

Impact of Predation Risk on Emergence by Little Brown Bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae), from a Maternity Colony

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[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.

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Abstract:

When bats emerge from their roosts in the evening to forage and drink, it appears as though their departure involves brief periods when many individuals emerge interspersed with periods during which few individuals emerge. Clustering is seen in many species of animals and probably has an anti-predator or information-transfer function. Regardless of its function, clustering in the emergence of bats may intensify as a result of large numbers of individuals trying to pass through a small exit hole in a short period of time.

A total of 31 observations of emergence were made from May to Aug. 1992 and 1993 at a maternity colony of little brown bats (*Myotis lucifugus*), in Cypress Hills, Saskatchewan, Canada. To determine the effects of a predator on clustering in the emergence, a plastic great horned owl (*Bubo virginianus*) was used as a predator model and mounted close to roost exits on 8 nights. Recorded calls of a great horned owl were played back towards the roost. The predator model and associated calls did not affect the number of bats that emerged, the median time of emergence, or the degree of clustering in the emergence. There was a significant positive relationship between the extent of clustering in the emergence and the number of bats that emerged. Emergences of more than 25 bats were clustered. Thus, we found no evidence to support clustering during emergence as being an anti-predator response. However, clustering may be intensified with increased numbers of individuals trying to pass through a narrow space in a short period of time.

Article:

Introduction

During the spring and summer in temperate regions, female insectivorous bats often aggregate in roosts to form nursery or maternity colonies. In these colonies, the young are born and raised to independence (BARCLAY et al. 1982; SPEAKMAN et al. 1992). The number of individuals in maternity colonies varies depending on species, ranging from as few as five in big-brown-bat (*Eptesicus fuscus*) colonies (KURTA & BAKER 1990) to as many as several million in Mexican free-tailed-bat (*Tadarida brasiliensis*) colonies (MCCRACKEN GUSTIN 1991). Given favourable conditions, each evening, shortly after sunset (BARCLAY 1984), individuals become

active and emerge from roosts. Environmental factors which may influence the emergence behaviour are ambient light levels and temperature, and, to some extent, wind and precipitation (ERKERT 1981). Because there can be many individuals exiting in a relatively short period of time, these emergences are conspicuous (SPEAKMAN et al. 1992).

Some studies have reported that the emergence of bats from maternity colonies appears to be clustered (SWIFT 1980; MCWILLIAM 1989). That is, the departure of individuals is non-random in timing, involving rapid outbursts of many bats interspersed with periods during which few bats emerge (SWIFT 1980; SPEAKMAN et al. 1992). Although this behaviour has been described as clustering, only a few studies have attempted to show statistically that emerging individuals are, in fact, exiting in groups (BRIGHAM & FENTON 1986; BULLOCK et al. 1987; SPEAKMAN et al. 1992).

If bats cluster when they emerge from roosts, two main hypotheses could explain this behaviour. One hypothesis is that the temporal clustering of individuals has an anti-predator function (Swim' 1980; BRIGHAM & FENTON 1986; BULLOCK et al. 1987). Anti-predator behaviour patterns are common in most groups of animals and one common strategy is to group with other individuals. This aggregation behaviour, which reduces an individual's probability of being taken as prey, is referred to as the selfish-herd phenomenon (HAMILTON 1971). The second hypothesis maintains that, like many socially roosting birds, bats are able to identify other bats that successfully foraged the previous night (WARD & ZAHAVI 1973; BRIGHAM & FENTON 1986) and then follow those individuals to high-quality feeding areas as they leave the roost.

Whether bats cluster because the risk of ambush predation is reduced through safety in numbers, or because information about food resources is shared, the size of the roost opening may also affect emergence behaviour. It has been shown that the likelihood of outbursts in pipistrelle-bat (*Pipistrellus pipistrellus*) emergences increases with the number of bats that emerge (BULLOCK et al. 1987). This has been described as 'the bottleneck effect', which is the result of a large number of animals attempting to move through a narrow space in a short period of time. Such a bottleneck should produce a regular stream of exiting bats. However, if each bat varies the time it waits to emerge, groups build up and then emerge behind those bats that had particularly long waiting times (SPEAKMAN et al. 1992).

