

Reproduction and growth in a Neotropical insectivorous bat

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Even though there is an abundance of data regarding the reproductive biology and postnatal growth of bats, comprehensive data on life history is still lacking for most species, particularly for rare families that have unique behavioral and ecological adaptations. In this study we provide a description of reproductive seasonality and length of reproductive activities such as gestation and lactation for *Thyroptera tricolor*, a small (3–4.5 g) Neotropical insectivorous bat and one of only four species in the family Thyropteridae. In addition, we also describe postnatal development, including growth rates and the onset of flight. Our results show that *T. tricolor* has long gestation (at least 3.5 months) and lactation (4 months) periods within a single annual reproductive event. Young are capable of sustained flight at two months of age, and attain adult forearm length at age 90 days and adult body mass at age 120 days. Offspring mortality was high, with 28% of young dying before age five months. Surviving young remained with their mother and natal group for at least one year. In addition, our field observations suggest that males attained sexual maturity earlier than females, at one year of age, while females became sexually active after their first year. These findings suggest that, among bats, *T. tricolor* may have an unusually slow life history, which could be attributed in part to its unique roosting ecology and social behavior.

Key words: gestation, lactation, life history, post-natal growth, reproduction

INTRODUCTION

The study of life histories encompasses all significant features of the life cycles of an organism, particularly as they relate to survival and reproduction. Life history characters include those associated with age-specific schedules of birth and death, such as phenology of reproduction, sex ratio, litter or clutch size, longevity, and number of litters, and those that include characters related to development, such as size of young at birth, stage of development at birth, growth rates, body size, and allometry (Roff, 2002). Optimization of these life history traits is ruled by the principle of allocation, which states that organisms must divide the energy available among reproduction, growth, and maintenance (Gadgil and Bossert, 1970). For example, nutritionally constrained juveniles allocate their scarce resources solely to maintenance, thus sacrificing growth (Wayne *et al.*, 1991; Woods and Armitage, 2003; Strauss *et al.*, 2007). Moreover, species time their reproductive activities to periods of greater resource abundance (Bronson, 1985), and may forego reproduction entirely during years when resource

abundance declines significantly (Guinet *et al.*, 1998; Chapman *et al.*, 2007).

Mammalian life histories are constrained not only by phylogeny and body size (Stearns, 1983), but also by features unique to this taxon, such as lactation (Pond, 1977; Dall and Boyd, 2004). Phylogeny places historical constraints that limit alternative directions for adaptation (Cheverud *et al.*, 1985), and body size may explain variation in gestation length, age of maturity, life span, and litter size within mammals (Stearns, 1983). Lactation forces extended periods of parental care, and imposes high energy, protein, and calcium demands on the mother (Speakman, 2008), thus limiting certain characters of mammalian life history evolution, such as litter size and rates of post-natal growth. Despite these constraints, mammals exhibit a great diversity in life history characters such as litter size, longevity, size of young at birth, and body size, as well as other differences in behavioral, physiological and anatomical adaptations (Feldhamer *et al.*, 2007).

Bats comprise the second largest mammalian order, and are unique among mammals in their ability to fly. They are also one of the most social and

diverse orders, and many of their life-history traits do not conform to typical mammalian patterns (Jones and MacLarnon, 2001; Barclay and Harder, 2003). For example, compared to similarly sized mammals such as shrews, insectivorous bats have significantly smaller litters, longer gestation and lactation periods, attain sexual maturity later, and have a lifespan that averages over 10 times that of shrews (Barclay and Harder, 2003). Thus, while most small mammals have life histories characterized by rapid reproduction and high mortality (Promislow and Harvey, 1990), bats have a life history characterized by extended longevity with multiple reproductive events, low litter size, and delayed onset of sexual maturity (Gaisler, 1989).

