

Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in north-eastern Costa Rica

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Abstract: Estimates of roosting habitat availability and population size using unbiased sampling regimes are completely lacking for any bat species. The use of conspicuous and accessible roosts in the developing, rolled leaves of *Heliconia* and *Calathea* plants by *Thyroptera tricolor* (Spix's disc-winged bat) provided an ideal opportunity to address this need. To assess roost availability and population size, the number of occupied and unoccupied leaves and bats in known areas in an area of lowland rain forest in north-eastern Costa Rica were quantified in 1998–99. A high density of leaves was available on any given day (mean: 43 leaves ha⁻¹), but the density of roost leaves was low (mean: 2.5 leaves ha⁻¹), corresponding with a low occupancy rate of 5.7 or 12% based on different methods of estimation. Developing leaves were 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. Using closed-population mark–recapture models, the 5.69-ha study area supported 261 individuals over a 4-mo period in 1998, corresponding to a density of 43 bats ha⁻¹. These results have important implications for the results of studies on bat community structure and rarity, and for the behaviour and ecology of *T. tricolor*.

Key Words: bats, *Calathea*, closed-population mark–recapture models, habitat availability, habitat longevity, *Heliconia*, population estimation, population size, rain forest, *Thyroptera tricolor*

INTRODUCTION

Environmental conditions can profoundly affect the ecology of vertebrates. The distribution and abundance of resources can directly or indirectly affect the density and dispersion of individuals (Clutton-Brock & Harvey 1984), thereby influencing a wide range of ecological and behavioural characteristics (Alexander 1974). For example, spatial and temporal variability in resources influences factors such as territorial behaviour, aggression, timing of dispersal and reproduction, habitat use, body condition, reproductive output, mating system, social organization and levels of inbreeding (Forsgren *et al.* 1996, Kie & Bowyer 1999, Lott 1991, Marshall *et al.* 2002, Marvin 1998, Ostfeld 1990, Pröhl 2002, Travis *et al.* 1995, Vincent *et al.* 1995). It is not surprising, then, that estimating the population size and density of organisms and the associated methods have received considerable attention in the ecological literature.

Bats present a particular challenge for estimating habitat availability and population size, because of their mobility, nocturnal lifestyle and secretive habits. The use of inconspicuous and inaccessible day roosts by most bat species has prevented the accurate assessment of roost density for any bat species using natural roost-sites, as it is virtually impossible to determine if all roosts have been found in a given area. Similarly, population estimation has been attempted for just a handful of bat species, and has often suffered from limitations of the methods available for sampling bats. While population estimation for some species using conspicuous roosts in the foliage of trees has been possible (e.g. Wiles 1987), most bat roosts are concealed, preventing accurate assessment of the numbers of individuals in a given area using direct visual observation. Most existing estimates have used radio-telemetry, direct searches and/or public involvement to locate and assess population size in individual roosts, from which minimum population estimates for a given area based on knowledge of the number of roosts are calculated (Boyd & Stebbings 1989, Gerell & Lundberg 1993, Speakman *et al.* 1991, Warren & Witter 2002). However, these studies are often unable to

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assess whether all roosts in a given area have been found, and may be biased towards females that group together in conspicuous maternity colonies. Furthermore, minimum population estimates may underestimate true population size, sometimes severely, and provide no estimate of precision (Alexander *et al.* 1997). The use of mark–recapture methods to provide more accurate population size estimates (Pollock *et al.* 1990, White *et al.* 1982) has been successfully applied to individual roosts (e.g. Entwistle *et al.* 2000), but has been applied on a larger scale in only one study. Leigh & Handley (1991) used data from captures in mist nets and recaptures of marked individuals to estimate the density of Jamaican fruit-eating bats (*Artibeus jamaicensis* Leach) on Barro Colorado Island, Panama. However, using captures in mistnets to estimate population size is problematic, because they are biased towards low-flying individuals, and are typically subject to negative behavioural responses (trap-shy behaviour; Kunz & Kurta 1988). What has been lacking to this point is an estimate of population size for any bat species using mark–recapture methods combined with an unbiased sampling regime.

Thyroptera tricolor Spix (Spix's disc-winged bat) is a small (3–4 g) insectivorous bat found in tropical forests from central Mexico to south-eastern Brazil (Wilson & Findley 1977). This species has typically been found roosting in the rolled, developing leaves of understorey plants of the order Zingiberales, including *Heliconia* and *Calathea* spp., as well as introduced banana (*Musa*) plants (Findley & Wilson 1974, Goodwin & Greenhall 1961, Handley 1976, Pine 1993, Simmons & Voss 1998, Villar-R. 1966), but may also occasionally roost in dead, rolled leaves (Simmons & Voss 1998). Suction discs on the wrists and ankles make *T. tricolor* morphologically specialized for using leaves, and virtually unable to make use of 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. In the only study addressing the ecology of *T. tricolor*, Findley & Wilson (1974) systematically searched a 1.9-ha area of secondary forest in south-western Costa Rica on a daily basis over a 2-wk period. They found that suitable leaves occurred at low densities and in clumps, approximately one in every four rolled leaves was occupied by bats, and estimated the density of bats in their study area to be 21.9 bats ha⁻¹ based on the number of known individuals per unit area.

Heliconia and *Calathea* plants are found in the understorey in tree-fall gaps, secondary forest, natural and man-made clearings, swamps and along stream banks (Seifert 1982, Stiles 1975). The leaves may be only available in the rolled form suitable for use by bats for a short period (approximately 24 h, Findley & Wilson 1974), and thus bats using these leaves are regularly forced to find

new roost-sites and depend on the availability of multiple sites to meet their roosting resource requirements over time. Furthermore, depending on the habitat and species present, plants with appropriate leaves occur from high density and almost uniform distribution in clearings or open woodland, to low density in discrete patches in primarily closed forest with canopy gaps (Dobkin 1984, Horvitz & Schemske 1994, Seifert 1982, Stiles 1975). 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, in turn, may have a strong influence on their behaviour and demography.

The consistent use of accessible and conspicuous rolled leaf-roosts by *T. tricolor* makes them the ideal subjects for studies on habitat availability and population size. Here we present the results of a 2-y study in Caribbean lowland rain forest in north-eastern Costa Rica to assess roost availability and population size in *T. tricolor*. Our specific objectives were to: (1) describe the characteristics of roosts used by *T. tricolor*, (2) determine the spatial and temporal availability of occupied and unoccupied rolled leaves by systematically sampling known areas and (3) estimate the size and density of the population of *T. tricolor* in those areas using closed-population mark–recapture methods. By systematically searching for rolled-leaf roosts we both provide an estimate of habitat availability over time in different patches of forest, and sample the population of *T. tricolor* in these patches using a relatively unbiased method. To our knowledge, we provide the first estimate of absolute population size and roost availability in a defined area for any bat species using an unbiased sampling regime and mark–recapture methods, and therefore provide fundamental and necessary ecological data that has been lacking to this point.

