Thermoregulation during reproduction in the solitary, foliage-roosting hoary bat (Lasiurus cinereus)

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The reproductive benefits of maintaining a high body temperature ($T_b$) are well understood, but costs may be prohibitively high. Many small mammals raise offspring in insulated nests, burrows, or roosts, and may form communal maternity colonies, all of which are behaviors that reduce the costs of maintaining $T_b$. However, some temperate-zone bats are solitary and raise young in exposed roosts. Little is known about how these species maintain energy balance in the face of high thermoregulatory costs, and whether they stay warm invariably for reproductive benefits, or use a more adaptive thermoregulatory strategy. We studied $T_b$ patterns in response to foraging conditions, weather, and pup age in free-ranging adult and juvenile hoary bats (Lasiurus cinereus). Lactating females regularly entered torpor, although its use was most extensive following poor foraging conditions, during inclement weather, and when pups were young. Juvenile L. cinereus appeared capable of staying warm from 3 days of age, but used torpor throughout development, gradually decreasing its use as they grew. Our results indicate that for this species, torpor is important throughout lactation, and torpor use changes in response to individually specific trade-offs between energetic cost and developmental benefit. We suggest that the costs of active thermoregulation during early development of L. cinereus pups outweigh the benefits of staying warm, and an extended growing season (as a result of their migratory nature) is more conducive to using torpor. Finally, we suggest that torpor use during lactation is dynamic and adaptive. Fine-scale changes within reproductive stages need to be considered, rather than broadly assessing thermoregulatory behavior among stages.

Key Words: Chiroptera, ecophysiology, heterothermy, hoary bat, lactation, Lasiurus cinereus, ontogeny, reproduction, thermoregulation, torpor

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The evolution of endothermy and of parental care in birds and mammals may have been linked, given the reproductive benefits of a high body temperature ($T_b$—Farmer 2000, 2003). Endothermy allows control of the temperature at which embryos and neonates develop, and maintenance of a high, stable temperature during development promotes rapid growth (Gillooly et al. 2002). However, endothermy is costly, especially for small birds and mammals (Kleiber 1932), and costs of maintaining a high $T_b$ may be difficult to meet under some circumstances. For example, in mammals, lactation is energetically expensive (Speakman 2008), and the combined costs of defending a high $T_b$ and lactating may create conflict between the energetic requirements of the parent and the thermal requirements of the developing offspring. This has favored the evolution of various mechanisms to reduce the costs of thermoregulation at a high $T_b$. These include morphological adaptations, such as increased insulation via fur and feathers, and behavioral adaptations, such as the use of insulated nests or dens (Hayes 2000; Kunz 1987) and social thermoregulation via clustering (Alberts 1978). These behavioral adaptations may be especially important in species with small neonates that are left alone while parents forage, and that have high surface area-to-volume ratios, generally lack significant insulation, and are often unable to maintain a high $T_b$ against low ambient temperatures ($T_a$—e.g., Geiser and Kenagy 1990; MacArthur and Humphries 1999). Raising young in colonial refuges may maximize the developmental benefits to offspring of a warm, stable environment and high $T_b$ while minimizing the physiological cost to the parent(s).

An alternative to homeothermy and adaptations that reduce its energetic costs is the evolution of adaptive heterothermy and the ability to carry out biological processes over a range of $T_b$. The evolution of endothermy and of parental care in birds and mammals may have been linked, given the reproductive benefits of a high body temperature ($T_b$—Farmer 2000, 2003).
Torpor is a physiological state involving lowered $T_b$ and metabolic rate, and has evolved in many species of mammals and some birds (Geiser 2008). Torpor can reduce energy consumption when the cost of defending a high $T_b$ becomes prohibitive (Wang and Wolowyk 1988), with even small drops in $T_b$ potentially saving considerable energy (Studir 1981). However, torpor also slows embryonic and neonatal development (e.g., Racey 1982), which may be detrimental, especially in seasonal environments with short growing seasons (Grindal et al. 1992). Furthermore, the use of torpor reduces the rate of production and protein composition of milk (Wilde et al. 1999). Use of torpor should thus be limited in individuals rearing offspring, thereby maximizing the benefits of parental care (Farmer 2000).