Although there is some information regarding the reproductive biology and postnatal growth of bats (reviewed in Crichton and Krutzsch, 2000), data are still lacking for most species. For example, life history events such as birth mass, gestation and lactation length, as well as age at maturity and longevity are only known for approximately 38% of all bat species (Barclay and Harder, 2003). Of those species studied to date, only partial data on life history traits are available, and the amount of information available per family varies considerably, with most data collected from larger families such as Pteropodidae, Vespertilionidae, and Rhinolophidae. Other speciose families such as Phyllostomidae, along with small families containing a low number of small-bodied species (e.g., Craseonycteridae, Natalidae, Furipteridae, Thyropteridae, Myzopodiidae), are very poorly known in general. Given their evolutionary histories, rare families have the potential to explain life history variation in bats independent of phylogenetic affiliations (Dobson, 1983). Some of these rare families, such as the disc-winged bats Thyropteridae, also have unique ecological and behavioral traits, which may affect life history evolution by changing production and/or mortality rates (Sibly and Brown, 2007). Thus, in order to increase our understanding of life history variation in bats, we provide the first description of the reproductive patterns of one of the four species of the New World family Thyropteridae, *Thyroptera tricolor*, specifically focusing on reproductive seasonality, and length of reproductive activities such as gestation and lactation. In addition, we also describe postnatal development, particularly regarding growth rates and the onset of flight. Given its small size (4 g), we expect age-specific schedules of birth and death and characters related to development to differ little between *T. tricolor* and other bats of comparable body

mass. However, life history evolution is not only subject to a size-dependent constraint, but also to an additional axis corresponding to lifestyle (Sibly and Brown, 2007). Thus, given the unique roosting and social ecology of this species, where very stable mixed-sex groups use exceptionally ephemeral roosts (Findley and Wilson, 1974; Vonhof and Fenton, 2004; Vonhof *et al.*, 2004), we anticipate differences among *T. tricolor* and other insectivorous bats in some of the life history traits addressed in this study, such as gestation period, offspring size, and age at maturity.

MATERIALS AND METHODS

Our study was conducted in and around the Golfito Wildlife Refuge (GWR) and Piedras Blancas National Park (PBNP), in South-western Costa Rica. The GWR is comprised of 2,810 ha, and the PBNP is comprised of 14,025 ha. Dense tropical broad-leaved evergreen lowland forests predominate in this area of the country, but other habitats such as pasturelands, mangroves, forest plantations, agricultural crops and human settlements are also common (Kappelle *et al.*, 2002). All sites surveyed within the GWR and PBNP were located on or near streambeds, and while some of these sites were located within primary forests, others were located in secondary forests with constant human disturbance, or were located in primary forests immediately surrounded by pasturelands. Some of the sites surveyed had an understory dominated by large patches of *Heliconia imbricata* and *Calathea lutea*, although others had sparse *Heliconia* spp. and *Calathea* spp. shoots.

We performed systematic surveys of tubular leaves at 16 study sites from August 2006 through April 2008. Most of these sites were only surveyed once, while five sites were surveyed an average of twice a month. Surveys at these five sites increased in frequency (up to once every week) during the parturition period. Bats were captured in all identified roosts by pinching the top of the leaf and directing them into a cloth-holding bag. They were then fitted with individually numbered metal wing bands, sexed, aged, and their reproductive condition was assessed. We used three age categories to classify individuals: juveniles, subadults, and adults. Bats were classified as juveniles if their ventral pelage was gray, if we observed the presence of cartilaginous epiphyseal plates in metacarpals and phalanges (Anthony, 1988), or if the individual was suckling. In addition, young with an umbilicus attached were classified as 1-day-old pups. Individuals were classified as subadults if they were already weaned (i.e., no females in the same roosting group were lactating), if their ventral pelage was white, and if there were no signs of reproductive activity, such as testicular descent or an increase in the size of the testes, which is associated with the growth of the seminiferous tubules and spermatogenesis in males, or a bare patch and enlarged keratinized nipples, which indicate parity in females (Racey, 1988). If there was evidence of current (i.e., enlarged testes, pregnancy, or lactation) or previous (i.e., testicular descent, keratinized nipples) reproductive activity, individuals were classified as adults. Adult females were classified as being pregnant if distension of the female's lower abdomen was present and if a fetus was also palpable; lactating if they had enlarged nipples which upon

