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Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats

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Spix's disc-winged bats, *Thyroptera tricolor*, roost in young, rolled leaves of *Heliconia* or *Calathea* plants. In this paper, we examined how the combination of high habitat availability, low occupancy rate and short longevity of those roosts may affect the pattern of interactions among individuals in the population. We regularly censused a 5.69-ha study area in northeastern Costa Rica and examined patterns of association using mark–recapture data. *Thyroptera tricolor* formed behaviourally cohesive social groups of mixed sex, ranging in size from four to 14 individuals. Approximately 85% of dyads maintained associations over time periods of up to 100 days, and 40% of dyads maintained longer-term associations of at least 420 days across sex classes. Individuals within social groups did not always roost together, but they shared a small common roosting home range, which averaged just 0.19 ha. Members of different social groups rarely associated, although limited associations between members of select social groups in one subunit were observed. However, roosting home ranges of adjacent social groups often overlapped (up to 39% of home ranges, and up to 92% of the area of the smaller home range), and home range centres were situated less than 100 m apart. Thus, social groups rarely interacted but overlapped in space. The features of this social system are unique among bats and mammals in general, and point to groupings based on kinship or cooperation.

Many social mammals live in groups of varying composition that facilitate some combination of feeding, reproduction, communication, learning and defence (Hamilton 1964; Alexander 1974; Axelrod & Hamilton 1981). Spatial proximity, or association, is usually a prerequisite for social interaction and the development and maintenance of social relationships (Smolker et al. 1992). The nature, quality and temporal pattern of behavioural interactions describe these social relationships, and, in turn, the content, quality and pattern of relationships between members of a population define their social structure (Hinde 1976). Thus, detailed knowledge of associations between individuals in a population and how they relate to sex, age, kinship and reproductive status is required to understand patterns of social structure within animal societies.

Bats show a wide diversity of social and mating systems (see reviews in McCracken & Wilkinson 2000; Burland & Worthington Wilmer 2001), yet detailed analyses of these systems are conspicuously lacking. Available descriptions (and categorization; see McCracken & Wilkinson 2000) of the social organization of bats are typically based on descriptive and qualitative assessments of the stability of social groups (typically of females in mating groups), where neither the patterns of association between individuals nor their significance are described in any detail (see references in McCracken & Wilkinson 2000). While informative, such qualitative descriptions may mask important patterns of preferential association or behaviours within groups, or the duration and temporal pattern of association. The lack of detailed analyses of association patterns for most species has limited our understanding of the complexity of social interactions among individuals within bat populations.

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To date, only five published studies have attempted to place social interactions in free-living bat populations in the context of the nature and quality of associations between individuals (Wilkinson 1985a; Williams 1986; McWilliam 1988; Kerth & König 1999; O'Donnell 2000). Williams (1986) found that harems of *Carollia perspicillata* were labile in composition, with only 3.3% of female pairs remaining together over 50% or more of observations. In contrast, McWilliam (1988) studied the social organization of *Chaerephon pumilus* roosting in buildings in Ghana, and found that 70% of females remained within their harem group from year to year. Similarly, Wilkinson (1985a) found that female *Desmodus rotundus* formed highly stable groups each attended by one to several males, with changes in group membership occurring approximately once every 2 years. Significant associations between females were not simply a consequence of shared habitat preferences, but rather pairs of females that formed stronger associations were more likely to share food, indicating a clear benefit to forming close social ties to other individuals (Wilkinson 1985a). All three studies found that males did not form significant associations with individuals of either sex, consistent with a polygynous mating system. Kerth & König (1999) found that female *Myotis bechsteinii* formed closed social groups in which group members formed nonrandom associations that were not based on genetic relatedness or common habitat preferences, and group members did not always roost together on the same day. Similarly, O'Donnell (2000) showed that groups of *Chalinolobus tuberculatus* in New Zealand roosted in discrete groups containing both males and females in exclusive roosting home ranges, but that members of these groups were spread among a number of roost trees on a given day. These studies highlight the variety and complexity of social interactions shown by bats, even within the same general mating system, thus underscoring the need for detailed studies of patterns of association and social behaviour within bat species.

In social species, interacting individuals may receive passive benefits, where individuals independently aggregate at a patchily distributed resource and benefit from increased vigilance, decreased predation risk or lower thermoregulatory costs. They may also receive active benefits, where individuals benefit directly from their repeated interactions with other group members in terms of cooperative behaviours (Wilkinson 1985a). The opportunity for animals to interact and the exact benefits they receive may be constrained by social factors, including various forms of competition, territoriality and aggression, and by environmental factors, such as the abundance, distribution and longevity of suitable habitat (Lott 1991; Travis et al. 1995). In this paper, we describe patterns of association and space use in the population of Spix's disc-winged bats, *Thyroptera tricolor*, near Tortuguero in northeastern Costa Rica. This species roosts in the rolled, developing leaves of *Heliconia* and *Calathea* plants (Findley & Wilson 1974; Vonhof & Fenton 2004). Suction discs on the wrists and ankles make *T. tricolor* morphologically specialized for using leaves, and virtually unable to use other roost structures that typically require gripping with the claws (Riskin & Fenton 2001). Therefore, *T. tricolor* is highly dependent on the availability of plants producing rolled leaves to meet its roosting requirements. The density of such plants varies considerably, from high densities and almost uniform distribution in clearings or open woodland, to low densities in discrete patches in primarily closed forest with canopy gaps (Stiles 1975; Seifert 1982). Thus, depending on the characteristics of the habitat, bats using rolled leaves as roosts are likely to experience a wide variety of resource distributions and densities, which may in turn influence how and when individuals are capable of interacting and the exact nature of the benefits they may receive.

The dependence of *T. tricolor* on this relatively transient (rolled leaves available for a single day) and patchy resource that varies in space and time led us to hypothesize that the distribution and abundance of suitable habitat will influence patterns of association between individuals. At our study site in Costa Rica, we found that rolled leaves were only available for 8–16 h in the preferred size range of leaves used by *T. tricolor*, and a maximum of 28–60 h, depending on the plant species. Suitable, unoccupied leaves occurred at high densities ($\overline{X} = 37$ leaves/ha), and outnumbered occupied roosts (2.5 leaves/ha), resulting in a low mean occupancy rate of 5.7–12% in the study area. Furthermore, the habitat supported a large population and high density of bats, and, between February and May 1998, we captured 261 bats in a total area of just less than 6 ha, corresponding to a density of 43 bats/ha (Vonhof & Fenton 2004). If grouping behaviour is passive and determined by the distribution and density of suitable leaves, we predicted that this combination of high habitat availability and population density, low occupancy rate and short longevity of roosts in our study area may limit the frequency of interactions between particular individuals, and we would observe extensive lability in the composition of roosting groups over time. The leaves provide no stable rallying point and no permanent structure to defend, individuals have multiple options as to where they may roost each day, and there are many individuals with which to potentially interact in a very small area.

Recent advances in the methodology used to characterize and analyse association patterns (Whitehead 1995, 1997, 1999a, b; Bejder et al. 1998; see review in Whitehead & Dufault 1999) allow for a detailed examination of associations between classes of individuals and their temporal stability. Here we use these analytical advances to describe the spatial and temporal patterns of association within and between sex classes of *T. tricolor*. This study will provide much needed data on fine-scale patterns of spatial and temporal patterns of association within a bat species, and allow us to address whether environmental constraints influence the social behaviour in a species using a specialized resource.