Indeed, the use of torpor by small birds and mammals varies with reproductive condition, with reproductive females generally using less torpor than other individuals (e.g., Csada and Brigham 1994; Geiser and Masters 1994).

Among temperate-zone bats, roosting colonially in insulated roosts, such as tree cavities, is common, especially for reproductive females, who frequently aggregate in maternity colonies (Kunz and Lumsden 2003). The combination of these roosts and clustering can significantly reduce thermoregulatory costs (Hollis 2004; Kurta 1985). However, not all bat species form maternity colonies or use insulated roosts. Species in the genus Lasiurus give birth alone among the foliage of trees (Koehler and Barclay 2000; Kunz and Lumsden 2003) in roosts that provide little thermal protection (but see Klug et al. 2012).

Lactating individuals use torpor (Willis 2006) and postnatal growth rates are relatively slow compared with other temperate insectivorous bats (Koehler and Barclay 2000). Such species may have evolved different adaptations to reduce thermoregulatory demands during reproduction compared with those of colonial species roosting in communal sheltered roosts.

Unlike most bats, lasiurines give birth to multiple young that are more precocial than neonates of most other species of bat (Barclay and Harder 2003; Koehler and Barclay 2000). Pups are born partially furred and a full pelage develops quickly compared with other bat species (Koehler 1991). The fur of adult Lasiurus also has the highest insulation value of any North American bat (Shump and Shump 1980). In addition, pups roost in close contact with one another, which may decrease heat loss and allow heat transfer between individuals (Alberts 1978). Given these features, and the fact that foliage roosts expose young to cool temperatures, and that the growing season is relatively short in much of the summer range of some of these migratory species (e.g., Lasiurus cinereus), the ability to thermoregulate immediately after birth may be possible and would be beneficial.

Actively maintaining a high $T_b$ may not always be the optimal strategy early in development, especially if a species is a thermal generalist whose performance has a broad thermal tolerance (Angilletta et al. 2010). When pups are small and lack a full pelage, the thermal benefits to growth may be offset by the cost of thermogenesis. Instead, solitary individuals may use torpor during lactation more often compared with colonial species. In addition, the costs and benefits to the family unit of using torpor likely change as offspring grow. However, studies investigating thermoregulatory behavior typically compare thermoregulatory patterns among broad reproductive stages, such as pregnancy versus lactation (e.g., Dzal and Brigham 2012; Turbill and Geiser 2006); changes in the use of torpor on a finer temporal scale (i.e., day to day) have not been investigated and adaptive changes within reproductive stages may thus be obscured.

Our objective was to determine how environmental and reproductive conditions influence the thermoregulatory strategy and use of torpor during lactation and early development by a small, solitary mammal. Specifically, we examined whether lactating L. cinereus defend a high $T_b$ to maximize reproductive benefits (Farmer 2000, 2003), or use an adaptive thermoregulatory strategy by adjusting the use of torpor to reflect changes in environmental and reproductive conditions (Angilletta et al. 2010). To do this, we monitored the $T_b$ patterns of free-ranging lactating and juvenile L. cinereus. We hypothesized that the solitary, exposed roosting behavior of L. cinereus makes maintaining a high $T_b$ more costly than for colonial-roosting species. Thus, we predicted that L. cinereus use torpor more regularly, and to a greater degree, than do species that roost colonially in insulated roosts. We further hypothesized that lactating females and juveniles use an adaptive thermoregulatory strategy reflecting changes in foraging success, energetic needs of developing young, and immediate costs of normothermy. L. cinereus is reported to maintain minimal energy reserves (Barclay 1989); thus we predicted that inclement weather and poor foraging conditions (i.e., wind, rain, and low $T_a$—Anthony et al. 1981) result in increased use of torpor. As thermal and energy requirements of the young change throughout the lactation period, we predicted that lactating females adjust the use of torpor to reflect the changing costs and benefits. Specifically, we predicted that the use of torpor by lactating L. cinereus declines as pups grow. Given the relatively large size of neonatal L. cinereus, and the presence of fur, we also predicted that neonate L. cinereus have the capacity to thermoregulate from birth.