palpation expressed milk (Racey, 1988); and post lactating if they had a swollen nipple similar to lactating females, but from which milk could not be expressed. Reproductive activity in adult males was presumed by presence of enlarged descended testes, even though seasonal testicular descent corresponding with seasonal spermatogenesis is not always observed in all species of bats (Racey, 1988). Emergent flight patterns of juveniles were determined as follows: 1) flapping occurred when young bats beat their wings as the researchers moved their arms in a downward motion while holding the bat; 2) short flight occurred when young were able to travel short distances (i.e., < 10 m) without having to land on a surface; and 3) sustained flight occurred when individuals were capable of flying long distances (i.e., > 10 m) without having to land on a surface.

We calculated average body mass and length of forearm for all sampled bats, and tested for a significant difference in body size among males and females using an independent samples *t*-test. Percent neonatal and juvenile body mass and length of forearm were then estimated as the average of young divided by the average of maternal post-parturition and pre-copulation (i.e., before pregnancy) body mass and length of forearm, multiplied by 100. This allows us to determine gestation effort, in addition to post-natal growth rates. To determine post-natal growth rates of juvenile bats, we first needed to estimate the date of birth of juvenile bats. We calculated growth rates of bats of known birth date (the reference bats, or RB) that had been frequently recaptured during the first 50 days after birth, and used linear regression to fit the growth curve for body mass. We then estimated the age of other juveniles whose birth date was unknown by comparing the first capture measurement of body mass with the RB's growth curve. We used the estimated age at first capture to draw empirical growth curves for mass and length of forearm for males and females. SPSS version 10 (SPSS Inc., Illinois, U.S.A.) was used in all statistical analyses, and significance was assessed at an alpha of 0.05. Values are given as $\bar{x} \pm SD$.

RESULTS

Reproductive Biology

We captured and marked a combined total of 432 individuals at our study sites, and recapture frequencies ranged from 0 to 16. Thus, including recaptures, we performed a total of 1556 captures during the study period of 21 months. Average body mass of the adult population was 3.89 g (± 0.25 , range 3.4–4.7, $n = 313$), and the body mass of females (4.00 ± 0.39 g, range 3.6–4.7, $n = 160$) was significantly larger than that of males (3.71 ± 0.24 g, range 3.4–4.3, $n = 153$; $t = 8.66$, $d.f. = 311$, $P < 0.001$). Mean length of forearm for all bats captured was 35.90 mm (± 0.78 , range 33.80–38.00). Females had significantly larger lengths of forearm (36.24 ± 0.65 mm, range 33.80–38.00) than males (35.54 ± 0.74 mm, range 33.80–37.20; $t = 8.76$, $d.f. = 311$, $P < 0.001$).

Males with enlarged testes were observed year-round (Fig. 1), although were more common during the second half of the year, starting in August. Pregnant females were first observed in December, and were observed until the month of April (Fig. 2). All adult females were pregnant during the month of January, and we did not observe any adult females that did not reproduce (Fig. 2). The first lactating females were observed in February, and in April 84% of females were lactating ($n = 44$). By June, a large

