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Real time observations of *Strix aluco* preying upon a maternity colony of *Myotis emarginatus*

Friederike Spitzenberger[1], Simon Engelberger[2] & Karl Kugelschafter[3]

[1] *BatLife Österreich*, *c/o Natural History Museum Wien*, *Burgring 7*, *1010 Wien*, *Austria*; *office@batlife.at*
[2] *Natural History Museum Wien*, *First Zoological Department*, *Mammal Collection*, *Burgring 7*, *1010 Wien*, *Austria*; *simon.engelberger@univie.ac.at*
[3] *ChiroTEC Hollersgraben 27*, *35102 Lohra*, *Germany*; *kugelschafter@chirotec.de*

Abstract. Contrary to other mammalian orders, bats face a very low risk of predation. Nocturnality and the capacity to reach remote shelters by active flight offer little opportunities for diurnal avian and terrestrial mammalian predators. Here, we report on direct real time observations of a tawny owl attacking Geoffroy's bats which may help to clarify the question if and how bats perceive, react to and avoid predators. During the reproductive periods 2011–2013, we monitored timing of emergence and return as well as fluctuations in size of a large (maximum number in 2011 was 598 adult bats) maternity colony of *Myotis emarginatus* in Burgenland/Austria by using an automatic registration device. Additionally, we recorded the behaviour of a tawny owl attacking the colony from a perch at the access window of the roost with an infrared camera from 2 June 2011 onwards. The tawny owl attacked the bats only in 2011. From 6 June through 5 July 2011, the owl visited the roost 20 times during 12 nights. In total, the owl perched for 294 minutes on the ledge of the access window. It never entered the roost. Attacks were performed exclusively on returning bats; the average time of arrival was 75 minutes before and of departure 58 minutes before sunrise. The maximum of attacks occurred 15–20 minutes before and 5–10 minutes after the peak of returning bats. We recorded 252 attacks, with only 31 being successful. Four days before and eight days after the onset of parturition (10 June 2011) the owl achieved the greatest capture success (n=30). At least 333 bats entered the roost by flying over or past the owl. We did not observe that bats were attracted to the perching owl when it was killing a bat or any other defence or predator avoidance behaviour. We observed a decline of the colony size from 598 bats on 9 June to 93 on 19 June when the continuous predation phase ended. By 4 July, the numbers increased again to 494 individuals, but dropped to 302 on 5 July after the owl had appeared on the roof near the exit hole without having performed any capture attempt. The fluctuations of the colony size were not in line with changes of the night temperature. Our results suggest that the owl hunted the fast and erratic flying Geoffroy's bats only when the preferred prey (voles) was not abundant enough, only during the phase of highest vulnerability (late pregnancy) of the bats and only when the range of night luminance levels provided enough resolution for a successful hunt. We assume that individuals that escaped capture attempts avoided returning to the roost during the following night(s).

Predation, predator perception, prey availability, prey vulnerability, reaction to predation, night luminance, capture success

Introduction

Recently, Lima & O'Keefe (2013) raised the question whether most species of bats actually experience a world largely free of the risk of predation or if there is an anti-predator behaviour in bats generally present which is not well understood. Indeed it is widely unknown, whether nocturnality (Speakman 1995, Rydell & Speakman 1995) in combination with the capacity to reach remote shelters by active flight (Pomeroy 1990) protect bats almost completely not only against diurnal avian predators but also against raptorial birds active during low light. There is evidence that in Europe more bats are preyed upon by owls than by diurnal birds of prey (Speakman 1991a). In the absence of large bat concentrations, predation of bats by owls is infrequent (e.g. Lesiński et al. 2009), but where bats are locally and temporally abundant they may become an important food resource for individual owls (García et al. 2005).

The tawny owl (*Strix aluco*) is the most significant predator of bats on the British Isles and in continental Europe (Ruprecht 1979). Speakman (1991a) estimated an annual intake of 168,850 bats by this species in the U.K. The impact of individual tawny owls on large aggregations of temperate bat species near hibernacula and in maternity roosts can be substantial. Kowalski & Lesiński (1990) and Obuch (1992) reported high numbers of bats in pellets of *Strix aluco* collected in chambers near the entrance and the vicinity of hibernation caves in Slovakia, respectively. Both authors assumed that the bats were caught during flight.

Several studies deal with the effect of potential predation risk on chiropteran sociality (Irwin et al. 2013), selection of roost (Kunz 1982), foraging sites (Russo et al. 2011) and commuting tracks of bats (Verboom & Spoelstra 1999) as well as on timing and pattern of emergence and return from and to roosts (Speakman 1991b, Jones & Rydell 1994, Speakman et al. 1995, Rydell et al. 1996, Duvergé et al. 2000, Lee & McCracken 2001). Some experimental studies investigated the response of bats to the presence of nocturnal avian predators. Plastic or stuffed owls of different species – with or without exposure to play back of recorded vocalisations – (Speakman et al. 1992, Kalkounis & Brigham 1994, Petrželková & Zukal 2001) as well as a trained live barn owl (*Tyto alba*) (Petrželková & Zukal 2003) were presented to bats emerging from their roosts. Baxter et al. (2006) studied the effect of the presence of an owl at the foraging site of bats by presenting tape-playbacks.

