Reproductive biology and postnatal development in the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae)

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Abstract

In this study we investigated the reproductive patterns and postnatal development in the tent-making bat *Artibeus watsoni*. We sampled two populations in the Golfito Wildlife Refuge and Corcovado National Park, south-western Costa Rica, from June 2003 to March 2005. Most females were pregnant during the months of January and June, and most were lactating in March and July, indicating that this species exhibits seasonal bimodal polyoestry, with the first parturition peak occurring in February–March and the second in June–July. Additionally, we observed a postpartum oestrus following the first parturition, but not after the second. Females entered oestrus again in November–December and had a gestation period of *c*. 3 months. A female-biased sex ratio of neonates was observed during the second parturition period, and young were born at 32 and 56% of their mothers' body mass and length of forearm, respectively. Adult proportions in length of forearm were attained faster than adult proportions in body mass, and sustained flight was only possible after 35 days of age, when pups had achieved 100 and 80% of adult length of forearm and body mass proportions, respectively. Weaning and roosting independence occurred when young were *c*. 30–40 days old, and young females appeared to remain close to their place of birth, at least for their first mating period, whereas adult males were never recaptured near their birth site. In addition, sexual maturity was reached in as little as 3 months in females born during the first parturition period, whereas females born during the second birth period in June–July seemed to reach maturity at 6 months of age. Our results show that *A. watsoni* belongs to the faster lane of the slow–fast continuum of life-history variation in bats, which may be attributed primarily to its roosting and feeding ecology.

Introduction

Among mammals, bats are unique 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 & MacLarnon, 2001; Barclay & Harder, 2003). For example, most small mammals have life histories characterized by rapid reproduction and high mortality (Promislow & Harvey, 1990), whereas bats have a life history characterized by extended longevity with multiple reproductive events, low litter size and delayed onset of sexual maturity (Gaisler, 1989).

Reproduction in bats is an energetically expensive and potentially risky activity (Studier, Lysengen & O'Farrell, 1972; Kurta *et al.*, 1989), and hence is usually synchronized to periods of high food availability (Bronson, 1985). Thus, in areas where food production is seasonal, individuals may only be able to meet the energetic requirements of reproduction during periods of maximum food availability (Racey & Entwistle, 2000). For example, temperate insectivorous bats

are known to synchronize their reproductive activities to a short period of high insect abundance (Wilson, 1979), and thus females are seasonally monoestrous because most of their reproductive activities (gametogenesis, gestation and lactation) are constrained to a few months per year (Tuttle & Stevenson, 1982), followed by long periods of reproductive quiescence during hibernation. In tropical environments, however, food appears to be available year-round, although variation in rainfall may affect the seasonality of peak food availability and thus the timing of reproductive activities. For example, frugivorous species such as *Artibeus jamaicensis* and *Carollia perspicillata* exhibit a seasonal bimodal polyoestry (Fleming, 1971; Heithaus, Fleming & Opler, 1975), and the two parturition events coincide with peak fruit abundance (Janzen, 1976; Leigh, 1999).

Gestation length in bats is highly variable, and ranges between 40 and 205 days (Barclay & Harder, 2003), and litter size per parturition period in most species is restricted to one (Badwaik & Rasweiler, 2000). Neonatal body mass ranges from 17.5 to 28.8% of maternal body mass (Kurta &

Kunz, 1987; Hayssen & Kunz, 1996), and pups may suckle for a period of 21–300 days (Kunz & Hood, 2000; Barclay & Harder, 2003). After birth, the forearm lengths of pups develop at rates of 0.4–2.0 mm day^{-1} and their body mass increases at rates of 0.1–1.3 g day^{-1} (Tuttle & Stevenson, 1982). Moreover, the onset of flight may occur in as little as 2 weeks in some insectivorous species or as long as 12 weeks in large frugivorous bats (Tuttle & Stevenson, 1982). Finally, reproductive maturity in bats is attained between 2 and 36 months of age (Barclay & Harder, 2003), and males usually reach sexual maturity at an older age than females (Tuttle & Stevenson, 1982).

Although there is some information regarding the reproductive biology and postnatal growth of bats (reviewed in Crichton & 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 less than 10% of the *c*. 128 species within the family Phyllostomidae (Barclay & Harder, 2003). Thus, the objective of this study was to provide a description of the reproductive patterns of the New World tent making bat *Artibeus watsoni*, specifically focusing on reproductive seasonality, length of reproductive activities such as gestation and lactation, and copulatory behaviour. In addition, this study also describes postnatal development, particularly regarding growth rate and the onset of flight and reproduction.

