



Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission–fusion model

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We used radiotelemetry to quantify roost switching and assess associations between members of maternity colonies of forest-dwelling big brown bats. Bats remained loyal to small roosting areas of forest within and between years and switched trees often ($\bar{X} \pm \text{SD} = 1.7 \pm 0.7$ days). For radiotagged bats from the colony in one of these areas, roost-switching frequency was positively correlated with the number of different individuals with which tagged bats shared roosts. We quantified associations between pairs of bats using a pairwise sharing index and found that bats associated more often than predicted when roost and roostmate selection were random but that all tagged bats spent at least some days roosting in different trees, apart from preferred roostmates. Our results suggest that forest-dwelling big brown bats conform to a fission–fusion roosting pattern. Roost switching in forests may reflect the maintenance of long-term social relationships between individuals from a colony that is spread among a number of different trees on a given night. In this fission–fusion scenario, switching between trees, within a local area, could serve to increase the numbers of individuals with which bats maintain associations. We contend that roosting areas in forests are analogous to spatially large roosts in caves, mines and buildings.

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Social interactions and intraspecific cooperation can result in fitness benefits for many animals (Alcock 2001). Group living in bats provides a number of fitness benefits (Kunz 1982). Clustering in maternity colonies reduces thermoregulatory costs, which are important for reproductive females because low roost temperatures and torpor delay the development of prenatal and juvenile offspring (Racey & Swift 1981; Wilde et al. 1995). Information transfer at roost sites can reduce costs associated with finding foraging areas (e.g. *Nycticeius humeralis*, Wilkinson 1992), or finding other suitable roosts (e.g. *Myotis bechsteinii*, Kerth et al. 2001a). Coloniality may reduce the costs of rearing young, via cooperative breeding (Kerth et al. 2001a), and may reduce individual predation risk, via clustering during emergence from roosts (e.g. Kalcounis & Brigham 1994; Speakman et al. 1999). In colonial birds, up to a certain colony size, the benefits of group living may

be positively correlated with the number of individuals in the colony (e.g. Ward & Zahavi 1973; Wittenberger & Hunt 1985). Bat colonies in physically large structures such as caves, mines and buildings can consist of thousands to millions of individuals (Kunz 1982). In forest ecosystems, however, the number of bats occupying a single tree cavity rarely exceeds tens to hundreds of individuals (Kunz 1982; Barclay & Brigham 1996).

Optimal group sizes of social animals may vary depending on a range of environmental constraints (Lefebvre et al. 2003). Differences in group size between bats roosting in tree cavities and those in larger structures (e.g. caves or buildings) may reflect constraints that favour smaller optimal group sizes in forests, such as the thermal properties of tree roosts, competition for space inside roost cavities, or competition for suitable roost sites on the landscape. However, recent evidence suggests that bat colonies using tree cavities are not restricted to individual trees. Instead, colonies may be spread among multiple trees on a given night, forming fission–fusion societies (Kerth & König 1999), which resemble those of some cetaceans and primates (Whitehead et al. 1991; Henzi et al.

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1997). Bats tend to be loyal to small, defined areas of forest within (e.g. Vonhof & Barclay 1996; O'Donnell & Sedgeley 1999) and between years (J. Vielleux, unpublished data) and also display loyalty to other individuals within their roosting area (O'Donnell 2000; Kerth et al. 2001a). Under the fission–fusion model, on a given night, the colony would consist of multiple roosting subgroups, spread among different trees within the roosting area (Kerth & König 1999; O'Donnell 2000; Kerth et al. 2001a). It is well known that tree-roosting bats switch roost sites every few days, but the motivation underlying roost switching is not well understood (Lewis 1995; Vonhof & Barclay 1996; Brigham et al. 1997; Kalcounis & Brigham 1998; O'Donnell & Sedgeley 1999; Cryan et al. 2001; Kurta et al. 2002). If a colony is composed only of those bats living in an individual tree, then roost switching will be costly because the group must dissolve during activity at night and re-form at a new roost site by the next morning (Lewis 1995). Roost switching in the context of fission and fusion, however, could provide a mechanism by which bats maintain long-term associations with colony members in other subgroups. During roost switching, subgroups may break apart and mix as they move to different trees within the roosting area. With repeated roost switching over time, bats may eventually associate with all other individuals resident to their roosting area (O'Donnell 2000). Loyalty to defined roosting areas, occupation of multiple trees within a roosting area, and frequent roost switching are consistent with the hypothesis that tree-roosting bats maintain stable social groups that are larger than the number of individuals occupying any given tree. Benefits associated with membership in a large colony, such as a reduced risk of energetically costly solitary roosting, reduced predation risk, information transfer about roost or foraging sites, cooperative breeding, and kin selection benefits if colony members are genetically related (O'Donnell & Sedgeley 1999; Kerth et al. 2001a) could all be positively correlated with colony size even if colony size exceeds the capacity of individual trees. Loyalty to small roosting areas of forest could reduce the time and energy invested in searching for roostmates during roost switching within the fission–fusion model.

One approach to testing the hypotheses that (1) bats form cohesive colonies that are larger than the numbers of bats in any given tree and (2) roost switching helps maintain a large colony is to determine whether individuals within a roosting area share cavities more often than would be expected if they selected roost trees and roostmates at random and whether a positive correlation exists between roost-switching frequency and the number of different colony members with which an individual roosts. Nonrandom roosting associations would provide evidence of colony fusion. A positive correlation between an individual's roost-switching frequency and its number of different roostmates would suggest the function of subgroup fission and roost switching. Subgroup fission could result from an active preference by bats to occasionally roost apart from certain individuals or, alternatively, it could be a consequence of limited space inside trees, where late arrivals to 'full' roosts on a given night are forced to find alternative sites. In either case, fidelity to small patches of

forest, a positive relationship between roost switching and the number of different associations between individuals, and nonrandom roosting associations would all provide evidence of a fission–fusion colony structure. This evidence would also lend support to the hypothesis that the potential benefits of colonial living extend beyond benefits accrued by roostmates sharing one tree cavity.

