used by the fal-
coner. Thus the presence of the observer/falconer
served as a neutral stimulus.

All observations on emergence and return activ-
ity were recorded verbally on a dictaphone, with each
emerging/returning individual recorded. Recordings
were later transcribed with accuracy to one second us-
ing TIMER software (J. R. Speakman, School of
Biological Sciences, University of Aberdeen, Scot-
land). The emergence model was characterized by the
following parameters: 1) onset of emergence (O) —
the time of the first bat to emerge, 2) median of em-
ergence (M) — the time of the middle bat to emerge,
3) end of emergence (E) — the time of the last bat to
emerge. All these parameters were given in seconds
with respect to sunset. In addition we recorded 4) the
duration of emergence (D) — length of the interval
between the first and the last bat to emerge (in min-
utes), 5) rate of emergence (R) — number of bats
emerging per minute, 6) degree of clustering (G) —
expressed as adjusted $G$-value (see data analysis). The
level of light intensity was measured at the onset of
emergence (L) using a luxmeter (GOSEN) placed
close to the roost of the colony. Because of the inac-
cessibility of the roost and because we did not want
to disturb the colony, the reproductive stage of the
females could not be directly reported. All bats left
the roost immediately after first emergence of weaned
bats and therefore the breeding season was divid-
ed only into two periods — ‘gravity’ and ‘lacta-
tion’. June 10th was defined as the transition date be-
tween gravity and lactation based on studies on oth-
er colonies, according to the information from litera-
ture (Schober and Grimmberger, 1993; Catto et al.,
1995), from previous studies on the colony under in-
vestigation (Petrželková and Zukal, 2001) and from
a study of another maternity colony of Eptesicus
serotinus near the study site (Pokorný, 1998) in pre-
vious years. We took account of the fact that bats
established the colony sooner than in previous years.
Air temperature was recorded at Troubsko, a village
near the study site (2 km), at 9 p.m. and atmospheric
pressure was recorded in Brno-Tuřany (ca. 15 km)
at 9 p.m. Climatic information were supplied by the
Hydrometeorological Institute in Brno, Czech Re-
public.

Data Analysis

The analysis of clustering behavior was perform-
ed by the behavioral temporal clustering analysis
program CLUSTAN (J. R. Speakman). This software
calculates an explicit comparison of the observed
distribution of intervals between two consecutive
individual emergence events to that expected if the
emergence was random, and tests the significance
of this difference using $\chi^2$- or $G$-tests, depending
on sample size. Clustering is indicated when there
is over-representation of the shortest and the long-
est intervals in the sequence. $G$-values and $\chi^2$-values
are used as measures of clustering. If the values
exceed the significance level then the distribution is
clustered. However, it is necessary to adjust $G$-values
and $\chi^2$ according to method of Speakman et al. (1999)
to eliminate the impact of sample size. Adjusted
$G$-values were chosen to express the degree of clus-
tering, because $G$-test is more robust to the small sam-
ple sizes (number of emerged bats). If the sample size
is smaller than 30, CLUSTAN is not able to analyze
clustering behavior.

To test whether temperature and atmospheric
pressure differed significantly among the three days
within each experimental set, we used repeated
measures ANOVA with type of night (control, treat-
ment, post-treatment) as a repeated factor. Repeated
measures ANOVA with reproductive period as a cat-
egorical factor was used to test differences in emerg-
ence parameters among control night, treatment
night and post-treatment night (repeated factor).
Non-normal distributed variables were transformed
by Box-Cox transformation. Spearman’s correlation
between adjusted $G$-values and other emergence pa-
rameters were performed to examine changes in rela-
tionships due to predation risk (Sokal and Rohlf,
1995).

RESULTS

We observed emergence from the roost
on total of 27 nights, but only 20 nights in
seven sets were used for analyses. The
remaining nights were single, and did not
form complete sets. Adjusted $G$-values
were counted only for 19 emergences. The
number of bats emerging from the roost was
stable after the establishment of the colony
(median of number of emerging bats was
56) and the bats commenced leaving the
roost immediately when their young began to
fly.

