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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 *Macheiramphus alcinus*, *Falco rufigularis* 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avian predators can specialize in preying on bats, e.g., *Tyto alba* (Bauer, 1956; Romano *et al*., 1999; authors' unpublished data), *Strix aluco* (Obuch, 1992; 1998) or *Falco tinnunculus* (Negro *et al*., 1992; Lee and Kuo, 2001).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,

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1994; Speakman *et al*., 1995; Catto *et al*., 1996).

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 co-ordinate 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 Petrželková 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 (Petrželková 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 (Petrželková 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

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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 falconer. Thus the presence of the observer/falconer served as a neutral stimulus.

All observations on emergence and return activity were recorded verbally on a dictaphone, with each emerging/returning individual recorded. Recordings were later transcribed with accuracy to one second using TIMER software (J. R. Speakman, School of Biological Sciences, University of Aberdeen, Scotland). 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 emergence (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 minutes), 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 (I) using a luxmeter (GOSEN) placed close to the roost of the colony. Because of the inaccessibility 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 divided only into two periods — 'gravidity' and 'lactation'. June 10th was defined as the transition date between gravidity and lactation based on studies on other colonies, according to the information from literature (Schober and Grimmberger, 1993; Catto *et al*., 1995), from previous studies on the colony under investigation (Petrželková and Zukal, 2001) and from a study of another maternity colony of *Eptesicus serotinus* near the study site (Pokorný, 1998) in previous 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 Republic.

Data Analysis

The analysis of clustering behavior was performed 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 χ^2- or *G*-tests, depending on sample size. Clustering is indicated when there is over-representation of the shortest and the longest intervals in the sequence. *G*-values and χ^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 χ^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 clustering, because *G*-test is more robust to the small sample 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, treatment, post-treatment) as a repeated factor. Repeated measures ANOVA with reproductive period as a categorical factor was used to test differences in emergence 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 parameters were performed to examine changes in relationships 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:

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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

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

$F_{2, 10} = 0.639$, $P = 0.55$) 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 corre-lated 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;

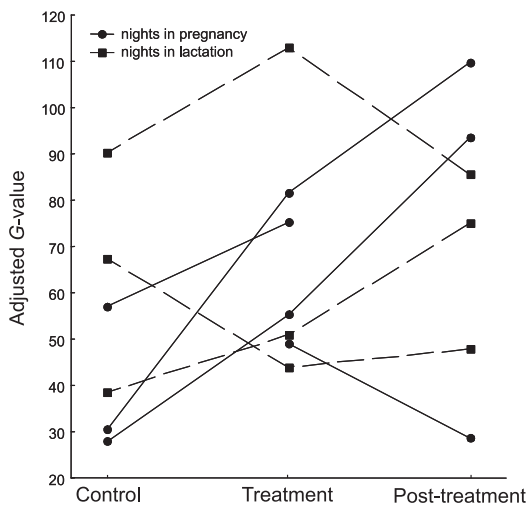

FIG. 1. Changes of adjusted *G*-values and type of night during control, treatment and post-treatment nights in respect to reproductive season

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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 ($P \leq 0.05$) in bold

Emergence parameter	Control		Treatment		Post-treatment	
	r	*P*	*r*	*P*	*r*	*P*
G & O	0.600	0.21	**-0.943**	**0.01**	0.143	0.79
G & M	0.486	0.33	**-0.886**	**0.02**	-0.029	0.96
G & E	0.486	0.33	-0.771	0.07	0.371	0.49
G & D	0.771	0.07	0.371	0.47	0.771	0.07
G & R	-0.257	0.62	0.029	0.96	**-0.886**	**0.02**
G & I	0.600	0.21	0.771	0.07	0.200	0.70

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* (Güttinger, 1990), with the colony abandoning its roost earlier than in previous years (R. Güttinger, pers. comm.). Attacks by *Falco columbarius* on emerging *Pteronotus fuliginosus* induced a disappearance of one of the emerging streams of the colony (Rodríguez-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

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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; Duvergé *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 (Petrželková and Zukal, 2001).