The individual interests of all members of a social group will not necessarily be equal (Conradt & Roper 2000). Reproductive bats have strict thermoregulatory requirements, relative to nonreproductive individuals, because low roost temperatures and torpor delay offspring development (Racey & Swift 1981; Kunz 1982; Wilde et al. 1995). Different thermoregulatory constraints may lead to differences in roost site selection between these groups. Among reproductive female bats, lactating individuals may select relatively warm roosts to avoid torpor, whereas pregnant bats, with higher flight costs, may choose cooler roosts during inclement weather to facilitate torpor (Kerth et al. 2001b; Willis, in press). These potential preferences lead to the hypothesis that, within colonies, the roost-sharing and roost-switching patterns of nonreproductive, lactating, and pregnant bats may differ.

The big brown bat is a common wide-ranging North American vespertilionid found from northern South America to southern Canada. They are most commonly associated with roost sites in buildings where maternity colonies may number in the hundreds, but are also found roosting in rock crevices and tree hollows, where numbers of bats in any one structure rarely exceed 30–40 individuals (Kurta & Baker 1990; Lausen & Barclay 2002; Kalcounis & Brigham 1998; Willis et al. 2003). Male big brown bats may roost solitarily, within maternity colonies or in male-only colonies (Kurta & Baker 1990). A high percentage of adult females return to the same building roosts each year but only 10–30% of juvenile bats have been found to return (Kurta & Baker 1990). It is unclear whether the low rate of juvenile returns reflects dispersal by juvenile females and low natal philopatry, or simply low overwinter juvenile survival. The degree of between-year fidelity of individual big brown bats to natural roost sites, such as trees, is not known, although individual tree maternity roosts may remain in use for up to 10 years (Willis et al. 2003). We report multiday patterns of roosting behaviour by radiotagged female big brown bats, within and between years, at a study site where they form maternity colonies exclusive of males and exclusively in trees. Our objective was to test the hypothesis that forest-living female big brown bats conform to a fission–fusion colony structure by quantifying associations between individuals and characterizing roost fidelity and switching. We posed the following questions. (1) Are big brown bats loyal to specific trees and/or nonoverlapping areas of forest within and between years? (2) Do individual bats associate with each other nonrandomly, within and between years? (3) Do roostmates locate each other if separated? (4) Does roost switching increase the number of bats with which an individual interacts over time? (5) Does reproductive condition influence roost-switching and roost-sharing behaviour?

METHODS

Study Area

We conducted fieldwork in Cypress Hills Provincial Park, Saskatchewan, Canada (49°34'N, 109°53'W). The Cypress Hills are the highest point on the Canadian prairies and run about 50 km in an east–west orientation. Sauchyn (1993) characterized the region as approximately 50% grassland, 45% woodland and 5% wetland. Woodland vegetation is characterized by lodgepole pine, *Pinus contorta*, forest in dry, high elevation (>1300 m) areas and white spruce, *Picea glauca*, forest with more substantial understorey in wetter areas (Sauchyn 1993). Big brown bats roost exclusively in cavities in trembling aspen trees, *Populus tremuloides* (Kalcounis & Brigham 1998), which are found throughout the study area (Sauchyn 1993).

Capture and Radiotracking

All protocols were approved by the University of Regina President's Committee on Animal Care and were in accordance with the Guidelines of the Canadian Council on Animal Care. Between June and August 2000–2002, adult female big brown bats were captured in mist nets when emerging from their roost trees and, occasionally, while foraging. To minimize disturbance to bats, we netted at roost trees infrequently and never more frequently than once every 7 days ($\bar{X} \pm SD = 15.6 \pm 8.5$ days, range 7–30). Roost trees housed reproductive and nonreproductive female bats, as well as juveniles of both sexes. We radiotracked only female bats because males were rare in the study area. Over 3 years, only two males were captured at foraging areas and none were captured during netting sessions at roost trees.

We identified pregnant bats by gentle palpation of the abdomen and lactating bats by the presence of bare patches around the nipples and/or the expression of milk. Bats were released within several hours of capture. Before bats were released, we clipped the fur between the scapulae and attached radiotransmitters (0.7 g BD-2B, Holohil Systems Ltd, Carp, Ontario, Canada) using surgical cement (Skin-Bond, Smith and Nephew United, Largo, Florida, U.S.A.). Transmitter mass represented less than 5% of body mass (Aldridge & Brigham 1988). During 2001 and 2002, all bats were permanently marked with blue numbered split-ring plastic bands (National Band and Tag Company, Newport, Kentucky, U.S.A.) on the forearm prior to release. This allowed us to assess reuse of areas of forest, and specific trees, by individuals based on captures at roosts, within and between years. We followed radio-tagged bats to roost trees on as many days as possible, using handheld telemetry receivers (R-1000, Communication Specialists Inc., California, U.S.A.) and five-element yagi antennas (AF Antronics, Inc., Urbana, Illinois, U.S.A.). We did not track bats to their roost trees every day, but on days when bats were not tracked to roosts, we determined their presence or absence within one of three roosting areas (see below) using telemetry. When possible, we performed exit counts at roost trees. We assessed whether roost trees used during 2000 were reused during 2001 and

2002 and compared the number of bats counted emerging at dusk from trees used only in 2000 to the number counted emerging from trees used in both 2000 and 2001.