METHODS

We conducted fieldwork in 1998–1999 at the Estación Biológica Caño Palma (hereafter Caño Palma), located in the Refugio Silvestre Barra del Colorado, at the northern

border of Tortuguero National Park in northeastern Costa Rica (83°32′W, 10°35′N). This region is situated in the Tropical Wet Forest Holdridge Life Zone (Holdridge et al. 1971) in the Caribbean lowlands, and forests consist of areas seasonally inundated by floods and dominated by palms (mainly *Raphia* and *Manikaria*), interspersed with mature or secondary evergreen forest. The study site ranged in elevation from below sea level to approximately 30 m. Fieldwork was conducted between 2 February and 26 May 1998, 21 and 26 October 1998, and 18 March and 30 May 1999.

We mapped the study area using a compass and measuring tape, and later created a GIS coverage in ArcInfo 3.0 and ArcView 3.2 (ESRI, Redlands, California, U.S.A.) to determine the size of areas searched. We divided the study area into three subunits easily searched within a day, and separated by short stretches of habitat containing few or no suitable leaves (Fig. 1). These subunits were the field station property (Station: total area = 1.50 ha), and two areas around the base of the only local hill, Cerro Tortuguero (Cerro1 and Cerro2: total areas = 3.27 and 0.92 ha, respectively). The size of the study area varied somewhat between years, due to land-clearing by local people, but the total area searched was similar between years (5.69 ha in 1998 and 5.63 ha in 1999). Each subunit consisted of a number of habitat types, including recently cleared areas where the majority of trees had been removed but which still contained considerable densities of herbs and shrubs, including *Heliconia* and *Calathea* (clearings; Cerro1 and Cerro2 only), secondary forest with a partial to complete canopy (mixed; Station and Cerro1), and the edge of primary forest with a closed canopy (forest; Cerro2; see Fig. 1). Forest to the north and west of the three subunits contained a low density of suitable leaves (<1 leaf/ha), and was not searched after an initial survey. Forest to the south of the Cerro2 subunit contained a similar density of leaves to the study area, but was separated from the main area by unsuitable habitat. This area was searched opportunistically for roosts ($N = 8$ searches), and never contained individuals captured in any of the three subunits regularly searched.

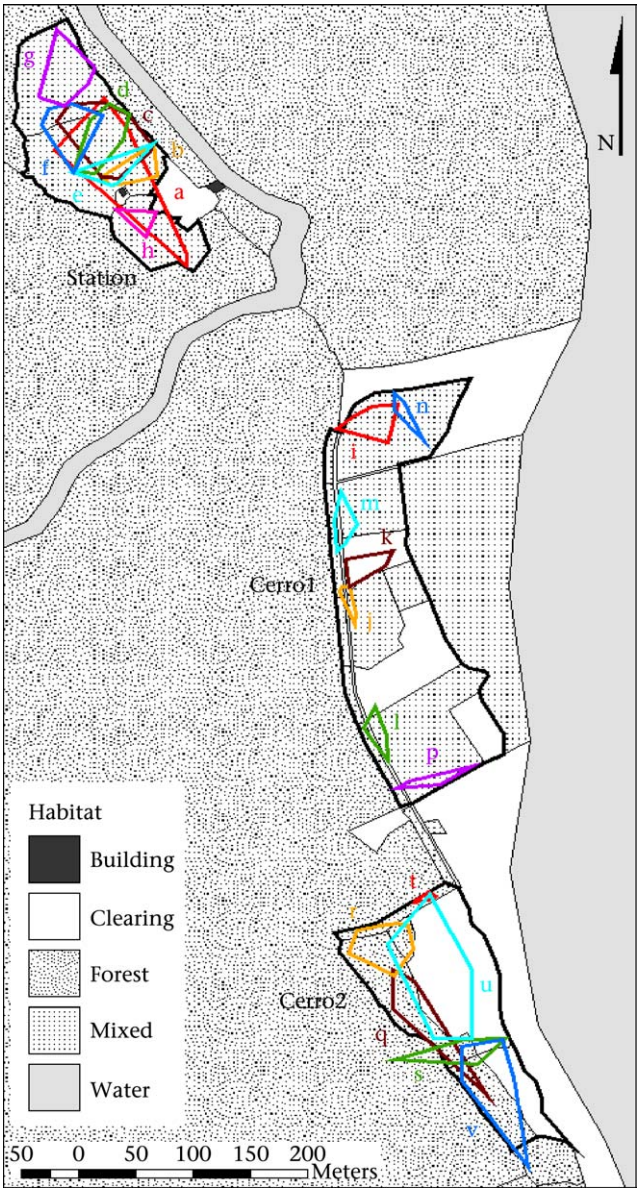


Figure 1. Map of the Caño Palma study area indicating different habitat types. Roosting home ranges (100% minimum convex polygons) for 21 social groups of *T. tricolor* in the Caño Palma study area are indicated in colour.

Roost Censuses

Two to six observers systematically searched subunits for suitable roosts. After a brief 3-week period of high-intensity searches, during which as many individuals as possible were captured and banded, censuses were reduced in frequency. Censuses of the study area took 3 days total, 1 day for each subunit, and each subunit was searched at intervals of greater than 1 week. This interval reflected a trade-off between accurately describing the behaviour of the bats, and both maintaining independence between subsequent captures and minimizing the stress of repeated captures. We performed 14 censuses, 10 in spring 1998, one in autumn 1998, and three in spring 1999. Suitable leaves were also checked opportunistically on an irregular basis while performing other field tasks throughout the study period. Censuses were typically carried out between 0700–1200 and 1300–1500 hours.

When we located potential roost leaves that were within reach (≤4 m high) we pinched the top of the leaf and directed any bats present into a plastic bag from which they were immediately transferred into a cloth holding bag. When we were unable to check leaves in this way (>4 m high), we gently shook the leaves to determine whether bats were present, but no bats were ever observed to roost in these leaves. Captured individuals were identified to species, sexed, and aged as adults or juveniles (young of the year) based on the degree of ossification of the metacarpal–phalange joints (Anthony 1988). Mass (to the nearest 0.25 g) and forearm length (in mm) were measured, and reproductive condition was assessed for all captured individuals (Racey 1988). All adults were marked with individually numbered split-ring plastic (in early

1998 only) or aluminium bands (1998 and 1999) on the forearm. Individuals were released directly outside their original roost immediately after processing to permit them to regroup, but they invariably flew to a new roost.

Patterns of Association

To describe social structure, we examined associations between individuals. Individuals were considered to be associating if they occupied the same leaf roost at the same time. Although presence in the same roost does not necessarily entail social interaction (Whitehead & Dufault 1999), the leaf roosts were small, and individuals were typically in contact with one another inside the roost (M. Vonhof, unpublished observation), suggesting that at least some interaction was taking place. A roosting group was defined as the individuals occupying a particular leaf roost on a given day.

We used the simple ratio association index (hereafter simple index) to describe associations between pairs of individuals (see Cairns & Schwager 1987; Ginsberg & Young 1992). The simple index is calculated for each pair of individuals as $X/(X + Y_{AB} + Y_A + Y_B)$, where X is the number of observation periods during which A and B were observed together, Y_{AB} is the number of observation periods during which A and B were both observed in separate groups, Y_A is the number of observation periods during which only A was observed, and Y_B is the number of observation periods during which only B was observed. Relative to other association indices (such as the half-weight or twice-weight indices; Cairns & Schwager 1987), the simple index is statistically unbiased (Ginsberg & Young 1992) and is more appropriate in situations where associations are determined by membership in the same group (Whitehead & Dufault 1999). The χ^2 index (Wilkinson 1985a), which can be used to discriminate between active associations versus passive habitat preferences, is not suitable for use with *T. tricolor* because it requires a finite population of roosts that individuals are able to use more than once. Our analyses were restricted to groups where all individuals had been captured, and within these, only individuals captured at least four times were included in the analyses, reflecting a compromise between including as many individuals as possible and accurately describing their social behaviour. Because no individuals were observed to move between subunits (Vonhof & Fenton, 2004), analyses were performed for each subunit independently. All analyses of associations were carried out using SocProg 1.3 (Whitehead 1999b; Whitehead & Dufault 1999).