As well as in our previous study (Petrželková 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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Literature Cited

Barclay, R. M. R., C. E. Thomson, and F. J. S. Phelan. 1982. Screech owl, *Otus asio*, attempting to capture little brown bats, *Myotis lucifugus*, at a colony. The Canadian Field-Naturalist, 96: 205–206.

Bauer, K. 1956. Schleiereule (*Tyto alba* Scop.) als Fledermausjäger. Journal of Ornithology, 97: 335–340.

Bullock, D. J., B. A. Combes, L. A. Eales. 1987. Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrellus*). Journal of Zoology (London), 211: 267–274.

Cade, T. J. 1987. The falcons of the world. Comstock/Cornell University Press, Ithaca, 188 pp.

Catto, C. M. C., P. A. Racey, and P. J. Stephenson. 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. Journal of Zoology (London), 235: 635–644.

Catto, C. M. C., A. M. Hutson, P. A. Racey, and P. J. Stephenson. 1996. Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. Journal of Zoology (London), 238: 623–633.

Duvergé, P. L., G. Jones, J. Rydell, and R. D. Ransome. 2000. Functional significance of emergence timing in bats. Ecography, 23: 32–40.

Eilam, D., T. Dayan, S. Ben-Eliyahu, I. Schulman, G. Schefer, and C. A. Hendrie. 1999. Differential behavioral and hormonal responses of voles and spiny mice to owl calls. Animal Behaviour, 58: 1085–1093.

Erkert, H. G. 1982. Ecological aspects of bat activity rhythms. Pp. 201–242, *in* Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, 425 pp.

Fenton, M. B., I. L. Rautenbach, S. E. Smith, C. M. Swanepoel, J. Grosell, and J. van Jaarsveld. 1994. Raptors and bats: threats and opportunities. Animal Behaviour, 48: 9–18.

Gerhardt, R. P. 1994. The food habits of sympatric *Ciccaba* owls in northern Guatemala. Journal of Field Ornithology, 65: 258–262.

Gillette, D. D., and J. D. Kimbrough. 1970. Chiropteran mortality. Pp. 262–281, *in* About bats (B. H. Slaughter and D. W. Walton, eds.). Southern Methodist University Press, Dallas, 313 pp.

Güttinger, R. 1990. Mausohren leben gefährlich. Fledermaus-Anzeiger, Regionalbeilage für die Kantone SG/AI/AR. September 1990.

Hamilton, W. D. 1971. Geometry of the selfish herd. Journal of Theoretical Biology, 31: 295–311.

Hendrie, C. A., S. M. Weiss, and D. Eilam. 1998. Behavioral response of wild rodents to the calls of an owl: a comparative study. Journal of Zoology (London), 245: 439–446.

Jenkins, E. V., T. Laine, S. E. Morgan, K. R. Cole, and J. R. Speakman. 1998. Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus*, in northeast Scotland. Animal Behaviour, 36: 909–917.

Jones, G. 1995. Flight performance, echolocation and foraging behavior in noctule bats *Nyctalus noctula*. Journal of Zoology, 237: 303–312.

Jones, G., and J. Rydell. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions of the Royal Society of London B, 346: 445–455.

Kalcounis, M. C., and R. M. Brigham. 1994. Impact of predation risk on emergence by little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae), from a maternity colony. Ethology, 98: 201–209.

Kunz, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology, 55: 693–711.

Lee, Y. F., and Y. M. Kuo. 2001. Predation on Mexican free-tailed bats by peregrine falcons and red-tailed hawks. Journal of Raptor Research, 35: 115–123.

McWilliam, A. N. 1989. Emergence behavior of the bat *Tadarida* (*Chaerephon*) *pumila* (Chiroptera: Molossidae) in Ghana, West Africa. Journal of Zoology (London), 219: 698–701.

Negro, J. J., C. Ibáñez, J. L Pérezjordá, and M. J. Delarivo. 1992. Winter predation by common kestrel *Falco tinnunculus* on pipistrelle bats *Pipistrellus pipistrellus* in Southern Spain. Bird Study, 39: 195–199.