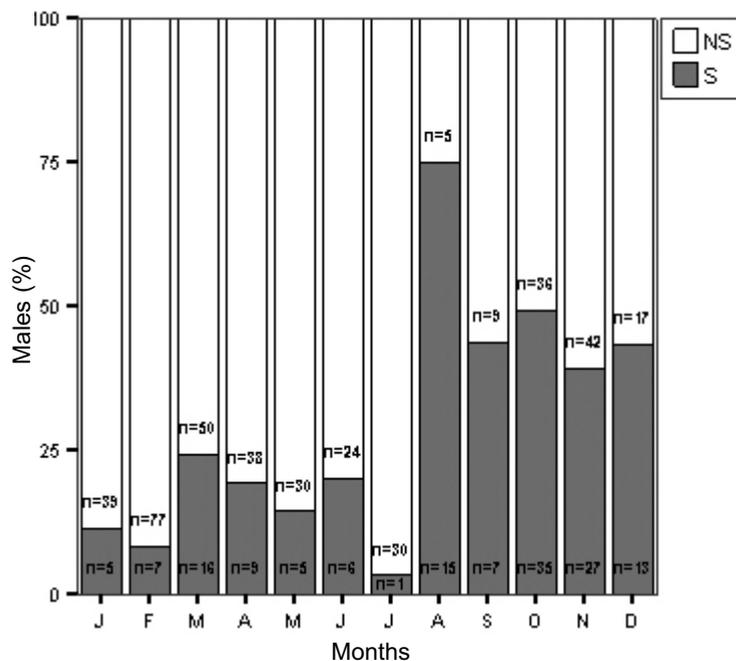


FIG. 1. Percent of males captured each month that were either scrotal (S) or non-scrotal (NS)

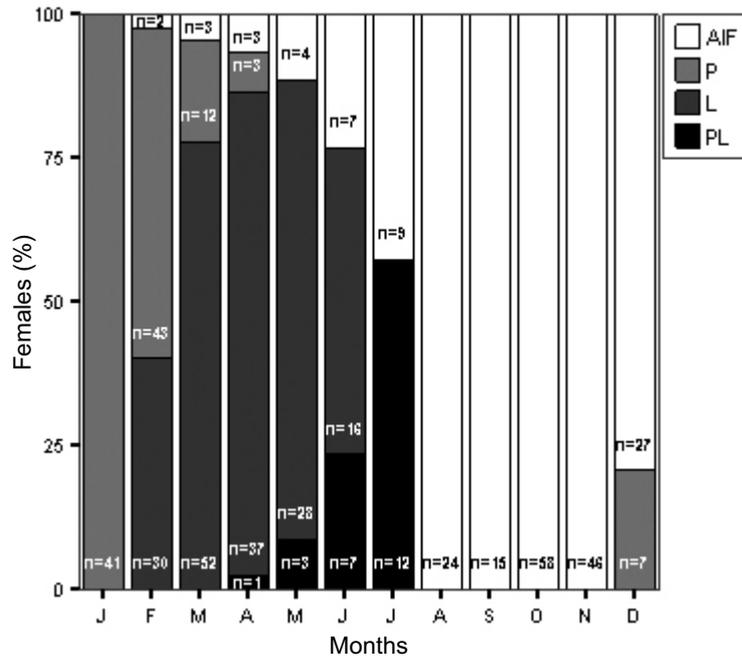


FIG. 2. Percent of females captured each month that were reproductively inactive (AIF), pregnant (P), lactating (L), or post-lactating (PL)

percentage (53%) of females were still lactating ($n = 30$), but all females stopped lactating by July. Post-lactating females were first captured in April, and were last observed in July. Thus, females exhibited only one parturition event per year, between the months of February and April.

When we tracked the change in body mass of several adult females ($n = 13$) whom we recaptured regularly, we noticed that a steady increase in mass was first recorded approximately 3.5 months before parturition occurred (Fig. 3). This suggests that the gestation period for *T. tricolor* is approximately 3.5 to 4 months. In addition, palpation of enlarged nipples in females that were frequently recaptured with their pups after parturition ($n = 7$) shows that individuals who had given birth in early and late February did not secrete any more milk after late May, early June, respectively. This indicates that the length of lactation in *T. tricolor* is approximately 3.5 to 4 months.

Postnatal Growth and Development

During the parturition period, we captured a total of 70 young, including 35 males and 35 females, and most of them (85%) were born during the months of February and March. The average size of pups at birth was 26.02% (± 2.24) and 31.43% (± 6.27) of maternal post-parturition and pre-copulation (i.e.,

before pregnancy) mass, respectively. Mean young to maternal length of forearm was 41.68% (± 2.38). The growth rates of the forearm were faster than the rates of increase in body mass (Fig. 4). When young were 30 days old, they had attained 67 and 80% of the average adult body mass and length of forearm, respectively. In 60 days, pups reached an average body mass of 3.2 g and a length of forearm of 35 mm (82 and 97% of the mass and length of forearm of adults); by day 90, pups had attained 87 and 100% of the adult body mass and length of forearm. The body mass of young reached adult proportions after 6–7 months of age (Fig. 4).

