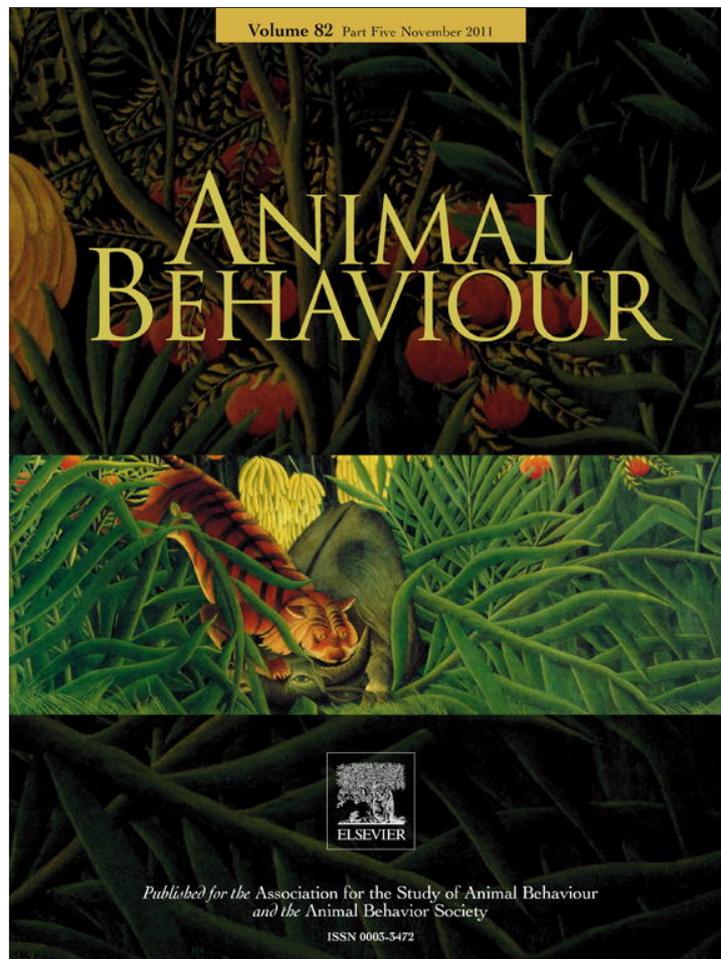


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All-offspring natal philopatry in a Neotropical bat

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Natal dispersal is a strategy employed by individuals to avoid reproducing with close relatives. In most bats, incestuous matings are prevented by the departure of one sex; thus, all-offspring philopatry has rarely been recorded in these mammals. Here we present evidence of all-offspring philopatry to natal groups in a Neotropical insectivorous bat. Our results are derived from behavioural observations of a long-term, capture–mark–recapture study conducted on three populations of Spix's disc-winged bat, *Thyroptera tricolor*. Results indicate that dispersal patterns of this species are characterized by low emigration rates (0.40–0.73 individuals per year), long residence times (492–1238 days) and high offspring retention of both sexes within natal groups. The retention of offspring resulted in groups being primarily composed of one or two matriline. Our study is the first to demonstrate such high amounts of male and female natal philopatry coupled with limited spatial movements in bats. These dispersal patterns may be explained by morphological and ecological constraints associated with costly flight dynamics and significant variation in the distribution and quality of habitat, in addition to social benefits accrued by remaining affiliated with close kin.

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Dispersal of individuals from their natal territory is considered a strategy used to reduce (1) negative fitness consequences associated with breeding with close relatives, (2) competition with kin at the natal territory and (3) variance in fitness caused by significant temporal variation in patch quality (Bowler & Benton 2005). To date, the vast majority of organisms studied engage in natal dispersal, although variation in life histories among taxa has resulted in characteristic trends (Greenwood 1980). For example, several studies have shown that most bird species show female-biased natal dispersal because of the substantial male investment in, and competition for, resources that are vital to the acquisition of breeding partners or to the rearing of young (Greenwood 1980; Clarke et al. 1997). In contrast, female mammals invest heavily in offspring and thus should benefit more from philopatry, whereas males gain access to breeding opportunities by defending groups of females, resulting in greater male–male competition and male-biased dispersal (Greenwood 1980; Wolff 1994). This pattern of female philopatry results in the formation of family groups or coalitions that may cooperate in the defence of resources (spotted hyaenas, *Crocuta crocuta*; Van Horn et al. 2004). This type of social structure, based on female kin

groups, is the most frequently observed among social mammals (Greenwood 1980; Clutton-Brock 1989a).