However, publications on personally witnessed real time observations of owls predating on bats are very rare. Gebhardt (1997) saw tawny owls attacking noctules (*Nyctalus noctula*) when they returned to their hibernation roost in a rock crevice and Barclay et al. (1982) described real time interactions between little brown bats (*Myotis lucifugus*) and an attacking screech owl (*Otus asio*) and the effects of the predation on the colony. Fippl (2013) provided observations of a tawny owl which hunted mouse-eared bats (*Myotis myotis*) flying back to their maternity roost in the early morning and described the subsequent decimation of the colony.

The aim of our paper is to describe the seasonal and diurnal timing of attacks of a tawny owl (*Strix aluco*) on a maternity colony of Geoffroy's bats (*Myotis emarginatus*) and to analyse responses to the predation by the bats.

Material and methods

Study site and date

During the reproductive seasons of the years 2011–2013, we studied the fluctuations of the colony size and the timings of emergence and return flights of a maternity colony of Geoffroy's bats, roosting in a castle in Lockenhaus (47°24' N, 16°24' E, 388 m a. s. l.) in Burgenland, Austria. Castle Lockenhaus is situated on a rocky promontory which is surrounded by the small river Güns and its narrow belt of alluvial forest. The slopes of the promontory are covered by mature deciduous woodland.

In 2011, the colony consisted of a maximum of 598 bats. It inhabited an attic in a north-facing roof located about 17 m above the ground. The attic had only one access hole, a rectangular dormer window (37×42 cm) (Fig. 1a, b) which was the only light source illuminating the roost. This window was visible from a window in an opposite roof.

All times herein are expressed as Universal Time (UTC) + 01:00 hour. Sunrise times were obtained from the NOAA Solar Calculator (http://www.esrl.noaa.gov./gmd/grad/solcalc/index.html).

Automatic registration device and infrared-illuminated video camera

An automatic registration device consisting of two infra-red light beams connected to a logger was installed in the frame of the access window of the maternity roost (Kugelschafter et al. 1994). This device counted incoming and outgoing bats with a temporal resolution of one second during the whole roosting periods of 2011–2013 between late April and late July/beginning of August. It also logged the ambient temperatures in hourly intervals. The temperature sensor was positioned at the frame of the access window. From the logged data the average ambient night temperature between 18:00 and 6:00 was calculated.

From 2 June 2011 onwards, we simultaneously recorded the bats during emergence and return and the behaviour of the tawny owl with an infrared-illuminated video camera (ABUS IR HD1.3 MPx) attached to the roof opposite the access window. We did not register calls emitted by bats.

Results

Hunting strategy of the tawny owl

Behaviour: From 6 June through 21 June 2011, the tawny owl always employed the following hunting strategy: It used the ledge of the access window as a perch from which it observed the bats flying in front of the window by turning its head constantly. When no bats were flying, the body was crouched and filled little more than half of the window space (Fig. 1a). When bats were sighted, the owl assumed an upright posture, blocking about three quarters of the window space. During peak times of returning flights, the owl showed its full front side, but when only single bats were flying, it often hid large parts of the body by stepping behind the window frame and looking out with stretched neck. Occasionally, the owl looked into the attic, but never entered it. During a successful attack it extended its legs, jumped upwards with raised wings and snatched and killed the entering bat with the talons of the foot, tore it apart and ate it on the spot or carried it away (Fig. 1b).

After two weeks, on 5 July, the owl appeared once more at the roost, but displayed a completely different behaviour. Perching motionless on the steep side of the dormer roof it watched the flying bats without attempting to pursue them (Fig. 2).

Timing and number of visits: Attacks of the tawny owl on the maternity colony of Geoffroy's bats were recorded only during the year 2011 (Fig. 3.) From 6 June through 5 July, the owl visited the

Fig 1. 1a (left) – Tawny owl (*Strix aluco*) perching on the ledge of the dormer window and observing Geoffroy's bats (*Myotis emarginatus*) returning to the maternity roost. 1b (right) – Tawny owl (*Strix aluco*) tearing apart a captured bat.

Fig. 2. Tawny owl (*Strix aluco*) perching on the side of the dormer roof on 5 July 2011.