**Materials and Methods**

**Study species and site.**—L. cinereus is a relatively large (mean mass = 27 g—Shump and Shump 1982), foliage-roosting, insectivorous bat (Vespertilionidae). It is migratory and found throughout most of North America, with individuals occurring in summer birthing grounds in Canada and overwintering possibly as far south as Mexico (Cryan et al. 2004). Our study was conducted near the University of Manitoba Field Station at Delta Marsh, Manitoba, Canada (50°11′02.44″N, 98°22′55.15″W). Reproductive female L. cinereus arrive in early June, give birth in mid- to late June, and begin southward migration in August (Barclay 1984). L. cinereus is monoestrus (Barclay and Harder 2003), with parturition typically resulting in litters of two (Shump and
Shump 1982). Unlike most temperate bat species, L. cinereus pups are born partially furred and become fully furred within days (Koehler 1991). Although L. cinereus are capable of using long-term torpor (i.e., bouts lasting multiple days—Geiser and Ruf 1995, Willis et al. 2006), we focus on diel patterns in the use of torpor (i.e., daily heterothermy).

Thermoregulatory patterns.—We monitored individuals from June through August 2009 and 2010. We accessed roosts using a portable tower and captured families using a modified bucket trap (Kunz and Kurta 1988). We measured mass (±0.1 g) and forearm length (±0.1 mm) for all members of the family. We estimated pup age from developmental features, such as presence of the umbilicus, fur coverage, and openness of the eyes and ears, as well as an equation developed at our site relating forearm length to age (Koehler and Barclay 2000). We trimmed hair between the scapulae and attached temperature-sensitive radiotransmitters (LB-2NT on pups, BD-2T on adults; Holohil Systems, Ontario, Canada) to the mother and 1 pup of each family using surgical adhesive (Skin Bond; Smith and Nephew United Inc., Florida). Before attachment, we confirmed that radiotransmitters and associated calibration curves were accurate to within 1°C by testing them in an environmental chamber of known temperature. The sensitivity of radiotransmitters can drift over time, but we did not detect any temperature drift in radiotransmitters that we recalibrated after recovery. To limit effects on behavior (Aldridge and Brigham 1988), the mass of each radiotransmitter was <5% of the mass of volant individuals (adults ~30 g, juveniles ~20 g; this study). Receiver data loggers (SRX400A; Lotek Wireless, Ontario, Canada) recorded skin temperatures (Tsk) every 10 min. Skin temperature recorded by external radiotransmitters is an accurate and relatively noninvasive method of determining core Tb in small mammals (Barclay et al. 1996).

We used mean daytime Tsk (°C), mean wind speed (m/s), and total daytime precipitation (mm) as indicators of the immediate energetic cost of normothermy. We used these same variables averaged over the previous night from sunset to sunrise as factors likely to influence foraging success via the density of flying insects. We recorded ambient temperature at each roost every 10 min, synchronized with Tsk readings, using a HOBO data logger (Onset Computer Corporation, Bourne, Massachusetts). We gathered all other environmental data (i.e., hourly wind speed and daily precipitation) from the Environment Canada Delta Marsh weather station located <5 km from all roost sites (Environment Canada 2010).

Definition of terms.—We defined torpor as periods when Tsk dropped ≥0.1°C below an individual’s active temperature (Tact), which is the lowest Tsk recorded from individuals within 10 min of their departure to forage (Barclay et al. 2001, Lausen and Barclay 2003). We modified this method to use the mean Tsk readings recorded within 10 min before emergence each night for the duration each radiotransmitter remained attached to an individual. Using this definition of torpor avoids some issues that may arise from using the single lowest Tsk as the threshold for torpor, such as underestimation of torpor (Willis and Brigham 2003), and accounts for individual differences in normothermic Tb and the effect of differences in calibration among radiotransmitters (Barclay et al. 2001). Although controversial (Boyles et al. 2011), using a Tb threshold to define torpor is a useful method to investigate thermoregulatory patterns in the field when metabolic rate cannot be measured (Brigham et al. 2011).

We used time spent in torpor, and mean and maximum torpor depth (Tact − Tsk) to quantify the use of torpor. We defined a bat day as the time between the adult female’s return to the roost and her emergence the following evening, whereas a bat night was the period when pups were alone in the roost while the mother foraged. A torpor day or night was defined as a bat day or night with at least one Tsk reading below Tact. Because individuals typically returned to the roost between 0400 and 0500 h and emerged between 2100 and 2200 h, we further separated bat days into morning (0400 to 1300 h) and afternoon (1300 to 2200 h). We excluded periods missing three or more consecutive readings from analyses.