If there is predation risk for bats in a maternity colony, the presence of a predator may affect emergence behaviour in different ways. If the perceived threat of predation is high, the risks of exiting to forage might outweigh the potential benefits and individuals may not emerge at all. Alternatively, to avoid a visually orienting predator, individuals may delay their emergence until ambient light levels decline, without forgoing foraging altogether.

Another possible response to a perceived high risk of predation is that emerging bats may increase clustering intensity to decrease the probability of the predator selecting a particular individual. Thus, we predict that a perceived threat of predation might cause fewer individuals to emerge, individuals to emerge later or individuals to increase clustering during emergence. If clustering is the result of large numbers of individuals trying to emerge at the same time, the behaviour should be more pronounced as the number of emerging bats increases.

Our three objectives were: 1. To test statistically whether individuals in a maternity colony of little brown bats (*Myotis lucifugus*) cluster during emergence; 2. To assess the effects of a predator model on the emergence behaviour of individuals in a maternity colony; and 3. To look for evidence of a bottle-neck effect in the emergence behaviour.

Methods

Study Colony and Roost

Field work was conducted between 1 May and 31 Aug. 1992 and 1993 at a maternity colony of about 40 little brown bats (*Myotis lucifugus*) in the Park Headquarters building in the West Block of Cypress Hills Provincial Park, Saskatchewan, Canada (49°34'N, 109°53'W). The bats roosted in the attic and under the cedar shingles of an east-facing section of the roof. Bats emerged from one of two exits: a small hole at the base of the chimney or a crack in the shingles on the east side of the roof. Although both holes were used as exits, the one at the base of the chimney was used more frequently (>80 %). Both exits were small enough that only one individual could pass through at any given time.

Emergence Behaviour

To record emergence, we positioned ourselves outside the roost where we could see the two exit holes. We used an ultrasonic mini-bat detector (Ultra Sound Advice, London, UK) to detect bats when it was too dark to see them. When the first bat emerged, the time was recorded to the nearest s. Subsequent emergences of individuals were spoken into a mini-cassette recorder as they occurred. Tapes were later transcribed to determine the time (to the nearest s) each individual emerged. Observations began about 30 min before the exit time of the first bat and lasted for 45 min thereafter, or until 15 min had elapsed without an emergence of an individual.

Visual and acoustic cues in the form of a predator model and song playbacks were presented to the bats to test the effect of predation risk on emergence behaviour. On treatment nights, a 51 cm high, plastic great horned owl (*Bubo virginianus*) was placed on the northeast corner of the roof about 7 m away from both exits. The predator model was in the line of sight and flight of emerging bats such that they often had to manoeuvre around it. In addition to the model, recorded calls of a great horned owl were played back towards the roost using a tape loop and a portable tape player. Playbacks began approximately 15 min before the first bat emerged and ended 30 min later. The tape consisted of call bouts lasting for 90 s with a 20 s interval between bouts. We chose this species of owl as a predator model because it is frequently seen and heard in the area and it has been reported to prey on bats (BAKER 1962). The playbacks often elicited responses from live great horned owls, confirming that they resembled natural calls.

Statistical Analysis

We used the 'behavioural temporal clustering analysis program' (J. R. SPEAKMAN, Department of Zoology, Univ. of Aberdeen, Aberdeen, Scotland) to analyse the clustering behaviour of bats during emergences. The program calculates the extent of temporal clustering in behavioural events by comparing the observed distribution of inter-event intervals to that expected if the events occurred at random. Clustering is expressed as a G value, which is the categorical statistic used to compare the

