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Azorean bats *Nyctalus azoreum*, cluster as they emerge from roosts, despite the lack of avian predators

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We tested the hypothesis that clustering in the behaviour of emerging bats is a response to the risk of avian predation. We hypothesised that if avian predation was the cause of clustering, bats in the prolonged absence of avian predators, would not cluster or would cluster less during their emergences. We studied the Azorean bat (*Nyctalus azoreum*) in the Azores Archipelago. The Azores have a depauperate fauna with no raptorial birds likely to predate bats. The Azorean bat is an endemic mammal to the archipelago, which has an unusually extensive degree of diurnal activity that has been hypothesised to reflect release from the risk of diurnal predation by raptors. Contrary to our prediction Azorean bats clustered during emergence to the same extent as bat species which occur where there are raptors. Two interpretations of these data are possible. First, the hypothesis that the behaviour is anti-predatory may be incorrect. Most of the variation in clustering was explained by variation in ambient temperature possibly suggesting the bats emerged in groups to aid exploitation of sparsely distributed food. Alternatively, the behaviour may be anti-predatory, but the key factor precipitating clustering may not be the risk from aerial predators, but terrestrial predators, such as rats (*Rattus norvegicus*) and cats (*Felis cattus*), both of which were common around the roost sites.

Key words: clustering, emergence, behaviour, bats, predation, group-feeding

INTRODUCTION

When bats emerge from their day roosts to feed they group together in 'clusters'. 'Clusters' are groups of bats of varying size (generally less than 10) that emerge together over a period of a few seconds, punctuated by periods when no bats emerge. Lapses in emergence may last several seconds to minutes. This pattern is overlaid on the general trend for colony emergence to follow a normal distribution in intensity, with few bats emerging at the beginning, more in the middle, and fewer at the end.

The functional nature of clustering behaviour has been a matter of debate. It has been suggested that the behaviour might reflect a defensive mechanism against the risk of avian predation. Avian predators are frequently observed taking bats as they exit roost sites (e.g., Fenton *et al*., 1994; Fenton, 1995; Jones *et al*., 1995). Clusters may thus represent a temporal equivalent of spatially distributed 'selfish herds' (Hamilton, 1964); the 'selfish cluster' hypothesis (Speakman *et al*., 1995). In other words by emerging temporally adjacent to another individual a bat reduces its own probability of being selected by a predator, because the predator

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has a choice to select one of several emerging bats within a cluster, whereas for a bat that emerges on its own the predator has no such choice. The spatial equivalent of this phenomenon 'the selfish herd' was rigorously modelled by Hamilton (1964) and is believed to be a major driving force influencing the spatial organisation of prey species.

Other authors have suggested that clustering is a behaviour by which bats parasitise information about other individuals' foraging success, or to synchronise group feeding or resource defence. For example, if bats are exploiting spatially complex resources they may differ enormously in their foraging success on a night by night basis. Individuals that return from foraging in energy surplus may be fatter than those which have less success. One strategy a bat that has had little success might adopt is to follow an individual that is fat that day, because that individual may know of a good food source that is currently available. Another way this might work is that teams of foraging bats may have greater success locating food sources and so groups of bats emerging in clusters may be teams that will subsequently forage together.

Alternatively, clustering may have no biological significance but reflect only an artefact of exit hole diameter — the 'bottleneck' hypothesis. On its own, a constriction through which only single individuals could pass might be expected to make the flow of individuals more regularly spaced. However, if the constriction was also combined by individual variations in the hesitancy of individuals to emerge, then clusters of bats eager to get out would form behind those individuals that were particularly hesitant. A clustering phenomenon might then develop without any biological function.

The Azores archipelago lies in the mid-Atlantic ocean approximately 1500 km due west of Lisbon in Portugal, and 2000 km due east of New York in the USA (49°N). No diurnal or nocturnal avian predators are known to inhabit the islands, apart from a large buzzard *Buteo buteo* which feeds mostly by scavenging. Nor is there evidence that predatory birds have ever inhabited the islands (Bannerman and Bannerman, 1966). Because of the release from predation over protracted periods several species that inhabit the islands have lost anti-predatory traits. For example, a subspecies of the European bullfinch (*Pyrrhula pyrrhula*) from the islands lacks the bright white rump patch found in the continental European form, which is believed to have a warning function against predators (Bannerman and Bannerman, 1966). The endemic Azorean bat (*Nyctalus azoreum*) also exhibits an unusually high frequency of diurnal flight (Moore, 1975; Speakman and Webb, 1993; Speakman, 1995). As nocturnality in bats has been hypothesised to result primarily from the risk of diurnal predation by raptorial birds (Speakman, 1990, 1991, 1995; Speakman *et al*., 1994; Rydell *et al*., 1996), diurnal activity in this bat is consistent with the release from the risk of avian predation. If clustering during emergence is a defensive mechanism against the risk of avian predation, as suggested by the Azorean bat, released from such predation risk, should exhibit no, or reduced levels of, clustering behaviour.