We used average linkage cluster analysis to visualize patterns of association within each subunit. Based on the cluster analysis, individuals were considered to form a distinct social group if they clustered above an arbitrary value of 0.1. This value was chosen because it is above the mean association value within all subunits (Table 1), and it allowed us to minimize the inclusion of transient individuals or interactions while including weak but repeated associations. We summarized mean and maximum simple index values by sex class (male–male, female–female, male–female), and for all associations involving either males (m) or females (f). We then tested whether associations between same-sex pairs (m–m and f–f) were stronger than mixed-sex pairs (m–f and f–m) using a Mantel test, with significance determined using Mantel's approximate analytic solution (Schnell et al. 1985; Sokal & Rohlf 1995). We also calculated the average number of associates in a roosting group of the first sex belonging to a member of the second sex for each sex class (e.g. for the m–f class, the average number of females found roosting with a particular male; for m–m, the average number of males found roosting with a particular male; for m, the average number of bats of both sexes roosting with a particular male, etc.). The average number of associates was calculated using both restricted (captured ≥ 4 times) and unrestricted data (captured any number of times).

Temporal Scale of Associations

We analysed two measures of the temporal stability of associations following Whitehead (1995). The lagged association rate is the probability that if two animals are associating now, they will still be associated at various time intervals (lags) later, and thus, it measures the rate of persistence of associations over a range of time periods. The intermediate association rate quantifies the consistency of relationships over various time lags, and is defined as an estimate of the probability that individuals remain associated between their first and last identification together. It is calculated by examining whether associations remain stable over the time period between each census and either the first or last recorded association, whichever is closest in time to the census in question. If individuals do not disassociate between observed associations, the intermediate association rate will approach 1.0 across all time lags (the individuals always remain together). Conversely, if long-term associations are characterized by periods of separation, the intermediate rate will be similar to the lagged association rate. These measures of temporal stability were compared to the null association rate, which is the expected value of the lagged association rate if there is no preferred association, given the capture histories of the individuals and the number of associations of each individual in each sampling period.

Lagged association rates were calculated for all individuals combined, and for each sex class separately. The intermediate association rate is data intensive, and was only calculated for the total pool of individuals (all sex classes combined). Both analyses are less sensitive to low recapture rates but are more sensitive to missing individuals, and therefore, we included all captures of all individuals across all three subunits with no restrictions on the number of captures. Lagged, intermediate and null association rates were then plotted continuously against time lag using a 100-data-point moving average. In addition, to describe the patterns of change in lagged association rates over time and to estimate the average length of association, we fitted exponential decay models to the lagged association rates as in Whitehead (1995). Models were fitted for all data combined, and each sex

Table 1. Mean and maximum simple index of association values (±SD) and mean number of associates (±SD) within and between different sex classes

			Mean number of associates (SD)	
Sex class	Mean association (SD)	Maximum association (SD)	Restricted*	Unrestricted†
Station				
m	0.10 (0.07)	0.77 (0.24)	3.62 (2.53)	3.71 (1.13)
m–m	0.11 (0.11)	0.61 (0.35)	1.92 (1.80)	2.26 (1.50)
m–f	0.09 (0.06)	0.60 (0.39)	1.70 (1.09)	1.45 (0.71)
f	0.08 (0.06)	0.73 (0.28)	3.00 (2.00)	3.04 (1.03)
f–f	0.08 (0.04)	0.69 (0.31)	1.39 (0.76)	1.07 (0.68)
f–m	0.09 (0.09)	0.68 (0.29)	1.61 (1.66)	1.96 (1.07)
Combined	0.09 (0.06)	0.75 (0.26)	3.30 (2.26)	3.42 (1.12)
Cerro1				
m	0.10 (0.02)	0.91 (0.14)	2.50 (0.64)	2.82 (1.28)
m–m	0.08 (0.06)	0.56 (0.39)	0.85 (0.58)	1.48 (0.97)
m–f	0.10 (0.03)	0.88 (0.18)	1.66 (0.47)	1.35 (0.82)
f	0.08 (0.04)	0.81 (0.30)	1.98 (1.10)	2.89 (1.12)
f–f	0.06 (0.03)	0.70 (0.30)	0.85 (0.52)	0.96 (0.63)
f–m	0.10 (0.08)	0.72 (0.39)	1.14 (0.85)	1.93 (0.86)
Combined	0.08 (0.04)	0.85 (0.25)	2.20 (0.96)	2.85 (1.21)
Cerro2				
m	0.09 (0.03)	0.79 (0.20)	3.01 (1.05)	3.14 (1.19)
m–m	0.09 (0.04)	0.69 (0.25)	1.78 (0.78)	1.81 (0.92)
m–f	0.09 (0.04)	0.60 (0.36)	1.23 (0.60)	1.34 (0.69)
f	0.08 (0.03)	0.80 (0.17)	2.74 (1.12)	2.64 (1.04)
f–f	0.06 (0.03)	0.63 (0.20)	0.81 (0.44)	0.97 (0.41)
f–m	0.09 (0.05)	0.74 (0.25)	1.93 (1.07)	1.67 (1.03)
Combined	0.08 (0.03)	0.80 (0.18)	2.91 (1.07)	2.92 (1.15)

*Includes data only for individuals captured on four or more occasions.
†Includes data for all individuals captured.

class separately, using maximum likelihood and binomial loss to select the best-fitting model (Whitehead 1999b). Standard errors of the lagged association rate were estimated by jackknifing (Sokal & Rohlf 1995) over 30-day periods. All models were of the form: $a \times e^{(-b \times \text{time lag})}$, where the units for parameter b are 1/day. Using these models, we calculated the average length of association between individuals in long-term associations using the expression $1/(0.5 \times b)$, which is expressed as the number of days over which one departure event is expected.

Roosting Home Range

We calculated the roosting home range, the geographical extent of all roost sites used by an individual, for individual bats with the 100% minimum convex polygon (MCP) method (White & Garrott 1990) using the program Calhome. MCP is the only method available when sample sizes are small (Harris et al. 1990). Only individuals for which at least four roost locations (range 4–14, $\overline{X} = 5.6$) were located were included. Roosting home ranges were also calculated for the social groups of bats delineated in the cluster analyses of association indices using the same method. Group O was excluded from the analyses because one of the four roosts used by this group was not mapped. Home range overlap between groups was examined by plotting the home range polygons in ArcView 3.2 and manually calculating the degree of overlap, defined as the percentage shared of the total combined areas of the two respective home ranges. Centroids of group home ranges were located using the gravity barycentre method in ArcView 3.2, which takes into account the shape of the polygon rather than simply computing the geographical centre. Differences between sexes in individual roosting home range size were analysed using a Kruskal–Wallis test. To determine whether group roosting home ranges differed between subunits, we used ANCOVA, with the number of locations as a covariate. The size of the MCP typically increases with increasing sample size, making home range estimates based on different sample sizes difficult to compare (White & Garrott 1990). To examine whether sample size affected the accuracy and comparability of our results, we plotted group roosting home range size as a function of sample size.

RESULTS

We found 255 roosts and made 927 captures of 308 adults (173 males, 135 females), as well as 28 juveniles, during the two field seasons at Caño Palma. The sex ratios within roosting groups and the sex ratio of our study population as a whole are slightly but significantly male-biased

(Vonhof & Fenton, 2004). Four juveniles captured in May 1998 were banded as adults in 1999, based on comparison of microsatellite genotypes of membrane samples between years (M. Vonhof, unpublished observation). Individuals were captured between one and 14 times, but overall, 66.8% of individuals (44% in the Station subunit, 82% in Cerro1 and 40% in Cerro2) were captured fewer than four times (Fig. 2).