Notwithstanding the general mammalian trend of female philopatry and male dispersal, female emigration is not uncommon among gregarious species with male-biased dispersal. In fact, evidence shows that female-biased dispersal may be the predominant pattern in mammals with resource-defence polygyny or in species where the average residency of males typically exceeds the average age of females at first conception. In these species, female dispersal and male philopatry result in the formation of kin-based male groups (Greenwood 1980; Clutton-Brock 1989b). Another dispersal pattern observed among mammals, albeit relatively rare, is the departure of both sexes and the formation of nonkin groups (Monard & Duncan 1996). In such cases, natal philopatry is apparently costly for young of both sexes because of high amounts of aggression and dominance of resident adults (Linklater 2000); thus, group formation may be predominantly explained by the availability, density and patchiness of resources and not by the benefits associated with breeding near conspecifics (Safran et al. 2007). In contrast, when parents benefit from the retention of offspring, and dispersal is costly because of a shortage of high-quality breeding territories, highly fragmented habitats or limited dispersal abilities, individuals from both sexes may remain in their natal territory (Emlen 1997; Kokko & Ekman 2002). This pattern has been observed in cooperatively breeding mammals such as meerkats (*Suricata suricatta*) and marmots (*Marmota* spp.; Blumstein & Armitage 1999; Clutton-Brock et al. 2001), and offspring typically

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remain within their natal group to assist their parents in raising young at the expense of their own reproduction. Thus, philopatry may be predominantly regarded as a temporary strategy until better breeding opportunities arise elsewhere (Emlen 1995). With the exception of cooperatively breeding species that show considerable differences in reproductive opportunities among dominant and subordinate group members (Emlen 1995, 1997), there are no other examples of terrestrial, nonvolant, mammals with all-sex natal philopatry.

Among mammals, bats are unique in their ability to fly. Compared with other forms of locomotion, such as running and swimming, flight is less energetically demanding (Alexander 1999) and provides an enhanced ability to escape predation (Pomeroy 1990). Thus, flight has probably decreased the costs of dispersal in bats by minimizing energetic expenditure and mortality risks. Notwithstanding, bats show morphological and ecological adaptations that could significantly constrain dispersal. For example, species that forage in cluttered spaces, such as foliage gleaners, have wing morphologies that increase manoeuvrability at the expense of aerodynamic efficiency and speed. Compared to insectivorous bats that forage above the canopy, foliage gleaners probably incur a greater energetic cost during long-distance dispersal flights than bats specialized for aerial hunting (Norberg & Rayner 1987). Many bat species also have roosting and foraging specializations that restrict them to specific locations, or their resources may be patchily distributed across the landscape, favouring site fidelity over dispersal (Law 1996; Miller-Butterworth et al. 2003). In addition to constraints imposed by morphological and ecological adaptations, there are also potential benefits of natal philopatry in bats, such as communal breeding in a familiar social environment and decreased parasite transmission among colonies (Kerth et al. 2002).

In general, bats show the typical mammalian trend of male dispersal and female philopatry (Kerth 2008), although there are also species with female-biased dispersal (Nagy et al. 2007) or all-offspring dispersal (Dechmann et al. 2007). To date, there are only two bat species known to show all-offspring philopatry: Schreiber's long-fingered bat, *Miniopterus schreibersii* (Miller-Butterworth et al. 2003), and the brown long-eared bat, *Plecotus auritus* (Burland et al. 1999; Entwistle et al. 2000). Both species are temperate, seasonally migratory bats, and while *P. auritus* has relatively high annual return rates to natal roosts, *M. schreibersii* shows high philopatry to natal subpopulations containing several colonies distributed along four distinct biomes, but does not show philopatry to natal roosts (Entwistle et al. 2000; Miller-Butterworth et al. 2003). Here we present evidence of all-offspring philopatry to natal groups in the Neotropical insectivorous Spix's disc-winged bat, *Thyroptera tricolor*, and attempt to understand intraspecific variation in patterns of dispersal based on the abundance of roosting resources. Given that studies on birds and mammals demonstrate a negative correlation between resource abundance and dispersal rates (Boulinier & Lemel 1996; Forero et al. 2002; Gaillard et al. 2008), we predicted that individuals inhabiting areas of high roost densities would show greater natal philopatry than individuals in areas of reduced roost availability. Our results are derived from behavioural observations of a capture–mark–recapture study conducted on three local populations of *T. tricolor* in southwestern Costa Rica.

