



Variation in body temperature and isolation calls of juvenile big brown bats, *Eptesicus fuscus*

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As occurs in some poikilotherms, the acoustic signals of young birds and mammals may be influenced by ambient temperature because young cannot maintain a constant body temperature. This may have consequences in colonial species in which individual recognition of offspring by parents is important if care is to be directed appropriately. In bats, mothers use isolation calls of pups to locate their own infants. For isolation calls to function effectively for individual recognition, they must vary among individuals while remaining relatively consistent for any given individual. We investigated the effect of variation in body temperature on the isolation calls of the big brown bat. Young pups are unable to thermoregulate and thus experience a wide range of body temperatures, potentially affecting their ability to produce consistent vocalizations. We recorded the isolation calls of pups at different body temperatures and measured various characteristics of the calls. Pups produced isolation calls at body temperatures ranging from 11 to 37°C. However, with increasing body temperature, the isolation call frequencies as well as the call interval decreased, while call duration increased, but changes in call structure with body temperature were not consistent among individuals. Overall, isolation calls produced at various body temperatures were identified no more accurately via discriminant function analysis when body temperature was accounted for than when it was not. Isolation calls produced by different individuals at approximately the same body temperature were classified most accurately (79%). Variation in body temperature of young therefore has the potential to hinder individual recognition by mothers in colonial situations. Other identification cues, such as odour and spatial memory, may be important.

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Ambient temperature has significant effects on the acoustic signals of many poikilothermic animals (e.g. frogs: Gerhardt 1978; Esteban et al. 2002; Lüddecke & Sánchez 2002; insects: Ritchie et al. 2001; Hedrick et al. 2002). Temperature-mediated variation in signal characteristics has the potential to influence the ability of a receiving animal to recognize the individual or species producing the signal, although in at least some species, the preference of the receiver is also influenced by ambient temperature ('temperature coupling': Gerhardt 1978; Ritchie et al. 2001).

In contrast to poikilotherms, the acoustic signals of adult homeotherms are unlikely to be affected by ambient temperature because the signaller's body temperature (T_b) remains relatively constant. However, the thermoregulatory ability of the young of many species of mammals and birds is initially poor, resulting in variation in body temperature (e.g. Whittow & Tazawa 1991; MacArthur & Humphries 1999; Holloway & Geiser 2000; Nichelmann

& Tzschentke 2002). Despite the importance of acoustic signals in parent-offspring communication (e.g. Halpin 1991), the effect of variation in the body temperature of newly hatched birds or neonatal mammals on their ability to vocalize or the characteristics of their calls has rarely been investigated (e.g. Okon 1970; Allin & Banks 1971; Branchi et al. 1998), and, to our knowledge, the ability of parents to recognize their young, has not been studied. Thus, the goal of our study was to determine whether variation in body temperature in neonatal mammals affects the ability to produce recognizable calls suitable for individual recognition.

Variation in vocalizations with body temperature should be particularly important among colonial birds and mammals in which parents must identify their offspring from among many young. Individual recognition also is especially critical in species in which parents are regularly separated from their young and need to reunite with the correct offspring. In many mammals, such reunions are facilitated via isolation calls ('i-calls'; e.g. Walser et al. 1982; Lent 1991; Smolker et al. 1993;

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Maestripietri & Call 1996; Phillips & Stirling 2000; van Parijs & Corkeron 2002), which are infant vocalizations uttered when the infant is lost, separated or removed from its mother (Brown 1976). The calls serve to inform the parent of the infant's location and thus function in reunions.

Many bats are colonial and mothers leave their young each night when they forage (Davis et al. 1968; Turner et al. 1972; Thomson et al. 1985). Mothers locate their own offspring using acoustic and odour cues (e.g. Loughry & McCracken 1991; de Fanis & Jones 1995), and probably spatial memory. Isolation calls are important in mother-infant reunions (e.g. Gould 1971; Thomson et al. 1985; de Fanis & Jones 1995) and consist of short, frequent, audible 'peeps' that are highly localizable. Mothers of some species can distinguish the i-calls of their own infant from those of others (Turner et al. 1972; Brown 1976; Thomson et al. 1985; Gelfand & McCracken 1986; Balcombe 1990; Jones et al. 1991; Scherrer & Wilkinson 1993; de Fanis & Jones 1995). For such individual recognition to occur, i-calls must contain vocal signatures. That is, they must be variable among individuals while remaining relatively consistent for any given individual, and they must contain unique characteristics that allow for discrimination among individuals (Scherrer & Wilkinson 1993).