Patterns of Association

In all subunits, small numbers of individuals were strongly associated, whereas the majority of pairs had simple index values of zero, indicating that they never associated during the course of our study (Fig. 3). Consequently, mean simple index values were low for each sex class within each subunit (Table 1). Individuals formed relatively strong associations with members of both sexes; maximum simple index values were relatively high for all sex classes (Table 1), and simple index values between same-sex pairs were not significantly different from mixed-sex pairs in any subunit (Mantel tests: Station: $t = -0.25$, $P = 0.60$, $r = 0.009$; Cerro1: $t = -1.44$, $P = 0.08$, $r = -0.077$; Cerro2: $t = -0.46$, $P = 0.32$, $r = -0.19$). Among those individuals captured at least four times, the number of associates of either sex averaged 2.9–3.4 (Table 1). Both males and females tended to associate with a greater number of males than females, although there was considerable variation within and between subunits (Table 1). Patterns were similar when the restriction on the number of captures was removed (Table 1), indicating that there was no sex bias among individuals not included in our analyses.

Cluster analysis of pairwise simple index values revealed that, within subunits, populations of *T. tricolor* were clearly differentiated into distinct social groups that rarely, if ever, interacted with one another (Fig. 4). Because of the obvious nonrandom pattern of associations between individuals, permutation tests such as those described by Bejder et al. (1998) and Whitehead (1999a) were redundant, and therefore, were not performed. The 22 social groups identified ranged in size from one to nine ($\overline{X} \pm \mathrm{SD} = 4.6 \pm 2.18$) individuals, and were typically composed of both males and females, with only one unisex group observed (group A; Table 2). However, social groups clearly differed in their cohesiveness, with considerable variation between groups in mean association index values (Table 2; see Fig. 4). All members of a social group rarely occupied the same roost at the same time, and roosting group sizes were significantly smaller than the overall size of the social group (Table 2). Furthermore, within groups, some individuals associated closely, whereas others rarely or never associated with one another (Fig. 4). For example, dyads within two social groups

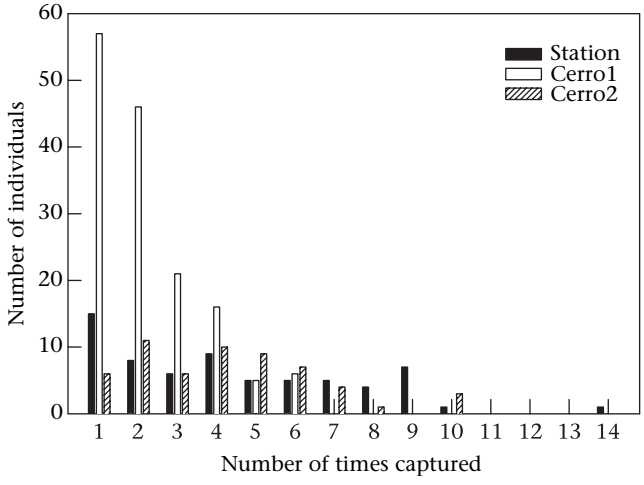


Figure 2. Distribution of the number of times *T. tricolor* individuals were captured in 1998–1999.

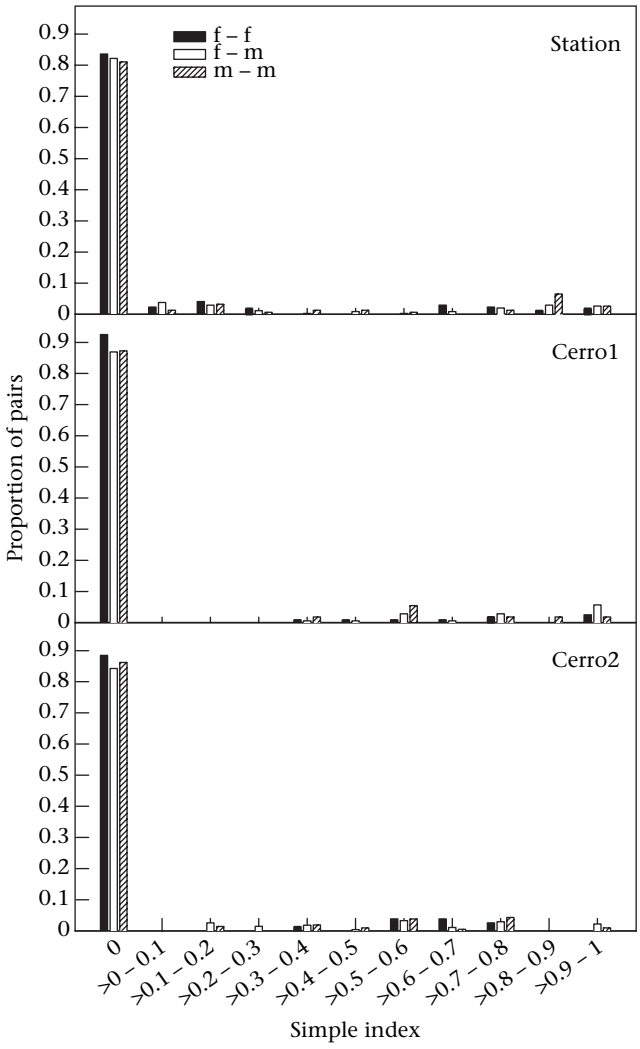
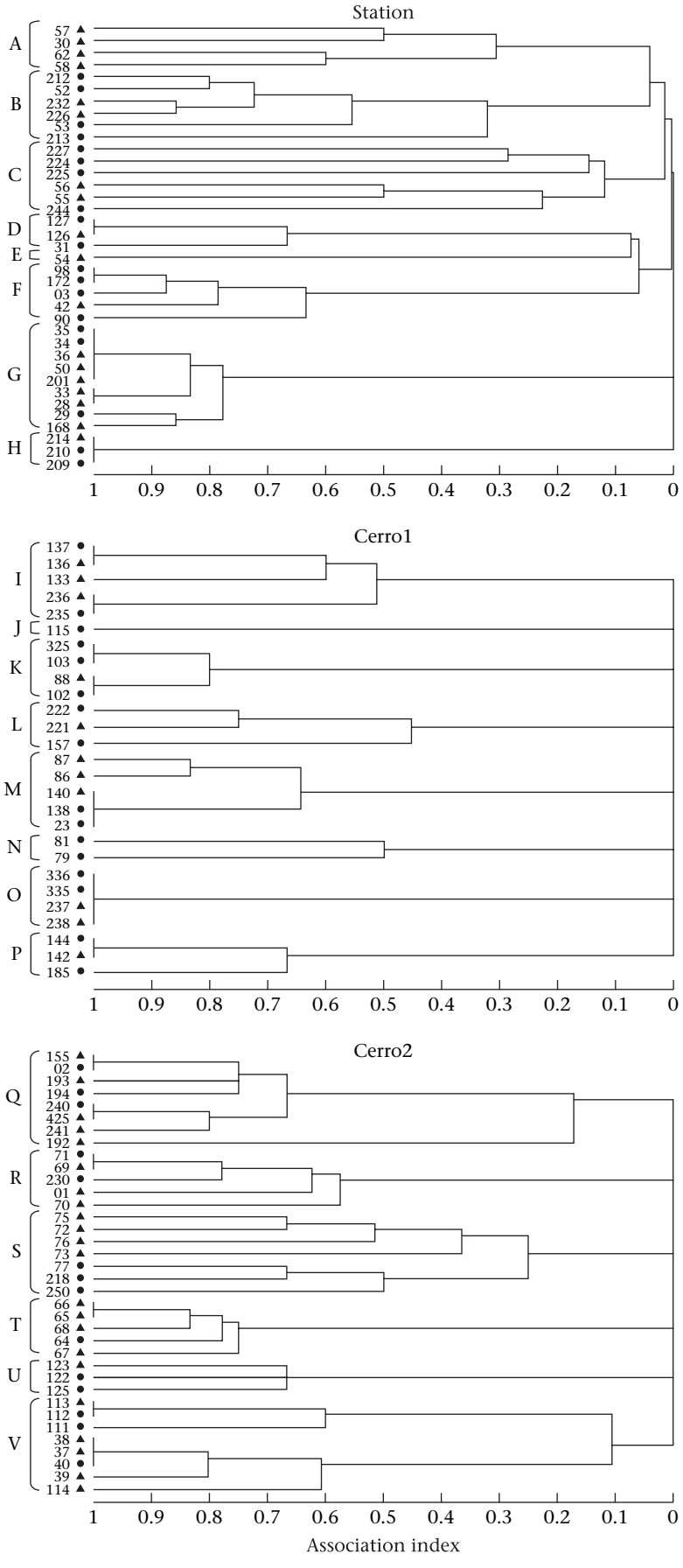


Figure 3. Distribution of pairwise simple ratio association index (simple index) values in *T. tricolor* by sex class and subunit.