Pups were born hairless (Fig. 5), but some hair had developed by day 10, and hair covered the entire body by the third week of age. Sustained flight was possible approximately two months after birth, when pups reached 77 and 95% of adult body mass and length of forearm, respectively. Wing flapping was observed in pups by the age of 25 days, when they had attained 65 and 70% of the average adult body mass and length of forearm, and short-distance flight was possible after day 40 (67 and 89% of adult body mass and length).

Offspring mortality seemed to be very common at our study sites. Of the 35 female-pup pairs we sampled frequently during our study, we were unable to recapture 10 pups after six months. However, we were still able to capture the females at

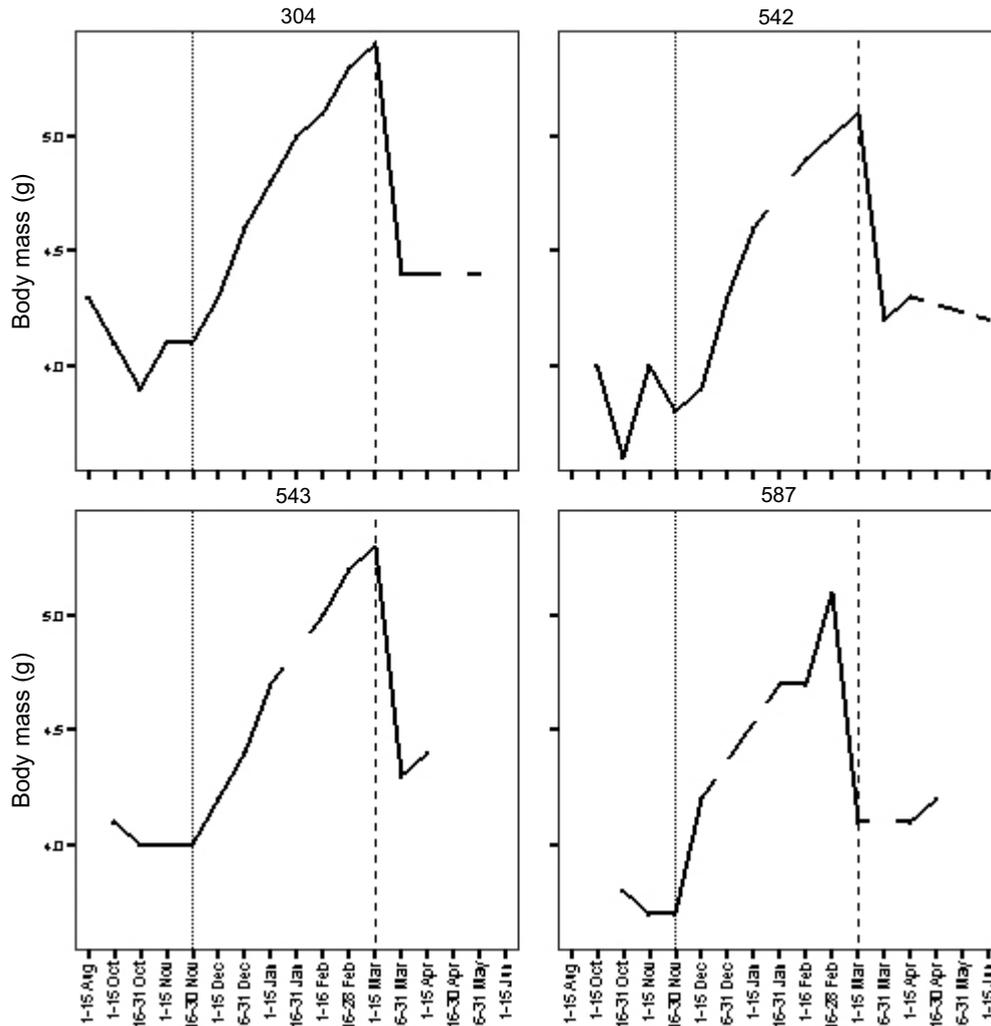


FIG. 3. Variation in body mass of four representative females (tag number on top of each graph) throughout the gestation period. Vertical lines represent the first time a steady increase in body mass was observed (dotted line), and the time when parturition occurred (dashed line)