We compared the frequency of the use of torpor by adult females across 3 stages of lactation that represent potential shifts in energetic demand on the basis of the stage of development of pups: early (parturition to day 17 when pups began roosting on their own—Klug 2011), middle (days 17 to 32, from shortly before to shortly after pups begin to fly), and late lactation (day 33 to weaning, when pups forage for themselves). Postlactation started at day 50. We categorized pups into 4 age classes that capture major developmental landmarks; early prevolancy was considered to be the period between parturition and 17 days of age (before density of pup fur is comparable with that of adult fur—Koehler 1991), late prevolancy as the remainder of the nonvolant period (17 to 27 days old, when pups begin roosting separate from their mother—Klug 2011), early volancy as the first 9 days of flight (28 to 36 days old; during which pups appear to learn to forage—Rolseth et al. 1994), and late volancy as the remainder of time to weaning (37 to 49 days old).

Statistical analyses.—We applied LOESS (local polynomial regression fitting) smoothing splines to daily Tsk data to minimize the effect of outliers and, although uncommon, to fill in values for periods missing less than 3 readings (see Lausen and Barclay 2003). We then visually inspected all data to ensure that the overall pattern was conserved. We could not claim independence in our measurements because data were sampled repeatedly from the same individual over time. In addition, most data quantifying the use of torpor in adults could not be normalized due to zero inflation, which precluded the use of parametric tests (Zar 1999) in some cases. Instead, we analyzed data using generalized linear mixed models (GLMMs) with individual bat as a random effect and appropriate correlation structures (e.g., compound symmetry or common unstructured covariance models) to account for autocorrelation where applicable. We transformed data quantifying the use of torpor in pups (e.g., log[y + 1]—Zar 1999) to best meet the assumption of normality (Shapiro–Wilk, W > 0.9), and analyzed with individual pup nested
RESULTS

In both years, parturition occurred between 10 and 22 June. We collected thermoregulatory data from 15 adult females and 25 pups. In total, we collected 188 bat days of data on adult females, 132 bat days of concurrent data on adult females and developing pups, and 157 bat nights of pup data. In brief, torpor was a regular part of the thermoregulatory behavior of *L. cinereus* adults and pups throughout lactation. Early in pup development, lactating females frequently entered torpor in the morning and passively rewarmed as *Tₐ* increased (Figs. 1A and 1B). However, these bouts decreased in frequency and depth as lactation progressed (Figs. 1A and 1C). Typically, adult females that returned to their pup at night between foraging periods remained warm. Pup temperature closely reflected that of the mother during the day (Fig. 2), and maintenance of high *Tₐ* in the absence of the mother was not common until 9 days of age. However, there was evidence that prevalent *L. cinereus* could actively thermoregulate as early as 3 days of age (Fig. 2B), which was the earliest age at which pups remained warm for a considerable period of time in the absence of their mother. Body temperature of early prevalent pups typically fell close to *Tₐ* immediately after the mother’s departure, and pups rewarmed only when their mother returned. As pups aged, they remained warm for longer periods at night. Late volant pups typically remained normothermic throughout the entire night between their own foraging bouts.

Adopt thermoregulation.—The *Tₐ*ₜₐₜₜ threshold for torpor in adults was consistent among individuals and radiotransmitters (X = 32.3°C ± 0.11°C, range = 31.2–33.4°C), below the normothermic *Tₐ* reported for *L. cinereus* (X = 35.7°C ± 0.7°C—Cryan and Wolf 2003). The frequency of adult torpor decreased as lactation progressed (z = -2.62, P = 0.001), with adult females remaining normothermic throughout the day more often as the pups aged. Adults used torpor on 92.3% (n = 65), 70.3% (n = 64), and 67.3% (n = 55) of available days during early, middle, and late lactation, respectively. The probability of adults using torpor was also influenced by mean daytime wind speed (z = -2.31, P = 0.021) and mean daytime *Tₐ* (z = -2.84, P = 0.009), with bats using torpor more often during days with higher wind speeds or lower *Tₐ* than on calmer, warmer days. Although torpor occurred equally during morning (123/142 days) and afternoon (117/142 days; χ² = 0.97, P = 0.325), more time was spent in torpor during the morning (273.6 ± 16.3 min) than the afternoon (227.7 ± 16.3 min; *F*₁,₁₃₉ = 15.20, *P* < 0.001).