Artibeus watsoni is a small (*c*. 11 g) phyllostomid bat that ranges from Veracruz, México through Central America to Colombia. It is usually found below 800 m above sea level, in semideciduous and evergreen lowland forests, second growth and fruit groves (Reid, 1997). It feeds primarily on fruits, although to a lesser extent may consume insects and pollen (LaVal & Rodríguez-H, 2002). This species roosts under modified leaves and is known to use more plant species for roosting than any other tent-making bat (Kunz & Lumsden, 2003).

Methods

This study was conducted at two protected areas in southwestern Costa Rica from June 2003 to March 2005. The first study area, Corcovado National Park (8°28′, 83°35′), is a 42 468 ha park with altitudes ranging from sea level to 550 m, and the second study area, Golfito Wildlife Refuge (8°38′, 83°11′), comprises 2810 ha and has altitudes that range from sea level to 505 m. Within Corcovado we sampled individuals located near the Sirena Research Station, and in Golfito individuals were sampled from the Playa Cacao sector.

We captured bats during the day at their roosts using hand nets with extendable poles and also captured them at night using mist nets (Kunz & Kurta, 1988). We then fitted all individuals with numbered, plastic wing bands (A. C. Hughes, Hampton Hill, Middlesex, UK) and recorded measurements such as length of forearm and body mass. The edges on all plastic bands were smoothed before using them to avoid injury to the bats. Finally, we collected

data on sex, age and reproductive status. Juveniles and subadults were distinguished from adults based on the presence of cartilaginous epiphyseal plates in metacarpals and phalanges (Anthony, 1988), and juveniles were further recognized from subadults if the former were still nursing and always roosting with their mother. Reproductive status was assessed in males by the presence of descended testes (reproductively active) and females were classified as being pregnant if distension of the female's lower abdomen was present and if a foetus was also palpable (Racey, 1988). Finally, females with enlarged nipples and when milk could be expressed when mammary glands were palpated were classified as lactating.

We attached radio transmitters (Holohil Systems Ltd, Woodlawn, Ontario, Canada, model BD-2 and BD-2N; 0.47–0.51 g; 3.9–4.25% of the bat's body mass) to some of the bats captured during the day using Skin Bond Cement (Smith and Nephew United, Largo, FL, USA), and located them at their roost using a radio receiver (TRX-1000S, Wildlife Materials Inc., Carbondale, IL, USA) with three-element Yagi antennae. We then observed and/or videotaped their behaviour at the roost using binoculars and a Sony NightShot (Model DCR-TRV120, Sony Corp., SSGE, Shanghai, China) digital video camera. Behaviour was recorded in these radio-tagged bats until all individuals in a group lost their radio transmitters (5–17 days).

We calculated the average body mass and length of forearm of all bats sampled, and significant differences among males and females were calculated using an Independent Samples *t*-test. We then estimated per cent neonatal and juvenile body mass and length of forearm based on the average of adult measurements. To estimate postnatal growth curves, we first calculated the curve of one bat of known birth date [the reference bat (RB)] that had been frequently recaptured, and used linear regression to fit the curve for body mass. We then estimated the age of other juveniles whose birth date was unknown (but which had been recaptured at least twice) by comparing the first capture measurement of body mass with the RB's growth curve. Finally, to estimate the best-fitting line of growth rates for body mass and length of forearm for all juveniles (RB and others with unknown birth dates), we used curve estimation analyses including body mass and length of forearm of all recaptured juveniles. The use of RB as the basis to estimate age for all other juveniles was considered to be appropriate if the line of best fit had high R^2 values. To test for significant deviations from a 1:1 sex ratio in pups born in the same parturition period (but for all years summed), we used a binomial test of a 0.50 proportion. SPSS version 10 (SPSS Inc., IL, USA) was used in all statistical analyses, and significance was assessed at an α of 0.05.

Results

Reproductive biology

We captured and marked a combined total of 1100 bats at both study sites. The average body mass of the adult

population was 11.51 g ($\pm$0.95), but the body mass of females was slightly larger (11.62 $\pm$ 1.05) than that of males (11.44 $\pm$ 0.87), although not significantly so ($t_{326} = 1.63$, $P = 0.10$). The mean length of forearm for all bats captured was 38.38 mm ($\pm$1.19), but females had significantly larger lengths of forearm (38.61 $\pm$ 1.11 mm) than males (38.23 $\pm$ 1.22; $t_{326} = 2.78$, $P = 0.006$).