STUDY SITE

We conducted fieldwork in 1998–99 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 north-eastern Costa Rica (83°32'W, 10°35'N; see Figure 1). This region is situated in the Tropical Wet Forest 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. Elevations in the study site ranged from below sea level to approximately 30 m. Unlike other parts of Costa Rica, there are no distinct wet and dry seasons, but January to April is typically driest, and the wettest months are October through December. The study area receives upwards of 5 m of rain

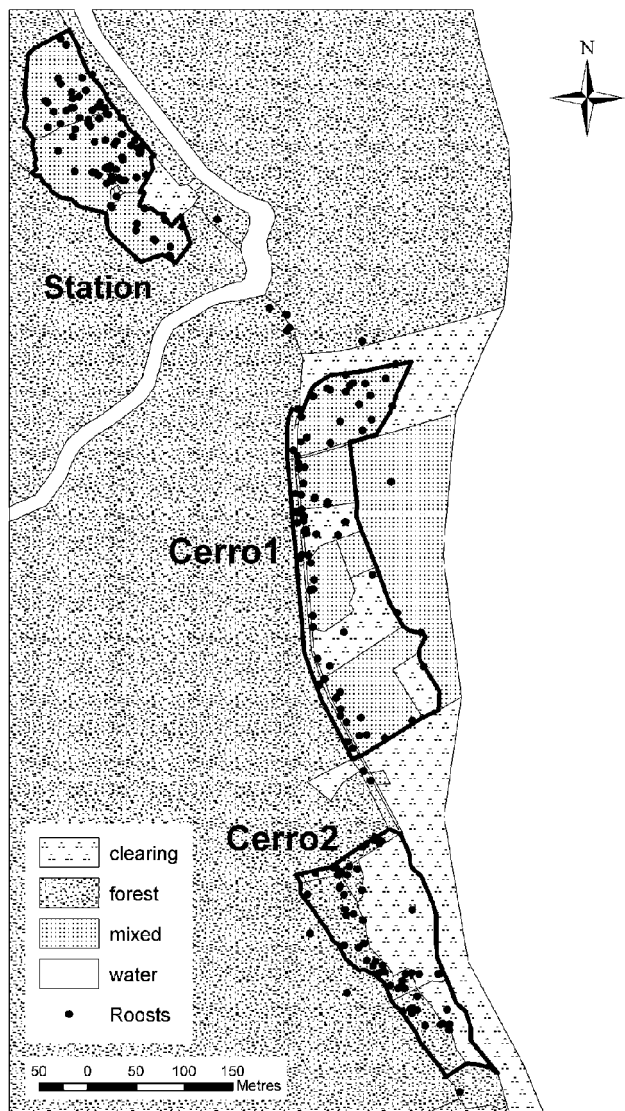


Figure 1. A map of the Caño Palma study area in north-eastern Costa Rica showing the location of the three subunits censused (Station, Cerro1 and Cerro2), the distribution of different habitat types within each subunit, and the location of all roost-sites used by *Thyroptera tricolor*.

annually. Fieldwork was conducted between 2 February and 26 May 1998, 21 and 26 October 1998 and 18 March and 30 May 1999.

After a brief initial survey, we determined the boundaries of areas containing abundant *Heliconia* or *Calathea* plants (Figure 1). Forest habitat surrounded the study area on three sides (south, west and north), and the Caribbean Sea bounded the study area to the east. We mapped the study area using a compass and measuring tape, and later created a GIS coverage in ArcInfo3.0 and ArcView3.2 (ESRI, Redlands, USA) to determine the size of areas searched. We divided the study area into three subunits that were easily searched within a day, and were separated by short stretches of habitat

containing few or no suitable leaves. These subunits were the field station property (Station; total area 1.50 ha), and two areas around the base of the local hill, Cerro Tortuguero (Cerro1 and Cerro2; areas 3.27 and 0.92 ha, respectively). In 1999, a clearing adjacent to Cerro2 developed into suitable habitat (area 1.11 ha), and was searched regularly as part of the Cerro2 subunit. Another small area was added to searches in the Station subunit (0.38 ha) in 1999, but several small forest patches originally included in Cerro1 were removed by squatters in late 1998. Thus, the study area varied somewhat between years, but the total area searched remained similar between years (5.69 ha in 1998 and 5.63 ha in 1999). Each subunit consisted of a number of habitat types, from recently cleared areas (Cerro1 and Cerro2 only) to secondary forest with canopy tree retention (mixed: Station and Cerro1) to the edge of primary forest (Cerro2; see Figure 1). Forest to the north and west of the three subunits contained a low density of suitable leaves ($< 1 \text{ leaf ha}^{-1}$), and was not searched after the 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, and contained only unique individuals not captured in any of the three subunits regularly searched.

METHODS

Roost censuses

Between 2–6 observers systematically searched subunits for suitable roosts. Observers quantified the number of unoccupied leaves, and leaves containing bats (roosts) in a given area, to provide estimates of the densities, and therefore the availability, of the different categories of leaves. All roost site locations were mapped relative to known points with a compass and measuring tape. After a brief 3-wk period of high-intensity searches, during which as much of the population was banded as possible, censuses were reduced in frequency to minimize disturbance to the bats. Censuses of the study area took 3 d in total, 1 d for each subunit, and each subunit was searched at intervals of at least 1 wk. Roost occupancy rate was calculated by comparing the number of occupied leaves to the total number of leaves searched during these systematic censuses. Differences between subunits and years in the density of unoccupied leaves and roost leaves, and the possible interaction of subunit by year in densities, were tested using a 2-factor ANOVA and Tukey's multiple comparisons. All dependent variables were natural log-transformed to satisfy the assumption of normality.

While searching, when we located leaves $\leq 4 \text{ m}$ in height 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. We were unable to check leaves > 4 m in height in this way, so instead, we gently shook tall leaves to determine if 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 individuals except juveniles were marked with individually numbered split-ring plastic (in early 1998 only) or aluminium bands (1998 and 1999) on their forearm for individual identification.

We measured the total height of the roost, the length of the roost leaf, and one-half the circumference of the opening (by flattening the opening and measuring at the point of overlap between the two sides of the leaf) with a measuring tape, and recorded the species of plant, for all roost leaves. *Heliconia* spp. plants were identified following Berry & Kress (1991), and the single species of *Calathea* was identified as *C. inocephala* (O. Kuntze) H. Kenn. & Nicolson based on floral and leaf morphology (H. Kennedy, *pers. comm.*). The circumference of the leaf was converted to a diameter assuming the opening was a perfect circle. The volume of each roost leaf was calculated as though the rolled leaf formed a perfect cone, with the length of the leaf as the height of the cone, and the diameter of the opening as the diameter of the base of the cone. This calculation assumes that the entire volume of the cone is usable by bats, which is unlikely to be true, and therefore likely provides a slight overestimate of roost volume. Spearman rank correlation was used to determine whether the number of bats using a roost was related to the characteristics of the leaf.