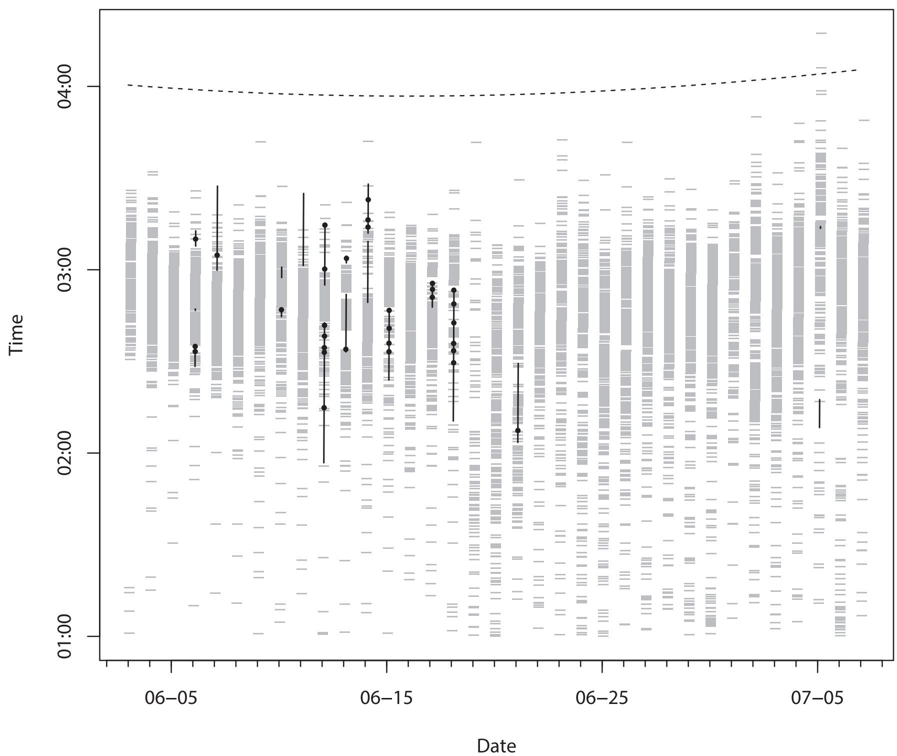

Fig. 3. Entering time of *M. emarginatus* individuals returning to the maternity roost between 3 June and 7 July 2011 as recorded by the infrared-illuminated video camera (grey dashes). Also indicated are the presence of the tawny owl (perpendicular black lines) and successful captures of bats (black dots) by the same. The dashed line indicates the course of daily sunrise times.

roost 20 times during 12 nights. Between 10 and 15 June, the owl perched each night in the access window. During a first phase (6–14 June) multiple visits per night occurred (three landings on 6, 13 and 14 June; two landings on 10 and 12 June). The length of the pauses between leaving and returning to the perch varied between 3 seconds and 20.5 minutes. Later (15–21 June), the owl appeared only once per night. During the last visit on 5 July, the owl perched for 9 minutes on top of the dormer, returned 56 minutes later to this place and flew off after one minute.

The individual visits started between 01:57 and 03:14 hours. On average, the owl appeared 74.6 min (range=44.9–120.4 min) before sunrise at the access window and flew off 57.6 min (28.9–106.5) before sunrise (n=18, 6–21 June). In total, the owl perched for 294 minutes in the window frame. The duration of one visit lasted on average 16.3 min (range=0.5–45.8, n=18, 6–21 June) and 5.0 min (range=0.6–9.2, n=2, 5 July) respectively (Fig. 3).

Timing of attacks: Attacks were performed exclusively on bats returning to the roost. They occurred between 113 and 34 minutes before sunrise (mean=74 min, n=252), coinciding with the period during which the bats returned to the roost. The maximum of attacks, however, did