Most females (83%, $n = 18$) were pregnant during January (Fig. 1), and no females were lactating during this month. In February, 75% of females were pregnant and 25% lactating ($n = 8$), and by March more females were lactating than pregnant (37 vs. 13%, respectively; $n = 52$). In June, most individuals were again pregnant (53%, $n = 19$), and the percentage of pregnant females decreased in the following months, although a slight increase occurred in September (Fig. 1). No pregnant or lactating bats were observed during the last 3 months of the year (October, November and December; $n = 107$). Thus, females exhibited two parturition peaks, one in February–March and another in June–July.

One or 2 days after their first parturition period (February–March), females entered oestrus, and copulated often for a period of up to 4 days. For example, for a period of 5 days we observed a group composed of an adult male and two females, one pregnant and one that had given birth the previous day. From 09:00 until 12:00 h, we observed repeated copulations between the oestrous female and the male, who attempted to mate with this female c. every 30 min. Each morning, however, only two or three copulations seemed successful (i.e. pelvic thrusts were observed). On the fourth day, mating attempts from the male were reduced, and by the fifth day no copulation occurred. No mating was observed among roosting bats after the second parturition period of June–July, at least for the observation period of 1–10 days after females gave birth. Females appear to enter oestrus again in late November–December, as we observed abnormally distended vaginal openings in most females captured in early December, suggesting repeated copulations. Males, in contrast, appeared to

be reproductively active year-round, because we observed individuals with enlarged testes in all months of the year.

Although direct data on gestation length in *A. watsoni* were not obtained, indirect evidence suggests that it extends for c. 3 months. For example, because most females appeared to copulate in December, parturition in February–March indicates that the length of gestation would be around 3 months. Similarly, after the postpartum oestrus (mid- to late February and March), females gave birth around June–July, indicating a second gestation period of about 3 months.

Postnatal growth and development

The sex ratio of pups was 1:1 (34 males, 34 females) after the first parturition period, but significant female-biased sex ratios were observed during the second parturition (1:2 sex ratio; 15 males, 31 females; significance based on a binomial test of a 0.50 proportion = 0.02). The body masses of two 1-day-old pups were 3.75 and 4.25 g (30 and 34% of the mother's body mass, respectively) and their lengths of forearms were 20 and 22 mm (54 and 59% of the mother's length of forearm, respectively). On the basis of evidence of other recaptured pups, the growth rates of the forearm appear to be faster than the rate of increase in body mass, and juveniles attained adult lengths of forearm faster than they achieved adult body mass (Fig. 2). For example, when the pups were 10 days old, they had attained 50 and 72% of the average adult body mass and length of forearm, respectively, and by day 20 the average body mass and length of forearm of pups had increased to c. 62 and 88% of adult proportions, respectively (Fig. 2). In 1 month, pups reached an average body mass of 8.68 g and a length of forearm of 37.58 mm (75 and 98% of the mass and length of adults); by day 40, pups had attained an adult length of forearm and 88% of adult body mass. The body mass of pups reached adult proportions by day 50 (Fig. 2).
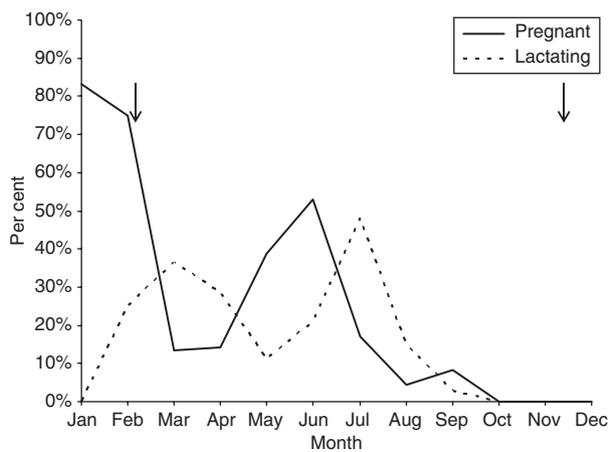
Figure 1 Annual breeding phenology of female *Artibeus watsoni* in south-western Costa Rica. Arrows indicate possible breeding dates for most females.