Roost permanency

To determine how long leaves were available to bats as roost-sites, we measured the opening rates of selected leaves of each of the three *Heliconia* species (*H. pogonantha* Cufodontis, $n = 25$; *H. latispatha* Bentham, $n = 26$; and *H. irrasa* Daniels & Stiles, $n = 21$) and *C. inocephala* ($n = 28$). We randomly selected new, tightly rolled leaves of each species and measured the diameter of the opening twice daily (within 1 h of local sunrise and sunset, respectively) until the leaf opened. Marking a random sample of leaves and following them through time in this manner also provided an independent measure of the roost occupancy rate, as a number of leaves were used as roosts (see Results). Two *H. pogonantha* and two *C. inocephala* leaves were damaged while removing bats,

and were not included in opening-rate calculations. The time leaves were available to bats was calculated by fitting quadratic polynomial regression equations to the opening-rate data for each leaf. Then the time each leaf was in the preferred size range was calculated using the regression equations, assuming that leaves were in the preferred size range if they had a diameter between the upper and lower 95% confidence limits of known roosts for that plant species. *Heliconia irrasa* was omitted from these opening-rate calculations and interspecific comparisons because the diameter of only two growth-rate leaves exceeded the upper 95% confidence limit of roost leaves. Ninety-five per cent confidence limits decrease with increasing sample size, and thus we also calculated the time leaves were between ± 1 SD of the mean of known roost leaves, and the maximum amount of time leaves were available in the rolled form for the four plant species. The lower limit for the latter measure was calculated by rounding down to the nearest cm from the smallest roost-leaf found for each plant species (4 cm for *C. inocephala*, and 3 cm for all others), and the upper limit was determined for each leaf by taking the final diameter measurement before the leaf opened. Growth-rate leaves measured in 1998 and 1999 were grouped, as sample sizes did not permit testing for differences between years. A Kruskal–Wallis test was used to compare opening rates of the different plant species, and a posteriori tests were conducted following Zar (1996) to determine which species differed.

Estimating population size

The population size of *T. tricolor* within the study area was estimated using the closed-population mark–recapture models in the program CAPTURE (Otis *et al.* 1978, White *et al.* 1982). These models assume both demographic closure, with no births, deaths, immigration, or emigration during the study, and geographic closure, where individuals do not move on and off the study area between trapping sessions. The basic mark–recapture model available in CAPTURE is model M_0 , which assumes equal capture probabilities for all individuals in the population, a condition which is rarely met in natural populations (White *et al.* 1982). Given that this is the case, CAPTURE uses a model-selection procedure to detect bias arising from unequal individual capture probabilities, and fits data to seven different models that allow for variation in capture probabilities between individuals (heterogeneity, model M_h), between capture sessions (time, model M_t), resulting from behavioural effects such as trap-happiness or trap-shyness (behaviour, M_b), and combinations of these effects (models M_{tb} , M_{th} , M_{bh} and M_{tbb}). Using seven different tests, the selection procedure compares how well the data

Table 1. Characteristics of roosts (mean \pm SD (range)) used by *T. tricolor* in each of the four most commonly used plant species.

Species	N	Diameter of opening (cm)	Leaf length (cm)	Total height (cm)
<i>Calathea inocephala</i>	35	7.3 \pm 1.78 (4.7–13.0)	63.1 \pm 11.95 (37–86)	121.2 \pm 27.30 (76–179)
<i>Heliconia irrasa</i>	33	7.1 \pm 2.33 (3.5–12.0)	54.3 \pm 14.24 (20–81)	123.2 \pm 31.60 (59–188)
<i>H. latispatha</i>	25	6.7 \pm 2.78 (3.7–17.8)	73.3 \pm 22.16 (32–108)	190.4 \pm 57.57 (41–254)
<i>H. pogonantha</i>	72	7.3 \pm 3.34 (3.5–27.6)	84.5 \pm 24.71 (36–141)	186.1 \pm 63.63 (66–340)

fit each of the models, and selects the simplest, best-fitting model. However, no estimator is provided for model M_{tbh} , in which all three factors play a role in the variability of capture probabilities. In practice, the model selection is based on knowledge of the biology of the animal, in addition to the statistical tests provided in CAPTURE. The validity of the assumption of closure was verified using the closure test in CAPTURE, which assumes that model M_h is the underlying model (White *et al.* 1982).

Only bats captured during surveys in February to May 1998 were included in the analyses, as this was the period of greatest effort, and no births took place during this time (M. Vonhof, unpubl. data). This period was divided into 10 censuses of approximately equal effort, which always included one systematic survey of the entire study area. For each period, all bats in the population were coded as captured or not, and a data matrix of captures by survey period was constructed for use in CAPTURE.

We used the Monte Carlo simulation procedure in CAPTURE to test the performance of the different models for each subunit. Following Mowat & Strobeck (2000), each model was tested under arbitrary conditions of weak and strong heterogeneity, with and without time variation. The effect of behavioural variation was not investigated, as our systematic sampling regime and capture method did not result in behavioural variation in capture probabilities (see Results). We used simulated populations of 66, 162, and 48 animals for the Station, Cerro1 and Cerro2 subunits, respectively, 1000 iterations, and time variation as estimated by model M_t for our data. To mimic weak and strong heterogeneity, we varied capture probabilities and the number of individuals assigned each capture probability to create distributions of individual capture probabilities (heterogeneity) that had the same average capture probability as measured by model M_h (0.15, 0.17 and 0.32, respectively). The exact settings may be obtained from the authors. Models with consistently low coefficients of variation (CV), bias (percentage difference from the true population size), and mean width of the 95% confidence intervals, and high coverage (the proportion of replications in which the constructed 95% confidence interval contained the true population size) across a range of influences were assumed to provide a more accurate estimate of population size than those with high CV, bias and interval width, and poor coverage (Otis *et al.* 1978).

RESULTS

We checked 3173 rolled leaves for bats during censuses in 1998–99, and found 255 roosts. Roosts were found wherever *Heliconia* and *Calathea* plants were present (Figure 1), including within secondary forest (Station and Cerro1 subunits) and along the edge of primary forest (Cerro2) where plants occurred singly or in narrowly dispersed clumps, and in clearings and along the edges of roadways (Cerro1 and Cerro2) where there was an almost uniform distribution of plants.

Roost characteristics

Four *Heliconia* species, *C. inocephala*, banana plants (*Musa* spp.) and one unidentified plant species were used as roosts by *T. tricolor*. *Heliconia pogonantha* ($n = 134$ of 231 roosts identified to species) was by far the most commonly used species, followed by *C. inocephala* ($n = 39$), *H. latispatha* ($n = 32$) and *H. irrasa* ($n = 23$). Single roosts were found in *Musa* sp., *H. mariae* J. D. Hooker and an unknown plant species.

The mean diameter of the leaf opening was consistent across plant species, at approximately 7 cm (Table 1), but diameters of used leaves ranged from 3.5 cm to 27.6 cm. Differences in leaf length and plant height reflected interspecific differences in plant and leaf morphology, but there was also considerable intraspecific variation (Table 1). Roost leaves typically opened symmetrically from the top down, with both edges of the leaf peeling back from the centre, but 12 roosts (5%) were in leaves where one edge opened away from the central tube while the other edge remained coiled. With only two exceptions, roost leaves were intact at the base. There was no significant correlation between the size of the roosting group and roost volume, diameter of the opening, or leaf length within or across plant species (Spearman correlations: $P > 0.05$ in all cases).

Spatial roost availability

Based on systematic censuses, the density of rolled leaves on a given day ranged from 5.3–130.3 leaves ha^{-1} , with a mean of 43 leaves ha^{-1} (Table 2). However, the majority

Table 2. The overall density (number ha⁻¹) of tubular, unoccupied, and roost leaves, and bats, and roost occupancy in each year and subunit of the Caño Palma study area. Numbers refer to mean (SD).