Methods

Site Selection

In a preliminary visit to the islands during 1988, we (JRS and P. I. Webb) visited four islands (San Miguel, Sao Jorge, Horta and Pico) but failed to locate any roost sites (Speakman and Webb, 1993). During a second trip (by P. Bloor) in 1993, a single roost was found on the island of Pico, but too late in the trip to make any emergence observations. During a third visit in 1994 (by NRI, P. Bloor, S. Darnell and A. Read), Pico was visited from the 1st of July, until the 1st of September. Between the 2nd and 14th of

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July we found several roost sites by active searching, interviewing local people, and distributing maps in villages. We found a colony of bats that occupied several buildings in the parish of San Antonio, Furnas. Site fidelity of the colony was low. Consequently, considerable time was spent relocating the colony each time it moved to a new roost site. Observations were made of 12 emergence sequences across a total of six different roost sites, all of which were located in buildings, which differed markedly in their exit topology.

Bat Activity Patterns

By definition, an individual emergence event was when a bat exited from an opening and flew away from its roost. Thus bats that crawled out along the wall and subsequently re-entered through a different hole were excluded. A 'return' occurred when a bat entered an exit hole from flight. Bats that returned but did not enter were not recorded until they entered a hole.

Although the Azorean bat flies frequently during daylight it is still most active at night (Speakman and Webb, 1993; Speakman, 1995). We therefore concentrated our observations at dusk when bats at the roosts were most active. In the literature, an evening emergence of bats has been variously described as the time at which the first bat leaves the roost, or the mean, or median, time of the total outflight (Swift, 1980; Avery *et al*., 1984; Bullock *et al*., 1987; McAney and Fairley, 1990; Speakman *et al*., 1992). For *N. azoreum*, 'evening' emergence was not so easily defined because bats would leave the roost in the afternoon sometimes as much as three and a half hours before sunset (Speakman, 1995). The start of an emergence stream was therefore arbitrarily defined, as the time at which approximately five bats exited within a five minute period. This start time varied from 1730 to 1930 across nights (n = 12) with no apparent causation for the variability. Sunset time over the same period varied between 1900 and 2000 h. Emergence activity was recorded until decreased visibility made observations unreliable (between 2150 and 2040, getting earlier as the season progressed).

Records of emergence behaviour were made using two methods. First, individual emergences and returns were dictated onto an audio cassette using a dictaphone. The audio tape was later played back, and the emergence event times transferred into a computer using a data logging program. Alternatively we observed the bats and recorded the times of emergence events using a continuously running stop watch (after Bullock *et al*., 1987). These data were entered later into a spreadsheet and converted from hours, minutes and seconds, into seconds. In total across both methods we recorded 34 hours of useful data.

Data Analysis

We have shown previously that standard time series analyses methods for detecting deviations from random in bat emergences (e.g., Bullock *et al*., 1987) may generate spurious illusions of clustering because the assumption of constant underlying intensity is violated (Speakman *et al*., 1992). We have devised a technique which overcomes this problem (Speakman *et al*., 1992) and written a software program that allows analysis of the inter-emergence event durations for their deviation from random (CLUSTAN: Speakman, 1993). Using this program deviations from the random expectation are quantified by a goodness of fit statistic (χ^2). Deviation from random in itself does not indicate clustering because other patterns of deviation are possible — such as over-dispersion. To demonstrate that the distribution of inter-event intervals is clustered it is necessary to show that the shortest and longest inter-event intervals (reflecting within cluster and between cluster durations) are over-represented, and inter-event intervals of intermediate duration are under-represented. The CLUSTAN software also performs such analysis.

Some studies using the CLUSTAN analysis method have shown that the degree of 'clustering' reflected by χ^2 is positively related to the numbers of emerging bats from a colony (Kalcounis and Brigham, 1994; Speakman *et al*., 1995). This has been inferred as support for the bottle-neck hypothesis — since one might expect the greater the number of bats emerging through a constriction the more clustered they would become. However, we have shown more recently that the χ^2-statistic generated by CLUSTAN is subject to an artefact generated by sample size, and that a size correction needs to be made to obtain a true estimate of clustering (Speakman *et al*., 1999).