The extent of torpor expression by lactating individuals was influenced by pup age and weather. Time spent in torpor per
day declined with pup age (Fig. 3; \( t_{164} = -2.83, P = 0.005 \)) and increased with precipitation (\( t_{164} = 2.63, P = 0.010 \)), and was influenced by the interaction between mean \( T_a \) and mean wind speed (\( t_{164} = -3.42, P = 0.001 \)). Mean torpor depth also declined as pups aged (\( t_{164} = -2.95, P = 0.004 \)) and increased with precipitation (\( t_{164} = -2.74, P = 0.007 \)), and was influenced by the interaction between \( T_a \) and wind speed (\( t_{164} = -4.18, P < 0.001 \)). Maximum torpor depth was influenced by the interactions between pup age and total precipitation (\( t_{162} = 2.17, P = 0.001 \)), and \( T_a \) and wind speed (\( t_{162} = -3.29, P = 0.001 \)). Individuals used deeper, longer bouts of torpor during windy days, especially when \( T_a \) was low. Conditions during the previous night’s foraging period influenced only the depth of torpor the following day. Nights with precipitation and concurrently low \( T_a \) increased the depth of torpor (\( t_{158} = -3.36, P = 0.001 \)). Adults did not forage on only 4 occasions, and in all cases the weather was unfavorable (i.e., \( T_a < 10 \degree C \), high winds, and rain) and torpor was used the entire night.

**Adult** *L. cinereus* in our study did not use torpor more frequently (77%) during lactation than did *E. fuscus* in the comparison study (88%, \( n = 50; \) Lausen and Barclay 2003; \( \chi^2_1 = 0.31, P = 0.578 \)). However, mean minimum \( T_{sk} \) (23.6\degree C \pm 0.55\degree C) throughout lactation and mean torpor depth (8.7\degree C \pm 0.56\degree C) of lactating *L. cinereus* were considerably lower than those recorded from lactating *E. fuscus* (29.0\degree C \pm 0.6\degree C and 5.4\degree C \pm 0.6\degree C, respectively—Lausen and Barclay 2003).

**Juvenile thermoregulation.**—Frequency of torpor by pups during the day decreased with age (\( \chi^2_3 = 39.55, P < 0.001 \)). Pups used torpor in 100.0% (\( n = 43 \)), 96.7% (\( n = 30 \)), 86.7% (\( n = 30 \)), and 69.0% (\( n = 29 \)) of available days during early prevolancy, late prevolancy, early volancy, and late volancy, respectively. At night, the frequency of pup torpor also decreased with age (\( \chi^2_3 = 51.36, P < 0.001 \)). Pups used torpor in 98.4% (\( n = 61 \)), 94.6% (\( n = 37 \)), 67.8% (\( n = 31 \)), and 39.3% (\( n = 28 \)) of available nights in the 4 age classes. Frequency of torpor did not differ between day and night.

**Fig. 1.**—a) Thermoregulatory pattern of adult *Lasiurus cinereus* over the course of 1 reproductive summer. Four-day temperature patterns are shown in more detail for the same female with 2 pups of age b) 5 through 8 days and c) 28 through 31 days. Gaps in skin temperature (\( T_{sk} \)) readings indicate foraging bouts.
during early prevolancy ($P = 0.587$), late prevolancy ($P = 0.579$), or early volancy ($P = 0.127$), but late volant individuals used torpor less often at night ($\chi^2 = 5.06, P = 0.024$).