METHODS

Study Species

Thyroptera tricolor is a small foliage gleaner specialized for roosting in the developing furled leaves of members of the order Zingiberales, which provide suitable roosts for approximately 1 day (Vonhof & Fenton 2004). The plants used by *T. tricolor* for roosting

are generally found within natural or disturbed areas where canopy cover is not complete. These plants can occur at high density and are almost evenly distributed in man-made clearings or open secondary forest. They occur at low density and in discrete patches along stream banks and in tree-fall gaps (Daniels & Stiles 1979). Thus, depending on the characteristics of the habitat, furled leaves show a wide variety of distributions and densities, which in turn probably has a strong influence on the distribution of *T. tricolor* bats. Despite significant spatial differences in the density of roosting habitat, furled leaf density within patches remains relatively constant through short timescales (G. Chaverri, unpublished results). *Thyroptera tricolor* forms mixed-sex groups composed of up to 14 individuals, which are known to maintain small, overlapping home ranges (mean = 0.19 ha.; Vonhof et al. 2004). Despite their spatial overlap, groups are highly cohesive, without immigration of individuals from other groups or emigration of group members for up to 22 months (Chaverri 2010). The maximum known life span of *T. tricolor* is approximately 6 years (G. Chaverri, unpublished results).

Study Sites and Field Methods

This study was conducted at three sites located in and around the Golfito Wildlife Refuge (GWR) and Piedras Blancas National Park (PBNP), in Southwestern Costa Rica, during August 2006 through April 2010. The first site, Finca (8°38'N, 83°05'W), is mostly surrounded by primary forests, and common understory plant species include *Heliconia imbricata* and *Calathea lutea*. The second site, Esquinas (8°42'N, 83°12'W), is surrounded by the PBNP. This site is mostly composed of primary and late secondary forests, and *Heliconia* spp. patches are small and scattered. The other site, Ureña (8°40'N, 83°12'W), is located inside the GWR within disturbed secondary forests, and its understory is dominated by dense patches of *C. lutea*.

At our study sites, we consistently surveyed a pre-established area (size: Finca = 0.78 ha, Ureña = 0.81 ha, Esquinas = 3.30 ha) once or twice each month. Each survey was conducted in a single day, and typically lasted less than 5 h. During these surveys, we captured bats in all identified roosts, then fitted them with individually numbered metal wing bands, sexed and aged them, and assessed their reproductive condition. To measure the abundance of roosting resources per site, we first quantified the total number of potential roosts per site by counting all unoccupied and occupied furled leaves of plant species known to be used by *T. tricolor* (Findley & Wilson 1974; Vonhof & Fenton 2004). Furled leaves were only counted if their diameter of opening ranged between 3.5 and 27 cm, as this is the preferred size range of leaves selected for roosting by *T. tricolor* (Vonhof & Fenton 2004). Then, to compare leaf density per site, we calculated the number of furled leaves per hectare, and compared leaf density among sites using a one-way ANOVA in SPSS v.17.0 (SPSS Inc., Chicago, IL, U.S.A.; data were normally distributed according to the Shapiro–Wilk test). All protocols for capturing and handling bats were approved by the Costa Rican government (permit number R-008-2009-OT – CONAGEBIO) and by Boston University's Institutional Animal Care and Use Committee (approval number 02-005).

Patterns of Residency, Emigration and Population Size

To address residence time within, and emigration rates from, study sites, we estimated the probability of individuals remaining in each area throughout the study period based on individual capture–mark–recapture records. We never observed movement of bats among study sites, and thus we assumed that the distance between sites was sufficiently large to separate populations. Hence,

we assessed how bats moved into, and out of, each study site separately. To model this process, we used lagged identification rates, which estimate the probability that an individual identified in a given study area at time t is the same as a randomly chosen individual from this area τ time units later (Whitehead 2001). Lagged identification rates were calculated using SOCPROG version 2.4 (Whitehead 2009) and plotted against time lag (τ), in days, to observe patterns of residency. These plots provided information regarding population size for each study site, as the intercept on the Y axis is an estimate of $1/N$. They also indicated how individuals used the study areas. For instance, a sharp fall in lagged identification rates would indicate that most bats departed when the drop in rate began. If populations were closed, the lagged identification rate should remain constant at all time lags, whereas a decrease in lagged identification rates would indicate that animals left the study area over a longer time, either through emigration or mortality. A levelling off at a large τ could be caused by some individuals being permanent residents of the study area and/or by reimmigration (Whitehead 2001).