There was no difference among days in
temperatures (repeated measures ANOVA:
Table 1. Effect of the presence of the predator on emergence activity. Results of repeated measures ANOVA on emergence factors (see Materials and Methods for details). Abbreviations: RF — repeated factor (type of night), CF — categorical factor (reproductive period). \( P \leq 0.05 \) in bold

<table>
<thead>
<tr>
<th>Emergence parameters</th>
<th>CF ( F )</th>
<th>CF ( P )</th>
<th>RF ( F )</th>
<th>RF ( P )</th>
<th>RF*CF ( F )</th>
<th>RF*CF ( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Onset of emergence (O)</td>
<td>0.122</td>
<td>0.75</td>
<td>1.538</td>
<td>0.27</td>
<td>0.056</td>
<td>0.95</td>
</tr>
<tr>
<td>Median of emergence (M)</td>
<td>0.638</td>
<td>0.47</td>
<td>2.037</td>
<td>0.19</td>
<td>0.021</td>
<td>0.98</td>
</tr>
<tr>
<td>End of emergence (E)</td>
<td>2.440</td>
<td>0.19</td>
<td>0.178</td>
<td>0.84</td>
<td>0.25</td>
<td>0.79</td>
</tr>
<tr>
<td>Degree of clustering (G)</td>
<td>0.007</td>
<td>0.94</td>
<td>6.914</td>
<td>0.03</td>
<td>5.458</td>
<td>0.05</td>
</tr>
<tr>
<td>Rate of emergence (R)</td>
<td>0.035</td>
<td>0.86</td>
<td>0.073</td>
<td>0.93</td>
<td>0.194</td>
<td>0.83</td>
</tr>
<tr>
<td>Duration of emergence (D)</td>
<td>3.948</td>
<td>0.12</td>
<td>0.573</td>
<td>0.59</td>
<td>0.395</td>
<td>0.69</td>
</tr>
<tr>
<td>Level of light intensity (I)</td>
<td>2.565</td>
<td>0.18</td>
<td>1.945</td>
<td>0.21</td>
<td>0.241</td>
<td>0.79</td>
</tr>
</tbody>
</table>

\( F_{2, 10} = 0.639, \ P = 0.55 \) or atmospheric pressure \( F_{2, 10} = 3.000, \ P = 0.13 \) within experimental sets of nights. Therefore, we ignored the effects of temperature and atmospheric pressure among control, treatment and post-treatment nights within experimental sets.

The presence of the barn owl did not induce any changes in most of the emergence parameters. No effect was also detected on the post-treatment days (Table 1). However, repeated measures ANOVA revealed significant variations in adjusted \( G \)-values among days within experimental sets, and a repeated measures factor versus reproductive period interaction was significant (Table 1, Fig. 1).

We found out that the presence of the owl influenced relationships among emergence parameters. The most important was the fact that the adjusted \( G \)-values correlated with the onset and median time of emergence on treatment nights, while there was no correlation between adjusted \( G \)-values and any parameter of emergence on control nights. Strong but non-significant correlations were also found between adjusted \( G \)-values and the level of light intensity and between adjusted \( G \)-values and the end of emergence. On post-treatment nights adjusted \( G \)-values correlated with rate of emergence (Table 2).

**Discussion**

Colonies of bats form resource patches that appear to offer excellent opportunities to predators. While concentrations of predators are commonly observed around the roost entrances of the enormous cave colonies of *Tadarida brasiliensis* (e.g., Lee and Kuo, 2001), at most bat colonies predators are seen rarely. However, predation may affect many aspects of bat behavior, like general coloniality and roost selection (Barclay *et al.*, 1982; Fenton *et al.*, 1994;
Table 2. Spearman’s correlation coefficients between G-values and other emergence parameters. Control, treatment, post-treatment nights are treated separately. G — degree of clustering, O — onset of emergence, M — median of emergence, E — end of emergence, D — duration of emergence, R — rate of emergence, I — level of light intensity at the onset of emergence. Significant correlations (P ≤ 0.05) in bold

<table>
<thead>
<tr>
<th>Emergence parameter</th>
<th>Control</th>
<th>Treatment</th>
<th>Post-treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>r</td>
<td>P</td>
<td>r</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G &amp; O</td>
<td>0.600</td>
<td>0.21</td>
<td>-0.943</td>
</tr>
<tr>
<td>G &amp; M</td>
<td>0.486</td>
<td>0.33</td>
<td>-0.886</td>
</tr>
<tr>
<td>G &amp; E</td>
<td>0.486</td>
<td>0.33</td>
<td>-0.771</td>
</tr>
<tr>
<td>G &amp; D</td>
<td>0.771</td>
<td>0.07</td>
<td>0.371</td>
</tr>
<tr>
<td>G &amp; R</td>
<td>-0.257</td>
<td>0.62</td>
<td>0.029</td>
</tr>
<tr>
<td>G &amp; I</td>
<td>0.600</td>
<td>0.21</td>
<td>0.771</td>
</tr>
</tbody>
</table>

Jenkins et al. (1998), use of linear landscape elements (Verboom, 1998), and both emergence and return behavior (Fenton et al., 1994; Jones and Rydell, 1994; Duvergé et al., 2000; Petrželková and Zukal, 2001; Petrželková, 2003). Avian predation is supposed to be the most important factor influencing bat nocturnality (Rydell and Speakman, 1994; Speakman, 1995), though there is still a lack of a clear consensus.