Subunit	Year	No. of censuses	Total leaves	Unoccupied leaves	Roost leaves	Bats	Occupancy (%)
Station	1998	8	27.4 (13.7)	20.2 (11.0)	3.5 (1.8)	13.7 (6.9)	13.6
	1999	3	19.6 (16.8)	16.1 (15.5)	1.6 (0.5)	4.5 (4.1)	8.1
	Both	11	25.3 (14.2)	19.1 (11.7)	3.0 (1.5)	11.9 (7.3)	12.1
Cerro1	1998	17	60.2 (27.5)	54.1 (25.8)	2.7 (2.1)	10.6 (8.7)	4.0
	1999	5	51.7 (33.0)	48.2 (32.6)	0.6 (0.9)	2.8 (4.1)	1.1
	Both	22	58.3 (28.2)	52.8 (26.8)	2.2 (2.1)	8.8 (8.5)	3.5
Cerro2	1998	9	34.6 (9.1)	28.5 (9.9)	3.5 (1.3)	14.2 (7.8)	10.1
	1999	5	32.8 (12.4)	29.1 (11.9)	1.1 (1.1)	4.1 (4.7)	3.1
	Both	14	33.9 (9.9)	28.8 (10.2)	2.6 (1.7)	11.1 (7.3)	7.6
All	1998	34	45.7 (25.5)	39.4 (24.6)	3.1 (1.8)	12.3 (8.0)	6.5
	1999	13	37.0 (25.2)	33.5 (24.8)	1.0 (0.9)	3.6 (4.0)	3.1
	Both	47	43.3 (25.5)	37.7 (24.6)	2.5 (1.8)	10.2 (8.1)	5.7

of leaves searched on a given day were not occupied by bats (mean: 37 leaves ha⁻¹), and roosts occurred at relatively low densities (mean: 2.5 leaves ha⁻¹; Table 2). The overall occupancy rate of rolled leaves was 5.7%, ranging from 1.1% in the Cerro1 subunit in 1999 to 13.6% in the Station subunit in 1998 (Table 2). Typically a number of leaves contained bat faeces but no bats (mean \pm SD: 3.1 \pm 2.54, range: 0–9.3 leaves ha⁻¹), and were likely used as night roosts during the previous 24 h. The density of bats on a given day averaged 10 bats ha⁻¹ (Table 2), ranging from 0–33 bats ha⁻¹.

The total density of leaves and the density of unoccupied leaves differed significantly between subunits (total: $F_{2,43} = 12.3$, $P < 0.01$; unoccupied: $F_{2,43} = 15.9$, $P < 0.001$; Table 2), but observed differences between years were not significant (total: $F_{1,43} = 2.70$, $P > 0.1$; unoccupied: $F_{1,43} = 1.52$, $P > 0.2$). More rolled leaves were present in the Cerro1 subunit than in either the Station or Cerro2 subunits, which did not differ from each other. In contrast, both the density of roosts and the density of bats differed significantly between years (roosts: $F_{1,43} = 23.5$, $P < 0.001$; bats: $F_{1,41} = 19.1$, $P < 0.001$) but not subunits (roosts: $F_{2,43} = 3.05$, $P > 0.05$; bats: $F_{2,41} = 1.55$, $P > 0.2$). Lower densities of both roosts and bats were observed in 1999, and corresponded with a drop in occupancy rate (Table 2). The interaction between year and location was not significant for any of the dependent variables ($P > 0.05$ in all cases).

Roost permanency

After a period of slow change in top diameter, where the leaves mainly grew in length, developing leaves opened rapidly (Figure 2). Opening-rate equations always explained a significant proportion of the variation ($P < 0.05$ in all cases), and the average R^2 value was 0.947, ranging from 0.84–0.99. Based on these equations, leaves of all three species were available between the 95% confidence

limits of the diameter of known roosts for approximately 1 d, but there was a significant difference among the three species in temporal availability (Kruskal–Wallis test; $\chi^2 = 20.6$, $P < 0.001$, $df = 2$). *Heliconia latispatha* was available for the longest period (mean \pm SD, range: 16 \pm 6.2, 8–31 h, $n = 13$), followed by *H. pogonantha* (11 \pm 3.0, 6–17 h, $n = 18$), and *C. inocephala* (8 \pm 2.4, 5–14 h, $n = 22$; Figure 2). Alternatively, if we assumed that leaves were available to the bats if the diameter fell between ± 1 SD of the mean of known roosts (*C. inocephala*: 23 \pm 6.7, 13–41 h, $n = 24$; *H. irrasa*: 15 \pm 7.2, 4–25 h, $n = 12$; *H. latispatha*: 27 \pm 12.5, 9–57 h, $n = 19$; *H. pogonantha*: 44 \pm 15.6, 12–74 h, $n = 20$), or if we calculated the maximum time leaves were available as roosts (*C. inocephala*: 50 \pm 25.5, 10–124 h, $n = 24$; *H. irrasa*: 28 \pm 9.9, 9–50 h, $n = 19$; *H. latispatha*: 37 \pm 13.9, 13–76 h, $n = 20$; *H. pogonantha*: 60 \pm 19.2, 23–98 h, $n = 20$), the interspecific differences remained (± 1 SD: $\chi^2 = 32.7$, $P < 0.001$, $df = 3$; maximum time: $\chi^2 = 30.0$, $P < 0.001$, $df = 3$), as did the central conclusion that the leaves are available to the bats for a limited period of time.

Twelve per cent of the 100 leaves marked in the opening-rate surveys (9 *H. pogonantha* and 3 *C. inocephala*) were used as roosts. In one case, bats were present in the late afternoon in a *H. pogonantha* leaf, but had not been there in the morning. Another six opening-rate leaves (five *H. pogonantha* and one *H. irrasa*) contained faeces from the previous night and had been used as night roosts, and one *H. latispatha* leaf contained a group of night-roosting bats when checked opportunistically 1 h after sunset.

Population size

Censuses resulted in 927 captures of 308 adults, as well as 28 juveniles, during the two field seasons at Caño Palma. Eighteen adults were sampled more than once based on