In this study, we analysed the data using CLUSTAN and plotted the goodness of fit statistic (χ^2) for successive inter-event interval duration classes to demonstrate that the deviation of the event distribution from random was due to clustering. For comparability to previous papers (Speakman *et al*., 1992, 1995, 1999; Kalcounis and Brigham, 1994) we present both the raw and size corrected χ^2-values as a function of the number of emerged bats.

We measured the ambient temperature with a digital thermometer (Digitron Ltd) 1m off the ground, in the middle of recording each evenings activity. Wind speed was measured on the Beaufort Scale, and cloud cover was measured on a scale of 0–8. We explored

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the effects of variation in the weather and exit topology on the extent of clustering using multiple regression analysis (with a stepwise backward deletion). The variables included were ambient temperature, wind speed, cloud cover, exit hole average size, and total number of exit holes being used.

Results

Pattern of Emergence

Twelve second-by-second emergence sequences were recorded (Table 1). The pattern of inter-emergence intervals differed significantly from random on all 12 nights (Table 1). The pattern of deviation from random was consistent with clustering, i.e., there was an over representation of the shortest and longest inter event intervals and an under-representation of intermediate inter event intervals (Fig. 1). There was a significant relationship between the number of bats in the emergence and the extent of clustering (Table 1, Fig. 2A) described by the equation: clustering (χ^2) = 1.03 (number of bats) + 16.83; r^2= 0.41, $P < 0.05$. This significant effect of the number of emerging bats on the extent of clustering disappeared however when the artefact effects of sample size were removed (Fig. 2B).

There was a significant positive relationship between the degree of clustering and ambient temperature ($r^2 = 0.74$, $d.f. = 1, 11$, $P < 0.001$; Fig. 3). The number of emerging bats and the number/size of exit holes were not significant predictors of the extent of clustering ($P > 0.05$) in a multiple regression analysis.

Discussion

Contrary to our a priori prediction, Azorean bats did cluster during emergence from their roosts. In addition, the degree of clustering in the Azorean bat was comparable to that reported for emergences of pipistrelle bats (*Pipistrellus pipistrellus*) in Scotland, UK, little brown bats (*Myotis lucifugus*) in Canada (Kalcounis and Brigham, 1994), and serotine bats (*Eptesicus serotinus*) in the Czech Republic (Petrželkova and Zukal, 2001, 2003). All of these species were recorded emerging in areas where avian predators are present and the bats are almost exclusively nocturnal.

Table 1. Summary for the evening emergences of *N. azoreum* between the 15/7/94 and the 27/8/94. The emergence data were recorded second by second over the time period stated. Clustering behaviour was described by the deviation of the inter-event interval distribution from that expected at random using the CLUSTAN software using procedures derived in Speakman *et al*. (1992). Speakman *et al*. (1999) provided additional methods that remove a size artefact in the raw χ^2 derived from CLUSTAN and these size corrected data are also presented in the table. '–' indicates data not recorded. Sunset time varied from 2000 h in mid-July to 1900 h in late August

Date	Time of emergence recording	χ^2	Deviation from random pattern (*p*)	Number of emerged bats (*n*)	Locality	χ^2 corrected for emergence size
15/7/94	17:48–21:30	242	>0.001	212	1	149.32
16/7/94	–	95	>0.001	134	1	106.97
16/7/94	19:41–21:35	45	>0.001	50	2	180.15
17/7/94	19:16–21:36	69	>0.001	70	1	179.70
19/7/94	18:33–21:50	320	>0.001	193	3	221.19
21/7/94	18:10–21:17	254	>0.001	309	4	97.07
08/8/94	19:50–21:17	93	>0.001	214	1	58.00
18/8/94	17:32–21:15	431	>0.001	146	5	435.19
19/8/94	20:30–21:02	35	0.001	39	3	192.66
23/8/94	19:13–21:15	13	0.05	41	6	66.29
24/8/94	19:15–21:00	312	>0.001	222	2	179.25
27/8/94	18:00–20:40	102	>0.001	130	2	119.46