the same site and within the same social group, and unable to recapture these pups in adjacent groups. This suggests that 28% of these pups died before age six months. Among the pups that died, most disappeared within 2–3 months (50%), but many also died in their first two weeks (40%). To determine if our capture efforts negatively affected survival of young, we compared recapture rates within the first three months of age of young that died and survived this period. We found that there were no significant differences between the number of times dying or surviving young were captured during their first three months of age (t -test = 1.37, $d.f.$ = 33, P = 0.18), which suggests that recapture rates did not increase mortality in juveniles. The pups that survived (n = 25) remained for at least one year with their mothers and natal group. Both males and

females born in February–March 2007 were recaptured within their natal group again in April 2008, even after their mother had given birth to a new young.

While direct evidence of age at sexual maturity was not collected, several observations suggest that males become sexually mature before females. Males born in February 2007 exhibited testicular descent and an increase in the size of the testes in March 2008. However, females born in 2007 were classified as reproductively inactive in 2008 given the absence of a bare patch and enlarged keratinized nipples. Sexual maturity in females most likely occurs after their first year, because subadult females captured in 2007 were pregnant in 2008. We presume these subadult females were born in 2006 because there were never more subadults than adult

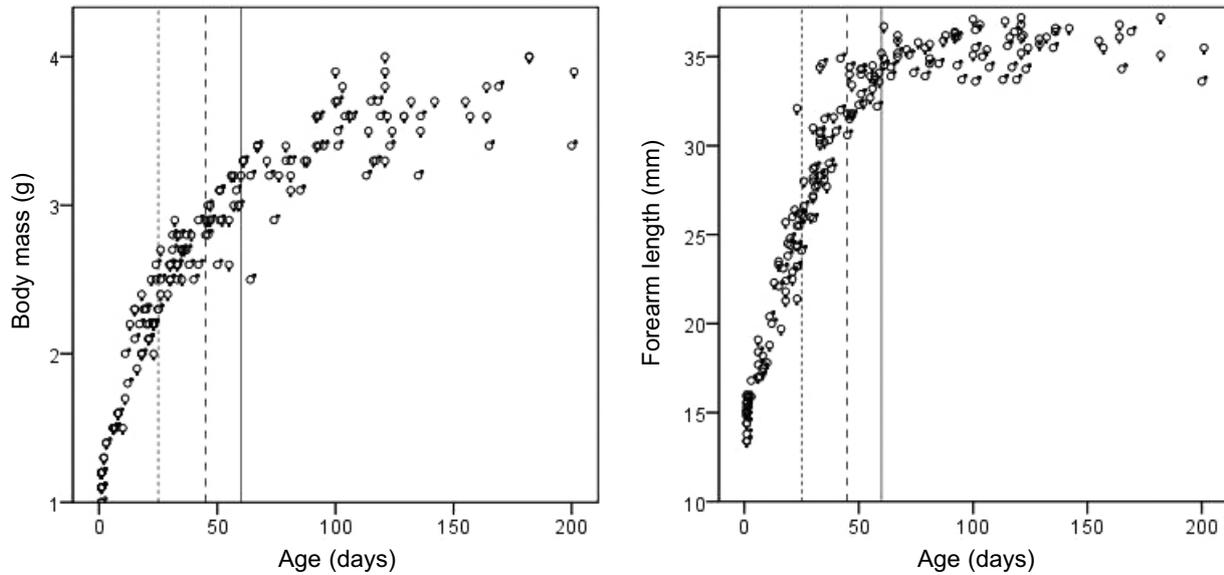


FIG. 4. Empirical growth curves for body mass and length of forearm for males and females in *T. tricolor*. Vertical lines represent the approximate age when wing flapping (dotted line), short flight (dashed line), and sustained flight (solid line) first occur

females within roosting groups, indicating that in any given year there is always only one subadult cohort.