Isolation calls of bats may vary within individuals depending on the infant's age (Turner et al. 1972; Gould 1975; Brown 1976; Moss 1988; Jones et al. 1991; de Fanis & Jones 1995) and stress or stimulation level (Gould 1971; Brown 1976). These factors may hinder recognition by mothers by increasing variation in the calls of each individual. However, with the exception of age, little research has been done on the effect of these variables on maternal recognition of offspring. In particular, i-call variation resulting from differences in juvenile body temperature could have important consequences for individual recognition of pups that undergo daily torpor. Some vocalizations of adult bats differ depending on whether the individual is torpid (Barclay et al. 1979), and juvenile bats are unable to thermoregulate for at least several days after birth (Noll 1979; Hollis 2004). Body temperature thus varies depending on ambient temperature. If such variation causes changes in the characteristics of isolation calls produced by each individual, recognition of offspring by mothers might be impaired. There is no evidence for any species that indicates whether juveniles are even able to produce i-calls at body temperatures below normothermic levels.

We tested whether juvenile big brown bats are able to produce i-calls at low T_b , and if so, whether characteristics of the calls vary with changes in T_b . We manipulated environmental temperature and recorded the isolation calls of pups at different T_b s. We predicted that variation in T_b would result in changes in the characteristics of i-calls, making them less identifiable as being produced by a particular individual.

METHODS

Eptesicus fuscus is a colonial species that often uses buildings as summer maternity roosts. During June and July

2003, we studied maternity colonies in the attics of two schools in Medicine Hat, Alberta, Canada. In this population, females give birth to a single pup between mid-June and mid-July. Pups are unable to maintain the normal adult T_b for the first 4 to 5 days after birth (Hollis 2004). By listening for i-calls, we located nonvolant pups after most adult bats had left the roost to feed in the evening. Pups were removed from the attic and were kept in dark cloth bags when not being handled. We returned pups to their point of capture within 4 h. We measured forearm length using calipers, and used the average of three measurements to estimate the ages of the pups, according to the equation: $\text{age} = 0.61(\text{forearm}) - 10.6$, $r^2 = 0.93$ (Holroyd 1993). All the pups used were 1–3 days old based on this equation. We measured skin temperature of pups using temperature-sensitive radiotransmitters (Holohil Systems Limited, Carp, Ontario, Canada), affixed between the shoulder blades of each pup, and a Lotek SRX 400 scanning receiver (Lotek Engineering Inc., Newmarket, Ontario, Canada). Skin temperature of bats reflects core T_b (Barclay et al. 1996), although Willis & Brigham (2003) pointed out some discrepancies, primarily during active rewarming.

We recorded the isolation calls of pups over a range of body temperatures using an environmental chamber to manipulate ambient temperature (T_a) over the range that pups encounter in both natural and building roosts (L. Hollis, personal observation; C. Lausen, personal communication). We recorded the i-calls from most pups at three T_a s each: room temperature (19–22°C), a higher temperature (25, 30 or 35°C) and a lower temperature (10, 15 or 20°C). We placed an individual in a small metabolic chamber and recorded i-calls at room temperature. We then placed the metabolic chamber in the environmental chamber set at one of the higher temperatures and waited until T_b of the pup was stable ($\pm 1^\circ\text{C}$) for at least 1 h before recording i-calls. We then lowered T_a by 15°C, waited for a stable T_b , and again recorded i-calls. We recorded i-calls using a custom-made ultrasonic microphone (Simmons et al. 1979) connected to a Racal 4DS instrumentation tape recorder operated at 38 cm/s (system flat ± 5 dB from 15 to >80 kHz). We recorded the calls from each bat for 2–7 min at each temperature and we noted the pup's T_b at the time of each recording.

We played isolation calls at 9.5 cm/s and digitized them using Real-Time Spectrogram for Disk (RTSD) version 1.10 (Engineering Design, Belmont, Massachusetts, U.S.A.) at a sampling rate of 25 kHz and a frequency resolution of 49 Hz. In most cases (20 of 24), our recordings of each individual at each environmental temperature had more than 20 clear (i.e. high signal-to-noise ratio) i-calls. From these, we randomly selected 20 calls for analysis. For the four recordings with fewer than 20 clear calls (10, 15, 16, 16), we used them all, thus resulting in unequal numbers of calls analysed for each individual. For each call, we measured several characteristics (Fig. 1): minimum frequency of the first harmonic (Min 1), maximum frequency of the first harmonic (Max 1), initial frequency of the first harmonic (Initial 1), final frequency of the first harmonic (Final 1), minimum frequency of the second harmonic (Min 2), maximum frequency of the second