$$y = -0.0106x^2 + 0.9168x + 19.612$$
$$R^2 = 0.9631$$

$$y = 0.1493x + 4.2046$$
$$R^2 = 0.985$$
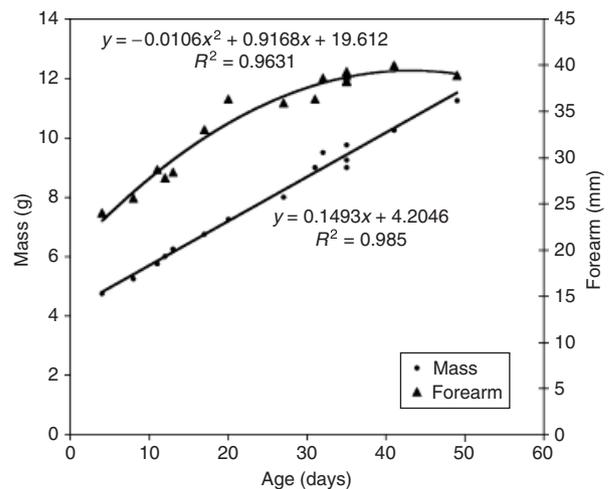
Figure 2 Empirical growth curves for body mass and length of forearm for the tent-making bat *Artibeus watsoni*.

Until flight was attained, pups were completely dependent on their mothers for relocation to alternate roosts. By the age of 14 days, when they had reached 55 and 80% of adult body mass and length of forearm, respectively, pups began to practise flight at their roosts by extending their wings and performing flapping movements. When the pups reached 64 and 90% of adult body mass and length of forearm (*c*. 20 days old), they exhibited extremely poor flight abilities, but by day 25 (69 and 94% of adult body mass and length of forearm) the young were capable of flying short distances. Sustained flight was only possible after day 35, when pups attained full adult length of forearm and 80% of adult body mass. Between 40 and 45 days old, pups were capable of longer foraging flights, and had almost reached adult body mass. The onset of flight also appeared to be associated with the onset of foraging independence, because females no longer produced milk when pups were 30–40 days old. After foraging independence was reached, juveniles began to gain roosting independence as well and were often found roosting alone.

Although data on juvenile dispersal from natal sites were not obtained, evidence gained from this study suggests that females remain close to their birth site, at least for their first mating period. Female #1322, for example, was initially captured in mid-July 2003 and then recaptured 85 m from her birth site on 3 March 2004, and female #1885 was captured first as a juvenile on 30 March 2004 and later recaptured 300 m from her birth site on 21 July 2004. Less than a year after initial capture, both females were pregnant, suggesting not only that nulliparous females mate near their birth site but also that they attain sexual maturity at a relatively early age. For example, on the basis of measurements of body mass and length of forearm at the time of initial capture, the birth date of female #1322 was extrapolated to 25 June 2003. She was later recaptured on 3 March 2004 with a *c*. 2 month-old foetus, suggesting she was 6 months old when she mated in mid-December. Female #1885, on the other hand, was probably born on 21 February 2004, and was pregnant with a *c*. 50-day-old foetus on 27 July 2004, indicating that she was *c*. 3.5 months old when she mated for the first time. Although the sample size is small, this suggests not only that females attain sexual maturity from 3.5 to 6 months of age, but also that females born in the first parturition period (February–March) are able to copulate early that same year, and that females born in June–July mate near the end of the year (December).

Discussion

Reproductive biology

On the basis of evidence collected in this study, we determined that *A. watsoni* has a seasonal bimodal polyoestry with a postpartum oestrus (Racey & Entwistle, 2000) following the first parturition period, and a period of sexual inactivity after the second parturition period. The first parturition period coincides with the middle of the dry season, and the second with the beginning of the rainy season. This seasonal bimodal reproductive pattern resembles that of other neotropical frugivorous bat species such as *A. jamaicensis*, *Uroderma bilobatum* and *C. perspicillata* (Fleming, 1972), although *A. watsoni* differs from *A. jamaicensis* in that a postpartum oestrus after the second parturition period is absent in the former (Fleming, 1971). *Artibeus watsoni* and other frugivorous species probably have birth peaks during the dry and early rainy seasons because fruit availability increases during this time (Fleming, 1972; Janzen, 1976), providing abundant resources not only for lactating mothers, which have high-energy expenditure (Kurta *et al.*, 1989), but also for the growing pups. These pups presumably lack appropriate flight skills (Kunz, 1974; Racey & Swift, 1985); thus having abundant food resources near their roosting sites likely increases survival.