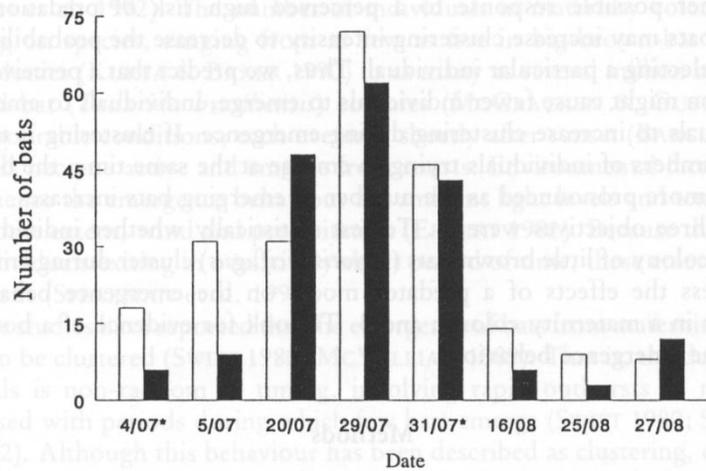


Fig. 1: Number of bats that emerged on nights without (open bars) and with (closed bars) predator model. Dates (d/mo) represent treatment nights in 1992 and 1993 (with asterisk)

expected and observed distributions for the purpose of assessing whether the observed emergence deviates from random. In addition, the program avoids spurious detection of clustering by trimming tails from distributions (see SPEAKMAN et al. 1992).

A paired t-test (ZAR 1984) was used to determine if the predator model affected the number of bats that emerged. Since colony size varies over the summer (Swift 1980), we paired each treatment night (with predator model) with the previous control night (without predator model) when comparing number of bats that emerged to minimize the seasonal effect of a changing colony size as well as varying environmental conditions. It has been documented that the time that the first bat emerges is correlated with sunset (VENABLES 1943; STEBBINGS 1968; SWIFT 1980). To establish whether bats emerged later on treatment nights, a single-factor analysis of covariance was used with sunset as the variate. Times of sunset were taken from tables prepared for the study site by Dominion Astrophysical Observatory, Victoria, B.C., Canada. We used median time of emergence in the ANCOVA since it best reflects the emergence pattern of the whole colony (BULLOCK et al. 1987). As small sample sizes and non-normal data precluded the use of a paired parametric test, we used a Mann-Whitney U test (ZAR 1984) to determine if the predator model affected clustering by comparing mean G values calculated for control and treatment nights. To test for a relationship between the degree of clustering and the number of bats that emerged, we used Model I least-squares regression analysis (ZAR 1984) and included control nights only to avoid any effect of the predator model. Data are presented as $X \pm 1$ SE and a rejection criterion of 0.05 was employed for all tests.

Results

We collected emergence data on 31 nights, of which 8 nights were controls for 8 treatment nights (paired). The mean number of emerging individuals was 22.5 ± 3.3 (range 2-72). The pattern of change in colony size observed over the summer (Fig. 1) is similar to published data for a pipistrelle maternity colony (SWIFT 1980). Colony size was small in early summer when adult females moved into the roost and peaked at the end of July when young began to fly. By mid Aug., mothers and young began to leave and the number of individuals in the colony declined.

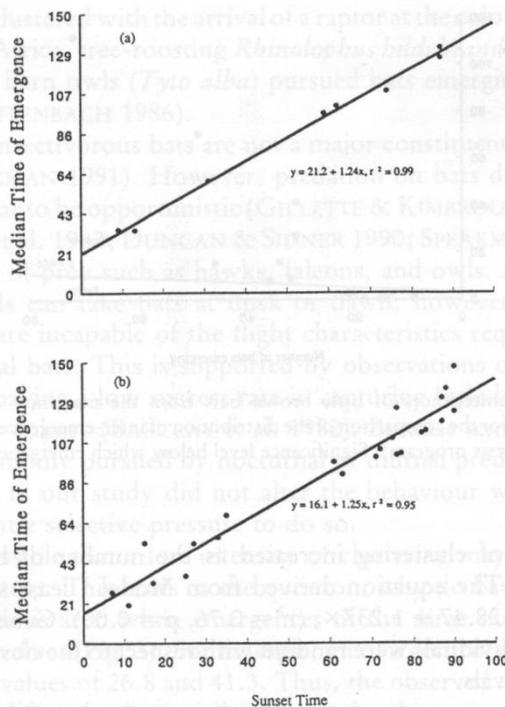


Fig. 2: Relationship between sunset time and time of median emergence (a) with and (b) without predator model. Lines indicate best-fit regression slopes with regression equation labelled below each line. There were no significant differences between the slopes ($T = 0.09$, $df = 27$) or the intercepts ($T = -0.70$, $df = 27$). Both sunset time and emergence times are plotted relative to 2000 h (C.S.T. = 0)