Roost Sharing and Individual Associations

We devised a pairwise sharing index (PSI) to quantify roost sharing between individuals that were radiotracked simultaneously. We only included pairs if we found the roost trees of both individuals on at least five simultaneous (although not necessarily consecutive) tracking days. We included a few days (11/346) on which we found the roost tree of only one member of the pair when we were certain that both members were not sharing a roost because we detected the signal of the transmitter from the other pair member in a different direction. For each pair, we calculated the observed roost-sharing proportion (OSP) by dividing the number of days during which the two individuals shared a roost by the total number of days during which we could account for both bats. For example, if we could account for both members of a pair of bats on 8 days and they shared roosts on 6 of those days, their OSP would be 0.75. We also calculated an expected roost-sharing proportion (ESP) based on the roost-switching behaviour of each bat in the pair and the number of days of simultaneous tracking (ST) as: $ESP = (1/(ST)(\text{Bat 1 roosts/day})) \times (1/(ST)(\text{Bat 2 roosts/day}))$. For each bat, 'roosts/day' is the total number of roosts at which that individual was found divided by the number of days that bat was tracked. This value incorporates individual variation in roost-switching behaviour into the ESP. For example, if Bat 1 of a hypothetical pair was tracked for 12 days to a total of six roosts, its roosts/day value would be 0.50. If hypothetical Bat 2 used four roosts over 10 tracking days, its roosts/day value would be 0.40. For each bat, we multiplied these values by the number of simultaneous tracking days (i.e. 8) to predict the number of different roosts each bat would be expected to use during the 8 days of simultaneous tracking. We assumed that if bats selected roosts and roostmates at random, the expected proportion of days when both bats should roost together would be the product of probabilities of finding each of them in one of their available roost trees on a given day. The pairwise sharing index, then, is the difference between observed and expected proportions: $PSI = OSP - ESP$. A positive PSI value represents a conservative estimate that a pair was found together more often than expected if the pair members were associating randomly. By definition, PSI scores must be less than 1 and greater than -1. A value of zero indicates that a pair of bats occupied the same roost at the same frequency as predicted by chance.

We compared the proportions of positive and negative PSI scores between pairs of bats captured during the same roost-netting session and pairs captured during different roost- or foraging-site-netting sessions. To determine whether reproductive status influenced sharing between individuals, we compared pairs composed of one pregnant and one nonreproductive bat to exclusively nonreproductive pairs. We were unable to compare pairs composed of

two pregnant or two lactating bats because of a small sample size. We also compared roosting behaviour between the three reproductive periods of the season. The timing of reproductive periods varied slightly between years, so we divided each year of the study into pre-pregnancy, pregnancy and lactation periods based on the reproductive status of the majority of bats captured during roost-netting sessions. Typically, we did not capture pregnant bats after catching lactating individuals. On one occasion in 2000, we netted a roost and captured both pregnant ($N = 2$) and lactating ($N = 4$) bats. This netting session was defined as delineating the start of the lactation period. For all other roost-netting sessions, all reproductive bats were either pregnant or lactating. Thus, the start of the pregnancy period was delineated by our first annual capture of at least one pregnant bat (mid-June) and the start of the lactation period was delineated by our first capture of lactating bats (mid-July). We defined a pre-pregnancy period because, in 2001 and 2002, some captured bats were not detectably pregnant in early June, but were pregnant or lactating when recaptured later in the season.

To determine whether roost switching or reproductive status affected the number of individuals with which bats associated over time, we devised an individual sharing index (ISI). This index is based on the number of radiotagged individuals with which a given radiotagged bat shared a roost, divided by the daily average number of potential radiotagged roostmates available for sharing. The ISI accounts for two potential biases of radiotracking data not encountered in census studies that account for all members of a roosting group during each sampling period (e.g. Kerth & König 1999; O'Donnell 2000). First, we could not identify all the members of roosting groups. Instead, our data come from a radiotagged subsample of group members. Furthermore, because some bats quickly groomed off their transmitters, not all bats were tagged for the same length of time (see Results). Therefore, the number of potential roostmates that we could detect each day was variable. Second, based on analysis of the PSI, we found that the likelihood of bats roosting together was significantly affected by whether they were initially captured from the same roost (see Results). To account for these potential biases, we calculated the ISI for individual Bat X as: $ISI = ((\text{roostmates caught with Bat X}/0.97) + (\text{roostmates caught separately from Bat X}/0.70)) / \text{average number of potential roostmates per day}$, where 'roostmates caught with Bat X' is the number of different radiotagged individuals originally captured from the same roost as Bat X with which it was later found roosting and 'roostmates caught separately from Bat X' is the number of radiotagged individuals caught at different roost or foraging sites from Bat X with which it was later found roosting. The correction factors, 0.97 and 0.70, are the probabilities of finding pairs of bats together more often than predicted with random roosting if they were caught at the same site or different sites, respectively (i.e. the proportion of positive PSIs for bat pairs caught at the same roost (0.97) and at different roost or foraging sites (0.70); see Results). The 'average number of potential roostmates per day' is the number of other bats carrying radiotags during Bat X's tracking days, divided by Bat X's tracking

days. A higher value of the ISI means that Bat X shared roosts with a greater proportion of its potential roostmates, whereas a smaller value indicates that Bat X shared roosts with fewer potential roostmates.

Effect of Experimental Separation on Roost Sharing

On 16 June 2002, during the prepregnancy period, 16 big brown bats were captured leaving a roost tree within Roosting Area 1 (see Results). All bats were banded and eight were outfitted with transmitters as described above. Four radiotagged and four untagged bats were randomly selected as a treatment group and the remaining four radiotagged and four untagged bats served as a control. Treatment bats were released approximately 4 km from the site of capture, within 100 m of three known roost trees found previously in Roosting Area 3 (see Results). Control bats were released simultaneously at the site of capture. We compared roost-switching frequencies and ISI scores between these two groups of bats. We also compared PSI scores of pairs composed of one control and one treatment bat to PSI scores of all other bat pairs captured during the same netting sessions.

Statistical Analysis

Values reported are means \pm SD. Nonparametric analyses were used where data violated normality, equal variance and/or equal sample size assumptions of parametric tests (Zar 1999). Significance was assessed at an alpha of 0.05.

RESULTS

Loyalty to Roosting Areas and Roost Trees

We collected 346 bat-days of radiotracking and census data from 61 adult female big brown bats during the 3-year study. The mean number of tracking days per bat was low (5.9 ± 4.4 days; range 1–18) compared to typical transmitter battery life (ca. 3 weeks) because bats groomed off transmitters relatively quickly. On 24 bat-days, we could not track individuals to specific trees but confirmed their presence within a roosting area by radiotelemetry.