Even though there is no direct evidence that sperm competition occurs in bats (Racey & Entwistle, 2000), a positive relationship between relative testis mass and promiscuity has been observed (Hosken, 1997; Wilkinson & McCracken, 2003), suggesting that sperm competition is widespread in this taxon. Thus, the repeated mating solicitations made by male *A. watsoni* may indicate that postcopulatory sexual selection occurs in this bat as well. Because *A. watsoni* exhibits low roost and mate fidelity (Chaverri & Kunz, 2006), and because females in oestrus may forage relatively far from their roosting sites, the probability of females mating with multiple males is high (Wilkinson & McCracken, 2003). Harem males may then solicit a high frequency of copulations to secure paternity, particularly because their sperm is likely to be competing with those of other males (Hunter *et al.*, 1993). The high frequency of mating events that we observed during the early morning may help dilute any possible sperm deposited by other males the previous night.

Similar to most bat species, *A. watsoni* only carries one conceptus to term during each pregnancy (reviewed in Badwaik & Rasweiler, 2000). Additionally, the observed gestation period of *c*. 3 months is within the documented range of 40 days–11 months reported for other bat species (Tuttle & Stevenson, 1982; Barclay & Harder, 2003). Notwithstanding, *A. watsoni* has a shorter gestation length than other frugivorous phyllostomids, such as *A. jamaicensis* and *C. perspicillata*. *Carollia perspicillata*, for example, has a gestation period of 4 months (Kleiman & Davis, 1979) and *A. jamaicensis* gestates for 3.5–4 months (Fleming, 1971; Wilson, Handley & Gardner, 1991). In addition, *A. watsoni* has a shorter gestation length than the average documented length for all phyllostomids studied to date (Barclay & Harder, 2003).

Sex ratio, size at birth, and postnatal growth and development

The female-biased sex ratio in newborns that we observed during the second parturition period may be explained by maternal condition. If a male's breeding success depends on his size and condition, and if such attributes depend in turn on the mother's ability to obtain sufficient resources during

gestation and lactation, then females should invest more in males at times of better body condition or greater resource abundance (Trivers & Willard, 1973; Trivers, 1974). Although we have no data on resource abundance during the two parturition periods, mothers may invest more in males during the first parturition because these males will encounter a longer period of high resource abundance than males born in the second parturition, thus conferring the former a potentially higher breeding success. Additional data, however, are required to understand if reproductive success in males depends on particular physical attributes or if producing males is really more expensive for females.

The average size of pups at birth (32% of female body mass) was larger than the average for most bat species (e.g. *C. perspicillata*: 28%; Kleiman & Davis, 1979; *Phyllostomus hastatus*: 20.7%; Stern & Kunz, 1998; *Tadarida brasiliensis*: 25%; Kunz & Robson, 1995; all microchiropteran bats: 28.3%; Kunz & Hood, 2000). Large neonatal size is likely to be possible in *A. watsoni* because females forage close to their roosting sites year-round (G. Chaverri *et al.*, unpubl. data), and thus carrying a heavier foetus during pregnancy will not have as detrimental an effect on the mother's foraging capabilities. Large neonatal body size probably confers advantages to *A. watsoni* because this species occupies roosts that are relatively unprotected compared with other sites such as caves and hollow trees. Thus, having a larger body size at birth most likely aids in the preservation of energy generated to maintain constant body heat when the mother leaves the roost to forage (Reiter, 2004). Moreover, a larger body size at birth probably confers greater neuromuscular maturity, allowing pups to cling tightly to their mothers or their roosts (Kurta & Kunz, 1987).

Growth rates and development patterns in *A. watsoni* are similar to those of most bat species studied to date, even those with different feeding and roosting requirements. For example, *Pipistrellus subflavus*, *Rhinolophus hipposideros*, *Eptesicus fuscus*, *Megaderma lyra* and *Ph. hastatus*, as well as *A. watsoni*, all have growth curves characterized by rapid growth in length of forearm and body mass accumulation after birth, reaching an asymptotic body size shortly before adult dimensions are achieved (Hoying & Kunz, 1998; Stern & Kunz, 1998; Rajan & Marimuthu, 1999; Hood, Bloss & Kunz, 2002; Reiter, 2004). The smaller species (*Pi. subflavus*, *R. hipposideros* and *E. fuscus*), however, reach their growth asymptote at *c.* 20 or 30 days, whereas the larger species (*M. lyra* and *Ph. hastatus*) reach it at *c.* 40 days. *Artibeus watsoni* seems to have an intermediate growth rate, because rapid growth in length of forearm continues until *c.* 30 days and rapid accumulation of body mass continues even after 40 days. These differences in growth rates among different bat species may be related to body mass and latitude, because larger species have been observed to develop at a slower rate and temperate bats grow faster than tropical species (Kunz & Stern, 1995).