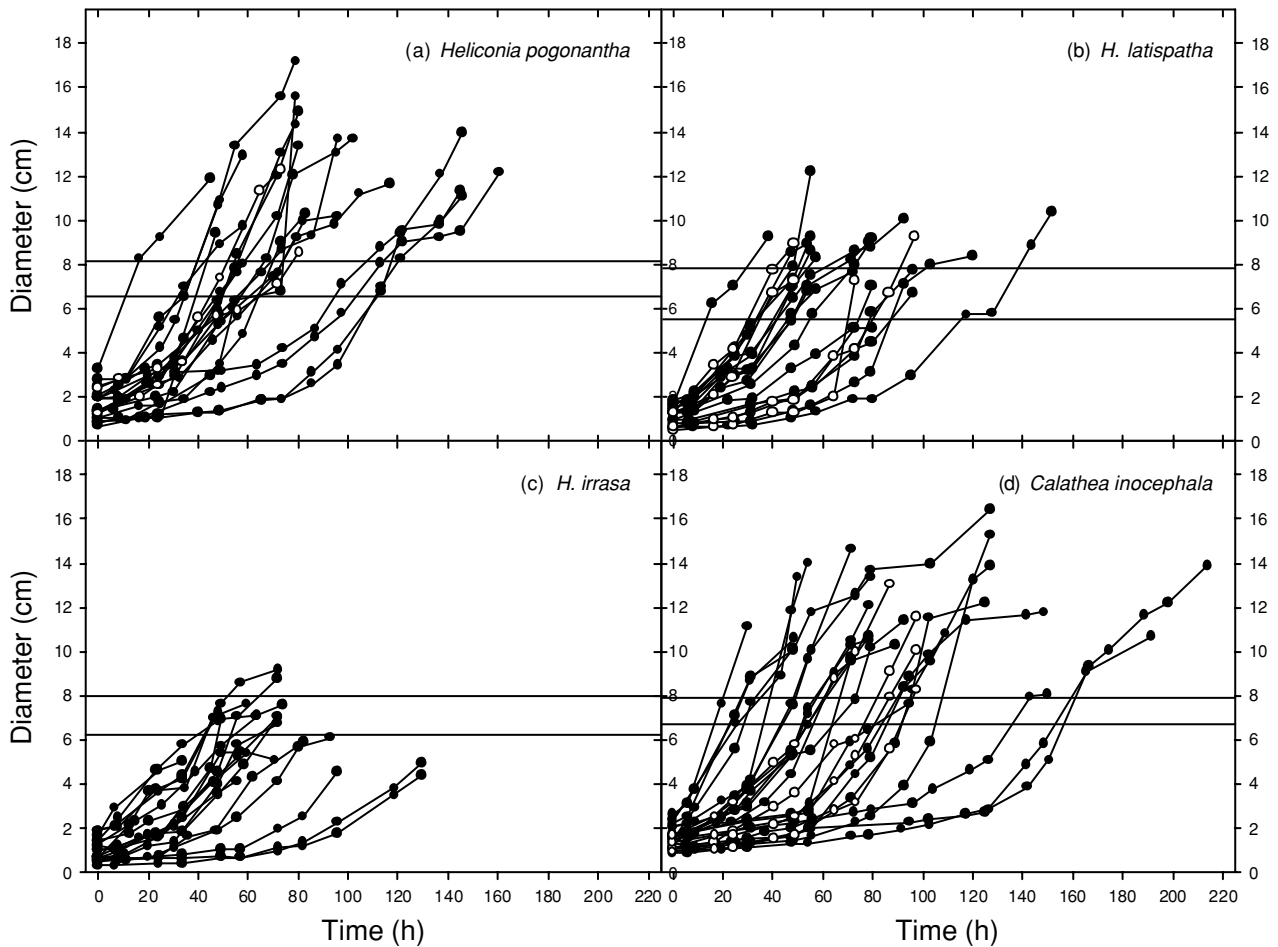


Figure 2. Growth rate curves of the diameter of the opening for leaves of the four most common plant species used as roosts by *Thyroptera tricolor*. The solid bars indicate the upper and lower 95% confidence limits of the diameter of known roosts. Closed and open circles represent leaves monitored in 1998 and 1999, respectively.

genetic identifications (Vonhof 2001), corresponding to a band-loss estimate of 6%.

Group sizes varied between 1 and 11, with a mean \pm SD size of 4.1 ± 2.07 individuals, and a modal size of five individuals ($n = 247$; Figure 3). The composition of groups was highly variable, from entirely female to entirely male. Of the 206 roosts (out of 255 total) in which all of the bats were captured, 12 roosts contained a single female and 8 contained a single male. A further 8 roosting groups were entirely female (4 roosts with 2 bats, 4 with 3 bats), and 12 groups were entirely male (9 roosts with 2 bats, 1 with 3 bats, 2 with 4 bats). The average proportion of females in mixed-sex roosting groups was 0.47 ± 0.16 ($n = 166$ groups), and the overall sex ratio in mixed-sex roosting groups (Replicated Goodness of Fit test; $G = 4.03$, $P < 0.05$, $df = 1$) and the entire population (Goodness of Fit test; $G = 4.28$, $P < 0.05$, $df = 1$) was significantly biased towards males. The proportion of females (or males) in a roosting group did not differ between subunits (Kruskal–Wallis; $\chi^2 = 3.50$, $P > 0.3$, $df = 2$) or censuses ($\chi^2 = 8.84$, $P > 0.3$, $df = 13$).

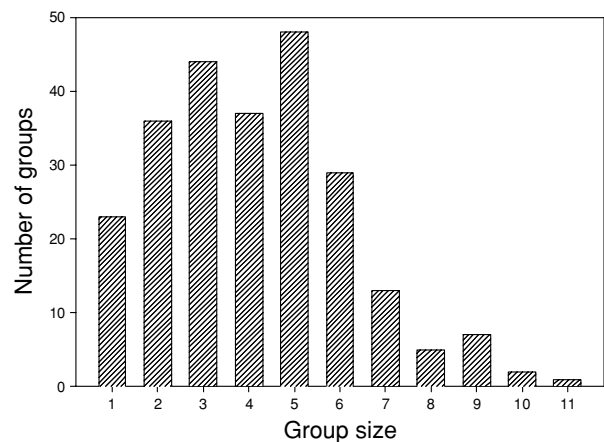


Figure 3. Distribution of the size of roosting groups of *Thyroptera tricolor*.

The capture histories for the 10 censuses of each subunit in 1998 are outlined in Table 3. There was considerable variation in the total number of bats captured in different census periods in all subunits (Table 3).

Table 3. Summary statistics for the 10 censuses of *T. tricolor* in February–May 1998 in each of the three subunits of the Caño Palma study area. Number caught is the total number of animals (marked and unmarked) captured during a census, newly caught is the number of unmarked animals in that sample, while cumulative marked is the cumulative number of marked animals in the population after the census in question. The value for cumulative marked in the 10th census is therefore the total number of unique individuals captured between February–May 1998. Proportion recaptures is the proportion of animals captured during a census that had been caught previously. Frequencies refers to the number of animals captured *j* times during the mark–recapture study, where *j* is the census period number.

	Census period									
	1	2	3	4	5	6	7	8	9	10
<i>Station</i>										
Number caught	26	17	12	33	14	10	4	30	12	30
Newly caught	26	4	0	13	4	2	0	7	0	0
Cumulative marked	26	30	30	43	47	49	49	56	56	56
Proportion recaptures	–	0.76	1.0	0.61	0.71	0.80	1.0	0.77	1.0	1.0
Frequencies	15	2	13	11	6	7	2	0	0	0
<i>Cerro1</i>										
Number caught	19	15	18	32	52	36	24	18	34	0
Newly caught	19	13	10	16	33	14	12	1	9	0
Cumulative marked	19	32	42	58	91	105	117	118	127	127
Proportion recaptures	–	0.13	0.44	0.5	0.37	0.61	0.5	0.94	0.74	–
Frequencies	48	49	21	6	3	0	0	0	0	0
<i>Cerro2</i>										
Number caught	18	26	10	24	20	5	20	25	5	10
Newly caught	18	18	3	4	4	0	0	2	0	0
Cumulative marked	18	36	39	43	47	47	47	49	49	49
Proportion recaptures	–	0.31	0.7	0.83	0.80	1.0	1.0	0.92	1.0	1.0
Frequencies	5	10	11	16	3	2	2	0	0	0

Individuals were always captured within the subunit in which they had originally been banded. The number of newly captured (unbanded) bats relative to the total number of captures decreased rapidly, and was clearly reaching an asymptote in the Station and Cerro2 subunits by the end of field work in 1998 and into 1999 (Figure 4). By the 5th or 6th census period virtually all individuals had been captured at least once in these subunits (Table 3), suggesting that the majority of individuals in the population had been captured and marked. In contrast, the proportion of recaptures was highly variable (Table 3), and the number of newly captured bats did not reach a clear asymptote (Figure 4) in the Cerro1 subunit. Because the subunits had different capture histories, and we never observed the movement of individuals between subunits, they were treated independently in population size analyses.