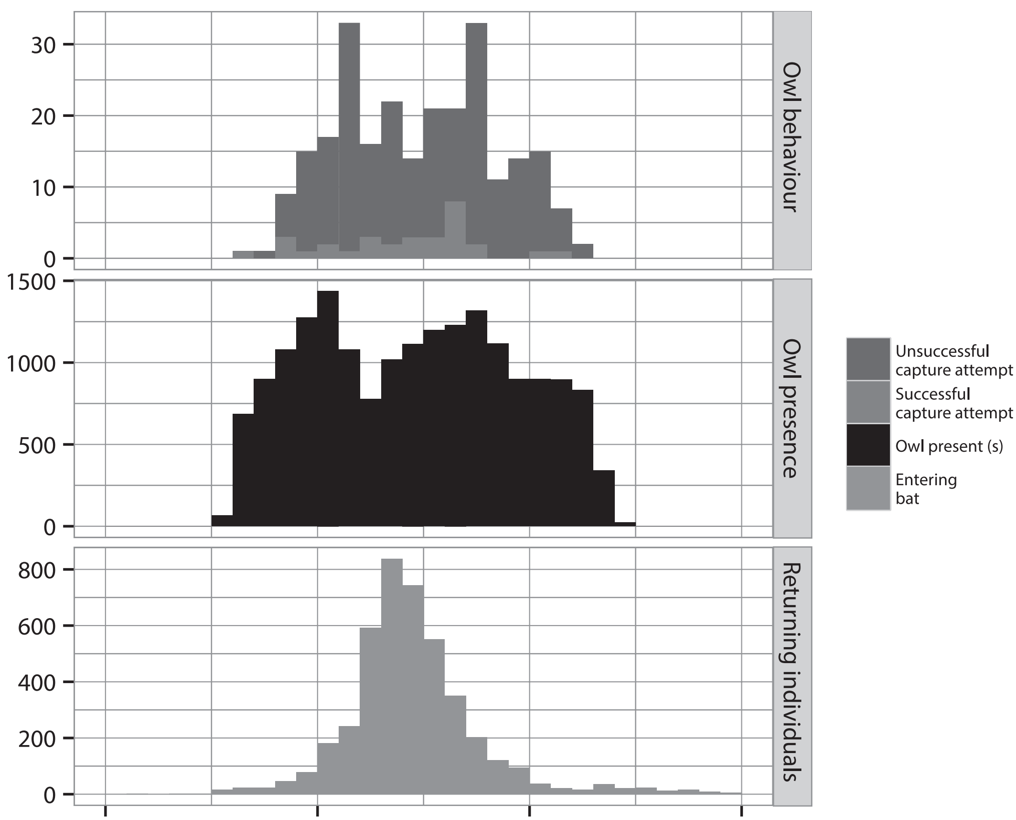

Fig. 4. Histogram (bar-width 5 min) of returning bats (bottom), overall presence of the owl (seconds per interval; middle), successful captures, and unsuccessful capture attempts (both top; stacked histogram) in relation to sunrise time. Contained are only data from nights between 6 June and 5 July 2011 when the tawny owl was perching at the bat roost.

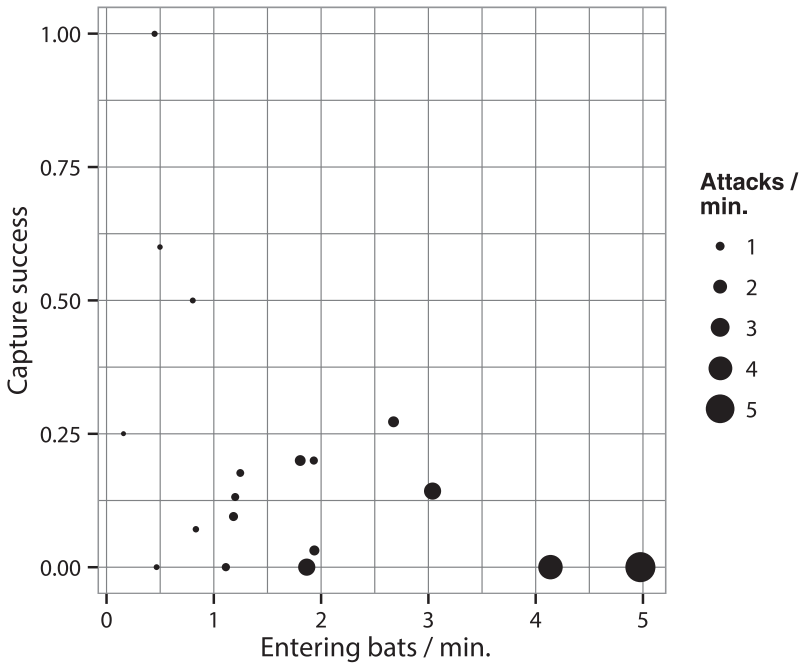

Fig. 5. Mean frequency of bats returning to the maternity roost during an uninterrupted visit of the tawny owl in relation to the capture success (successful / total capture attempts). Symbol size is proportional to the mean number of total capture attempts per visit.

not occur during the peak of returning bats, but ca. 15–20 minutes before and 5–10 minutes after this peak (Fig. 4).

Capture success: We recorded 252 attacks, with 31 being successful. Thus, the owl was successful in 12.3% of capture attempts. On average, it attacked 2.99 times per minute (range=0.38–6.65), the median number of captured bats per hour was 0.54 (range=0.00–26.87) (6–21 June). Per night it killed 0–7 (median=2.5), per visit 0–6 bats (median=1). Of 20 visits, in 13 the owl was successful in capturing a bat. In 2011, the first parturitions in the maternity roost of Geoffroy's bat occurred on 10 June. In the period four days before and eight days after the onset of parturition (6–18 June), the owl achieved the greatest capture success. Of a total of 31 captured bats, 30 were obtained during this reproductive phase.

Most bats were captured on the nights of 12 June (7 bats) and 18 June (6 bats) when the owl perched for 66 and 43 minutes respectively. Only during two nights the owl was not successful in catching a bat: On 11 June nine capture attempts performed within 24 minutes failed and on 5 July the owl made no attempt to capture a bat.