All individuals were loyal to one of three nonoverlapping roosting areas, each less than 2 km², within the approximately 100-km² study area (Fig. 1). Our capture and radiotracking effort was highest in one of these roosting areas, hereafter called Roosting Area 1 (RA1). On average, we tagged approximately four bats (3.7 ± 1.7 bats, range 1–8) in RA1 each day. No bat captured or found roosting within RA1 was ever found roosting outside it ($N = 317$ days from 47 bats). On 1.8% of bat-days (5/280), we failed to locate a bat with an active transmitter in RA1 when we searched for it. This small percentage may be explained by the fact that several roost trees, not found until August 2002, were located in a low-lying area within RA1, where obtaining signals was

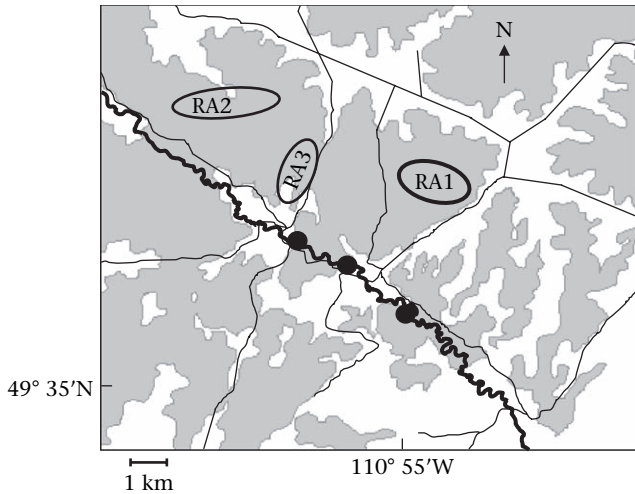


Figure 1. Map of the study area in Cypress Hills Provincial Park, Saskatchewan, Canada. Grey shading represents forested area. Roads are indicated by thin black lines and the heavy black line represents the Battle Creek. Roosting areas (RA) are indicated by ovals. Closed circles mark capture locations along Battle Creek.

difficult. Bats that we failed to locate earlier in the study could have roosted in these trees without being detected. Within years, during 20 roost-netting sessions in RA1, we recaptured 18 previously banded bats. Successive captures of banded individuals were separated by 28.5 ± 14.5 days (range 11–43). During the study, nine bats were captured at three foraging areas along Battle Creek. Two of these bats always roosted in RA1 ($N = 22$ bat-days). The remaining seven bats displayed loyalty to two other roosting areas (RA2 and RA3; Fig. 1) and never roosted in RA1 ($N = 42$ bat-days). We never failed to locate these bats with active transmitters in RA2 ($N = 23$ days from four bats) and RA3 ($N = 19$ days from three bats) when we searched for them. In addition, bats captured at roosts in RA2 were loyal to this area ($N = 24$ days from three bats). We did not capture bats at roosts in RA3.

Bats from RA1 were loyal to the area between years. Three individuals captured from RA1 in 2000 and held captive over the winter as part of another study were found only in RA1 after being released in 2001 ($N = 19$ bat-days). One of these bats was recaptured in the roosting area on two occasions in 2002, the last being more than 3 years after her initial capture. This individual was also radiotracked to roosts in RA1 on 6 additional days in 2002. These three bats were excluded from further analyses to control for a potential captivity effect. Additionally, noncaptive bats from RA1 that were banded in 2001 only roosted in RA1 in 2002, based on recaptures at roosts ($N = 10$ bats) or radiotracking ($N = 50$ days from six bats). We also found evidence of interseason loyalty to specific trees by individuals in RA1. In 2002, two bats were captured from a roost tree they had shared in 2001 and, later, one of these individuals was radiotracked to another tree it had used the previous year.

We found 47 roost trees during the study, 36 of these in RA1. In general, the RA1 bats were loyal to specific trees in the area between years. Seventy-three per cent of roosts

(8/11) found in RA1 during 2000 were reused in 2001 and/or 2002. We performed 52 exit counts at 21 RA1 trees on 40 nights over 3 years. Roosting group sizes were variable (18.1 ± 12.1 ; range 1–45, $N = 52$) but bats rarely roosted alone. Solitary bats were observed during only 9.6% of exit counts (5/52). There was no difference between roosting group sizes during the pregnancy period (15.21 ± 9.7 , $N = 19$) and the lactation period (19.3 ± 10.6 ; t test: $t_{37} = -1.3$, $N = 20$, $P = 0.22$). During 2000, significantly more bats emerged from trees that were reused the following year (37.4 ± 9.7 , $N = 5$) compared with trees that were not reused (6.5 ± 5.5 ; t test: $t_7 = -5.7$, $N = 4$, $P = 0.001$). During roost-netting sessions, we never captured all the bats in a roost tree and significantly fewer were captured, on average (6.5 ± 4.9 ; range 1–19, $N = 11$), than the mean roosting group size (Mann–Whitney U test: $U = 118$, $N_1 = 11$, $N_2 = 52$, $P = 0.003$). Radiotagged bats were spread among more than one roost tree on 52% of days when more than one bat was tagged (31/60).

Loyalty between Bats

Bats from RA1 associated with each other between years. Although we never captured all the bats in a roost tree, 40% of bats (4/10) banded during 2001 and recaptured at roost trees in 2002 were found roosting with bats with which they had roosted the previous year. These four bats formed nine different pairwise combinations but, within years, only one of these pairs (bats 34 and 28) was tracked for 5 simultaneous days for calculation of PSI scores. Their score was low but similar in both 2001 (0.13) and 2002 (0.12). Within years, we obtained at least 5 simultaneous days (7.1 ± 1.8 days per pair; range 5–12 days) of tracking data from 39 bat pairs in RA1. These pairs consisted of different combinations of 26 individuals. For 89.7% of pairs (35/39), PSI scores were positive, indicating that these bats roosted together more frequently than expected if they selected roosts at random. However, despite the high proportion of days that bats spent roosting with known individuals, no two bats spent 100% of their simultaneous tracking days together. We found a significant difference in the ratio of positive to negative PSI scores for individuals captured at the same roost (28:1) relative to those captured at different roost or foraging sites (7:3; Fisher's exact test: $P = 0.045$; Fig. 2). In other words, bats captured at the same roost were more likely to be found together again than bats captured at different roost trees or at foraging sites. These proportions were used as correction factors in our calculation of the ISI (see Methods). There was no correlation between the number of simultaneous tracking days and PSI scores for bats captured together ($r^2 = 0.05$) or bats captured separately ($r^2 = 0.002$).