Estimates of population size varied widely for the Station and Cerro1 subunits, ranging from 56–121 animals (Table 4), based on the capture of 56 animals (Table 3) for the Station subunit, and from 146–674 (Table 4) based on the capture of 127 individuals (Table 3) for the Cerro1 subunit. In contrast, all of the population estimates for the Cerro2 subunit fell between 49–51 individuals, based on the capture of 49 individuals (Table 4), suggesting that virtually all individuals in this subunit were captured during the censuses. Assuming model M_h –jackknife, male and female average capture probabilities were similar in all subunits (Station: males: 0.15, females: 0.19; Cerro1:

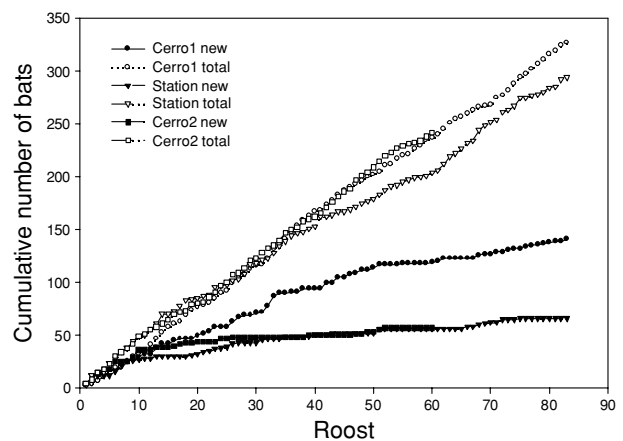


Figure 4. The cumulative number of bats (open symbols) and newly captured bats (closed symbols) captured in the Station, Cerro1 and Cerro2 subunits as new roosts were located in 1998–99. The first 66, 71 and 45 roosts were found in 1998 in the Station, Cerro1 and Cerro2 subunits, respectively.

males: 0.14, females: 0.17; Cerro2: males: 0.30, females: 0.28) when analysed separately, and the assumption of closure was met in the Station and Cerro2 subunits (Station: $Z = 1.54$, $P > 0.9$; Cerro2: $Z = -0.21$, $P > 0.4$), but not the Cerro1 subunit ($Z = -2.87$, $P < 0.001$).

The model selection procedure in CAPTURE detected significant variation in capture probabilities due to time in all three subunits, and either M_t (Station) or M_{th} (Cerro1,

Table 4. Population estimates of *T. tricolor* at Caño Palma Biological Station in north-eastern Costa Rica in February–May 1998, using eight closed mark–recapture models in the program CAPTURE. Estimates for the Station and Cerro2 subunits are based on 10 censuses, whereas those for the Cerro1 subunit are based on the first nine censuses only. Model M_{bh} –Removal failed in all cases. Model M_o assumes equal individual capture probabilities. Other models account for variation in individual capture probabilities (heterogeneity – model M_h), between capture sessions (time– M_t), a behavioural response to capture (behaviour – Model M_b), or various combinations of these effects.

Model	Station			Cerro1			Cerro2		
	Estimate	SE	95% CI	Estimate	SE	95% CI	Estimate	SE	95% CI
M_o – Null	56	1.05	56–62	151	6.99	142–169	49	1.00	49–55
M_h – Jackknife	121	25.15	88–191	167	9.59	153–190	51	3.21	50–68
M_h – Chao	112	49.82	69–305	151	8.99	139–175	50	1.63	50–57
M_b – Zippin	57	1.57	57–64	222	54.36	161–396	49	0.47	49–49
M_t – Darroch	56	0.34	56–58	150	6.53	140–166	49	0.34	49–51
M_t – Chao	79	18.62	62–148	146	7.60	137–167	50	1.19	50–55
M_{th} – Chao	65	4.87	60–80	150	7.47	140–169	50	1.55	50–57
M_{tb} – Burnham	67	11.00	59–112	674	973.59	180–5813	49	0.70	49–49

Cerro2) were identified by the model-selection procedure as the best-fitting models. Significant heterogeneity in capture probabilities was detected for the Station subunit only, and behaviour effects were not detected for any subunit. Based on low bias combined with low CVs and a high per cent coverage relative to width of the confidence intervals during Monte Carlo simulations (see Methods; detailed results are available from the authors), we selected M_{th} as the best-fitting model for the Station subunit, and M_t –Chao as the best model for the Cerro1 and Cerro2 subunits. Using the point estimates from these best-performing models for each subunit, there were 65, 146 and 50 individuals, corresponding to densities of 34.6, 44.6 and 54.3 bats ha^{-1} , in the Station, Cerro1 and Cerro2 subunits, respectively. Overall, in the entire study area, there were 261 individuals, or 43 bats ha^{-1} , in February–May 1998.

DISCUSSION

Population size

The 5.69-ha Caño Palma study area supported a high density of bats. Based on mark–recapture data, the estimated population size of *T. tricolor* in February–May 1998 was 261 individuals, and over the course of two field seasons we captured 336 individuals. The high population size in this small area translates into a high density of bats (43 bats ha^{-1} in spring 1998), despite the low rate at which available rolled leaves were occupied. Although differences in methods and scope prevent an in-depth comparison, our overall density estimate is almost double the 21.9 bats ha^{-1} for *T. tricolor* provided by Findley & Wilson (1974) in south-western Costa Rica.

Several factors may influence the accuracy of closed-population mark–recapture estimators, including model

choice, sample size, number of trapping occasions, overall capture probabilities, and whether the assumptions of the models have been met (Manning *et al.* 1995, Menkens & Anderson 1988, Pollock *et al.* 1990, White *et al.* 1982). The choice of models influences the size and accuracy of the population estimate, and, in turn, is influenced by the relative magnitude of the different sources of variation (behaviour, time and heterogeneity) present in the data. Although many studies have detected significant heterogeneity in individual capture probabilities (Boulanger & Krebs 1994, Corn & Conroy 1998, Greenwood *et al.* 1985, Hallet *et al.* 1991), we found heterogeneity only for the Station subunit population, and there it was weak. Differences in behaviour between males and females are often a source of heterogeneity in capture probabilities, but our systematic sampling regime and a capture method that did not rely on an individual's choice to enter a trap minimized this source of variation. Furthermore, capture probabilities of males and females were similar in all subunits, and, although consistently male-biased, no differences in sex ratio within captured groups between sampling periods was observed, suggesting that males and females were equally likely to be captured at all times. Despite capturing bats within roosts, we found no evidence of negative or positive behavioural influences (trap-shy or trap-happy), and the numbers and proportions of recaptures actually increased as sampling progressed in all subunits. Although models including heterogeneity (M_h , M_{bh} , M_{th}), particularly M_h –Jackknife, are typically the most reliable, and least affected by other sources of variation, such as behaviour or time (Boulanger & Krebs 1994, 1996; Manning *et al.* 1995, Otis *et al.* 1978), especially when population size is large (Manning *et al.* 1995), differences in mean capture probabilities among censuses were correctly identified by the model-selection procedure as the dominant source of variation in our data for all subunits. The results of our simulations indicated that for our data sets, models

including time variation (M_t – Chao and M_{th} – Chao) provided the most accurate estimates of population size under conditions of weak and strong heterogeneity, both with and without time variation, highlighting the necessity of testing the selected models with a range of conditions using simulations for each data set.