Although our data are strongly biased due to uneven sample sizes, there seems to be a tendency towards increased capture success with the decrease of the density of arriving bats despite of increasing hunting effort (Fig. 5).

Handling time: The average handling time of a bat from capture to end of eating was 1.5 min (range=0.4–4.6, sd=1.01, n=24).

Behaviour of the bats

Independent of the presence of the owl, the returning flight of Geoffroy's bats to their maternity roost was very fast and erratic. The bats performed circles and loops with small radii in front of the window before they swooped into the opening. Some bats turned back after they detected the owl as an obstacle in the window frame by echolocation, but we recorded at least 333 occasions of bats entering the roost flying over or past the perching owl. Collisions between entering bats and the owl were not observed. Seventeen bats entered the roost while the owl was eating a killed bat.

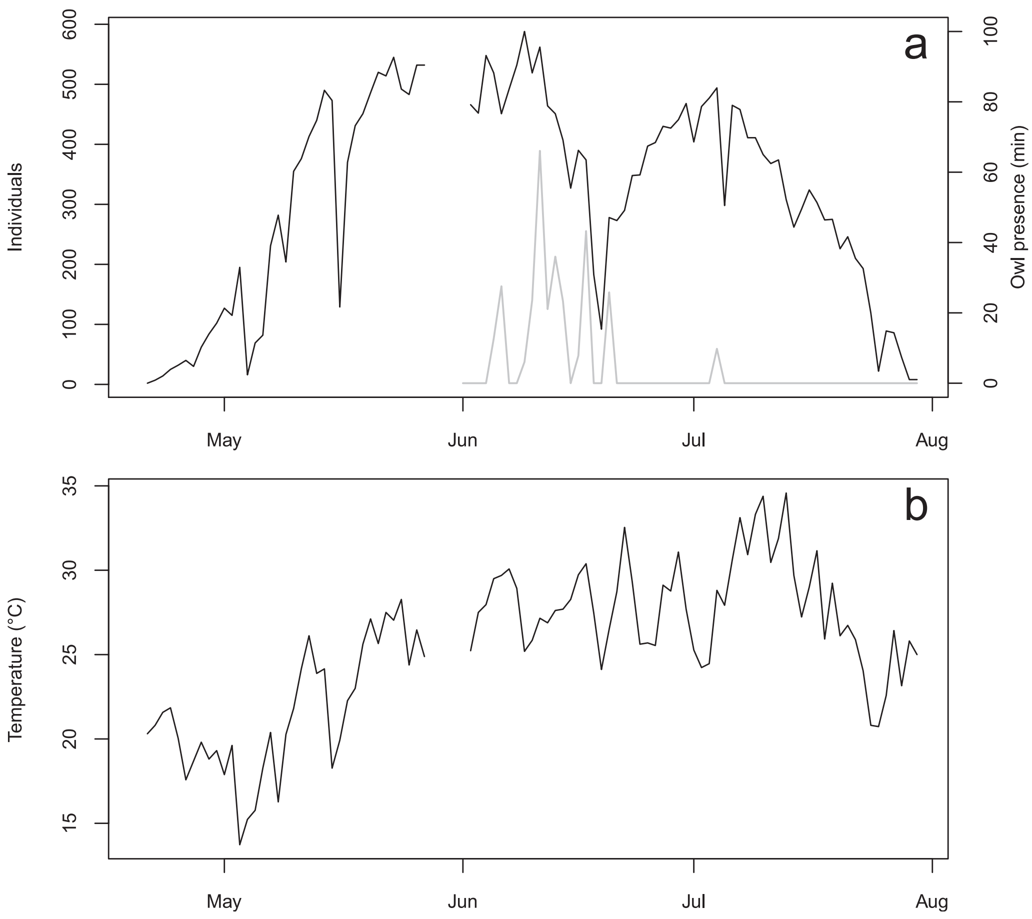

Fig. 6. Development of colony size over the whole reproductive period 2011. a – Black lines (left axis) maximum numbers of *M. emarginatus* individuals counted per night; grey lines (right axis): presence time of the tawny owl at the entrance of the roost. b – Development of the average night temperature during the same period.

We neither observed bats that were attracted to the perching owl as a consequence of potential distress calls emitted by attacked or captured bats (Jung et al. 2011) nor bats swooping towards the owl and approaching it within few centimetres (Fenton et al. 1976). As the body of the perching owl modified the shape of the access hole, it was impossible to discern if potential modifications of the usual returning flight patterns (onset and end, duration, clustering) were caused by the owl as a simply physical barrier or a potential predator.

Although seemingly unaffected by the frequent attacks, there was a considerable decline of the colony size from a peak of 598 bats on 9 June, to 384 on 12 June and to 93 on 19 June, when the continuous predation phase ended. By 4 July, the numbers had increased again to 494 individuals. However, upon the return of the owl in the following night, the colony size dropped to 302 individuals although the owl had not perched on its usual place and not performed capture attempts (Fig 6).