DISCUSSION

Life in the Slow Lane

Body size has traditionally been acknowledged as an important correlate of life history evolution in mammals, whereby small species typically have

short gestation and lactation periods, produce small offspring which mature early, and die at an early age (Harvey and Read, 1988; Promislow and Harvey, 1990; Millar and Hickling, 1991; Dobson and Oli, 2007; Sibly and Brown, 2007). However, our study shows that, for its body size, *T. tricolor* has an unusually slow life history among bats, with long lactation and gestation periods, and later age at sexual maturity compared to other insectivorous bats (Barclay and Harder, 2003). For example, compared to other insectivorous bats of similar size, such as



FIG. 5. Photograph of a mother *T. tricolor* and its ca. 1-week-old pup

Myotis thysanodes (5–8 g, gestation 50–60 days — O'Farrell and Studier, 1980), *M. nigricans* (3–5 g, gestation 60 days — Wilson and LaVal, 1974), and *Perimyotis subflavus* (4–8 g, gestation 44 days — Fujita and Kunz, 1984), *T. tricolor* has a gestation period at least 1.5 months longer. Similarly, the duration of lactation is at least twice as long (3.5 to 4 months) in *T. tricolor* compared to other species such as *M. nigricans* (3–5 g), *Balantiopteryx plicata* (6 g), and *Saccopteryx leptura* (4–5 g), which lactate for 1.5, 2, and 2.5 months, respectively (Wilson and LaVal, 1974; Arroyo-Cabrales and Jones, 1988; Yancey *et al.*, 1998b). *Thyroptera tricolor* also has a single young per year, whereas other tropical insectivorous bats such as *Eptesicus furinalis* (7–8 g), *M. nigricans*, *Rhinonycteris naso* (4 g), and *S. leptura* may have one or two young twice a year (Wilson and LaVal, 1974; Plumpton and Jones, 1992; Mies *et al.*, 1996; Yancey *et al.*, 1998b). Sustained flight is also possible in as little as one week in other insectivorous species, such as *R. naso* (Plumpton and Jones, 1992), but *T. tricolor* is only capable of sustained flight at two months of age. Some of these other small species also reach adult proportions in as little as two weeks (i.e., *R. naso* — Plumpton and Jones, 1992), whereas it takes *T. tricolor* four months to reach adult proportions in body mass. Furthermore, our study shows that sexual maturity in female *T. tricolor* occurs later than in other small insectivorous bats, some of which are able to breed within their first year (i.e., *Tadarida pumilia* and *Saccopteryx bilineata* — Happold and Happold, 1989; Yancey *et al.*, 1998a). Compared to *Pipistrellus nanus*, another small insectivorous species that roosts in the developing tubular leaves of members of the order Zingiberales, *T. tricolor* has longer gestation and lactation periods (*P. nanus*: gestation 10 weeks, lactation eight weeks), and twins have also been reported in the former but not the latter (Lausen and Barclay, 2005).

Although body size is a strong correlate of life history evolution in mammals, evidence also suggests that life history traits co-vary systematically even when body size effects are removed. These size-independent correlations among life history traits are mostly attributed to adaptation to environmental predictability and lifestyle, which affect mortality rates (Harvey and Zammuto, 1985; Read and Harvey, 1989; Promislow and Harvey, 1990; Sibly and Brown, 2007). For example, high adult mortality and low juvenile mortality favor early and high reproductive output, while low adult mortality and high juvenile mortality favor a delayed onset of

sexual maturity and low reproductive output (Charnov and Schaffer, 1973; Michod, 1979; Promislow and Harvey, 1990). The later onset of reproductive activities and low reproductive output of *T. tricolor* may be a result of high rates of juvenile mortality, whereby nearly 30% of pups died within their first five months of age, and presumably higher adult survival rates compared to other similarly-sized insectivorous bats.

