Suckling behaviour in the brown long-eared bat (*Plecotus auritus*)

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Thirty-two adult female brown long-eared bats were taken into captivity. Eight individuals gave birth to single young in captivity (known mother–young pairs), 10 were lactating when captured (putative mother–young pairs), and the remaining 14 bats were non-reproductive. Bats were maintained in five groups consisting of females from single (n = 3) or mixed (n = 2) wild roosts. All bats were housed in outdoor, free-flight enclosures and fed mainly on free-flying noctuid moths. Bats were individually marked with exclusive codes using black and white plastic split rings. Suckling associations were determined daily (n = 152) for a single group of bats containing four known mother–young pairs and five non-reproductive bats. The probability of a bat being attached to the nipple declined from 100% of records at 1–5 days of age to 5% of records at 36–40 days of age. Females were always found suckling their own young. Suckling associations were determined using infra-red sensitive video-recordings of bat behaviour within the roost box. For both known (n = 8) and putative mother–young pairs (n = 10), there were no records of young attached to lactating females other than their own mothers (from the same or different wild roosts).

**Introduction**

For a female mammal, lactation represents the most energetically costly aspect of reproduction (e.g. Hanwell & Peaker, 1977; Oftedal, 1985; Gittleman & Thompson, 1988). Hence, lactating females would be expected to be selective regarding the young that they nurse to minimize wasted investment. However, indiscriminate suckling behaviour (i.e. suckling of young born to females other than the parent female) has been documented in a wide range of species (reviewed in Riedman, 1982; Gittleman, 1985; Packer, Lewis & Pusey, 1992).

In most bat species, females indiscriminately nurse only their own offspring (e.g. Davis, Barbour & Hassell, 1968; Davis, 1969; Brown, 1976; Fenton, 1985; Thomson, Fenton & Barclay, 1985; Marimuthu, 1988), but the extent to which indiscriminate nursing occurs in bats is unclear (Fenton, 1985). Nursing of offspring that are not the female’s own progeny has been well documented in some species (e.g. McCracken, 1984; McCracken & Gustin, 1987, 1991; Wilkinson, 1989). However, reports of discrimination in nursing behaviour are often contradictory. For example, there are several records of indiscriminate suckling in captive vampire bats, *Desmodus rotundus* (Schmidt & Manske, 1973; Mills, 1980; Schmidt, Schmidt & Manske, 1980). In contrast, Wilkinson (1985) noted that banded vampire bats in the wild nursed only from their own mothers. Wilkinson (1987) studied spear-nosed bats, *Phyllostomus hastatus*, using night vision scopes in caves, and reported that 1 to 4-week-old young occasionally nursed from more than one female, yet McCracken & Bradbury (1981) reported no occurrence of indiscriminate suckling in the same species. Indiscriminate suckling has been recorded in pipistrelle bats, *Pipistrellus pipistrellus* (Kleiman, 1969; Eales, Bullock & Slater, 1988). However, more recent work in the same species suggests it is a selective suckler (Hughes et al., 1989; Bishop et al., 1992).
In noctule bats, *Nyctalus noctula*, there are records of both discriminate (Kleiman, 1969) and indiscriminate nursing (Alexeeva, 1982; Kozhurina, 1993).

In theory, 'indiscriminate' suckling might evolve in bats by the processes of kin selection or reciprocal altruism (Wilkinson, 1987). However, these processes may be compromised in large bat colonies because of the low average relatedness of females in a colony and the difficulties associated with reciprocating selectively (Hughes *et al.*, 1989; McCracken & Gustin, 1991). Indiscriminate suckling is thus more likely to be found in small colonies of bats, particularly where relatedness between individuals is high (Wilkinson, 1987). Alternatively, non-offspring nursing may occur as a result of parasitism by milk thieves (either orphan young or hungry opportunistic young), or errors in pup recognition in large colonies (e.g. Mexican free-tailed bats, *Tadarida brasiliensis*, McCracken, 1984; McCracken & Gustin, 1987, 1991). Kozhurina (1993) reported that 14% of nursing associations in captive *N. noctula* were non-parental, and perhaps reflected milk stealing rather than voluntary provisioning of non-descendant offspring. Hughes *et al.* (1989) suggested indiscriminate suckling reported in *P. pipistrellus* (e.g. Eales *et al.*, 1988) could be due to milk dumping by lactating females whose own offspring had died.