As reductions of the colony size can also be caused by deterioration of the weather, we analysed the fluctuations in numbers in relation to changes of the ambient temperature (e.g. Petrželková & Zukal 2011). Fig. 6 shows that severe drops in the average night temperature in the period 3 to 5 May and on 8 May, when the owl had not yet started preying on the colony, caused sharp declines of the colony size. Conversely, the gradual decrease of the colony size between 9 and 19 June was not in line with the temperature trend and appeared to be a consequence of predation. The sharp fall of the colony size in the night of 4/5 July, when the temperature remained on a relatively high level, supports this hypothesis.

Discussion

Impact and timing of attacks

Given the small size typical of the home range of *Strix aluco* (25–30 ha) and the strong territoriality of the species (Glutz von Blotzheim & Bauer 1994), as well as the fact that this owl takes only prey species which are available in its own home range (Southern 1954), it can be taken for granted that all attacks on the Lockenhaus bat colony were performed by one single breeding pair. It can be assumed, however, that only one of the pair was catching the bats, as both partners normally do not use the same hunting technique (Julian & Altringham 1994). The owl killed 5.3% of the maximum number of females roosting in the attic in the course of 12 nights in 2011.

We noticed remarkable limitations of the hunting activities of the owl. In the course of three reproductive periods of the maternity colony of Geoffroy's bats in Lockenhaus, the owl restricted its attacks to one year (2011) and to returning individuals. With some caution due to the lack of video recordings before 2 June, it can also be stated that the owl attacked only during a short part (12 nights) of the presence of the colony in the roost. These limitations might best be explained in the context of cost-benefit relations. The capture success of 12.3% of capture attempts seems to indicate that the costs of capturing Geoffroy's bats from the air are quite high.

As tawny owls are long-lived and stay in their territory for years, and as the availability of the prey was predictable, a replicate of the predation of bats in 2012 and 2013 could have been expected, but did not happen. A possible reason for the absence of attacks in these years was that the owl preferred the most common prey of this species, voles, which were abundant in 2012 (own observations) and probably in 2013 also.

Many authors (Speakman et al. 1992, Fenton et al. 1994, Jones & Rydell 1994, Kalcounis & Brigham 1994, Speakman et al. 1995, Rydell et al. 1996, Irwin & Speakman 2003, Petrželková & Zukal 2003, Russo et al. 2007) assumed that bats face the greatest danger of attacks during emergence from their roost. In Lockenhaus, however, the tawny owl attacked the Geoffroy's bats exclusively during their return to the roost. About the reasons can only be speculated. We assume that the very low light levels prevailing in the completely dark loft hampered discerning of emerging bats, whereas the range of night luminance levels always provided enough resolution to successfully catch returning bats when the owl was looking towards the sky. This assumption is supported by the fact that the owl never tried to hunt inside the bat roost. Another possible explanation for the restriction on returning bats is that the owl became aware of this source of food only after having hunted voles during the first part of the night unsuccessfully.

The owl chose the time for hunting bats both on the basis of abundance and vulnerability, as described as a rule guiding the decision of predators when and where to hunt successfully (Qinn & Cresswell 2004). The large size of the maternity colony of Geoffroy's bats in Lockenhaus (almost 600 females) and the predictable influx at dawn were certainly attractive for the tawny owl. Unable to hunt a dense crowd successfully (Hamilton 1971), it tried to maximise its profit by focusing the attacks to the intervals 15–20 minutes before and 5–10 minutes after the peak of return flights (Fig. 4).

By restricting its attacks to the period of late pregnancy, the owl took advantage of the state of highest vulnerability of the bats. During late pregnancy, the body weight of the females increases rapidly (Speakman 1991b, Rydell 1993) and the flight due to high wing loading is slower and less manoeuvrable (Speakman 1991b, Duvergé et al. 2000, Russo et al. 2007) than in earlier stage of pregnancy and after parturition.

The cause for restraining from attacking the returning bats on 5 July might have been the owl's inability to hunt the fast flying, lightweight lactating females successfully both from the usual perch in the window ledge and when pursuing flying bats from the dormer roof. But why the owl refrained from capturing young inexperienced bats during their first flights and why it did not resume its attacks on heavyweight bats in late stage of lactation when high demands for milk production for the almost independent young led to high food consumption remains unclear.