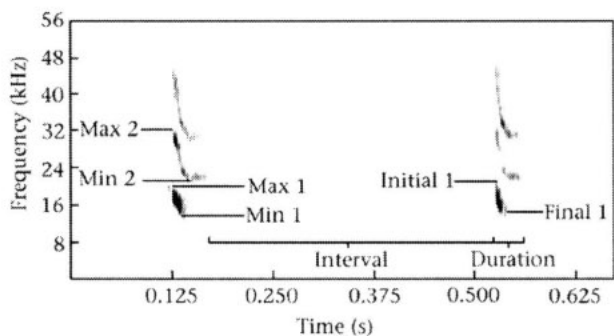


Figure 1. A frequency–time display of two consecutive isolation calls from a juvenile *Eptesicus fuscus* illustrating the variables measured. Note the shift in emphasis of frequencies from the first to the second harmonic.

harmonic (Max 2), call duration (Duration) and the interval between the end of one call and the beginning of the next one (Interval). Frequency measures from the two harmonics were not perfectly correlated because sound energy within a call frequently shifted from one harmonic to the other (Fig. 1). Likewise, variation in call shape meant that Max 1 and Initial 1 were not always the same, nor were Min 1 and Final 1 (Fig. 2).

We analysed the data using SAS 8.1 for Windows (SAS Institute Inc., Cary, North Carolina, U.S.A.). Univariate analyses using analysis of covariance (ANCOVA) were first performed to assess whether there was an effect of T_b on each call parameter. Isolation calls in this population are individually distinct (Rasmuson & Barclay 1992), so we included both individual and the interaction between individual and T_b in the models.

To determine which of the call variables that we measured best discriminated calls from different individuals, we used forward stepwise discriminant function analysis (DFA). To avoid multicollinearity, we included only one of each pair of parameters with Pearson correlation coefficients greater than 0.5. We used the variables identified in this analysis in all subsequent analyses.

We examined the potential effect of T_b on call recognition by comparing the distinctiveness of calls produced by different individuals from three perspectives: gross characteristics of calls recorded at different body temperatures, characteristics of the same calls after removal of the general effect of T_b , and gross characteristics of calls recorded at the same body temperature. The distinctiveness of calls was assessed by the ability of DFA to associate calls correctly with the individuals that produced them (Tabachnick & Fidell 2001). To remove the general effect of T_b from variation in call characteristics, we considered all characteristics simultaneously as dependent variables in a multivariate regression against T_b . The residuals from this analysis were then used in the DFA, with cross-validation to determine the proportion of calls that were identified correctly to the pups that produced them. The analyses of gross call characteristics similarly considered residuals from the overall mean call characteristics. If variation in T_b increases variation in each individual's calls predictably, then removing the general effects of T_b by regression should allow better identification. We tested this expectation using paired t tests on the arcsine-transformed proportions of correctly classified calls of each individual when T_b was or was not included in the model, and when T_b did not vary. We used one-tailed tests, because we predicted that variation in T_b would decrease the ability to correctly identify calls.

RESULTS

We recorded i-calls from nine individuals (five males and four females) at the various environmental temperatures. Six individuals were recorded at room temperature, a higher temperature and a lower temperature, and the other three were recorded at only two temperatures each. Body temperatures during i-call recordings varied with T_a and ranged from 11 to 37°C. Pups spontaneously produced i-calls at all T_b s.