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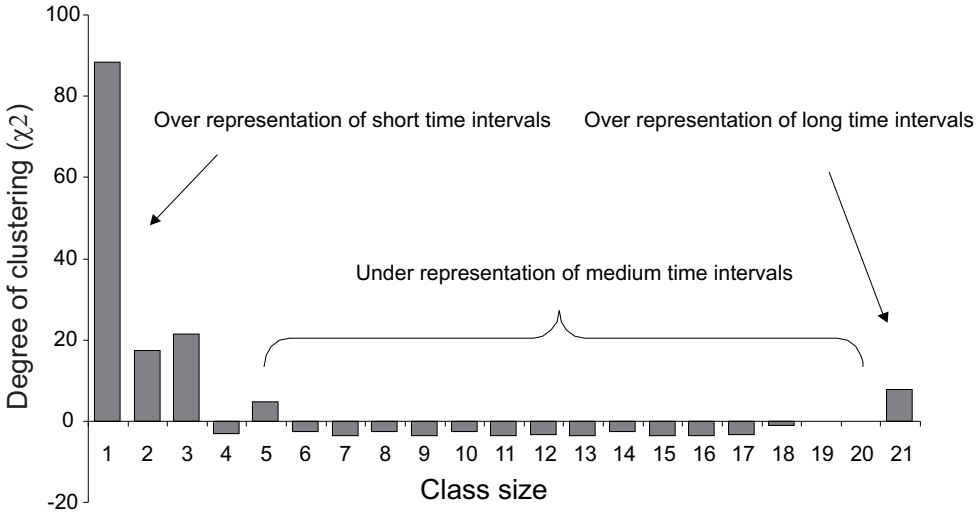


FIG. 1. The pattern of deviation from random of the inter-event time intervals for a typical emergence of the Azorean bat. Class size (x-axis) refers to inter-event interval classes of increasing duration from 1 the shortest duration intervals (0 to 0.3 s duration) to 21 the longest duration intervals (< 1 minute). The y-axis (χ^2) expresses the difference between the number of inter-event intervals in that particular size class compared to the number expected at random. Positive values reflect over-representation and negative values under-representation. Clustering can be inferred from an over representation of the shortest and longest inter-event intervals (reflecting within cluster events and between cluster intervals respectively) and under-representation of intermediate intervals. (Data presented from one emergence on the 15th of July 1994)

The results from this study can be interpreted in several different ways. First, the bats may be only recent additions to the fauna of the Azores (Ulfstrand, 1961) and have consequently not had time to adapt their emergence behaviour to the absence of predators. An alternative version of this interpretation is that although there are currently no predators in the Azores they may have been present historically, and eliminated only recently, again allowing insufficient time for the behaviour to adapt. Both explanations seem unlikely. There has been substantial morphological divergence indicating the bats have probably been there a long time. It seems unlikely that these bats could have diverged morphologically as much as they have (see Palmeirim 1991; Speakman and Webb, 1993) in the 100 years or so that Ulfstand (1961) suggests they have been on the islands. Moreover there is no evidence that raptorial birds have ever inhabited the islands (Bannerman and Bannerman, 1966). Behavioural changes generally evolve faster than morphological changes and these bats have also lost other anti-predatory behaviours, like strict nocturnality, suggesting sufficient time may have elapsed for clustering behaviour to have been lost. However, the rate of evolution will reflect the extent of selection and while clustering may confer little advantage to Azorean bats, it may also confer no disadvantages and be evolutionarily 'neutral'. It may therefore be a relict behaviour originating through phylogeny.

Second, although there are no aerial predators, terrestrial animals may exert a significant predation pressure on emerging bats in the Azores. Domestic cats (*Felis cattus*) and brown rats (*Rattus norvegicus*) were both observed close to the exit holes at the roosts, on occasion within 30 cm of exit holes. Although neither were observed

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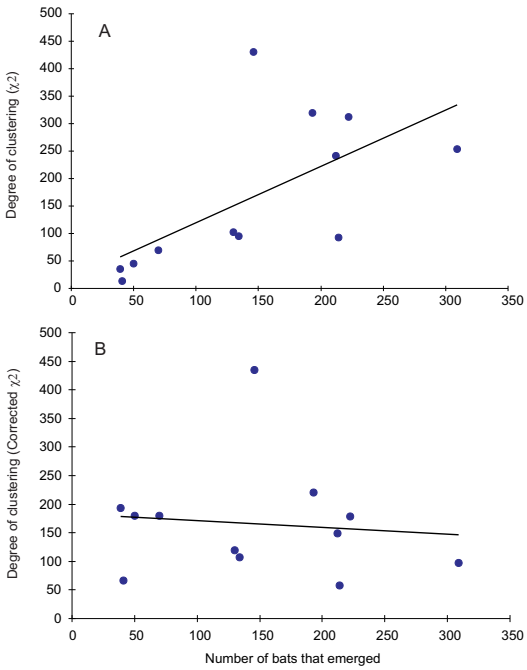