In addition to estimating trends in lagged identification rates, we also calculated population size, emigration rates and residence time based on an emigration/mortality model in SOCPROG for each population. The emigration/mortality model assumes a population with permanent emigration (or mortality) of individuals with no reimmigration (Whitehead 2007). We fitted three other default models in SOCPROG to our data, namely (1) closed, (2) emigration + reimmigration and (3) emigration + reimmigration + mortality, to determine whether the emigration/mortality model used in our analysis fit our data well. A closed model assumes a population with no birth, death, immigration or emigration, while the other two models assume permanent emigration (or mortality) of some individuals. These last two models also assume that some individuals within a population may often live outside the study area, often re-entering it (Whitehead 2007). We used the quasilielihood version of the Akaike Information Criterion (QAIC) to estimate the best-fitting models (Whitehead 2009). To determine the fit of our data to the four models, we first calculated QAIC for each model. We then selected the model with the lowest QAIC and used it to compare the fit of the other three models to the data based on Δ QAIC. Small Δ QAIC (i.e. 0–2) indicate strong support for the model, while differences of 4–7 indicate considerably less support, and large differences (i.e. >10) indicate no support for the model (Burnham & Anderson 2002). In SOCPROG, we used a maximum time lag of 1200 days in the analysis, with 100 bootstrap replicates to obtain standard errors of the three variables (i.e. population size, emigration rates and residence time).

Offspring Retention and Matrilines

Patterns of offspring retention within study sites and roosting groups were assessed based on capture–mark–recapture data. For each offspring born during the parturition season of 2007 (February–April), we recorded residence time at the study site and natal group, and determined whether bats attained reproductive maturity while being resident at the study site. We only analysed data of bats born in 2007 to observe patterns of offspring retention over a longer period. Because of high mortality rates of bats under

5 months old, and because individuals do not attain full adult proportions until they are about 4 months old (Chaverri & Vonhof 2011), we considered any disappearance of individuals under this age to be caused by mortality, and any disappearance after this age to be from dispersal. We also determined whether young remained within their natal group by analysing data on group composition based on associations at roost sites. In our study, individuals were considered to be associating if they were captured at the same roost at the same time. We evaluated whether bats born in 2007 attained sexual maturity at the study sites based on pregnancy and lactation records for females, and on testicular descent or an increase in the size of the testes for males.

Based on maternity records of individuals captured at our study sites, we traced maternally inherited lineages within roosting groups. To observe patterns of matrilineality, we constructed pedigrees depicting matrilineal relationships among group members using SmartDraw version 2010 (SmartDraw Software, LLC, San Diego, CA, U.S.A.). Because females become sexually active after their second year (Chaverri & Vonhof 2011), females that were captured during our first field season in 2006 were presumed to be less than 1 year old if they were first pregnant in 2008; females that showed no signs of parity (such as the presence of a bare patch and enlarged keratinized nipples) at capture in 2006 but became pregnant in 2007 were presumed to be at least 1 year old; and females that showed signs of parity in 2006 were presumed to be 2 years or older. For this pedigree analysis we only used groups for which we had at least 3 years of data, to increase the probability of detecting maternal affiliation among group members, and only for groups captured during the last parturition season (February–April 2010).

RESULTS

During the study period of almost 4 years, we captured a total of 230 individuals across the three study sites. We captured 58 individuals in Finca, 63 in Ureña and 109 in Esquinas. Recapture rates, measured as the proportion of individuals identified per sampling period, were highest in Finca (0.27), followed by Ureña (0.15) and Esquinas (0.09). We conducted 40 surveys in Finca, 38 in Ureña and 41 in Esquinas, and estimated leaf density based on data collected from 73 surveys (Finca = 24, Ureña = 23, Esquinas = 26). All sites differed significantly in the density of furled leaves (one-way ANOVA: $F_{2,70} = 130.06$, $P < 0.001$). Finca had the greatest amount of furled leaves per hectare followed by Ureña. The lowest density of leaves was observed at Esquinas. Population densities, based on model fitting, followed the same pattern, with a high density of 31.7 individuals/ha at Finca and a low density of 9.7 individuals/ha at Esquinas (Table 1).