Sources of Juvenile Mortality

The possible reasons for higher levels of juvenile than adult mortality in *T. tricolor*, and higher levels of mortality in juvenile *T. tricolor* relative to other tropical insectivorous bat species are unclear. *Thyroptera tricolor* is one of the few species of bats known to roost in the developing tubular leaves of members of the order Zingiberales, which are suitable for use by *T. tricolor* for one day or less (Findley and Wilson, 1974; Vonhof and Fenton, 2004). This means that before juveniles achieve flight, females have to transport young between roosts on a daily basis, which may be particularly costly for *T. tricolor* given the extended duration of lactation and parental care. If suitable roosts or food resources are highly unpredictable or limiting, then offspring abandonment may occur more frequently in this species to minimize current costs and increase future reproductive success. However, this possibility requires further evidence, particularly as other species with similar roosting habits have different life-history patterns. At the onset of flight, young *T. tricolor* may be more prone to mortality from starvation and/or predation because of the costs involved in changing and locating roosts on a daily basis. However, once offspring can fly, survival may be enhanced by cooperation with other group members, since social groups in *T. tricolor* maintain contact while foraging (Vonhof *et al.*, 2004) and while locating roosts (Chaverri *et al.*, 2010).

Reproductive Phenology

The results of our study show that, at least in our study sites, *T. tricolor* exhibits a reproductive pattern characterized by seasonal monoestry (Jerrett, 1979; Racey and Entwistle, 2000), with most births occurring during the dry season (January through March), and only a few occurring during the early rainy season (April). Happold and Happold (1990) described two patterns of synchrony among species

exhibiting seasonal monoestry: restricted, in which there is close synchrony in birth dates, or extended, where births occur in a relatively longer period of time. While births in *T. tricolor* are synchronized to a specific season, these occur throughout a period of four months. Thus, its reproductive pattern should be classified as extended seasonal monoestry. Other species with extended seasonal monoestry include *Rousettus aegyptiacus* (Smithers, 1983), *Rhinolophus blasii* (Happold and Happold, 1990), and *Hipposideros caffer* (Bernard and Meester, 1982). In addition, many other bats in the Neotropics are thought to have a somewhat extended birth season once per year, coinciding with the beginning of the wet season (Reid, 1997; LaVal and Rodríguez-H., 2002). *Thyroptera tricolor* and other bats probably have birth peaks during the late-dry/early-rainy season because insect availability apparently increases during this time (Janzen, 1973; Wagner, 2001; Richards and Windsor, 2007), providing abundant resources not only for lactating mothers which have high energy expenditure (Kurta *et al.*, 1989), but also to newly-volant offspring. However, not all insects have a peak of abundance during the late-dry/early-rainy season. Thus, specific data correlating year-round abundance of preferred prey and reproductive activities in *T. tricolor* and other insectivorous bats are needed to understand how environmental cues influence reproduction.

In conclusion, our study shows that *T. tricolor* belongs to the slower lane of the slow-fast continuum of life-history variation in bats (Barclay and Harder, 2003). For example, *T. tricolor* produces fewer offspring per year than many insectivorous species, and the gestation and lactation periods are also longer. Pups are born relatively small, develop more slowly, and acquire feeding independence and flight capabilities later than many other bats of similar size and with similar ecological requirements. These findings suggest that, among bats, *T. tricolor* may have an interesting and unusual life history, which could be attributed in part to its unique roosting ecology and social behavior. Unfortunately, given the lack of basic data on many other tropical insectivorous bat species, understanding the causes of such a unique pattern is challenging. Thus, until more data are collected not only on tropical species' ecology and behavior, but also on their phenology of reproduction, litter size, longevity, number of litters, size of young at birth, stage of development at birth, and growth rates, testing hypotheses of life-history evolution will always be troubled by a taxonomical bias.

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