The brown long-eared bat (*Plecotus auritus*) is generally found in small roosting groups of 10-30 individuals (Swift, 1991), although the size of the colonies (or populations) which contribute to these groups is probably larger (average colony size estimated from mark-recapture data at 15 roosts over nine years of ringing = 48, Entwistle, 1994). In addition, ringing studies have indicated some degree of matrilineral recruitment, with minimal movement of bats between studied roost sites (Heise & Schmidt, 1988; Entwistle, 1994), hence females in a colony, and probably also roosting groups, are likely to be closely related. These conditions are likely to favour the evolution of indiscriminate suckling. Likhachev (1980) reported female *Plecotus auritus* in the wild simultaneously suckling two young which were of different ages. In contrast, Swift (1981) individually marked 10 lactating females and their attached young (presumed to be biological offspring) in the wild and on subsequent visits to the roost; each female was always associated with the same young as at the first ringing. Although the number of subsequent visits to the roost is not quoted, the logistical difficulties of repeatedly entering roosts without disturbing bats, and the inability to observe the bats inside roosts for prolonged periods, suggest that the sample size for these observations was probably low. Consequently, if suckling of alien young is only an infrequent and/or short duration behaviour, this protocol may have been insufficient to detect it. In the present paper, we further investigated the suckling behaviour in captive brown long-eared bats (comprising known and assumed mother-young pairs) using daily records of female-young attachments, combined with suckling associations observed from infra-red sensitive video-recordings of roosting bats.

**Methods**

Thirty-two adult female brown long-eared bats were taken into captivity under licence from Scottish Natural Heritage (SNH) between May and July in 1992 and 1993. Bats were obtained from nursery roosts in Grampian and Highland regions, north-east Scotland. Palpably pregnant individuals (Racey, 1974) were selected, although this criterion proved unreliable in the early stages of gestation in May and June. In 1993, 10 individuals were captured with their young attached, and taken into captivity. All bats were housed in free flight enclosures subject to natural photoperiod and temperature variations. Bats were maintained on a diet of free-flying noctuid moths occasionally supplemented with live mealworms (*Tenebrio molitor*). Whilst in captivity, bats chose to roost in a single, heated roost box (0.4 m x 0.4 m x 0.4 m).
Eight individuals gave birth in captivity, 10 were lactating when captured and the remaining 14 bats were non-reproductive. Bats were maintained in 5 groups (discrete over time) consisting of 3–15 individuals. Groups varied in the proportion of non-reproductive females and lactating females. The composition of groups also varied; they either contained females from the same wild roost, or females taken from different roosts. The extent of indiscriminate suckling among these groups might then indicate the importance of previous roosting associations in the evolution of indiscriminate suckling behaviour. Bats were checked twice daily for new births, hence the stage of lactation of all females giving birth in captivity was known (±12 hours). These offspring could be unequivocally attributed to their true mothers. For those bats that were already lactating when captured, the age of young was estimated from the linear portion of forearm growth curves obtained previously in captivity (J. A. McLean, pers. obs). All bats were marked on each forearm with exclusive codes using combinations of up to 3 black and white plastic split rings (A. C. Hughes). Two types of observation were conducted to investigate the pattern of nursing behaviour.

**Daily suckling associations**

Data were obtained for a single group of bats containing 5 non-reproductive females and 4 mother-young pairs over days 1 to 40 of lactation (taking parturition as day 1). The adult bats were originally captured from 3 different roosts. Each morning, the bats were removed from the roost box and individual suckling associations were recorded \( n = 152 \) (after Hughes et al., 1989); young bats were recorded as either attached to the nipple of an adult bat or not attached. Where attachment was recorded, the identifications of both mother and young were noted. Bats were then returned to the roost box.