Bats' response to predation

Experimental studies using plastic (Speakman et al. 1992 , Kalcounis et al. 1994), stuffed (Petrželková & Zukal 2001) or live owls (Petrželková & Zukal 2003) as predator models have attempted to determine whether bats emerging from roosts perceived owls as predators and whether predator presence affects bat behaviour. They came to the conclusion that responses, if they exist at all, consist of subtle differences in the degree of clustering during the emergence flight. Similarly, the Geoffroy's bats of Lockenhaus did not display behaviours that could be interpreted as defence or predator avoidance when the owl was attacking them. This statement seems to be confirmed by the fact that we could not furnish proof that the tawny owl caught less bats the longer it perched on the window ledge. Nevertheless, Petrželková & Zukal (2003) supposed that bats might be able to perceive a silhouette of an avian predator as a potential threat.

The only reaction of the *Myotis emarginatus* colony that can be unanimously related to the predation by the owl were the conspicuous fluctuations in the colony size. During the phase of continuous owl attacks, the numbers decreased to 10% of the initial value but recovered almost completely after the owls had ceased preying. Interestingly, we recorded again a sudden drop to 60% between 4 and 5 July, when the owl perched on the dormer roof without attacking. Previous publications e.g. (Barclay et al. 1982) reported already that predation by owls leads to decrease in numbers of individuals in the colony, change of exit holes (e.g. Petrželková & Zukal 2003), short- and long-term and even permanent abandonment of the roost (Bernd et al. 2000). Fippl

(2013) provided a report on a decimation of a large German maternity colony of mouse-eared bats by a tawny owl from 1100 individuals to zero.

Our study proves that Geoffroy's bats perceive and react to predation by a tawny owl by leaving the roost. However, how this was achieved is not clear. Due to the lack of audio recordings, we cannot assess the role of distress calls probably emitted by attacked bats as reported for other bat species (Fenton et al. 1976, McGuire & Fenton 2010, Russ et al. 1998, Russ et al. 2004). However, as we did not observe reactions of colony members to attacks on a colony mate we hesitate to assume that distress calls might have acted as alarm signals to provide social information transfer on the predation risk (Galef 1976, Griffin 2004). The most likely explanation seems to be that the direct experience of an unsuccessful attack on themselves triggered the learning to avoid predation by leaving the roost. The instantaneous reaction of the *Myotis emarginatus* colony to the mere presence of the owl perched on the dormer roof on 5 July (Fig. 6) can be discussed controversially. Whether the Geoffroy's bats had learned to recognise the owl as enemy or they merely registered a change in the vicinity of their access window remains unclear.

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References

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

Baxter D. J. M., Psyllakis J. M., Gillingham M. P. & O'Brien E. L., 2006: Behavioural response of bats to perceived predation risk while foraging. *Ethology*, **112**: 977–983.

Bernd D., Eppler G. & Kappes D., 2000: Vertreibung von Fortpflanzungskolonien des Großen Mausohrs (*Myotis myotis*) durch die Schleiereule (*Tyto alba*) sowie Vorschläge zu Vermeidung dieses Kohabitationsprozesses. *Collurio*, **18**: 113–124.

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

Fenton M. B., Bellwood J. J. & Fullard J. H., 1976: Responses of *Myotis lucifugus* (Chiroptera: Vespertilionidae) to calls of conspecifics and to other sounds. *Canadian Journal of Zoology*, **54**: 1443–1448.

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

Fippl R., 2013: Waldkauz versetzt Fledermäuse in Panik. *Arbeitsgemeinschaft Fledermausschutz in Hessen*, **7**: 6–8.

Galef B. G. B., 1976: Social transmission of acquired behavior. *Advances in the Study of Behavior*, **6**: 77–100.

García A. M., Cervera F. & Rodríguez A., 2005: Bat predation by long-eared owls in mediterranean and temperate regions of southern Europe. *Journal of Raptor Research*, **39**: 445–453.

Gebhardt J., 1997: *Fledermäuse*. Birkhäuser, Basel, Boston, Berlin, 381 pp.

Glutz von Blotzheim U. N. & Bauer K. M., 1994: *Handbuch der Vögel Mitteleuropas. Band 9: Columbiformes – Piciformes. 2nd Edition*. Aula Verlag, Wiesbaden, 1148 pp.

Griffin A. S., 2004: Social learning about predators. A review and prospectus. *Learning and Behavior*, **32**: 131–140.

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

IRWIN N. R. & SPEAKMAN J. R., 2003: Azorean bats *Nyctalus azoreum*, cluster as they emerge from roosts, despite the lack of avian predators. *Acta Chiropterologica*, **5**: 185–192.

IRWIN A., BRODERS H. & RODRIGUES B., 2013: The social behaviour of little brown bats at maternity colonies. P.: 73. In: ANONYMOUS (ed.): *Abstracts. 16th International Bat Research Conference. 43rd North American Symposium on Bat Research. San Jose, Costa Rica. August 11–15, 2013*. San Jose, 178 pp.

JONES G. & RYDELL J., 1994: Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **346**: 445–455.

JULIAN S. & ALTRINGHAM J. D., 1994: Bat predation by a tawny owl. *Naturalist* (*London*), **119**: 49–56.