During the day, time spent in torpor by pups varied significantly ($F_{36,95} = 17.99, P < 0.001$). Duration of daytime torpor was positively correlated with that of the mother ($F_{1,131} = 193.41, P < 0.001$), but also varied with the interaction between age class and mean $T_a$ ($F_{3,128} = 5.06, P < 0.003$). More time was spent in torpor during early prevolancy than during late prevolancy, early volancy, or late volancy ($P < 0.013$ in each case). Variation in daytime torpor depth varied significantly ($F_{36,95} = 10.88, P < 0.001$), and was influenced by adult torpor depth ($F_{1,131} = 196.47, P < 0.001$) and minimum $T_a$ ($F_{1,131} = 34.89, P < 0.001$). Torpor depth also varied among age classes ($F_{3,128} = 32.50, P < 0.001$); late volant individuals used shallower torpor than individuals of all other age classes ($P < 0.001$).

At night, time in torpor varied among pup age classes ($F_{43,113} = 20.72, P < 0.001$) and was influenced by the interaction between age class and mean $T_a$ ($F_{3,128} = 2.94, P = 0.036$), with less time spent in torpor as pups aged. Torpor depth at night varied significantly ($F_{33,98} = 11.61, P < 0.001$), and was influenced by minimum $T_a$ ($F_{1,131} = 133.85, P < 0.001$) and age class (Fig. 4; $F_{3,128} = 64.44, P < 0.001$). Torpor depth decreased with age, and late volant individuals

**Fig. 2.**—Thermoregulatory patterns of an early prevolant *Lasiurus cinereus* and its mother. The pup was a) 1 and b) 3 days old. Gaps in adult skin temperature ($T_{sk}$) readings indicate foraging bouts and arrows indicate initial emergence (E) and final return (R).

**Fig. 3.**—Mean daily torpor minutes by lactation stage of adult *Lasiurus cinereus*. Bold bars represent the median. Upper and lower box limits are the 75th and 25th quartiles, respectively. Whiskers extend to the minimum and maximum values of each stage, excluding possible outliers, which are represented by open circles.
used shallower torpor than all other age classes \((P < 0.001 \text{ for all comparisons})\). The rate of change in \(T_{sk}\) of pups after their mother’s emergence varied significantly \((F_{3,108} = 21.76, P < 0.001)\), and was influenced by the interaction between pup age and \(T_a\) \((t_{108} = -2.57, P = 0.012)\). The rate of change in pup \(T_{sk}\) varied from \(-0.48^\circ C/min\) to \(0.15^\circ C/min\) \((\bar{X} = -0.1^\circ C \pm 0.01^\circ C/min)\) and decreased with age. Following the mother’s departure, individual \(T_{sk}\) dropped as much as \(14.3^\circ C\) in 30 min during early prevolancy \((\bar{X} = -4.0^\circ C \pm 0.81^\circ C/min)\), compared with \(1.3^\circ C\) in late volancy \((\bar{X} = 0.1^\circ C \pm 0.20^\circ C/min)\). In general, pups remained warmer on their own than expected if they were to thermoconform given their mass and prevailing weather conditions (Fig. 5).

**DISCUSSION**

Our results support the hypotheses that lactating female and juvenile \(L. \text{cinereus}\) use torpor throughout early development, and that torpor expression is adapted in response to environmental and reproductive conditions. Use of torpor by \(L. \text{cinereus}\) varied with the age of the young, as we predicted. Lactation is the most energetically costly period in the life of small mammals (Speakman 2008), and the most demanding period of lactation occurs as pups become volant (Kunz 1987; Kurta et al. 1987); pups are relatively large at fledging, and spend energy learning to fly, yet may not forage well enough to fully meet their own energy demands (Hamilton and Barclay 1998). Thus, it might be expected that torpor would be most beneficial around the time of fledging, as a way of reducing the peak overall energy demand on the female. Instead, our data support our prediction that the opposite would occur; females used less torpor as lactation progressed and energy demand increased. We suggest that the peak energy demand at fledging is offset by a peak in foraging duration (Barclay 1989), and that changes in the use of torpor over the lactation period are explained by a trade-off between energy savings and reduced milk production. Early in lactation, when demand for milk is relatively low due to the small size of the young, even a reduced rate of milk production due to the use of torpor is sufficient to provide enough for the young. Torpor at this time reduces overall energy demand on the mother and therefore the duration of foraging (Barclay 1989). Females can thus spend longer at night with their young at a time when young may be particularly vulnerable (e.g., from winds that could cause them to fall from their roost). However, as pups grow and require more resources, we suggest that females use less torpor because reduced milk production at that time could slow growth of the offspring. In addition, the metabolic mass of the family unit increases over time and pups begin to actively thermoregulate on their own. Therefore, for the mother, staying warm becomes less costly as her pups grow, and the benefits in terms of milk production increase.