In addition to growth curves, we also found remarkable convergence in the onset of flight among our study species and other bat taxa. In our study we found that *A. watsoni* flew short distances when *c.* 20 days old. Similarly, Isaac &

Marimuthu (1996) and Rajan & Marimuthu (1999) found that *Pipistrellus mimus* and *M. lyra* began to flutter and fly short distances at 21 and 18 days of age, respectively. Short flight distances were attained in *A. watsoni* at 25 days of age, and *Pi. mimus* and *M. lyra* were able to cover small distances when 24 days old. Sustained flight in *A. watsoni* seemed to occur after day 35, whereas both *Pi. mimus* and *M. lyra* were able to fly continuously when they were 28 days old. Flight in these three species was only possible when the length of forearm had reached more than 90% of adult proportions, although body mass at the onset of flight was less than 80% of adult body mass for all three species. Even though these three species differ in their adult body mass (*Pi. mimus*: 3.5 g; *M. lyra*: 50 g; *A. watsoni*: 11.5 g) and have different feeding requirements (*Pi. mimus* is insectivorous, *M. lyra* is carnivorous and *A. watsoni* is frugivorous), convergence in the onset of flight among them may occur from similar selective pressures to attain independence from parental care and thus increase survival of both juveniles and their mothers. Additionally, having smaller body size at the onset of flight may be advantageous to all three species because wing loading would be smaller, thus increasing manoeuvrability and decreasing the cost of flight at such vulnerable times (Hoying & Kunz, 1998).

Weaning in *A. watsoni* occurred at *c.* 1 month of age, which is faster than the average length of lactation for all microchiropterans (mean 60.44 days, range 21–300) and phyllostomids (mean 95.6 days, range 49–300) studied to date (Barclay & Harder, 2003). However, *A. watsoni* was weaned when its body mass reached 80% of adult proportions, lower than the average of 96% for all microchiropterans, but similar to the average of 78% for phyllostomids (Barclay & Harder, 2003). Thus, because *A. watsoni* lactates for shorter periods of time and still gains a similarly proportional pup–mother body mass of other phyllostomids, it is possible that the larger size at birth provides this species with an important head start, promoting early foraging independence and thus decreasing the costs of lactation to the mother.

The onset of sexual maturity in female *A. watsoni* appears to be faster than in most bat species. The average age at maturity in microchiropterans, for example, is 10.44 months (range 3–36), with an average for phyllostomids of 4.6 (range 3–8; Barclay & Harder, 2003), whereas female *A. watsoni* reached sexual maturity in as little as 3 months. However, females born in the second parturition period seemed to attain sexual maturity at an older age. Females from the first breeding period are probably capable of breeding earlier because fruits are more abundant at the time when they are born. In contrast, the availability of resources after the second parturition period is lower, which may lead to slower rates of development. Breeding earlier, however, may have serious implications for female bats, and individuals that delay reproduction may show a reduction in mortality and an increase in body condition and lifespan (Ransome, 1995).

In conclusion, this study showed that *A. watsoni* belongs to the faster lane of the slow–fast continuum of life-history

variation in bats (Barclay & Harder, 2003). For example, *A. watsoni* breeds at an earlier age and produces more offspring per year than most species, and the gestation and lactation periods are also shorter. Pups also are born larger, develop faster and acquire roosting and feeding independence sooner than many other bats. It is possible that the small size and foraging and roosting ecology of this species are important determinants of its reproductive biology and development. For example, interspecific differences in body mass are known to be important determinants of mammalian life-history traits (Western, 1979; Stearns, 1983); thus it is reasonable to hypothesize that because *A. watsoni* is a relatively small bat, some of its life-history traits will be inclined towards the faster lane. The correlation between life-history variation and body mass, however, has had little empirical support in bats (Jones & MacLarnon, 2001). It is possible then that the relatively vulnerable roosting conditions experienced by this bat will promote having larger pups that attain flight and foraging independence faster. This faster development of juveniles is subsequently facilitated by the apparently abundant and relatively nearby feeding resources. More data are required to understand the factors affecting life-history traits of *A. watsoni*, and analyses of intraspecific variation in these traits will likely provide additional insight into the selective pressures that shape them.