Roostmates captured together and then separated before release roosted together again following release. We tracked all radiotagged control and treatment bats used in the separation experiment for 4.5 ± 1.5 days after capture (range 3–6). There was no significant difference between ISI scores of treatment bats (1.36 ± 0.16 , $N = 4$) and control bats (1.25 ± 0.08 , $N = 4$; Mann–Whitney

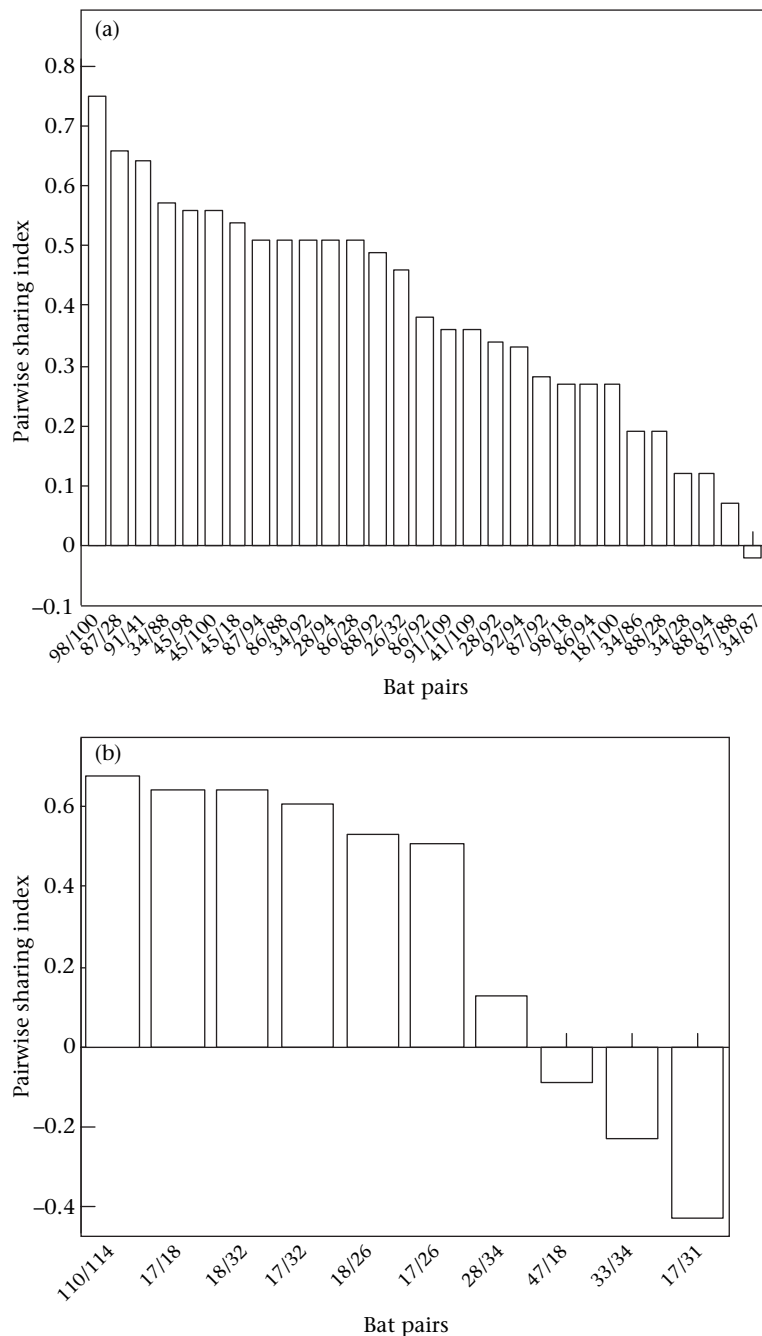


Figure 2. (a) Pairwise sharing indexes (PSI) calculated for 29 pairs of female *E. fuscus*. Both members of each pair were captured while emerging from the same roost. Values represent the difference between the observed proportion of simultaneous tracking days that both bats in a pair roosted together and an expected value calculated based on the probability of finding both bats in the same roost if they were selecting roosts and roostmates at random (see text). Positive values suggest that bats were sharing roosts more than would be predicted with random roosting. (b) PSI scores of 10 pairs of *E. fuscus* captured from different roost or foraging sites.

U test: $U = 12$, $P = 0.24$), indicating that bats of both groups were equally likely to share roosts with similar numbers of potential roostmates after separation. There was no difference in roost-switching frequency between control (2.0 ± 0.6 days, $N = 4$) and treatment bats (1.6 ± 0.5 days, $N = 4$; Mann–Whitney *U* test: $U = 5$, $P = 0.38$) and no difference between PSI scores of pairs composed of

one control and one treatment bat (0.31 ± 0.22 , $N = 12$) and PSI scores of all other bat pairs composed of individuals captured together (0.46 ± 0.17 , $N = 12$; Mann–Whitney *U* test: $U = 44$, $P = 0.11$). Most telling, even given our small sample size, all eight bats tracked in the experiment were roosting together in the same tree, within 200 m of the roost tree from which they were captured, the

morning after release. Furthermore, of the eight bats banded but not radiotagged during the experiment, we later captured three of four control bats and all four treatment bats during three roost-netting sessions in RA1. During one of these sessions, three banded treatment bats and two banded control bats were captured from the same roost, along with one of the control bats that had been radiotagged.

Roost Switching and Individual Associations

On average, bats switched roosts every 1.7 ± 0.7 days (range 1–4.5). On nine occasions, radiotagged individuals left a roost tree and then returned to it several nights later. Based on exit counts, we know that on three of these nights, the roosts remained occupied during the bats' absences, but we do not know whether, on the remaining six nights, roost trees were abandoned by the entire group or just by radiotagged individuals. Following 91% of roost-netting sessions (10/11), bats that were radiotagged during a particular session had moved to a different roost tree by the following day. Overall, however, there was no difference between switching frequencies of bats captured at roost trees (every 1.7 ± 0.7 days, $N = 29$) and bats captured at foraging areas (every 1.8 ± 0.7 days, $N = 9$; Mann–Whitney U test: $U = 144.5$, $P = 0.63$). Roost switching did lead to an increase in the number of novel associations between different bats. There was a significant positive relationship between ISI scores of individuals and the number of times they switched roost trees while tagged (linear regression: $r^2 = 0.67$, $F_{1,34} = 69.31$, $P < 0.001$; Fig. 3).