Female \(L. \text{cinereus}\) do not appear to carry large energy reserves in the form of fat (Koehler and Barclay 2000), perhaps as a means of increasing foraging efficiency (Norberg 1981) and the amount of time available to stay with the young (Barclay 1989; Henry et al. 2002). As a consequence, weather
that either increases the cost of maintaining a high $T_h$, or reduces foraging success, should make torpor more beneficial. Indeed, our results show an increased use of torpor during inclement weather, as studies on other species have found (e.g., Willis et al. 2006). However, $T_a$ alone did not influence the use of torpor by adult *L. cinereus*, which may be due to their relatively low thermoneutral zone (30–34°C—Cryan and Wolf 2003) compared with some other sympatric species, such as *Myotis lucifugus* (39–42°C—Stones and Wiebers 1965). Convection and evaporation are more effective modes of heat transfer than thermal radiation (Bakken and Kunz 1988; Willis and Brigham 2005). Therefore, wind and precipitation appear to increase the cost of thermoregulation more than low $T_a$ alone, to a point that benefits of increased torpor expression are realized. Furthermore, our data also suggest that poor foraging conditions cause increased use of torpor. Bats, including *L. cinereus*, are less active in high winds due to reduced insect availability (Baerwald and Barclay 2011), and forage for shorter durations as $T_a$ declines (Anthony et al. 1981; Barclay 1989; Hamilton and Barclay 1998). We found an increase in the use of torpor following nights with rain, low temperatures, and high winds, likely as a result of less energy intake.

That lactating *L. cinereus* used torpor more during the morning than the afternoon may be explained by the fact that temperatures are lowest just before sunrise. The large gradient between bat and environment results in substantial energy savings if torpor is used. In addition, less energy is required to achieve normothermia if individuals passively rewarm as $T_a$ increases (Geiser and Drury 2003). Indeed, roosts of *L. cinereus* in our study area predominantly face south, thus allowing individuals the thermal benefits of solar radiation (Klug et al. 2012).

Although lactating *L. cinereus* in our study did not use torpor more frequently than lactating individuals of their colonial, crevice-roosting counterparts (*E. fuscus*—Lausen and Barclay 2003), they had lower $T_b$ throughout lactation. Natural selection in solitary bats may favor the ability to perform (e.g., produce milk) across a wide $T_a$ range and to use torpor adaptively to cope with environmental and reproductive stressors compared with colonial, cavity-roosting species that are more at the mercy of their roosts and roostmates. Milk production by foliage-roosting bat species may be less influenced by temperature than that of colonial species, allowing them to use torpor with reduced consequence. Furthermore, colonial bats may be constrained on both ends of the thermal spectrum; performance may decline if the temperature gets too hot (Speakman and Kröl 2010), an issue that may be mitigated in foliage-roosting species exposed to cooling winds.

The timing and development of homeothermic ability in neonate small mammals depends on phylogeny (Geiser 2008) and prenatal development, is often gradual, and results from a combination of physiological ability and physical growth (i.e., accumulation of mass and insulation—Studier and O’Farrell 1972). Determining when the use of torpor develops in neonatal heterotherms is difficult. The difference between forced hypothermia (heat loss exceeds capacity for heat production—IUPS Thermal Commission 2003) and regulated hypothermia (reduction in $T_h$ despite the capacity to stay warm; i.e., torpor or hibernation—IUPS Thermal Commission 2003) is not easy to ascertain in free-ranging individuals. Our data suggest that *L. cinereus* neonates had the ability to maintain a high $T_h$ within 3 days of parturition and used torpor thereafter. Although active thermoregulation in the absence of the mother was not common until 9 days of age, there were extended periods during which pup $T_sk$ exceeded adult $T_sk$ early in development (see Fig. 2B). In addition, pups had smaller than expected changes in $T_sk$, and the variation in this change exceeded what was expected from environmental conditions (i.e., $T_a$ and wind speed) alone (Fig. 5), which suggest an influence of endogenous heat. Therefore, our results indicate that the onset of full thermoregulatory ability in *L. cinereus* is considerably more rapid (11% of fledging age; 3 of 28 days—Koehler and Barclay 2000) than in other insectivorous species that raise young in temperate regions. For example, *E. fuscus* and *M. lucifugus* are poikilothermic until at least 39% (7 of 18 days—Hollis and Barclay 2008) and 47% (9 of 19 days—Studier and O’Farrell 1972) of fledging age, respectively. Likewise, the fringed Myotis (*Myotis thysanodes*) can thermoregulate at 5 days of age, but this is 28% of fledging age (Studier and O’Farrell 1972).