There were 18 control and 6 treatment nights in 1992, and 5 control and 2 treatment nights in 1993. On 10 nights (7 control and 3 treatment) too few bats (<14) emerged for the behavioural temporal clustering analysis program to generate a G value. Thus, we analysed 21 emergences for clustering. On 11 of those nights, the observed distribution of intervals between individual exits differed significantly from that which would be expected if individuals were emerging at random, representing 52.4 % (8 control, 3 treatment) of the emergences (with >14 bats).

The presence of the predator model did not affect the number of bats that emerged (Fig. 1; $t = -1.2$, $df = 7$, $p = 0.26$). In addition, there was no significant difference between the mean median emergence times for nights with and without the predator model (Fig. 2; ANCOVA: $F = 1.7$, $df = 30, 28$, $p = 0.49$). Placing the predator model outside the roost exits had no significant effect on clustering (Mann-Whitney: $U = 28$, $df = 15, 4$, $p = 0.84$). On one treatment night (5 Jul. 1993) a live great horned owl responded to our play backs by calling while perched in a lodgepole pine (*Pinus contorta*) less than 10 m from the roost. The live owl had no obvious effect on the emergence behaviour.

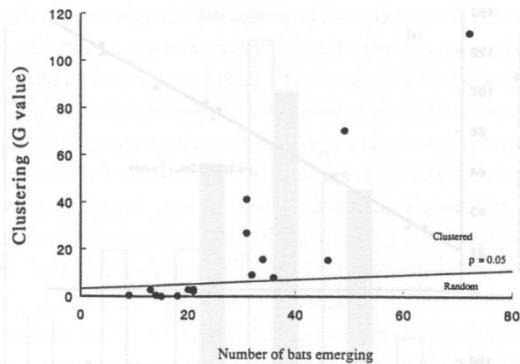


Fig. 3: Clustering in emergences of little brown bats from the maternity colony. Clustering is expressed as the G value for the comparison of the distribution of inter-emergence intervals (behavioural temporal clustering analysis program). Significance level below which emergence is random: $p = 0.05$

The intensity of clustering increased as the number of bats that emerged increased (Fig. 3). The equation derived from Model I least squares regression analysis was $y = -28.47 + 1.237x$, ($r^2 = 0.76$, $p = 0.00$). Generally, emergences of fewer than 25 individuals were random with respect to the observed distribution of inter-event intervals.

Discussion

It is difficult to assess whether or not bats cluster as they emerge solely by observing the emergence from a roost. What may appear as clusters may simply reflect random groupings of bats (SPEAKMAN et al. 1992). We determined statistically that more than one-half of the emergences analysed involved individuals clustering as they exited. This result is lower than that reported by SPEAKMAN et al. (1992) for emergences of pipistrelles in northern Scotland. They found roughly 70 % of emergences to be clustered. However, this may reflect the colonies they studied which, in some cases, were four times larger than the one we studied.

The placement of a predator model at the little-brown-bat maternity roost had no effect on the number of bats that emerged, the median time of emergence, or the clustering behaviour of emerging individuals. Bats inside the roost may not have altered their behaviour in the presence of the predator simply because they did not perceive the predator model as a potential threat. Perhaps the duration and intensity of the owl playbacks did not reflect what occurs naturally. However the response of live owls to our playbacks suggest that this is not the case. Additionally, echo-locating bats might perceive a plastic owl as something quite different from a real owl.

Accounts of clustering in the emergence behaviour of bats in Africa suggest that, in the presence of a predator, individuals will modify their behaviour. For example, *Tadarida pumila* in Ghana, West Africa, switched emergence behavior from random to clustered with the arrival of a raptor at the colony site (MCWILLIAM 1989). In South Africa, tree-roosting *Rhinolophus hildebrandtii* began using night roosts once two barn owls (*Tyto alba*) pursued bats emerging from a day roost (FENTON & RAUTENBACH 1986).