Effect of Reproductive Condition on Sharing and Switching

For bats captured together, there was a significant difference between PSI scores of bat pairs composed of

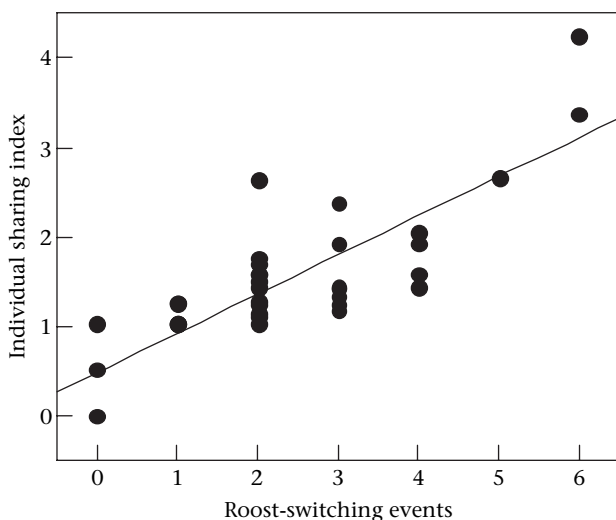


Figure 3. Relationship between the individual sharing index and the number of roost-switching events for 36 female *E. fuscus* radiotagged in Roosting Area 1.

two nonreproductive individuals (0.35 ± 0.18 , $N = 22$) and pairs composed of one pregnant and one nonreproductive bat (0.52 ± 0.17 , $N = 6$; Mann–Whitney U test: $U = 30.5$, $P = 0.046$). Small samples sizes of other reproductive class combinations precluded statistical analysis. There was no difference in roost-switching frequency between bats of different reproductive status (ANOVA: $F_{2,28} = 0.36$, $P = 0.70$). Using ANCOVA with number of roost-switching events as a covariate, we compared ISI scores of seven pregnant, six lactating and 10 nonreproductive bats, as well as eight bats captured during the prepregnancy period. The effect of switching was significant ($F_{1,9} = 56.1$, $P < 0.001$) but there was no effect of reproductive condition on ISI scores ($F_{3,26} = 1.1$, $P = 0.37$). However, we found a significant difference between ISI scores of bats tracked during the prepregnancy, pregnancy and lactation periods (ANCOVA: $F_{2,27} = 3.68$, $P = 0.039$; Fig. 4). Irrespective of their own reproductive condition, individuals had more novel associations with other bats during the pregnancy period relative to the prepregnancy (Tukey test: $P = 0.01$) or lactation (Tukey test: $P = 0.008$) periods.

DISCUSSION

Our objective was to characterize patterns of roost fidelity and roost switching and test the hypothesis that forest-dwelling, female *E. fuscus* conform to a fission–fusion colony structure. Data on the social structures of forest bat populations are rare. Those studies that do exist rely on census data collected at a population of known tree roosts (O'Donnell 2000) or, more commonly, artificial bat houses (Park et al. 1998; Kerth & König 1999; Kerth et al. 2001a). Very few studies have addressed the social behaviour of bats in natural forest roosts and fewer still have relied on radiotracking to quantify pairwise associations between individuals. The use of radiotracking is important because obtaining census data from natural roosts in forests is

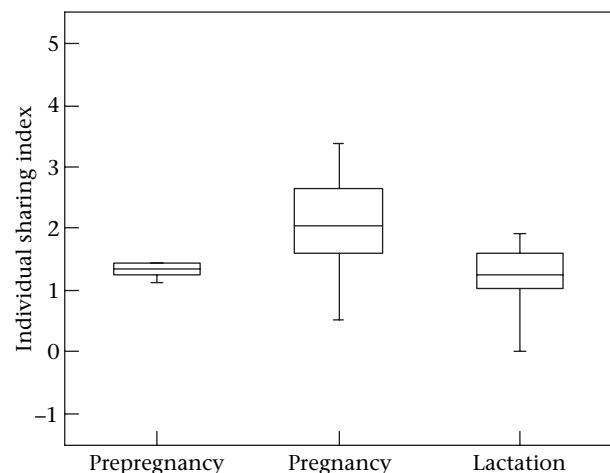


Figure 4. Boxplots showing individual sharing indexes for bats during prepregnancy ($N = 8$), pregnancy ($N = 9$) and lactation ($N = 14$). Middle lines represent the median, boxes represent the quartile range, and whiskers represent the 5th and 95th percentiles.

logistically challenging. Radiotelemetry is commonly used to study roost site preferences, foraging behaviour and, more recently, thermoregulation in forest-dwelling bats (e.g. Vonhof & Barclay 1996; Sedgely & O'Donnell 1999; Cryan et al. 2001; Willis, in press). Our analytical approach may prove useful for future radiotracking studies that address the social structure of populations in addition to describing roost site preferences and foraging behaviour.

Loyalty to Roost Trees and Roosting Areas

Previous studies suggest that, within years, forest-roosting bats are loyal to a defined area containing many potential roost trees (Barclay & Brigham 1996; Vonhof & Barclay 1996; Brigham et al. 1997; O'Donnell & Sedgely 1999; O'Donnell 2000; Cryan et al. 2001; Kurta et al. 2002). Our results substantiate these findings. We found that all bats were loyal to one of three defined, non-overlapping areas of forest within years, and that individuals from one roosting area were loyal to the area between years. Most studies addressing this question report radiotracking data, which account for individuals over the relatively short-term life of transmitters (days to weeks; e.g. Barclay & Brigham 1996; Vonhof & Barclay 1996; Brigham et al. 1997; Cryan et al. 2001). Our recapture data show that individual bats used the same trees in RA1 for a maximum of 43 days within years, and for over 3 years. Additionally, between years, specific trees were reused by individuals and the RA1 colony in general. These roosting patterns are consistent with long-term colony stability. Loyalty, by colony members, to a relatively small area should mitigate costs associated with searching for occupied roosts or colonymates, and will reduce the risk of having to roost alone.