Lagged identification rates at the three study sites decreased steadily through all time lags, and appeared to reach zero at lags greater than 1200 (Fig. 1). This constant decrease indicates permanent emigration or mortality from all sites and no permanent residency or reimmigration. Based on values of the QAIC, the emigration/mortality models were always a good fit to the data, with Δ QAIC between 0 and 4 (Table 2). Other models with good support included those describing populations with reimmigration. These models were not considered for further analyses because our

Table 1

Density of furled leaves and emigration rate, population size and residence time of Spix's disc-winged bats measured from the fitted models of residency at each study site

Site	Leaf density (furled leaves/ha)	Emigration rate (individuals/day)	Population size (number of individuals)	Population density (individuals/ha)	Residence time (days)
Finca	70 (3.85)	0.0011 (0.0002)	24.75 (2.98)	31.73	908 (228.64)
Ureña	55 (3.47)	0.0013 (0.0005)	21.75 (3.05)	26.85	732 (271.44)
Esquinas	7 (0.52)	0.0020 (0.0004)	32.00 (3.49)	9.69	492 (120.85)

Values are means. Standard errors are given in parentheses. Variables were measured from emigration/mortality models.

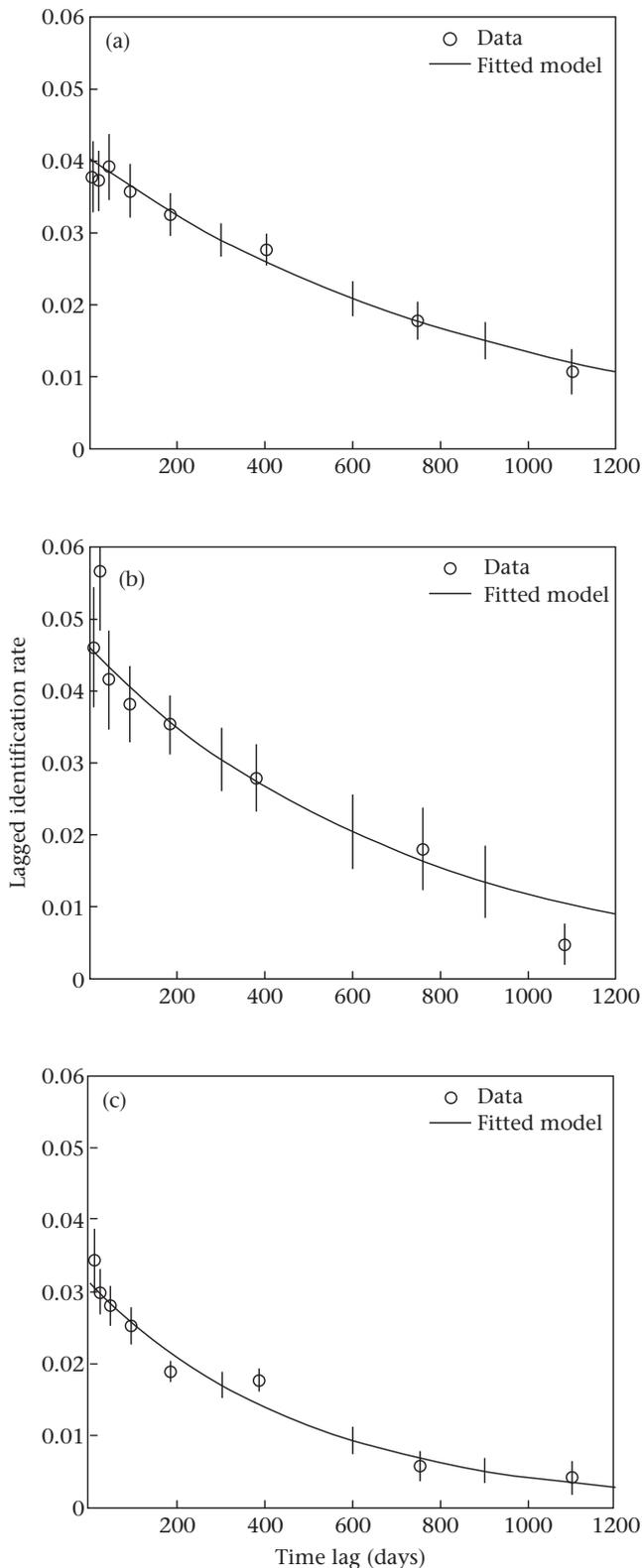


Figure 1. Lagged identification rates for Spix's disc-winged bats at the three study sites: (a) Finca, (b) Ureña and (c) Esquinas. Fitted model represents the expected lagged identification rate from an emigration/mortality model.