Effective anti-predator defence mechanisms depend on efficient recognition of possible predators. Kalcounis and Brigham (1994) and Speakman et al. (1992) disputed that bats were able to distinguish models and playback calls of predators, used during their experiments, from real ones. Both authors presented plastic models of owls to emerging bats, Kalcounis and Brigham (1994) together with recorded owl calls. Our previous results indicated that E. serotinus perceived a stuffed owl and kestrel, along with playbacks of their calls, as a predation threat (Petrželková and Zukal, 2001). In the current study, E. serotinus responded to the live owl, which did not utter any calls. Therefore, we suppose bats could perceive a silhouette of an avian predator as a potential threat. Nevertheless, experiments with plastic owls have proven unsuccessful (Speakman et al., 1992; Kalcounis and Brigham, 1994), and we can speculate that bats may discriminate between a plastic (not stuffed) and a real owl. It is also possible that more than one stimulus are used by bats (silhouette plus movements or silhouette plus calls). Moreover, the vocalisation of an attacked bat could alert the rest of a bat colony (Fenton et al., 1994). In desert rodents, playbacks of calls of Strix aluco were sufficient to induce anti-predator defence behavior and increased corticosterone levels of rodents (Hendrie et al., 1998; Eilam et al., 1999).

There are a few observations which have recorded direct changes in emergence or return behavior directly in response to a predator. A part of a colony of Myotis lucifugus was reported to leave their roost in response to the activity of Otus asio nearby (Barclay et al., 1982). Also, Myotis myotis changed their emergence exit from a roost to avoid the attacks of S. aluco (Güttlinger, 1990), with the colony abandoning its roost earlier than in previous years (R. Güttlinger, pers. comm.). Attacks by Falco columbarius on emerging Pteronotus fuliginosus induced a disappearance of one of the emerging streams of the colony (Rodriguez-Durán and Lewis, 1985). Fenton et al. (1994) studying colonies of Tadarida pumila and T. condylura attacked by raptors, described several anti-predation strategies of bats. In colonies of less than 100 individuals, bats decreased their risk of attack by switching
roosts, and by adjusting the times and durations of emergence. Bats from larger colonies emerged earlier, despite the increased risk of predation by raptors. At all colonies, increasing numbers of bats decreased the risk of predator attack (Fenton et al., 1994).

Kalcounis and Brigham (1994) and Speakman et al. (1992) proposed that bats should increase their clustering in the presence of a predator to decrease their probability of attack. However, their experiments with models of owls did not reveal any significant effect of predation risk on the extent of clustering during emergence. Nevertheless, Speakman et al. (1992) discussed that development of clustering may be sufficient to act as an anti-predation device. In contrast, the results of our experiments indicate that in pregnancy, bats increased their clustering in the presence of the live owl and also on the night following the treatment. We speculate that this effect of the reproductive period might be connected with differences in other emergence parameters between pregnancy and lactation. In comparison with other reproductive periods, bats can emerge during pregnancy earlier (e.g., Jones, 1995; Shiel and Fairley, 1999) or later (Kunz, 1974; Duverge et al., 2000). There could also be intra-colony differences in the effect of the reproductive period on emergence times, which could be related to different food availability in each year (Petřželková and Zukal, 2001).

As well as in our previous study (Petřželková and Zukal, 2001), predation risk induced changes in relationships among emergence parameters. When bats emerged early in the presence of owl, they increased their degree of clustering. Early emergence increases exposure to raptorial birds (Jones and Rydell, 1994; Rydell et al., 1996), but emerging late results in missing the peak abundance of aerial insects (Racey and Swift, 1985; Rydell et al., 1996). Therefore, we conclude that if bats emerged earlier and thus were exposed to increased potential predation pressure, they increased their degree of clustering to thereby decrease the individuals’ probability of being attacked. This behavioural tactic may be expressed if bats perceive an actual risk of predation. The correlation between the degree of clustering and rate of emergence probably reflected the fact that faster emergence could disrupt clustering.

Ambient temperature and atmospheric pressure can affect emergence behaviour (e.g., Negro et al., 1992; Catto et al., 1995; Rydell et al., 1996). Our analyses showed no differences among nights within the experimental sets, so we neglected the effects of climatic factors on the perception of predation threat.

Tadarida pumila switched their emergence behaviour from random to clustered with the arrival of Macheiramphus alcinus at their roost site (McWilliam, 1989). With maternity colonies of Pipistrellus pipistrellus in Scotland, the extent of clustering behaviour was the greatest during the first half of emergence, when light levels were high, suggesting an anti-predation function (Speakman et al., 1995). Based on the results of our studies on bat anti-predation behaviour during emergence, we suggest that clustering during emergence is an important anti-predation strategy.

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