Loyalty between Bats

Previous studies reporting pairwise roosting associations of bats have used Fager's (1957) symmetrical index of sharing or other techniques designed to analyse census data (e.g. Wilkinson 1985; Kerth & König 1999; O'Donnell 2000; Kerth et al. 2001b). These methods were not appropriate for our study because we did not necessarily obtain the same number of census (or in our case, tracking) days from each bat in a pair. Thus, we did not have an equal probability of finding both individuals every day. The PSI score we derived is appropriate to radiotracking data because it is based only on tracking days during which we account for both members of a pair. It also incorporates observed individual differences in roost-switching behaviour into the calculation of the proportion of days a pair is expected to share a roost. Our expected roost-sharing proportion is a conservative estimate. During the study, we located 47 roost trees and, although all of these trees may not have been available to bats on a given night, more roosts were probably available than the number per simultaneous tracking period we used in our calculation of PSI scores (4.1 ± 1.0 roosts per bat pair; range 2.9–8.0; see Methods). Therefore, any error

in the sharing index will underestimate, rather than overestimate, the degree to which bats share roosts with known individuals.

Based on recaptures and PSI scores, we found convincing evidence of colony fusion among bats in RA1. Forty per cent of bats recaptured in 2002 were found with roostmates from the previous year. This is likely to be an underestimate because, during most netting sessions, we captured only a small fraction of bats in a given tree. Therefore, marked individuals probably escaped detection. Within years, despite frequent roost switching, almost 90% of bat pairs were found together more often than predicted if they selected roosts and roostmates at random. Indeed, bat pairs often switched roosts together. These data lend strong support to the conclusion that bats roosting in defined areas of forest form cohesive social groups, and are consistent with previous studies (Kerth & König 1999; O'Donnell 2000).

Wilkinson (1985) suggested two explanations to account for nonrandom roosting associations between bats. Passive aggregation would occur at roosts that are attractive to the same individuals at the same time, whereas active aggregation would result from preferences of individuals for each other. Kerth & König (1999) found evidence for active associations among *M. bechsteinii* roosting in bat houses. The results of our separation experiment suggest that active aggregation occurs in big brown bats as well. The treatment group in this experiment was released within 100 m of three known roost trees within one roosting area, yet these bats returned to a roost tree in their original roosting area. Furthermore, all eight radiotagged bats were found in the same tree the next morning and they associated repeatedly during the days that followed. Despite a relatively small sample size, the probability of this occurring by passive aggregation is remote because the bats had many roost trees available to them. It is highly unlikely that the tree selected by all eight bats on the night of release had conditions so ideal as to preclude any of them from using another tree.

Roost Switching and Individual Associations

Lewis (1995) suggested that the permanence of roost sites like caves, mines and buildings, in contrast to the ephemeral nature of sites like trees, could account for patterns of roost switching observed in free-ranging bats. The intra- and interseasonal fidelity to roosting areas, documented in this and other studies, is not consistent with the ephemerality hypothesis. In the Cypress Hills, we have documented reuse of roost trees by the *E. fuscus* population for up to 10 years and reuse probably occurs over much longer time frames (Willis et al. 2003), but bats still switch roosts about every 2 days. This contradicts the idea of ephemerality as a driver of roost switching for tree-cavity-roosting bats. O'Donnell & Sedgely (1999) suggested the alternative explanation that roost switching could serve to maintain associations between members of the larger colony if the colony is spread among multiple trees on a given night. Our data are consistent with this hypothesis. We found bats spread among multiple trees within RA1 and that roost switching between trees in RA1

led to an increase in novel associations between individuals. Furthermore, despite very high PSI scores for most bat pairs, no two individuals spent all of their tracking days together. This shows that, although bats roost with the same individuals most of the time, they occasionally leave preferred colony members to roost with other bats. This pattern of fission may represent active decisions by individuals to roost apart from certain colony members at certain times. Alternatively, group fission may be an artefact associated with limited space available inside roosts. Bats arriving late to a roost tree may be forced to find an alternative site. The latter case seems less likely because *E. fuscus* subgroups in the Cypress Hills often use very large cavities (>2 m long), which could potentially house much larger groups (Willis 2003). This suggests that space inside roosts may not be the only limit on roosting group size and provides some evidence for active fission. Kerth & König (1999) found that the size of roosting subgroups of *M. bechsteinii* was stable despite variable ambient conditions, which suggests there may be some optimal subgroup size. However, further work is needed to determine conclusively if fission events are the result of active choices by bats. It is also important to quantify the relative influence of other factors, such as microclimate, parasite load and guano accumulation within tree cavities, on patterns of roost switching in forests. Regardless of the underlying causes of roost switching, however, switching and fission within the larger cohesive colony could allow bats to maintain associations with more colony members over time.

One hypothesis suggested by the results of this and other studies is that relatively large colonies provide fitness benefits for bats in forest habitats. Surprisingly, recent evidence suggests that colony size is not necessarily positively correlated with fitness in forest-roosting bats. O'Donnell (2002) found that a large colony of *Chalinolobus tuberculatus* in New Zealand had low juvenile recruitment and poor body condition relative to a smaller colony in the same area. O'Donnell (2002) suggested that this reduced fitness could reflect increased competition between members of the large group, or genetic differences between groups. However, O'Donnell (2002) did not suggest a causal relationship between the larger colony size and reduced fitness in this group. On the contrary, one possibility is that bats form larger colonies as a response to suboptimal habitats. Members of the large colony described in O'Donnell's (2002) study were only found roosting in an area characterized by the lowest-quality roost trees, and only foraged in areas with low insect abundance compared to the smaller social group. Although questions remain, arguably, O'Donnell's (2002) findings lend support to the hypothesis that forming large colonies can be beneficial to bats, especially if they are restricted to poor habitats. In any case, our data are consistent with those of O'Donnell (2000, 2002) in that both *C. tuberculatus* and *E. fuscus* form colonies that are spread among multiple trees on a given night and that contain more individuals than those counted emerging from single trees.