Increasing the number of capture sessions, and sample sizes within sessions, typically increases the accuracy and precision of population estimates (Koper & Brooks 1998, Manning *et al.* 1995). Constraints imposed by the methods or behaviour of the target animals mean that many population estimates using mark–recapture methods are based on a small number of captures in a limited number of capture sessions (Greenwood *et al.* 1985, Koper & Brooks 1998, Mowat & Strobeck 2000). The accuracy of estimates is further eroded by low mean capture probabilities, particularly when sample sizes are low (White *et al.* 1982). In contrast to many other studies, our population estimates were based on a relatively large number of censuses (10), and a high capture rate (typically > 15% of the total estimated population within each session). By the 10th session we had captured virtually all of the animals in the Cerro2 and Station subunit populations, thereby providing more precise and accurate estimates (Alexander *et al.* 1997). The quality of data also likely countered the negative effect of the low mean capture probability and small population size (White *et al.* 1982) on the accuracy of the estimate in the Station subunit. Although we clearly captured a smaller proportion of the population, and mean capture probability was also low in the Cerro1 subunit, our estimates for the population there were still relatively precise, with small standard errors and narrow confidence intervals.

Demographic closure in this study was ensured, in part, by restricting surveys used for population estimation to the dry season, when no births took place (Vonhof 2001; see also Wimsatt & Enders 1980). Deaths, immigration and emigration likely had little effect on our analyses, as our sampling period was short, we captured few new individuals after the first month of sampling, and the number of recaptures remained consistently high for the rest of the sampling period. The assumption of geographic closure was likely met in the horizontal dimension, as the study area was largely surrounded by unsuitable habitat, the ocean on one side and closed-canopy forest with a low density of *Heliconia* and *Calathea* plants on two of the other three. Although there were *Heliconia* plants in the forest to the south of the Cerro2 subunit, movements of banded bats were always within subunits, suggesting that individuals rarely move out of the small patch of forest they inhabit for the purposes of roosting. A small number of roosts (12) were found outside of the boundaries of the study area during opportunistic searches, but with only two exceptions these roosts always

contained individuals not previously captured within the areas normally searched.

Despite demographic and geographic closure, the density of bats during systematic censuses was far lower than our estimate based on mark–recapture analysis, indicating that we did not capture all individuals during each survey. Although we made every effort to systematically locate and check all available leaves during our censuses, and the rolled leaves are quite conspicuous, we may have missed a small number of roosts. However, this likely did not occur commonly enough to account for all of the bats missed. *Thyroptera tricolor* sometimes uses roosts other than rolled leaves, for example in pendant dead leaves of *Phenakospermum guyannense* (Strelitziaceae; Simmons & Voss 1998). Although we regularly checked dead leaves, we never found *T. tricolor* roosting in leaves of this type. We did, however, regularly observe bats flying during the day in the areas we were searching, presumably because of disturbance even when we had clearly not encountered any suitable rolled leaves. On several occasions, we observed individuals landing on the underside of open *Heliconia* leaves after disturbance of their roost leaf, and we made similar observations of light-tagged individuals night-roosting on the underside of open leaves while foraging at night (M. Vonhof, unpubl. data). In addition, on one occasion, a single *T. tricolor* was disturbed from its roost on the underside of an open leaf in a clearing at the beginning of a census (M. Vonhof, unpubl. data), when we clearly could not have previously disturbed any bats in their original roost.

If the use of the underside of leaves or dead leaves is a common feature of the roosting behaviour of *T. tricolor*, then these bats may occur in habitats previously considered unsuitable, such as those with low densities of *Heliconia* or *Calathea* plants, or in the foliage of subcanopy or canopy trees. The use of such roosts could have affected the accuracy of our population estimates in three ways. First, the use of alternate roosts could have been responsible for a lack of closure in either the horizontal (but see discussion above) or vertical dimension, resulting in inflated population estimates (White *et al.* 1982). Second, if some individuals in the population never use rolled leaves as roosts, then they would have entirely escaped detection, and we would have underestimated population size. Third, if we assume that all individuals used rolled leaves at some point, differences in the frequency with which they use alternate roosts may account for heterogeneity in individual capture probabilities despite the fact that we sampled available rolled roosts systematically. However, heterogeneity in individual capture probabilities was detected in one subunit only, and then only weakly, arguing against individual differences in the use of alternate roost-sites. The degree to which each of these factors influenced

our population estimates cannot be assessed without determining the extent of use of alternate roosts by *T. tricolor*.

Availability of rolled leaves

We found that *T. tricolor* occupied rolled leaves at a density of 2.5 rolled leaves ha⁻¹, representing 5.7% to 12% of the available leaves, depending on the method of estimation. These results suggest that *T. tricolor* is not roost-site limited in our study area (cf. Humphrey 1975), and, in fact, only uses a small proportion of available leaves. However, there are a number of reasons why these data may not demonstrate that roost availability does not limit local populations of *T. tricolor*. First, all of the rolled leaves examined may not have been suitable for roosting bats, because of their size, microclimate or exposure to rain or sunlight. Nevertheless, there was considerable variation in the dimensions of occupied leaves and the microhabitats they occurred in, and approximately 5% of roost leaves had growth defects, suggesting that *T. tricolor* is flexible in its use of roosts, and could have made use of the majority of leaves searched. Second, on any day, roosting *T. tricolor* may use more than one leaf roost, because of unfavourable conditions or disturbance, as demonstrated by the afternoon movement of bats into a leafroost not occupied in the morning. Furthermore, over a day, the rapid growth rate of leaves could render a roost unsuitable, obliging the bats therein to move. However, changing roosts during the day presumably comes at the cost of increased exposure to diurnal predators, such as hawks and falcons (Fenton *et al.* 1994), and individuals are likely under pressure to select leaves that will provide them with a roost-site for the duration of the roosting period. Third, disturbance of roosting bats may have caused them to emerge from one roost and move to another without detection, a hypothesis which is difficult to assess, but was unlikely in our study because of the presence of multiple observers searching small areas of habitat. The high density of rolled leaves is counterbalanced by the short time that any one is suitable for use by roosting bats (on average 8–16 h, maximum longevity of 28–60 h, depending on the plant species and method of estimation). Individual plants typically produce only one new leaf at a time, at intervals of at least 2 wk (Vonhof 2001), and therefore individual bats require access to a moderate number of plants (> 15–20) to meet their roost requirements over time.