Figure 4. Cluster diagram of simple ratio association index (simple index) values for individuals in the Station, Cerro1 and Cerro2 subunits. Individuals with association values greater than 0.1 were considered to belong to the same social group, and are denoted by brackets. The sex of individuals is denoted by triangles for males and circles for females.


Station
A
57
30
62
58
B
212
52
232
226
53
C
213
227
224
225
56
55
244
D
127
126
E
31
54
F
98
172
03
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90
G
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201
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214
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Cerro1
I
137
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Cerro2
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425
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250
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1 0.9 0.8 0.7 0.6 0.5 0.4 0.3 0.2 0.1 0
Association index

Table 2. Size and composition of social and roosting groups, mean association within social groups, and group roosting home range size for the 22 social groups of *T. tricolor* identified at Caño Palma including individuals captured on four or more occasions

		Number of			Social group members/roosting group			
Group	Total size	Males	Females	Mean ± SD association index (range)	Mean ± SD number (range)	Mean proportion	Number of roosts	Group home range size (ha)
Station								
A	4	4	0	0.39 ± 0.146 (0.2–0.6)	2.0 ± 1.00 (1–4)	0.50	9	0.616
B	6	2	4	0.56 ± 0.210 (0.2–0.86)	3.3 ± 2.09 (1–6)	0.54	15	0.099
C	6	2	4	0.18 ± 0.133 (0–0.5)	1.7 ± 0.89 (1–4)	0.28	18	0.376
D	3	1	2	0.78 ± 0.191 (0.67–1)	2.6 ± 0.53 (2–3)	0.86	7	0.179
E	1	1	0	—	—	—	5	0.094
F	5	1	4	0.77 ± 0.137 (0.57–1)	4.0 ± 1.05 (2–5)	0.80	10	0.190
G	9	6	3	0.86 ± 0.105 (0.71–1)	6.5 ± 2.98 (2–9)	0.71	11	0.197
H	3	1	2	1.00 ± 0.000 (1)	3.0 ± 0.00 (3)	1	4	0.041
Cerro1								
I	5	3	2	0.63 ± 0.226 (0.33–1)	3.3 ± 1.63 (1–5)	0.67	6	0.110
J	1	0	1	—	—	—	5	0.022
K	4	1	3	0.87 ± 0.103 (0.8–1)	3.5 ± 0.84 (2–4)	0.88	6	0.070
L	3	1	2	0.55 ± 0.180 (0.4–0.75)	2.2 ± 0.98 (1–3)	0.72	6	0.049
M	5	3	2	0.77 ± 0.180 (0.57–1)	4.1 ± 1.21 (2–5)	0.83	7	0.062
N	2	0	2	0.50 ± 0.000 (0.5)	1.5 ± 0.55 (1–2)	0.75	5	0.029
O	4	2	2	1.00 ± 0.000 (1)	4.0 ± 0.00 (4)	1	4	—
P	3	1	2	0.78 ± 0.191 (0.67–1)	2.4 ± 0.89 (1–3)	0.8	5	0.038
Cerro2								
Q	8	5	3	0.59 ± 0.282 (0–1)	4.1 ± 2.23 (1–7)	0.51	9	0.222
R	5	3	2	0.67 ± 0.144 (0.55–1)	3.4 ± 1.61 (1–5)	0.68	13	0.190
S	7	4	3	0.36 ± 0.175 (0.13–0.67)	3.3 ± 1.58 (1–6)	0.47	10	0.124
T	5	4	1	0.80 ± 0.103 (0.67–1)	4.5 ± 0.55 (4–5)	0.9	6	0.007
U	3	1	2	0.67 ± 0.000 (0.67)	2.4 ± 0.53 (2–3)	0.81	7	0.621
V	8	5	3	0.41 ± 0.377 (0–1)	3.8 ± 1.29 (2–5)	0.47	12	0.338
Overall								
Mean	4.5	2.3	2.2	0.66	3.3	0.71	8.2	0.175
SD	2.18	1.73	1.11	0.218	1.15	0.193	3.75	0.1778

(H and O) were always found together, whereas members of dyads in some other social groups (groups C and S, in particular) never spent more than 70% of their time with any particular social group member, and a number of individuals in the social group were never captured together.

Members of social groups in subunits Cerro1 and Cerro2 never associated with members of other social groups, and group membership was apparently closed (Fig. 4). However, in the Station subunit, individuals from select groups associated with one another on a few occasions (Fig. 4). On one occasion in spring 1998, two members of group A roosted with five members of group B and one member of group C. On a separate occasion, an entirely different subset of individuals from groups B and C (one and two individuals, respectively) roosted together. However, each of these groups was behaviourally isolated both before and after these mixing events. Similarly, the sole member of group E (54), which was an offspring of a member of group B (52, Vonhof 2001), roosted together with another member of group B (53) on four of the five occasions each bat was captured. This individual was found with bats from groups D and F only once in late spring 1999. Lastly, in spring 1999, four members of group F roosted with two members of group D. Later in the session, two members each of groups D and F and the sole member of group E roosted together.

Social groups typically included a number of individuals (range 0–8) not included in association analyses because they were captured on fewer than four occasions (Table 3). An average roost occupied by members of a social group included a mean of one of these individuals, ranging from zero to six individuals (Table 3), with the highest numbers in Cerro1, where the greatest proportion of individuals were excluded from association analyses. In no case was any individual captured on three or fewer occasions ever found to associate with members of more than one social group, indicating that their exclusion from the analyses was not likely to be a result of differing behaviour or social strategies. Instead, their exclusion was typically a result of appearance or disappearance at some point during the study. Thirty-six of the 73 individuals (49.3%) were found in spring 1998 only, and disappeared by autumn 1998. Fourteen individuals (19.2%) appeared for the first time in autumn 1998, and another 14 (19.2%) appeared in spring 1999. Five individuals (6.8%) were present in both spring and autumn 1998, but were not captured in 1999. Only four individuals (5.5%) were captured in both years. When we counted individuals captured three or fewer times as belonging to the social groups, then sizes of social groups

Table 3. Number of unrestricted individuals (captured on <4 occasions) in each social group, the mean (±SD) number per roosting group and total social group size incorporating unrestricted individuals