JUNG T. S., LAUSEN C. L., TALERICO J. M. & SLOUGH B. G., 2011: Opportunistic predation of a little brown bat (*Myotis lucifugus*) by a great horned owl (*Bubo virginianus*) in southern Yukon. *Northwestern Naturalist*, **92**: 69–72.

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

KOWALSKI M. & LESIŃSKI G., 1990: The food of the tawny owl (*Strix aluco* L.) from near a cave in Poland. *Bonner Zoologische Beiträge*, **41**: 23–26.

KUNZ T., 1982: Roosting ecology of bats. Pp.: 1–55. In: KUNZ T. (ed.): *Ecology of Bats*. Plenum Press, New York, xviii+425 pp.

KUGELSCHAFTER K., KIMPEL, W., HORVATH T. & VOLK T., 1994: Neue Techniken zur Überwachung von Fledermäusen. Pp.: 373–382. In STUBBE M., STUBBE A. & HEIDECKE D. (eds): *Methoden feldökologischer Säugetierforschung*. Martin-Luther-Universität, Halle-Wittenberg, 474 pp.

LEE Y. F. & MCCRACKEN G. F., 2001: Timing and variation emergence and return of *Tadarida brasiliensis*. *Zoological Studies*, **40**: 309–316.

LESIŃSKI G., IGNACZAK M. & MANIAS J., 2009: Opportunistic predation on bats by the tawny owl (*Strix aluco*). *Animal Biology*, **59**: 283–288.

LIMA S. L. & O'KEEFE J. M., 2013: Do predators influence the behaviour of bats? *Biological Reviews*, **88**: 626–644.

MCGUIRE L. P. & FENTON M. B., 2010: Hitting the wall: Light affects the obstacle avoidance ability of free-flying little brown bats (*Myotis lucifugus*). *Acta Chiropterologica*, **12**: 247–250.

OBUCH J., 1998: Tawny owl (*Strix aluco*) preying on bats. Pp.: 119–121. In: HORÁČEK I. & VOHRALÍK V. (eds.): *Prague Studies in Mammalogy*. Charles University Press, Praha, xxi+245 pp.

PETRŽELKOVÁ K. & ZUKAL J., 2001: Emergence behaviour of the serotine bat (*Eptesicus serotinus*) under predation risk. *Netherlands Journal of Zoology*, **51***: 395–414.*

PETRŽELKOVÁ K. & ZUKAL J., 2003: Does a live barn owl (*Tyto alba*) affect emergence behavior of serotine bats (*Eptesicus serotinus*)? *Acta Chiropterologica*, **5**: 177–184.

POMEROY D., 1990: Why fly? The possible benefits for lower mortality. *Biological Journal of the Linnean Society*, **40**: 53–65.

QUINN J. L. & CRESSWELL W., 2004: Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology*, **73**: 143–154.

RUPRECHT A. L., 1979: Bats (Chiroptera) as constituents of the food of the barn owl *Tyto alba* in Poland. *Ibis*, **121**: 489–494.

RUSS J. M., RACEY P. A. & JONES G., 1998: Intraspecific responses to distress calls of the pipistrelle bat, *Pipistrellus pipistrellus*. *Animal Behaviour*, **55**: 705–713.

RUSS J. M., JONES G., MACKIE I. J. & RACEY P. A., 2004*:* Interspecific responses to distress calls in bats (Chiroptera: Vespertilionidae): a function for convergence in call design? *Animal Behaviour*, **67**: 1005–1014.

RUSSO D., CISTRONE L. & JONES G., 2007: Emergence time in forest bats: the influence of canopy closure. *Acta Oecologica*, **31**: 119–126.

RUSSO D., CISTRONE L., GARONNA A. P. & JONES G., 2011: The early bat catches the fly: Daylight foraging in soprano pipistrelles. *Mammalian Biology*, **76**: 87–89.

RYDELL J., 1993: Variation in foraging activity of an aerial insectivorous bat during reproduction. *Journal of Mammalogy*, **74**: 503–509.

RYDELL J. & SPEAKMAN J. R., 1995: Evolution of nocturnality in bats: Potential competitors and predators during their early history. *Biological Journal of the Linnean Society*, **54**: 183–191.

RYDELL J., ENTWISTLE A. & RACEY P. A., 1996: Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos*, **76**: 243–252.

SOUTHERN H. N., 1954: Tawny owls and their prey. *Ibis*, **96**: 384–410.

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

SPEAKMAN J. R., 1991b: Why do insectivorous bats in Britain not fly in daylight more frequently? *Functional Ecology*, **5**: 518–524.

SPEAKMAN J. R., 1995: Chiropteran nocturnality. *Symposia of the Zoological Society of London*, **67**: 187–201.

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

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

VERBOOM B. & SPOELSTRA K., 1999: Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Canadian Journal of Zoology*, **77**: 1393–1401.

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