capture–mark–recapture data clearly indicated that reimmigration never occurred once individuals had left a specific group or study site. Emigration rates were low, with the lowest rate in Finca, the site with the largest density of roosting habitat. Individuals at

Table 2

Model fit (τ is time lag in days) to the data on lagged identification rates, $R(\tau)$, of Spix's disc-winged bats at each study site

Site	Model	Fitted function	QAIC	Δ QAIC
Finca	C	$R(\tau)=0.027124$	49 034	595
	EM	$R(\tau)=0.040398e^{-0.0011008\tau}$	48 443	4
	E+R	$R(\tau)=0.027131\pm 6.834e^{-2.7645\tau}$	49 033	594
	E+R+M	$R(\tau)=-4.3653e^{-2.3416\tau} + 0.040464e^{-0.0011035\tau}$	48 439	0
Ureña	C	$R(\tau)=0.029993$	15 744	252
	EM	$R(\tau)=0.045971e^{-0.0013648\tau}$	15 492	0
	E+R	$R(\tau)=0.030012\pm 0.28629e^{-1.5138\tau}$	15 745	253
	E+R+M	$R(\tau)=-0.25324e^{-1.2704\tau} + 0.046099e^{-0.0013702\tau}$	15 492	0
Esquinas	C	$R(\tau)=0.016162$	9908	347
	EM	$R(\tau)=0.031243e^{-0.0020313\tau}$	9561	0
	E+R	$R(\tau)=-0.00062748 + 0.031637e^{-0.001924\tau}$	9563	2
	E+R+M	$R(\tau)=-0.15355e^{-2.3348\tau} + 0.031252e^{-0.0020318\tau}$	9565	4

Models tested: closed (C), emigration/mortality (EM), emigration + reimmigration (E + R) and emigration + reimmigration + mortality (E + R + M). The best-fitting model was determined using the quasiliikelihood version of the Akaike Information Criterion (QAIC) (Whitehead 2007).

this site also remained within their habitat the longest. Conversely, emigration rates were the highest, and residence time the lowest, at Esquinas, the site with the lowest density of furled leaves (Table 1, Fig. 2).

Of the 25 bats born in 2007 (8 in Finca, 8 in Ureña, 9 in Esquinas), survival past their fifth month of age was recorded for six males and 10 females. Most (11 of 16) remained as residents at their natal site for 2 years or longer, largely within their natal group (9 of 11), and there seemed to be a relatively equal proportion of philopatric males and females (6 females, 5 males). The majority (3 of 5) of individuals that dispersed before 2 years of age apparently did so with their mothers, and often with other members of their group, as they disappeared from the study sites at the same time. In fact, we observed the dispersal of an adult female and her approximately 10-month-old offspring to a site 900 m away from the offspring's birth site. All individuals that were recaptured for 2 years or longer at the study sites attained reproductive maturity, and all females recaptured for 2 years or longer at the study sites reared offspring. Offspring produced by philopatric females typically also remained in the natal group, resulting in a matrilineal composition of roosting groups. This was observed at the three study sites, with two traceable matrilineal lines in Finca, one in Ureña and one in Esquinas (Fig. 3), which resulted in groups being formed by a maximum of three matrilineal lines.

DISCUSSION

Evidence to date gathered on bats shows that individuals from one sex typically leave the natal group and territory to breed elsewhere, and that the other sex remains philopatric, albeit with various degrees of philopatry ranging from most individuals dispersing to most individuals being philopatric (Kerth 2008). Our study shows that dispersal patterns in *T. tricolor* are characterized by low emigration rates from, and long residence times within, natal territories, coupled with high amounts of offspring retention from both sexes within natal groups that result in a matrilineal social organization. This is the first study to show such high amounts of all-sex natal group philopatry coupled with limited spatial movements in any bat species. These results complement previous findings of unusually high group stability in *T. tricolor* (Vonhof et al. 2004; Chaverri 2010), showing that groups are primarily formed by highly related individuals whose long-term associations may be partly explained by kinship.