Social group	Number of unrestricted individuals: In each social group (males, females)	Number of unrestricted individuals: Mean±SD/ roosting group (range)	Total group size
Station			
A	4 (0, 4)	1.3±2.18 (0–4)	8
B	0	0.3±0.46 (0–1)	6
C	5 (2, 3)	0.4±0.60 (0–2)	11
D	1 (1, 0)	0.6±0.98 (0–2)	4
E	0	0.4±0.89 (0–2)	1
F	1 (1, 0)	0.5±0.85 (0–2)	6
G	2 (1, 1)	0.5±0.93 (0–2)	11
H	4 (2, 2)	2.5±1.29 (1–4)	7
Cerro1			
I	4 (2, 2)	1.5±1.22 (0–3)	9
J	7 (4, 3)	2.4±2.07 (0–5)	8
K	5 (3, 2)	1.3±0.82 (0–2)	9
L	4 (2, 2)	1.3±1.51 (0–3)	7
M	2 (2, 0)	0.3±0.49 (0–1)	7
N	7 (7, 0)	2.5±2.07 (0–5)	9
O	0	0.0±0.00 (0)	4
P	8 (6, 2)	3.4±1.67 (2–6)	11
Cerro2			
Q	0	0.0±0.00 (0)	8
R	2 (0, 2)	0.3±0.75 (0–2)	7
S	7 (2, 5)	1.2±1.19 (0–4)	14
T	2 (2, 0)	0.7±1.03 (0–2)	7
U	3 (2, 1)	0.9±0.69 (0–2)	6
V	5 (1, 4)	0.8±1.11 (0–3)	13
Overall			
Mean	3.3	1.1	7.9
SD	2.53	0.92	3.00

ranged from one to 14 ($\overline{X}\pm\text{SD} = 7.8\pm3.02$) individuals (Table 3).

To determine whether the repeated captures involved in our census methods influenced the strength of associations, we tested for an association between the simple index values and total number of captures for each dyad (the sum of captures for both individuals) within all social groups (when sample sizes allowed, $N = 14$ of 22 groups) using Mantel tests. The number of captures did not significantly influence the simple index values in any social group (NS in all cases).

Temporal Scale of Associations

The observed lagged and intermediate association rates for all individuals combined (Fig. 5), as well as each sex class (Fig. 6), were well above the null association rate for all time lags, indicating that there were preferred associations at all timescales over all sex classes. This result was consistent when the null association rate was calculated by subunit rather than for the overall population (data not shown). In any roosting group, the majority (~85%) of individuals were likely to remain associated over short to moderate time lags of up to 100 days (Fig. 5). Conversely, there was a small proportion (~15%) of individuals that spent short periods as brief as 1 day associating with the individuals that they had been captured with (Fig. 5). Approximately 40–45% of associated individuals maintained preferred associations over longer time lags of 150–420 days (Fig. 5). However, the intermediate association rate followed, but was slightly higher than, the lagged association rate, indicating that, although there were preferred associations at all time lags, individuals regularly spent short periods apart from long-term companions. Similar patterns of temporal persistence of associations were observed when the different sex classes were analysed independently (Fig. 6). Although there was a tendency for same-sex pairs, and particularly f–f pairs, to have a higher probability of remaining together over

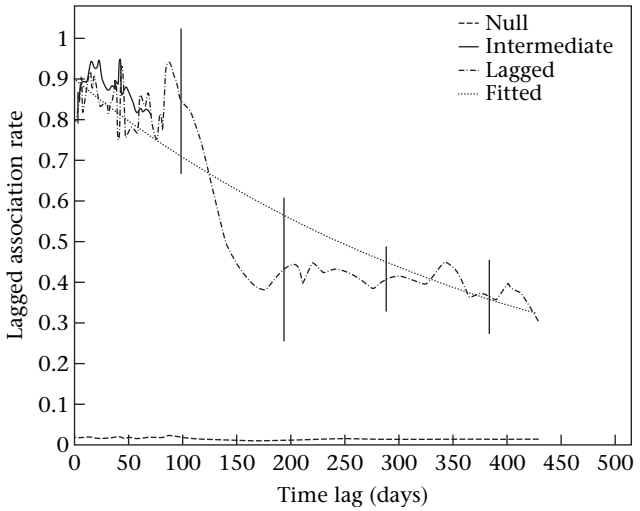

Figure 5. Lagged, intermediate and null association rates, and the fitted model to the lagged association rate, using unrestricted data across all subunits. Standard errors were calculated by jackknifing over 30-day periods.

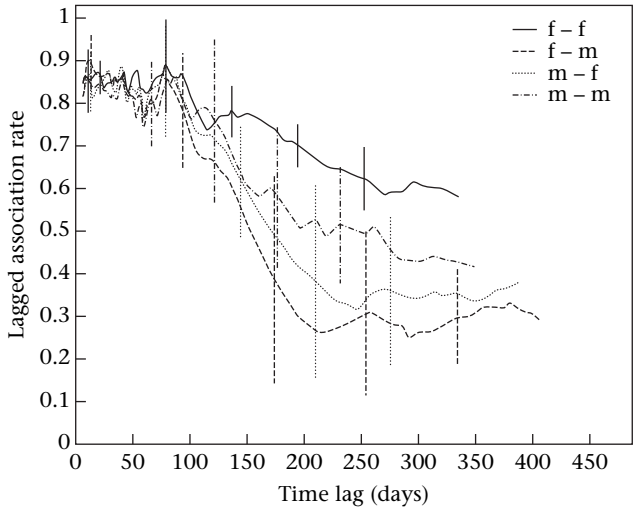

Figure 6. Lagged association rates for each sex class. Standard errors were calculated by jackknifing over 30-day periods.

Table 4. Results of model fitting procedure on lagged association rates

Sex class	Parameter *a* (SE)	Parameter *b* (SE)	Average length of association (days)
m−m	0.8750 (0.0495)	0.0022 (0.0006)	909
m−f	0.9001 (0.0354)	0.0025 (0.0006)	800
f−m	0.9239 (0.0260)	0.0032 (0.0008)	625
f−f	0.8903 (0.0122)	0.0014 (0.0002)	1429
Combined	0.8973 (0.0213)	0.0024 (0.0004)	833

All models are of the form: $a \times e^{(-b \times \text{time lag})}$, where the units for parameter *b* are 1/day. Standard errors were computed by jackknifing over 30-day periods. Based on the models, the average departure rate for individuals in long-term associations was calculated using the expression $1/(0.5 \times b)$, and is expressed as the number of days over which one departure event is expected.

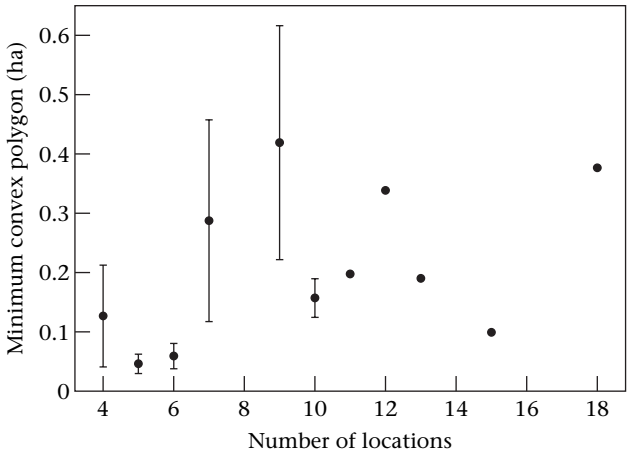

Figure 7. The relationship between mean (±SE) group roosting home range size and sample size.

longer time lags, this result was not significant, because the lagged association rates for each sex class were associated with large standard errors (Fig. 6).

Models fitted to the lagged association rate data for all individuals combined and each sex class separately described a pattern of casual acquaintances and rapid disassociation, reflecting the fact that a small proportion of individuals interacted with other members of the same social group (or very rarely different social groups; see above) for brief periods, but also maintained long-term associations with select members of their social group (Table 4). Extrapolating from the fitted models, the average period of time that individuals in long-term associations may continue to roost together typically extends for periods of approximately 2 years or more. The estimated average length of association for f−f pairs (3.9 years) was noticeably, but not significantly greater than that for other sex classes (because of large standard errors associated with the lagged association rate; see Figs 5−6), which ranged from 2.5 years for m−m pairs, to 1.7−2.2 years for mixed-sex pairs (Table 4).