**Suckling associations determined from video recording of roosting bats**

Roosting behaviour for 5 groups of bats, containing a total of 18 mother-young pairs and 14 non-reproductive females, was recorded on video during July and August in 1992 and 1993. The adult bats (non-reproductive, pregnant, or lactating with attached young) were originally captured from 9 different roosts. There were 3 single-roost groups and 2 mixed-roost groups. Video-recording produced 14.5–16.5 hours coverage per day. Each group containing lactating females was followed for several sequential days (range = 3–22), and data were obtained for bats over a period ranging from day 1 to 51 of lactation (parturition = day 1, data pooled across groups and nursing pairs) \( n = 97 \) bat days). A total of 49 days of observations, representing approximately 735 hours of recorded film, was gathered over the 2-year period. It was possible to identify all individuals on the film from their exclusive forearm codes. When the bats were present in the roost box, instances of direct contact between lactating females and young, i.e. the young was directly underneath a lactating female, apparently attached to the nipple, were noted during 1 minute sampling periods in every 10 minutes of video. These instances were recorded as positive associations if they occurred for more than 25 seconds in the sampled minute. Data were analysed as percentage positive records per day for each mother-young combination in each group. Data were analysed separately for bats that had given birth in captivity (and hence were known to be mother-offspring pairs) and bats that were captured with attached young (putative mother-offspring pairs).

**Results**

**Daily suckling associations**

The probability of a bat being attached to the nipple declined from 100% of records at 1–5
days of age, to 5% of records at 36–40 days of age (based on observations from four known mother–young pairs: Fig. 1).

Of 152 records of daily suckling associations, 40.1% involved young attached to their mothers and 59.9% involved young not attached to any adult (data obtained from four known mother–young pairs over days 1–40 of lactation: Table I). There were no records of young attached to lactating females other than their own mothers (from the same or different wild roosts) (Table I).

**Suckling associations determined from video-recording of roosting bats**

For bats born in captivity (i.e. known mother–young pairs), young were attached to their mothers in 29.4% of records and not attached to any adult in 70.6% of records (data were obtained from video-recordings of eight known mother–young pairs over a period ranging from day 1 to 51 of lactation (n = 40 bat days), data were averaged across individuals and days: Table I). There were no records of young attached to lactating females other than their own mothers (from the same or different wild roosts) (Table I).

For putative mother–young pairs, young bats were attached to their mother in 70.1% of records and not attached to any adult female in 29.9% of records (data were obtained from video-recordings of 10 nursing pairs over a period ranging from day 4 to 31 of lactation (n = 57 bat days), data were averaged across individuals and days: Table I). There were no records of young attached to lactating females other than their own mother (from the same or different wild roosts) (Table I).

**Discussion**

This study suggests that brown long-eared bats, kept in captivity, suckled only their own young throughout lactation. The bats used for the video recording of roosting behaviour consisted of eight females with known biological offspring and 10 females which were taken into captivity with attached young. We cannot be certain that these latter females were nursing their own offspring when they were captured. However, there were no cases of females suckling more than one young. In combination with the data for known mother–young pairs, these latter data

<table>
<thead>
<tr>
<th>% Records</th>
<th>From daily suckling associations (known M–Y pairs)</th>
<th>From video of roosting bats (known M–Y pairs)</th>
<th>From video of roosting bats (putative M–Y pairs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attached to mother</td>
<td>40.1</td>
<td>29.4</td>
<td>70.1</td>
</tr>
<tr>
<td>Not attached to any female</td>
<td>59.9</td>
<td>70.6</td>
<td>29.9</td>
</tr>
<tr>
<td>Attached to other female (from same roost)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Attached to other female (from different roost)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

TABLE I

Distribution of suckling associations determined from daily records of attachment and from infra-red sensitive video-recording of roosting bats. Values represent percentage records. Daily suckling associations were obtained from four known mother–young pairs, n = 152 records. Video-recording data were obtained from (a) eight known mother–young (M–Y) pairs over days 1 to 31 of lactation, n = 40 bat days; (b) 10 putative mother–young pairs over days 4 to 31 of lactation, n = 57 bat days.
suggest that this species nurses discriminately. This finding contrasts the previous report of indiscriminate suckling in this species (Likhachev, 1980).

There may be problems in extrapolating these data, collected on captive brown long-eared bats, to those living in the wild. The groups of bats we kept in captivity were in temporary associations which included females drawn from the same and from different colonies. This may have disrupted social structure sufficiently to suppress any expression of indiscriminate suckling behaviour, even between individuals captured from the same colonies. Thus, in more stable wild colonies comprising undisturbed groups of potentially closely related individuals, indiscriminate suckling may occur. Nevertheless, the current extensive data are consistent with the evidence of discriminant nursing found in a wild colony of *P. auritus* (Swift, 1981).

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REFERENCES