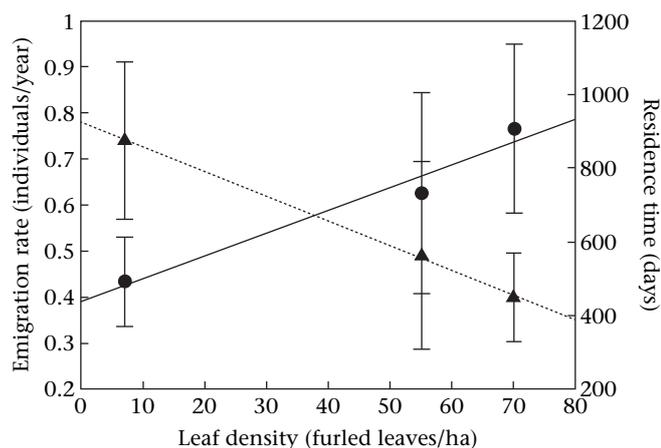


Figure 2. Linear relationships between leaf density and emigration rate (triangles) and residence time (circles) of Spix's disc-winged bats. Values are means \pm SE.

With the exception of bats and pilot whales, *Globicephala melas* (Amos et al. 1993; Entwistle et al. 2000; Miller-Butterworth et al. 2003), natal philopatry by both males and females has not previously been reported in noncooperatively breeding mammals. In pilot whales, social benefits accrued by both males and females remaining with close kin could explain natal philopatry (Amos et al. 1993), while ecological and morphological constraints, such as an extreme adaptation to local conditions and costly flight dynamics, may be primarily responsible for subpopulation and roost philopatry in *M. schreibersii* and *P. auritus* (Burland et al. 1999; Entwistle et al. 2000; Miller-Butterworth et al. 2003). Morphological and ecological constraints, coupled with social benefits, could also explain natal group and site philopatry in *T. tricolor*. Wing dimensions in *T. tricolor* suggest that flight in this species is highly manoeuvrable but aerodynamically inefficient and slow (Norberg & Rayner 1987), increasing the costs of long-distance movements. *Thyroptera tricolor* is also highly habitat specific and apparently incapable of using roosts other than furlled leaves (Riskin & Fenton 2001). Furlled leaves show significant spatial, but not temporal, differences in patch quality, which is known to favour residency over dispersal (Johnson & Gaines 1990). Moreover, because kinship and social stability favour the evolution of cooperative behaviours (Ferriere & Michod 1996; Griffin & West 2003), individuals may benefit by remaining within natal groups, as this could promote

cooperative interactions among group members during the location of roosts (Chaverri et al. 2010).

While our study shows that individuals of both sexes typically remained within their natal group and territory for extended periods, our emigration/mortality models suggest that philopatry is only a temporary strategy, with lagged identification rates constantly declining throughout the study period. These apparently contradictory results could be explained by the properties of the models used to understand dispersal patterns, which cannot differentiate between disappearances from emigration or mortality (Whitehead 2001). Thus, the observed emigration/mortality rates of 0.40–0.73 individuals per year could well be attributed primarily to mortality and not to emigration. In fact, even if these departure rates were solely attributed to mortality, they would still be lower than those known for many other bird or mammalian species for which data on annual mortality rates are available (Ricklefs 1998). Notwithstanding, the departure and arrival of a small number of adult individuals among groups and territories suggest that dispersal, while rare, is a strategy used occasionally by *T. tricolor*. Other philopatric bat species are also known to engage in low rates of dispersal (Entwistle et al. 2000; Kerth et al. 2000; Nagy et al. 2007), but the factors favouring this strategy remain unknown.

One hypothesis most often cited to explain the evolution of dispersal is that individuals emigrate from their natal territory to avoid reproducing with close relatives. When significant social benefits or ecological constraints favour all-offspring retention within natal groups, inbreeding can be prevented either by suppressing the reproduction of offspring, which could lead to highly unstable groups, or by selecting mating partners from outside the family group (Emlen 1995). By actively seeking extragroup copulations, individuals avoid the costs of inbreeding and dispersal while still maintaining high group cohesion and intragroup relatedness (Cant et al. 2002), which should favour the evolution and maintenance of cooperative behaviours. In *T. tricolor*, the observed patterns of natal philopatry, which resulted in a matrilineal social organization and high intragroup relatedness, coupled with high social cohesion and rare exchanges of individuals among adjacent groups, suggest that mating partners are selected from outside social groups. Preliminary results of parentage analysis suggest that individuals travel outside areas of genetic similarity to find mates (M. R. Buchalski, unpublished data). These preliminary findings, with observations of extracolony copulation in the only other bat known to show all-sex philopatry to natal groups (*P. auritus*; Burland et al. 2001), support this hypothesis.