Group Roosting Home Ranges

Individual roosting home ranges were small for both females (100% MCPs: $\overline{X} \pm \text{SD} = 0.12 \pm 0.127$ ha, range 0.001−0.621 ha, $N = 49$) and males (0.11 ± 0.101 ha, 0.001−0.502 ha, $N = 53$). Individual roosting home range size did not differ between sexes (Kruskal−Wallis test: $\chi^2_1 = 0.06$, $P = 0.93$). Combined roosting home ranges for social groups were also small, ranging from 0.007 to 0.62 ha, with an overall mean of 0.18 ± 0.178 ha ($N = 21$). Group roosting home range size did not differ significantly between subunits when we accounted for differences in sample size (ANCOVA: $F_{2,17} = 1.28$, $P = 0.30$; Station: 0.22 ± 0.188 ha, $N = 8$; Cerro1: 0.05 ± 0.030 ha, $N = 7$; Cerro2: 0.25 ± 0.212 ha, $N = 6$). Although MCP size increased with increasing sample size, home range sizes were similar across all sample sizes, and the largest home ranges were associated with moderate sample sizes (Fig. 7). Almost half of all possible pairs of group roosting home ranges overlapped in both the Station and Cerro2 subunits (Station: 14 of 28 possible pairs; Cerro2: 7 of 15 pairs; Fig. 1), but the degree of overlap between adjacent home ranges was typically small ($\overline{X} \pm$SD: Station: $16 \pm 12.1\%$, range 0.1−38.8%; Cerro2: $6 \pm 4.4\%$, range 0.3−8.5%). However, the measure of overlap is influenced by the difference in home range size, and overlap values increased when we calculated the proportion of the smaller home range that overlapped with the larger home range for all overlapping pairs of home ranges (Station: $54 \pm 30.2\%$, range 0.1−92.3%; Cerro2: $22 \pm 12.9\%$, range 0.7−38.6%; Fig. 1). Average distances between group roosting home range centroids were small among all groups (Station: 56.5 ± 35.65 m, range 3.5−154.7 m; Cerro2: 96.1 ± 47.38 m, range 40.2−192.8 m) and among groups with overlapping roosting home ranges (Station: 31.0 ± 16.59, range 3.5−58.5 m; Cerro2: 61.2 ± 18.74, range 40.2−87.5 m). In contrast, only two group roosting home ranges overlapped in the Cerro1 subunit, and then only marginally (groups I and N, 1.4%; Fig. 1), but our recapture rate in this subunit was low (only 18% of individuals were captured >4 times; see above) relative to the others. An unknown number of groups were probably not included in the analyses, and thus, the lack of overlap most likely represents an artefact of low sample sizes in this subunit.

DISCUSSION

Environmental Influences on Social Organization

Based on the high density of available habitat and bats in our study area, and the transient nature of the rolled leaves in which they roost, we predicted that *T. tricolor* would show a fluid social organization, with extensive mixing of individuals in the population and labile roosting-group composition. However, we observed that *T. tricolor* of both sexes maintained close associations in clearly defined social groups within small roosting home ranges ($\overline{X} = 0.2$ ha). The vast majority of individuals in the population never associated with one another, and individuals had a small number of regular associates of both sexes. Associations within social groups were typically

stable across all sex classes, with approximately 85% of dyads remaining together over short periods (up to 100 days), over 40% of individuals remaining together over longer periods of up to 420 days, and some dyads potentially persisting for up to 4 years or more. Within subunits, social groups were not spatially isolated from one another, as there was considerable home range overlap between groups and short distances between home range centroids, yet interactions between members of different social groups while roosting were exceedingly rare.

We suggest two possible reasons why *T. tricolor* formed stable mixed-sex groups. First, the close patterns of association among group members in spite of overwhelming habitat availability and close proximity to other social groups suggest that passive benefits alone are unlikely to explain the formation of groups in *T. tricolor*. Instead, individuals within social groups may actively maintain associations with other group members, although it is presently unclear what the active benefits of association group members may receive. *Thyroptera tricolor* is insectivorous, thus, reciprocal food sharing (Wilkinson 1985a) and coordinated foraging (Packer & Ruttan 1988; Wilkinson & Boughman 1998) are unlikely. We have limited observations on light-tagged roosting groups that suggest that individuals in social groups may maintain contact while foraging (M. Vonhof, unpublished observation), but whether groups of *T. tricolor* defend group-foraging territories, as has been observed for some other tropical bat species (Bradbury & Vehrencamp 1976), remains to be determined. Documenting other active benefits, such as social learning (Johnston 1997), communal nursing (McCracken 1984; Wilkinson 1992a) or information transfer (Wilkinson 1992b; but see Kerth et al. 2001), would require observations currently not feasible given the lifestyle and small size of *T. tricolor*. Nevertheless, the presence of closely related individuals within roosts would support an argument for active benefits based on kin selection.

Second, the abundance of available habitat at Caño Palma may be temporary. If a more patchy distribution and lower density of plants is the norm, or if the density of plants varies over short timescales, then the bats may simply not respond behaviourally to a temporary increase in habitat abundance following disturbance. For example, we observed a significant decrease in the density of leaves and roosting bats between the 2 years of our study (Vonhof & Fenton 2004), as well as considerable changes in the quality of habitat as new openings were created or became overgrown. Over the long term, in the context of a spatially and temporally heterogeneous environment, individuals (and groups) may ensure a long-term supply of roosts by remaining faithful to a habitat patch that provides a consistent supply of roosts, the suitability of which is likely to be determined by the lower limit of plant density. Findley & Wilson (1974) found much lower densities of plants and bats at their field site in southwestern Costa Rica than we found at Caño Palma, yet also observed mixed-sex groups of *T. tricolor* roosting in small sections of habitat that were stable over their 2-week study.

Roosting in rolled leaves appears to have evolved independently from *T. tricolor* in two bat species in the distantly related family Vespertilionidae, but these species have social systems in which interactions between males and females are limited to mating activities, and in which males rarely associate with one another. In Gabon, *Myotis bocagei* roost in rolled leaves distributed in discrete patches of banana plants, and single males roost with two to seven females in year-round harems (Brosset 1976). Turnover of both males and females is highly variable, but individuals of both sexes have been observed to remain in the same group for 3 years or more. In Malawi, *Pipistrellus nanus* roost in rolled leaves in isolated banana plantations but do not form stable harems; instead they show a seasonal, promiscuous mating system in which single (or rarely two) males occupy leaves in closely spaced clumps of banana plants that are visited consecutively by groups of females (Happold & Happold 1996). During parturition and lactation, males show fidelity to the same clump of banana plants that they use for mating, but typically roost alone, whereas females regularly move between clumps and roost in labile groups with other females.

The difference in social structure among the three species of bats roosting in rolled leaves may be related to differences in the availability and permanency of the habitat. Banana leaves may be available for up to 3 days (Brosset 1976; Happold & Happold 1996), possibly making them more defensible than *Heliconia* or *Calathea* leaves, which are available for 1 day only (Vonhof & Fenton 2004). In Gabon, the distribution of banana plants is extremely patchy, with up to a kilometre between clumps of plants (Brosset 1976), and thus, both males and females are probably restricted to distinct patches of habitat. Increasing habitat patchiness may enable males to defend habitat features or a group of females using a particular habitat (Clutton-Brock 1989), and therefore, the existence of year-round polygynous mating groups in *M. bocagei* may be related to the extremely patchy nature of the habitat. Male *P. nanus* in Malawi occupy and appear to defend successive leaves within individual clumps of banana plants, but clumps are closely spaced, and females are free to move between males in different clumps (Happold & Happold 1996). Male territoriality and promiscuous mating probably reflect the inability of males to prevent females from visiting other nearby males. These systems contrast significantly with what we found for *T. tricolor*, in which leaves are available for an extremely short duration, but are evenly and abundantly distributed.