Despite the high degree of fidelity between bats in this study, there was considerable variation in the PSI scores of

different pairs. About three per cent of bats captured together and 30% of bats captured separately were found together less frequently than expected. This could be attributed to the relatively short time we were able to radiotrack bats. As observed by O'Donnell (2000) for *C. tuberculatus*, it is possible that with longer-term monitoring, eventually we would have found that all bats in RA1 associate as they continue to switch roosts (Fig. 3). Other previous work, however, does not support this explanation. Based on long-term census data from bat houses, Kerth & König (1999) reported results similar to ours in that most members of an *M. bechsteinii* colony roosted together preferentially but some shared roosts much less frequently than predicted with random roost site selection. As for nonrandom associations, patterns of individual avoidance could represent either a passive by-product of roost selection, where trees with certain characteristics are attractive to some bats but unattractive to others, or an active process where certain individuals avoid each other. One possibility is that closely related females roost together most often, perhaps to exploit kin selection benefits associated with cooperative breeding. However, Kerth & König (1999) found that reproductive status was a better predictor of positive associations than genetic relatedness. Further work is needed to resolve this question in *E. fuscus* but, given predicted differences in microclimate requirements of different reproductive classes of bats, passive avoidance might be expected between pregnant and lactating individuals (see below).

Effects of Reproductive Condition on Individual Associations

Reproductive condition accounted for some of the variation in pairwise sharing. Pairs of nonreproductive bats were less likely to be found together than pairs composed of one pregnant and one nonreproductive individual. Again, Kerth & König (1999) found a similar pattern for lactating and nonlactating *M. bechsteinii*. This species does not reproduce every year and roosting groups consist of both reproductive and nonreproductive individuals. Kerth & König (1999) argued that the close associations between reproductive and nonreproductive bats provide evidence for cooperative breeding. If related bats roost together, and stagger reproduction between years, they would still benefit from social thermoregulation while lowering annual costs and risks associated with reproduction. Kerth & König (1999) found evidence of cooperative breeding but little evidence of kin selection in *M. bechsteinii* because subgroups were not necessarily composed of related females. However, in systems where roostmates are close relatives, kin selection could help nonreproductive bats recoup some of the fitness costs of a reduced reproductive output. We have no data on relatedness of individuals, but *E. fuscus* in our study area display an identical pattern to *M. bechsteinii* in that they typically do not reproduce every year (C. Willis, unpublished data) and nonreproductive bats are consistently found roosting with reproductive individuals. Although equivocal, our data are consistent with Kerth & König's (1999) cooperative breeding hypothesis.

Surprising to us, bats roosted with fewer different individuals during the pre-pregnancy and lactation periods compared with the pregnancy period despite there being no difference in roost-switching frequency. One explanation for this observation could be that active associations between colony members are enhanced by passive, roost selection requirements during energetically stressful periods (Kerth et al. 2001b). Some evidence suggests that lactating bats select warm roosts to avoid torpor, whereas pregnant bats, with higher flight costs and reduced foraging efficiency, select cooler roosts that facilitate torpor (Kerth et al. 2001b; Willis, in press). If warm roost trees are relatively rare, then passive aggregation of lactating bats at such trees would be expected. This passive aggregation, combined with established active associations, could reduce the occurrence of novel associations between aggregating bats and other individuals. Passive aggregation at warm roost trees could also account for lower novel associations during the early season pre-pregnancy period. During the gestation period, bats are commonly exposed to ambient temperatures below freezing in the Cypress Hills, so microclimate selection during pre-pregnancy could lead to an increase in passive aggregation. A small sample size precluded analysis of pairwise associations between other reproductive classes of bats and further work is required to address these hypotheses.

Management Implications

Our radiotracking results show that forest-roosting female big brown bats are loyal to colony-defined roosting areas and that colonies conform to a fission–fusion social structure in which they form preferential, but not exclusive, roosting associations with other colony members. In other words, bats form long-term associations with some individuals in their colony but they also occasionally roost apart from preferred roostmates. Our data suggest that associations in this species are active, but we suggest that passive aggregation at certain roost sites may occur as well, especially as a result of changing microclimate requirements throughout the season.

We contend that roosting areas of forest are analogous to physically spacious, more ‘permanent’ roosts. Physically large roosts containing hundreds to thousands of bats probably offer a range of roosting opportunities, particularly in terms of spatial variability in microclimate (Kunz 1982), but also in terms of opportunities for social interaction. Bats can move freely between microclimates during the day, selecting warm sites to avoid torpor when reproductive and cool sites to facilitate torpor when necessary (Hamilton & Barclay 1994; Willis, in press). Physically spacious roosts also afford bats the opportunity to interact with many different colonymates throughout the day. Roosting areas of forest offer similar opportunities. Roost switching between trees would facilitate the maintenance of social relationships between many different bats while also fulfilling changing microclimate requirements. The obvious difference between physically large cave or building roosts and a forest-roosting area is that the forest-roosting bats must do their switching at

night whereas cave- or building-roosting bats are free to do so throughout the day. We suggest that, in a functional and evolutionary sense, roost fidelity to caves, mines and buildings represents an essentially identical behaviour to the fidelity shown by bats to areas of forest. If this is the case, then the definition of a functional ‘bat roost’ for tree-cavity-roosting bats needs to be expanded, just as the concept of what constitutes a ‘bat colony’ has changed to include multiple roosting groups in different trees (e.g. Vonhof & Barclay 1996; O’Donnell & Sedgely 1999; O’Donnell 2000). This argument may appear semantic but it has important implications for forest management. Harvesting prescriptions such as clear-cutting would remove the majority of trees comprising the functional ‘roost’ in the same way that the collapse of a cave could make much or all of that roost unavailable. Defining the spatial boundaries of forest bat roosts, quantifying numbers of trees required within the roost to maintain colonies, and managing these roosts as defined entities are important for ensuring the stability of bat populations. If roosting areas of some species are indeed discrete, non-overlapping areas of forest, then restricting forest harvesting to areas between the boundaries of forest roosts could mitigate impacts of forestry on bat populations.

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