Acknowledgements

References

Anthony, E.L.P. (1988). Age determination in bats. In *Ecological and behavioral methods for the study of bats*: 47–58. Kunz, T.H. (Ed.). Washington, DC: Smithsonian Institution Press.

Badwaik, N.K. & Rasweiler, J.J. (2000). Pregnancy. In *Reproductive biology of bats*: 221–293. Krichton, E.G. & Krutzsch, P.H. (Eds). London: Academic Press.

Barclay, R.M.R. & Harder, L.D. (2003). Life histories of bats: life in the slow lane. In *Bat ecology*: 209–253. Kunz, T.H. & Fenton, M.B. (Eds). Chicago: University of Chicago Press.

Bronson, F.H. (1985). Mammalian reproduction: an ecological perspective. *Biol. Reprod.* **32**, 1–26.

Chaverri, G. & Kunz, T.H. (2006). Roosting ecology of the tent-roosting bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in southwestern Costa Rica. *Biotropica* **38**, 77–84.

Crichton, E.G. & Krutzsch, P.H. (2000). *Reproductive biology of bats*. San Diego, CA: Academic Press.

Fleming, T.H. (1971). *Artibeus jamaicensis*: delayed embryonic development in a neotropical bat. *Science* **171**, 402–404.

Fleming, T.H. (1972). Three Central American bat communities: structure, reproductive cycles, and movement patterns. *Ecology* **53**, 555–569.

Gaisler, J. (1989). The r–K selection model and life history strategies in bats. In *European bat research*: 117–124. Hanak, V., Horácek, I. & Gaisler, J. (Eds). Prague: Charles University Press.

Hayssen, V. & Kunz, T.H. (1996). Allometry of litter mass in bats: comparisons with respect to maternal size, wing morphology, and phylogeny. *J. Mammal.* **77**, 476–490.

Heithaus, E.R., Fleming, T.H. & Opler, P.A. (1975). Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* **56**, 841–854.

Hood, W.R., Bloss, J. & Kunz, T.H. (2002). Intrinsic and extrinsic sources of variation in size at birth and rates of postnatal growth in the big brown bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *J. Zool. (Lond.)* **258**, 355–363.

Hosken, D.J. (1997). Sperm competition in bats. *Proc. Roy. Soc. Lond. Ser. B Biol. Sci.* **264**, 385–392.

Hoying, K.M. & Kunz, T.H. (1998). Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus* (Chiroptera: Verspertilionidae). *J. Zool. (Lond.)* **245**, 15–27.

Hunter, F.M., Otronen, M., Birkhead, T. & Møller, A.P. (1993). Why do females copulate repeatedly with one male? *Trends Ecol. Evol.* **8**, 21–26.

Isaac, S. & Marimuthu, G. (1996). Postnatal growth and age estimation in the Indian pygmy bat *Pipistrellus mimus*. *J. Mammal.* **77**, 199–204.

Janzen, D.H. (1976). Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* **21**, 620–637.

Jones, K.E. & MacLarnon, A. (2001). Bat life histories: testing models of mammalian life-history evolution. *Evol. Ecol. Res.* **3**, 465–476.

Kleiman, D.G. & Davis, T.M. (1979). Ontogeny and maternal care. In *Biology of bats of the New World family Phyllostomatidae*: 387–402. Baker, R.J., Jones, J.K.J. & Carter, D.C. (Eds). Lubbock: Special Publication of the Museum, Texas Tech University.

Kunz, T.H. (1974). Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* **55**, 693–711.

Kunz, T.H. & Hood, W.R. (2000). Parental care and postnatal growth in the Chiroptera. In *Reproductive biology of bats*: 415–468. Krichton, E.G. & Krutzsch, P.H. (Eds). London: Academic Press.

Kunz, T.H. & Kurta, A. (1988). Capture methods and holding devices. In *Ecological and behavioral methods for the study of bats*: 1–29. Kunz, T.H. (Ed.). Washington: Smithsonian Institution Press.