Obuch, J. 1992. Tawny owl (*Strix aluco*) preying on bats. Pp. 119–121, *in* Prague studies in mammalogy (I. Horaček and V. Vohralík, eds.). Charles University Press, Prague, 245 pp.

Obuch, J. 1998. The representation of bats (Chiroptera) in the diet of the owls (Strigiformes) in Slovakia. Vespertilio, 3: 65–75.

Petrželková, K. 2003. Impact of predation on bats. Ph.D. Thesis, Masaryk University, Brno, Czech Republic and Institute of Vertebrate Biology, Brno, Academy of Sciences of the Czech Republic, 93 pp.

Petrželková, K., and J. Zukal, 2001. Emergence behavior of the serotine bat (*Eptesicus serotinus*) under predation risk. Netherlands Journal of Zoology, 51: 395–414.

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POKORNÝ, M. 1998. Prostorová a časová aktivita netopýra večerního (*Eptesicus serotinus*) v zemědělské krajině [Temporal and spatial activity of serotine bat (*Eptesicus serotinus*) in agrocoenoses]. M.A. Thesis, Masaryk University, Brno, Czech Republic, 91 pp. [In Czech].

RACEY, P. A., and S. M. SWIFT. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behavior. Journal of Animal Ecology, 54: 205–215.

ROBERTS, K. J., F. D. YANCEY, and C. JONES. 1997. Predation by great-horned owls on Brazilian free-tailed bats in north Texas. Texas Journal of Science, 49: 215–218.

RODRÍGUEZ-DÚRAN, A., and A. L. LEWIS. 1985. Seasonal predation by merlins on sooty mustached bats in western Puerto Rico. Biotropica, 17: 71–74.

ROMANO, M. C., J. I. MAIDAGAN, and E. F. PIRE. 1999. Behavior and demography in an urban colony of *Tadarida brasiliensis* (Chiroptera: Molossidae) in Rosario, Argentina. Revista de Biologia Tropical, 47: 1121–1127.

RYDELL, J., A. ENTWISTLE, and P. A. RACEY. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos, 76: 242–252.

SCHOBER, W., and E. GRIMMBERGER. 1993. Bats of Britain and Europe. Kosmos Verlag, Stuttgart, 265 pp.

SHIEL, C. B., and J. S. FAIRLEY. 1999. Evening emergence of two nursery colonies of Leisler's bat (*Nyctalus leisleri*) in Ireland. Journal of Zoology (London), 247: 439–447.

SOKAL, R. R., and F. J. ROHLF 1995. Biometry: the principles and practice of statistics in biological research. Third ed. W. H. Freeman and Company, New York , 887 pp.

SPEAKMAN, J. R. 1991. The impact of predation by birds on bat population in the British Isles. Mammal Review, 21: 123–142.

SPEAKMAN, J. R., D. J. BULLOCK, L. A. EALES, and P. A. RACEY. 1992. A problem defining temporal pattern in animal behavior: clustering in the emergence behavior of bats from maternity roosts. Animal Behaviour, 43: 491–500.

SPEAKMAN, J. R., R. E. STONE, and J. E. KERSLAKE. 1995. Temporal patterns of pipistrelle bats, *Pipistrellus pipistrellus*, from maternity colonies are consistent with anti-predator response. Animal Behaviour, 50: 1147–1156.

SPEAKMAN, J. R., N. IRWIN, and R. STONE. 1999. Effect of roost size on the emergence behavior of pipistrelle bats. Animal Behaviour, 58: 787–795.

VERBOOM, B. 1998. The use of edge habitats by commuting and foraging bats. IBN Scientific Contributions 10, DLO Institute for Forestry and Nature Research (IBN-DLO), Wageningen, 120 pp.

WILKINSON, G. S. 1992. Information transfer at evening bat colonies. Animal Behaviour, 44: 501–518.

WILKINSON, G. S., and J. W. BOUGHMAN. 1998. Social calls coordinate foraging in greater spear-nosed bats. Animal Behaviour, 55: 337–350.

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