Temperate insectivorous bats are not a major constituent in the diet of many predators (SPEAKMAN 1991). However, predation on bats does occur, although most events appear to be opportunistic (GILLETTE & KIMBROUGH 1970; RUPRECHT 1979; BARCLAY et al. 1982; DUNCAN & SIDNER 1990; SPEAKMAN 1991). Predators are usually birds of prey such as hawks, falcons, and owls. BAKER (1962) found that diurnal birds can take bats at dusk or dawn, however, he suggested that nocturnal birds are incapable of the flight characteristics required to pursue and capture individual bats. This is supported by observations of an eastern screech owl (*Otus asio*) having a low success rate in capturing little brown bats emerging from a maternity colony (BARCLAY et al. 1982). Because temperate insectivorous bats are not commonly pursued by nocturnal or diurnal predators, it may be that the *M. lucifugus* in our study did not alter the behaviour we examined because there has been little selective pressure to do so.

It is also possible that a low intensity of clustering may act as a mechanism to confuse predators. This leads to the question, why do bats increase clustering on occasion? This is seen when emergences of the same number of individuals have different G values (Fig. 3). For example, on two control nights, 31 individuals emerged with G values of 26.8 and 41.3. Thus, the observed distributions of these two emergences differed substantially from each other, as well as deviating from random.

In this study, there was a significant positive relationship between the extent of clustering and the number of bats that emerged, with emergences of greater than 25 individuals being clustered. These results provide evidence in support of a bottleneck effect occurring in the emergence of little brown bats, similar to that described for pipistrelles (BULLOCK et al. 1987). That is, individual bats vary the waiting time at roost exits and groups build up behind those bats with particularly long waiting times. Nightly variation in the order and waiting times of exiting individuals would explain why two emergences of the same number of individuals had different G values.

In their study of the activity patterns of the lesser horseshoe bat (*Rhinolophus hipposideros*) in Ireland, McANEY & FAIRLEY (1988) found no indication of clustering in emergences. To our knowledge, theirs is the only published study to report that bats do not cluster during emergence. Whether anecdotal or statistical, most studies describe emergences as clustered (SWIFT 1980; BRIGHAM & FENTON 1986; BULLOCK et al. 1987; McWILLIAM 1989; SPEAKMAN et al. 1992). What separates McANEY & FAIRLEY (1988) from other emergence studies is the size of the emergence hole. Whereas most building roost exits are small holes in roofs (BRIGHAM & FENTON 1986) or eaves (McWILLIAM 1989), the roost exits of the lesser horseshoe bat were open trap doors and windows with missing panes up to 1 m² in area.

If clustering in the emergence of bats has an adaptive value (e.g. antipredator function), we would expect that, even if individuals are not constrained by roost exit size, they should still exit in groups. If, on the other hand, clustering is an artifact of the bottleneck principle, we would predict that, if bats are not constrained by exit size, as in McANEY FAIRLEY (1988), they should not group. Acknowledging the fact that our sample sizes were small and that a small number of bats emerged from a second hole, we found no direct evidence in support of an anti-predator strategy but did find evidence to suggest that a bottleneck effect may be occurring in this behaviour. To show that clustering behaviour in the emergence of bats is a result of more

than an antipredator strategy, further field tests on a variety of species with diverse roosting habits are needed. For example, a controlled and rigorous experiment which manipulates the size of the emergence hole should show differences in clustering behaviour during emergence if a 'bottleneck effect' occurs.

Acknowledgements

We thank the park conservation officers for allowing access to the colony and the Biology Department at the University of Regina for use of the field station. We are grateful to Dr. J. R. SPEAKMAN for providing us with a copy of his 'behavioural temporal clustering analysis' program, and instructing us in its use. We would particularly like to thank D. J. BENDER, D. L. GUMMER, K. WANG and Dr. J. R. SPEAKMAN for useful and stimulating discussion about various aspects of this work. Dr. H. J. BROCKMANN and two anonymous reviewers provided valuable comments on the original manuscript. This project was supported by the Sigma-Xi and Theodore Roosevelt Memorial Fund (American Museum of Natural History) grants to M. C. KALCOUNIS and Natural Science and Engineering Research Council operating and equipment grants and a University of Regina President's NSERC grant to R. M. BRIGHAM.

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