Kunz, T.H. & Lumsden, L.F. (2003). Ecology of cavity and foliage roosting bats. In *Bat ecology*: 3–87. Kunz, T.H. & Fenton, M.B. (Eds). Chicago: University of Chicago Press.

Kunz, T.H. & Robson, S.K. (1995). Postnatal-growth and development in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*) – birth size, growth-rates, and age estimation. *J. Mammal.* **76**, 769–783.

Kunz, T.H. & Stern, A.A. (1995). Maternal investment and post-natal growth in bats. *Symp. Zool. Soc. Lond.* **67**, 123–138.

Kurta, A., Bell, G.P., Nagy, K.A. & Kunz, T.H. (1989). Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiol. Zool.* **62**, 804–818.

Kurta, A. & Kunz, T.H. (1987). Size of bats at birth and maternal investment during pregnancy. *Symp. Zool. Soc. Lond.* **57**, 79–106.

LaVal, R.K. & Rodríguez-H, B. (2002). *Murciélagos de Costa Rica*. Heredia, Costa Rica: Instituto Nacional de Biodiversidad.

Leigh, E.G.J. (1999). *Tropical forest ecology: a view from Barro Colorado Island*. New York: Oxford University Press.

Promislow, D.E.L. & Harvey, P.H. (1990). Living fast and dying young: a comparative analysis of life-history variation among mammals. *J. Zool. (Lond.)* **220**, 417–437.

Racey, P.A. (1988). Reproductive assessment in bats. In *Ecological and behavioral methods for the study of bats*: 31–45. Kunz, T.H. (Ed.). Washington, DC: Smithsonian Institution Press.

Racey, P.A. & Entwistle, A.C. (2000). Life-history and reproductive strategies of bats. In *Reproductive biology of bats*: 363–414. Krichton, E.G. & Krutzsch, P.H. (Eds). London: Academic Press.

Racey, P.A. & Swift, S.M. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* **54**, 205–215.

Rajan, K.E. & Marimuthu, G. (1999). Postnatal growth and age estimation in the Indian false vampire bat (*Megaderma lyra*). *J. Zool. (Lond.)* **248**, 529–534.

Ransome, R.D. (1995). Earlier breeding shortens life in female greater horseshoe bats. *Philos. Trans. Roy. Soc. Lond. Ser. B Biol. Sci.* **350**, 153–161.

Reid, F.A. (1997). *A field guide to the mammals of Central America and Southeast Mexico*. New York: Oxford University Press.

Reiter, G. (2004). Postnatal growth and reproductive biology of *Rhinolophus hipposideros* (Chiroptera: Rhinolophidae). *J. Zool. (Lond.)* **262**, 231–241.

Stearns, S.C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* **41**, 173–187.

Stern, A.A. & Kunz, T.H. (1998). Intraspecific variation in postnatal growth in the greater spear-nosed bat. *J. Mammal.* **79**, 755–763.

Studier, E.H., Lysengen, V.L. & O'Farrell, M.J. (1972). Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae) – II. Bioenergetics of pregnancy and lactation. *Physiol. Zool.* **57**, 457–467.

Trivers, R.L. (1974). Parent–offspring conflict. *Am. Zool.* **14**, 249–264.

Trivers, R.L. & Willard, D.E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**, 90–92.

Tuttle, M.D. & Stevenson, D. (1982). Growth and survival of bats. In *Ecology of bats*: 105–150. Kunz, T.H. (Ed.). New York: Plenum Press.

Western, D. (1979). Size, life-history and ecology in mammals. *Afr. J. Ecol.* **17**, 184–204.

Wilkinson, G.S. & McCracken, G.F. (2003). Bats and balls: sexual selection and sperm competition in the Chiroptera. In *Bat ecology*: 128–155. Kunz, T.H. & Fenton, M.B. (Eds). Chicago: University of Chicago Press.

Wilson, D.E. (1979). Reproductive patterns. In *Biology of bats of the New World family Phyllostomatidae, Part III*: 317–378. Baker, R., Jones, K. & Carter, D.C. (Eds). Lubbock: Special Publications of the Museum of Texas Tech University.

Wilson, D.E., Handley, C.O.J. & Gardner, A.L. (1991). Reproduction on Barro Colorado Island. In *Demography and natural history of the common fruit bat, Artibeus jamaicensis, on Barro Colorado Island, Panamá*: 43–52. Handley, C.O.J., Wilson, D.E. & Gardner, A.L. (Eds). Washington, DC: Smithsonian Institution Press.