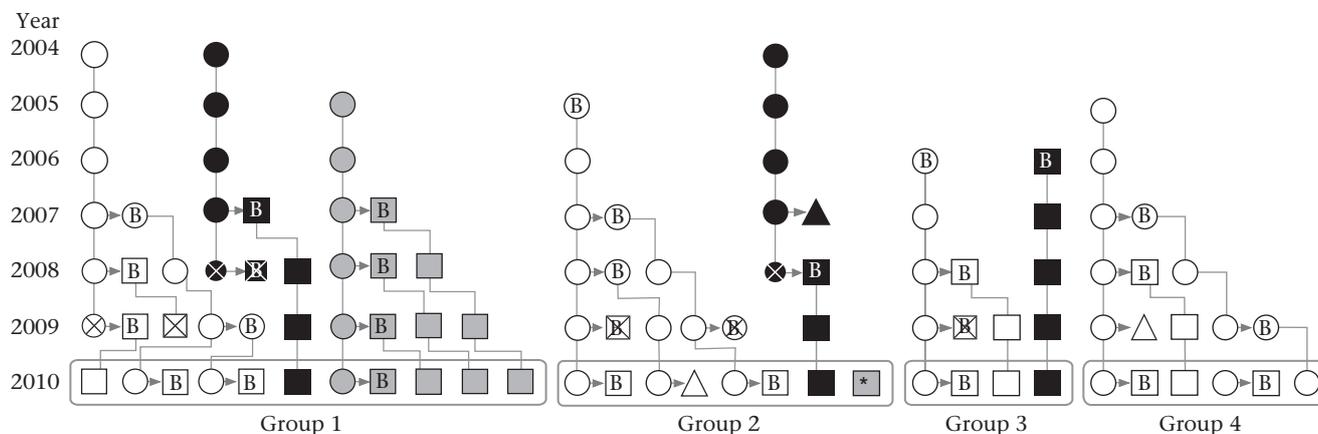


Figure 3. Pedigrees illustrating matrilineal relationships among group members of Spix's disc-winged bats (males: squares; females: circles) at the three study sites (groups 1, 2: Finca; group 3: Ureña; group 4: Esquinas). Each member of a group is traced back to its year of birth (B) and matriline (white, black or grey shading), with arrows indicating mother–infant relationships. Crossed symbols denote individuals that disappeared during the year; triangles denote infants whose presence was presumed by the female's pregnancy but that died soon after birth before being tagged; asterisks denote individuals for which matrilineal origin was unknown.

Resource availability has been recognized as an important correlate of dispersal, and some studies show that emigration is more frequent when resources are scarce (Bowler & Benton 2005). Our findings of greater emigration rates and shorter residence times with a decreasing density of roosting resources support our prediction of a negative relationship between resource abundance and dispersal in *T. tricolor*. Thus, while dispersal may generally be costly for *T. tricolor*, given its wing morphology, the costs from limited roosting sites could entail significant fitness costs to individuals that remain in the habitat. These costs may include greater offspring mortality, greater energetic expenditure while locating suitable roosting sites and greater risks of predation (Altmann 1987; Panzacchi et al. 2009; Chaverri & Vonnhof 2011).

The movement of animals through space is a life history trait that has profound consequences for populations. In this respect, studies show that ecological pressures that favour dispersal over philopatry may increase colonization rates and metapopulation persistence but increase the extinction risk of local populations and decrease cooperative interactions (Bowler & Benton 2005; Kümmerli et al. 2009). Conversely, ecological and morphological constraints that favour philopatry over dispersal may reduce mortality risks associated with long-distance movements and increase cooperative interactions among individuals (Emlen 1997; Kokko & Ekman 2002). Nevertheless, this increases the detrimental effects of crowding and competing with kin (Hamilton & May 1977), in addition to significantly limiting the ability to colonize new areas (Holt 2003), thereby increasing extinction risk in metapopulations (Higgins & Lynch 2001). Thus, all-offspring philopatry in *T. tricolor* may improve the survival of local populations by increasing survival of young and promoting cooperative interactions among group members.

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