Variation in the Strength of Association within Groups

The majority of individuals in social groups maintained long-term associations. However, based on analyses of lagged association rates and their fitted models, there was a small proportion (~15%) of individuals that spent only short periods associating with the individuals that they had been captured with. Furthermore, intermediate association rates indicated that even among long-term

associations, individuals often disassociated for short periods. These observations probably reflect the fact that not all members of each social group were together during each census, with averages of 28–100% (overall $\overline{X} = 71\%$) of social group members roosting together on a given day. Within social groups, individuals typically associated with all other individuals, but formed associations of differing strengths among them, and rarely formed perfect associations. O'Donnell (2000) found that *Chalinolobus tuberculatus* roosting in trees in New Zealand could be differentiated into three distinct social groups, but bats belonging to each group were spread over a number of roosts each day. Similarly, female *Myotis bechsteinii* roosting in bat boxes in Germany formed socially and genetically closed social units that frequently split into subgroups that occupied different roosts (Kerth & König 1999; Kerth et al. 2000).

The fission–fusion nature of these societies challenges the traditional definition of the term 'bat colony', which is typically used to refer to individuals occupying a roost at the same time (Bradbury 1977b). The results from this study, Kerth & König (1999) and O'Donnell (2000) indicate that this static definition of social groups based on roost occupancy may not apply to all bat species, and that the functional social unit may be broader than the individuals found in a given roost on any day. Therefore, definitions of bat colonies based on relative levels of interaction (e.g. Burland & Worthington Wilmer 2001) may be much more appropriate. The idea that networks of social relationships may exist raises questions about the benefit of maintaining these associations, and whether cooperative behaviours, if they occur, are apportioned with respect to strength of association among social group members. From a conservation perspective, if social units are spread among a number of habitat features, then it is clear that larger numbers of those features must be protected, and thus, a greater amount of habitat is required to allow for the conservation of multiple social units.

A Novel Social Organization?

Long-term interactions between both males and females and the overlap of mixed-sex social groups in space is exceedingly rare among bats specifically and other mammals in general. In some temperate bat species, males roost in maternity colonies, but they are typically spatially separated from the females within the roosts, and during migration or hibernation, mate only with members of other colonies (e.g. Petri et al. 1997; Entwistle et al. 2000; Burland et al. 2001). The social systems of the majority of bats (and other mammals) described so far are characterized by the formation of seasonal or year-round polygynous mating groups, where a limited number of males are found with a group of females for the purpose of mating (McCracken & Wilkinson 2000). Males and females may resist intrusion by members of the same or opposite sex, and thus defend roosting sites and possibly also feeding areas. Although females in these groups may form highly stable, long-term associations (see references in McCracken & Wilkinson 2000), associations between males and females are typically limited to the breeding tenure of the males, and intense competition for breeding status probably prevents long-term associations between males or between males and females (e.g. Wilkinson 1985a, b; Williams 1986; McWilliam 1988). Other mixed-sex groupings are found in several species of flying foxes that display lek mating systems in which males establish nocturnal display sites away from mixed-sex daytime roost sites (Brosset 1966; Wickler & Seibt 1976; Bradbury 1977a). However, there is no evidence of stable associations between members of either sex in these species.

Only one study has provided evidence of stable, mixed-sex groups not associated with mating in a bat species. O'Donnell (2000) showed that a population of *Chalinolobus tuberculatus* roosting in trees in New Zealand could be divided into three discrete groups of 166–234 individuals containing both males and females. Although social groups were delineated only on the basis of interactions between reproductive females, and males were significantly more likely to transfer between social groups, it was clear that both sexes regularly interacted within these social groups. Like *T. tricolor*, these bats switch roosts nearly every day, and not all group members are found together in a roost on a given day. However, unlike *T. tricolor*, groups of *C. tuberculatus* are very large and use exclusive roosting home ranges. Clear differences in group size, space use, and the nature of associations between males and females between these two species suggest that their social systems are not equivalent.

In mammals other than bats, stable, mixed-sex groups not associated with mating are rare outside of cooperatively breeding species. Several cebid (squirrel and spider monkeys) and cercopithecine (talapoins) primates form multimale and female social units that superficially resemble social groups in *T. tricolor* (long-term associations between all sex classes and formation of subgroups), but these primate societies differ in a number of respects. Interactions between males and females in these primate social groups are dominated by behaviours associated with mating or ensuring mating access, and linear dominance hierarchies and/or coalitions among same-sex individuals are the norm (Melnick & Pearl 1987; Robinson & Janson 1987), neither of which appears to be the case in *T. tricolor*. Furthermore, home ranges in primates are typically exclusive, although squirrel monkey groups may coalesce into large aggregations for extended periods (Baldwin & Baldwin 1981), whereas spider monkeys and talapoins vigorously defend territories (Melnick & Pearl 1987; Robinson & Janson 1987), neither of which resembles the rare contact and yet extensive spatial overlap observed between groups of *T. tricolor*.

The system of stable relationships involving all sex classes and overlapping home ranges of *T. tricolor* most closely resembles the social organization of some cetaceans (e.g. *Orcinus orca*, Bigg et al. 1990; *Globicephala melas*, Amos et al. 1993). These species form highly cohesive social groups that overlap in space and consist of matrilines with retention of offspring of both sexes. Mating between members of different matrilines is thought to occur either when groups come together for

short periods, or during short periods when males leave their natal pod in search of mates. However, at least in killer whales, cooperative behaviours such as coordinated foraging, alloparenting and group defence of offspring provide obvious benefits for maintaining associations (Bigg et al. 1990; Baird & Dill 1996), whereas any active benefits of grouping for *T. tricolor* are unclear at this point (see above).

The stable, mixed-sex groups, male-biased sex ratio, variable roosting group composition and lack of bachelor groups or seasonal patterns in sex ratio within roosting groups observed for *T. tricolor* (see also Vonhof & Fenton 2004) argue against a year-round, socially polygynous mating system. Given the density of available leaves and overlapping use of habitat by neighbouring social groups, it is unlikely that males could feasibly defend even a small habitat patch or prevent other males or females from roosting in nearby leaves. In addition, opportunities for female choice are high, because individuals presumably make independent decisions each day whether to join other group members in a particular roost, and it is unclear how males could prevent females from mating with other males after the bats have left the roost each night, unless group members forage together in exclusive, defended feeding areas. Our observations on *T. tricolor* suggest that mating and parturition are seasonal, with births recorded only in April and May, and no juveniles or subadults recorded at other times of year (M. Vonhof, unpublished observation). The 5-month gestation period of *T. tricolor* (Wimsatt & Enders 1980) places the mating period in December and January, at the boundary of the wet and dry season. The mating system of *T. tricolor* is currently unclear, but evidence based on microsatellite data indicates that males never mate with members of their social groups (M. Vonhof, unpublished observation), much like the cetaceans discussed above. Whether *T. tricolor* groups are composed of matrilines, how social organization changes during the mating season, and whether groups coalesce or males transfer between groups (as in killer whales), or set up mating territories during the mating season (as in *P. nanus*), requires further observation.

In conclusion, we have described a novel social structure among bats wherein *T. tricolor* forms mixed-sex social groups that are behaviourally cohesive over both short and long periods, and in which members of each social groups almost never interact with members of other social groups despite extensive overlap in space. Within social groups, however, there is considerable variation in the strength of association between dyads, and only rarely do all group members occupy the same roost at once. What remains to be examined are patterns of parentage and relatedness within and between social groups to determine whether social groups in the same or different habitat patches are connected by dispersal and mating, whether social groups are matrilineal in nature, and whether the strength of observed associations are based on relatedness. Such studies promise to uncover other distinctive aspects of this unique social system, and help us to better understand the observed patterns of stable relationships between members of both sexes.

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