Torpor expression by juvenile *L. cinereus* during the day was heavily influenced by the thermoregulatory patterns of their mother. Pups typically roost under the wing of the mother for the first 17 days (Klug 2011), and contact results in heat transfer between family members and buffers offspring from ambient conditions (Jones 2000). Therefore, we suggest that it is most efficient for pups to thermoconform, with $T_h$ similar to that of their mother, thus allowing energy to be allocated to growth (Kunz 1987). Although pups did not actively thermoregulate often during early prevolancy, it would be beneficial for them to have the capacity to do so. For example, it would reduce the time needed to rewarm, thereby allowing pups to nurse soon after the mother returns between foraging bouts.

Although *L. cinereus* neonates are partially furred at birth (Koehler and Barclay 2000), twins can huddle to reduce heat loss, and they demonstrate the ability to actively thermoregulate early in development, our data suggest that the costs of maintaining a high $T_h$ outweigh the benefits to development during prevolancy. Contrary to our prediction, pups used torpor throughout most of postnatal development. Trade-offs in energy allocation are likely the result of the roosting ecology of *L. cinereus*. Colonial bats often raise young in sheltered roosts with relatively high $T_a$ (Kunz and Lumsden 2003), which offers thermal benefits to both juveniles and lactating females; pups can allocate energy to growth instead of maintaining high $T_h$, and lactating females can allocate more resources to milk production. However, given the often unstable low $T_a$ and convective cooling in foliage roosts, the energy required to compensate for heat loss is large and
benefits gained by remaining normothermic appear to be outweighed. As offspring grow, mass and fur density increase, reducing the costs of normothermy to a point where staying warm becomes beneficial under most conditions (i.e., mild $T_n$, low wind speed, and no precipitation), but periods of inclement weather still evoke use of torpor.

Despite the reproductive benefits of maintaining high $T_b$ (Farmer 2000), and adaptations of $L$. cinereus that may mitigate the cost of thermoregulation, torpor appears necessary given their solitary nature and use of unsheltered roosts. However, solitary roosting, the use of relatively exposed foliage roosts, and migration may combine to allow $L$. cinereus greater use of torpor than colonial bats, such as $E$. fuscus, and in an individually strategic, adaptive fashion. Although hibernating and migrating species both face short reproductive seasons at our study latitude, there may be less developmental constraint for migratory species. Hibernators have the additional burden of accruing sufficient fat stores to survive through the winter, but once migrants become efficient fliers, they may have developed sufficiently to migrate; $L$. cinereus pups begin migration at ~80% adult mass (Koehler and Barclay 2000). In addition, if long-distance migrants remain active on their wintering grounds and do not need to develop fat reserves for hibernation, they can continue to grow during and after migration (Ewing et al. 1970). Overall, a longer growing period for migratory species may allow thermoconformity early in development and frequent use of torpor by mother and pup throughout the reproductive period, because the resulting slowed growth is less costly than for resident, hibernating species.

Although many studies have investigated thermoregulation in small mammals, few have focused on the development of thermoregulatory capabilities in bats, and even fewer have done so using free-ranging juveniles (Hollis and Barclay 2008). Studying thermoregulation under natural conditions is important because captive mammals may not behave like free-ranging individuals (Geiser et al. 2000). Lactation is often viewed as a single stage, and the use of torpor during lactation is compared with that of other reproductive stages, such as pregnancy and postlactation. However, our results indicate that the use of torpor during lactation is higher for reproductive female $L$. cinereus than for non-reproductive females, suggesting that lactation should not be considered a single, static stage, and that use of torpor reflects current energetic conditions on a finer temporal scale.

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