The plants used by *T. tricolor* (*Heliconia* and *Calathea*) are typically found in natural or disturbed habitat where canopy cover is not complete (Seifert 1982, Stiles 1975). As such, there is considerable spatial variation in the availability and density of suitable habitat on a landscape scale. This variation is influenced by the

size and distribution of habitat disturbance and natural openings, which, in turn, are likely to determine the distribution of *T. tricolor*. The Caño Palma study area was an island of suitable habitat surrounded by vast stretches of unsuitable habitat, with ocean to the east, swamp forest to the north and west, and cleared agricultural areas some distance to the south. Although *Heliconia* and *Calathea* plants occurred in small patches along some rivers and tree-fall gaps, our study area was atypical in terms of the area of suitable habitat, and may thus have had an unnaturally high density of plants and bats. Similarly, plant density may also vary over time, with initially high densities following disturbance tapering off as succession proceeds and canopy cover increases. For example, even over the course of our 2-y study, we observed a decrease in the density of leaves and roosting bats between years, as well as considerable changes in the quality of habitat as new openings were created or became overgrown. Thus, the local abundance of available habitat at Caño Palma during our study, largely due to recent land-clearing activities, may be temporary. If the presence of *T. tricolor* is tied to the presence of rolled leaves, then the lower limit of fluctuations in the density of suitable leaves is likely to determine maximum sustainable population size in a given area. Therefore, the distribution and abundance of *T. tricolor* is likely to depend both on the distribution of suitable habitat at a landscape scale, and on the local dynamics of the population of rolled leaves.

The estimation of roost availability is complicated by the presence of different habitats within the study area, because the growth and density of *Heliconia* and *Calathea* plants may be much higher in clearings and tree-fall gaps where the canopy has been removed (Horvitz & Schemske 1994, Stiles 1975). The high density of rolled leaves in the Cerro1 subunit relative to the other two subunits reflected the number of cleared areas and the presence of a roadway, but did not translate into significantly greater densities of roosts or bats. The prediction that *T. tricolor* uses only rolled leaves in shaded forest (Findley & Wilson 1974, Villa-R. 1966) was not supported in this study, as we regularly found bats roosting in rolled leaves that were fully exposed to direct sunlight and rain. Therefore, the concentration of plants along edges and in clearings in the Cerro1 subunit is unlikely to have resulted in the relatively lower occupancy rate and bat density observed.

The marked decrease in the density of roosts and roosting bats between 1998 and 1999 did not correspond to a decrease in the density of unoccupied leaves, and could reflect three factors. First, massive flooding in the entire region in November 1998 (R. Ballard, *pers. comm.*) inundated the understory for almost 2 wk. This flooding may have reduced the population of *T. tricolor* either through direct mortality, via the temporary loss

of roost-sites or foraging habitat, or changes in prey abundance. Second, succession-driven changes in the plant community may have decreased the availability of roost-sites. In Cerro1 in particular, patches of *Heliconia* were eclipsed by fast-growing tree (mainly *Cecropia* spp.) and shrub species, and many *Heliconia* plants became completely surrounded by other vegetation. Although these plants still produced rolled leaves, their decreased conspicuousness and the increased amount of vegetation surrounding them may have reduced their use by *T. tricolor*. Third, disturbance associated with our regular censuses and captures may have decreased survivorship or increased emigration. Had this been the case, however, we would have expected an immediate decrease in the overall numbers of captures and recaptures in the first 4 mo of our study. We found no such consistent trends in overall captures per census, and the proportion of recaptures actually increased over time.

Conclusions

In the only other study to estimate population density for a tropical bat species using mark-recapture techniques, Leigh & Handley (1991) estimated the density of Jamaican fruit bats, *Artibeus jamaicensis*, at 200 bats km⁻² (= 2 bats ha⁻¹) using captures in mistnets on Barro Colorado Island, Panama. Although the methods behind the estimate are problematic, based on well-documented biases associated with captures in mistnets (Kunz & Kurta 1988), if taken at face value their estimate translates into a biomass of 80 g ha⁻¹ of *A. jamaicensis*, compared with 172 g ha⁻¹ of roosting *T. tricolor* (based on our average density estimate from spring 1998 and a mean adult body mass of 4.0 g; M. Vonhof, unpubl. data). *Artibeus jamaicensis* was the most commonly captured bat in mistnets on BCI, Panama, with 8907 individuals marked in a 4-y period (Leigh & Handley 1991), and if their estimate of density based on mistnet captures is accurate, *T. tricolor* may occur at densities over an order of magnitude higher. Aside from other leaf- (Brosset 1976, Happold & Happold 1990) or tent-roosting species (Brooke 1990, Kunz & McCracken 1996, Timm 1987), unbiased sampling regimes may be difficult to apply to other bat species. This situation raises the question of how to determine which bats are common, the answer to which could strongly affect our views of bats and their conservation status (Hutson *et al.* 2001).

While captures in mist nets indicate that *A. jamaicensis* is a common species at many neotropical sites, *T. tricolor* is rarely captured in mistnets, and is considered to be a rare component of the mammalian fauna in studies on community structure and mammalian diversity throughout the neotropics (see review in Voss & Emmons

1996). In practice, studies on community structure that estimate relative abundance, animal biomass, or vertical distribution make the assumption that the numbers of bats captured in mistnets is equivalent to their absolute abundance in the area sampled (Arita 1993, Kalko *et al.* 1996, Lim & Engstrom 2001, Medellín *et al.* 2000, Simmons & Voss 1998, Voss & Emmons 1996). The apparent ability of *T. tricolor* to avoid mistnets may result in misleading or erroneous conclusions as to their presence and/or abundance. For example, despite the large population size and high density of *T. tricolor* at Caño Palma, only two individuals were captured in mistnets out of 142 bats, in 121 mistnet-hours over 18 nights in 1999 (D. Riskin, *pers. comm.*). Although limited in scope, the mistnetting data would have led to the conclusion that *T. tricolor* is rare in the study area, and the estimate of biomass would have been 130 times smaller than one based on searching for roosts in the same study area. Searches of roosts have been included in some studies (Simmons & Voss 1998), but are generally used only for species presence, as effort often cannot be standardized in the same way as for mistnets. Our results indicate that the difference between perceived and actual abundance needs to be better appreciated in studies on bat community structure and rarity.

Having said this, we do not argue that *T. tricolor* is abundant wherever there are rolled leaves. It appears that *T. tricolor* is very local in its distribution, and intensive surveys at 11 sites in Costa Rica and Panama across a range of elevations and habitats containing *Heliconia* or *Calathea* plants yielded only three other populations (M. Vonhof, unpubl. data). Furthermore, all of the sites in which we have found *T. tricolor* have been dominated by forested habitat, and *T. tricolor* was completely absent from large clearings and landscapes dominated by agriculture, even when the abundance of suitable rolled leaves was high. Although we regularly observed *T. tricolor* roosting in previously cleared areas with little or no canopy cover at Caño Palma, these clearings were small in size (< 1.2 ha), and were always adjacent to forest on at least two sides. Thus, it is unlikely that they will be associated with large cleared areas or habitats and landscapes not dominated by forest. Clearly, more surveys involving searches for roosts are required to better characterize the distribution of *T. tricolor* in different habitats within its range.

The use of spatially abundant but impermanent roosts likely influences other aspects of the biology of *T. tricolor*, such as their social organization, mating system, home range, and foraging behaviour. The combination of large population size, abundant potential roosts but low actual roost-site density, and low permanency of those roosts may limit the opportunity for *T. tricolor* to maintain stable social relationships with other individuals in the population. This may lead to a more fluid social structure

than reported for bats using more permanent, rarer structures (references in McCracken & Wilkinson 2000). Alternatively, if individuals remain faithful to a patch of suitable habitat, they may be able to rally with other group members by searching the available leaves in that patch. This may permit the maintenance of stable relationships among group members, assuming there is some benefit to doing so, and predicts that roosting home ranges will be small.

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