FIG. 2. A: Degree of clustering on emergence, uncorrected for the size artefact plotted against emergence size, B: The degree of clustering after removal of the artefactual effects of emergence size as a function of the number of bats which emerged

taking bats as they emerged during these observations, both are known to take emerging bats at other sites (Gillette and Kimborough, 1970). The clustering behaviour of the bats may still be anti-predatory therefore in the absence of avian predation risk.

Finally, the predation hypothesis may be wrong. Two alternative hypotheses present themselves — the 'bottleneck' hypothesis and the 'information transfer hypothesis'. The data collected here do not support the bottleneck hypothesis. When the artefact effect of emergence size was removed there was no effect of emerging numbers on the extent of clustering (χ^2). In addition, number and size of exit holes was not a significant predictor of the extent of clustering, indicating that the animals were not constrained by a bottleneck. Clustering might therefore reflect 'information transfer' about food availability. In some bat species, group feeding has been shown to be possibly advantageous (Barak and Yom-Tov, 1989; Wilkinson and Boughman, 1998). By emerging together, and following a conspecific which knew of a potentially abundant food resource, bats may increase the efficiency of their foraging. For example, in the evening bat *Nycticeius humeralis*, successful foragers (those that had increased in weight after a foraging bout) were followed

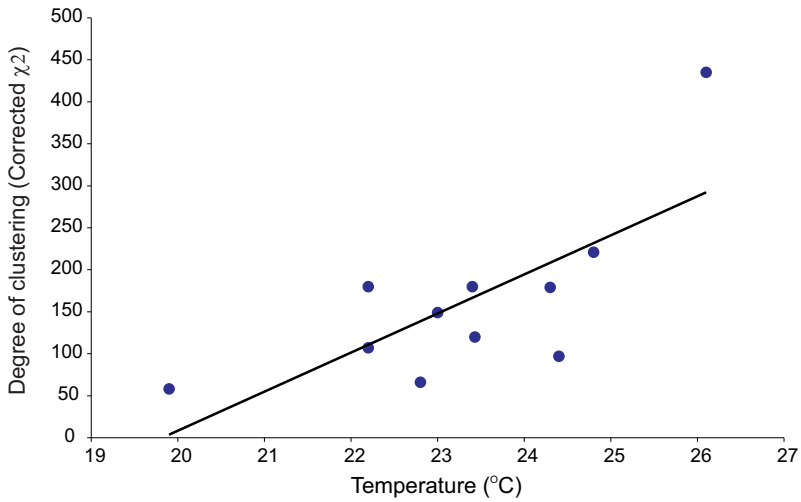


FIG. 3. Regression of temperature and degree of clustering ($y = 46.57x - 923.15$, $r^2 = 0.534$, $P < 0.01$)

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in the next emergence by those which had been less successful.

We have previously observed *N. azoreum* foraging during daylight (Speakman and Webb, 1993) and they generally do not forage in groups. In the present study, bats were observed leaving the roost together, but they did not appear to aggregate when feeding. At night, however, the foraging behaviour may differ and the significant relationship we found between the degree of clustering and ambient temperature may support the hypothesis that the bats emerged in groups to forage together as their prey may become more patchily distributed with increased ambient temperature. Alternatively, Negro *et al*. (1992) found that predation by European kestrels (*Falco tinnunculus*) on pipistrelle bats (*P. pipistrellus*) was dependent on weather conditions — so an association with climate need not necessarily implicate a link to feeding behaviour. Moreover, this positive relationship was heavily dependent on a single datum at high temperature and this effect clearly requires further confirmation. Similar effects of temperature were not reported on clustering in *E. serotinus* (Petrželkova and Zukal, 2001).

In summary, although we could not reject the anti-predation hypothesis, because of the potential effects of terrestrial predators, our data suggest that the risks of avian predation are not the cause of clustering behaviour in the Azorean bat. Avian predation has been inferred as the dominant cause of clustering in other bat species and the current data may question such an interpretation. The current data were not consistent with the bottleneck hypothesis and provide limited support for the information transfer hypothesis.

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