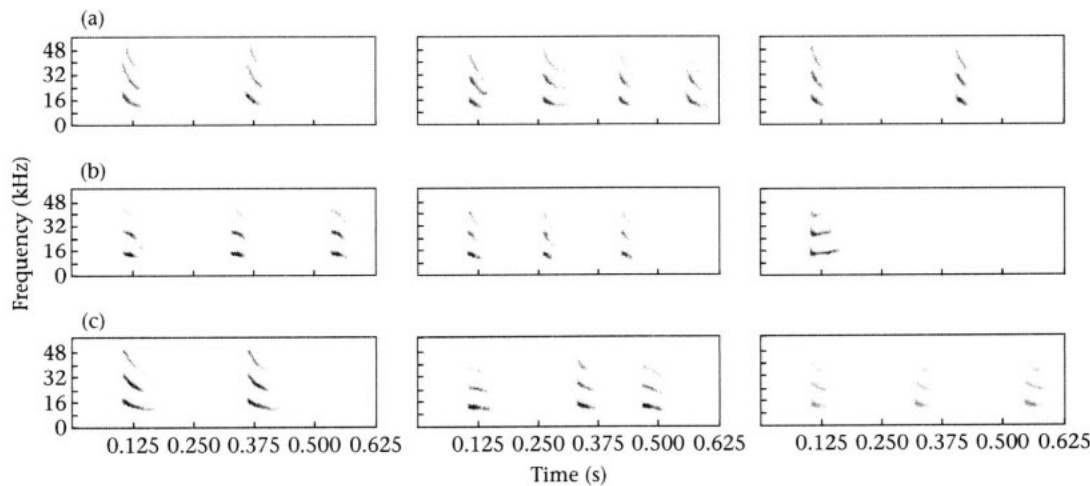


Figure 2. Frequency–time displays of calls from three different juvenile *Eptesicus fuscus* pups (a–c). For each individual, each panel presents calls produced at a different body temperature (a: 23.7, 35.1, 20.4°C; b: 24.2, 28.6, 12.2°C; c: 24.9, 35.0, 22.4°C).

The ANCOVA model that included individual, T_b and the individual $\times T_b$ interaction, explained a significant amount of variation of each call parameter that we measured (Table 1). Estimates of the partial regression coefficient revealed that, with the exception of Min 1, T_b had a statistically significant effect on all call parameters measured (Table 1). All frequency measurements, as well as Interval, increased with decreasing T_b , and Duration decreased. However, in each case there was also a significant $T_b \times$ individual interaction (Table 1), indicating that the effect of T_b on call characteristics was not consistent among individuals.

Min 1 was highly correlated with Final 1 and Min 2, and Max 1 was highly correlated with Initial 1 and Max 2. The inclusion of Min 2 and Max 2 into the forward stepwise DFA model occurred earlier than did Min 1 and Max 1 or Initial 1 and Final 1, indicating that Min 2 and Max 2 were of greater importance for identifying groups. We therefore used Min 2, Max 2, Interval and Duration in the standard DFAs used to identify groups.

The DFA using the residuals from the MANOVA indicated that there were significant differences in call parameters among the nine individuals, whether T_b was included in the model (Wilk's $\lambda = 0.248$, $F_{32,1646} = 23.60$, $P < 0.001$) or not (Wilk's $\lambda = 0.270$, $F_{32,1646} = 21.94$, $P < 0.001$). Not all individuals were recorded at the same ambient temperatures, so we conducted a separate analysis for the six pups that were recorded at three ambient temperatures. There were significant differences in call parameters among individuals, whether T_b was included in the model (Wilk's $\lambda = 0.366$, $F_{20,956} = 16.91$, $P < 0.001$) or not (Wilk's $\lambda = 0.368$, $F_{20,956} = 16.83$, $P < 0.001$) for these bats as well. Finally, we analysed calls from the six individuals when they were held at room temperature. Their body temperatures were relatively consistent (range 24–27°C), thus minimizing the potential effect of T_b variation on call characteristics. When T_b variation was limited in this way, there were again significant differences in call parameters among individuals (Wilk's $\lambda = 0.032$, $F_{20,356} = 32.21$, $P < 0.001$).

For the model involving data from all nine pups and no T_b , the first three discriminant functions accounted for 90.8% of the total variation, with canonical variable 1 (Can 1) weighted most heavily towards Max 2, Can 2 weighted towards Min 2, and Can 3 towards Interval.

With the addition of T_b as a covariate, the first three discriminant functions accounted for 95.2% of the variation, with Can 1, Can 2 and Can 3 weighted towards Max 2, Min 2 and Duration, respectively. For the model involving six individuals and no T_b , the first three functions explained 92.9% of the variation, with Min 2, Duration and Max 2 contributing heavily towards Can 1, 2 and 3, respectively. With inclusion of T_b , the first three discriminant functions accounted for 97.1% of the total variation, with the same parameters contributing to the canonical functions. Finally, for calls recorded from individuals with T_b between 24 and 27°C, the first three discriminant functions accounted for 98.4% of the variation, with Interval, Duration and Min 2, respectively, as the main contributing factors.

We used DFA to determine the probability of classifying calls produced at any T_b to the correct individual, using a cross-validation approach. When calls from all nine bats were included without accounting for variation in T_b , 52.8% of the calls ($N = 458$) were correctly assigned. This value did not change significantly when T_b was accounted for (48.2%; paired t test: $t_8 = 0.85$, $P = 0.42$). Overall prior probability of correct classification, assuming random assignment, would have been 11.1%. Similarly, for the six individuals recorded at all temperatures, correct classification declined slightly when T_b was accounted for (52.2% versus 61.3%, $N = 297$ calls). However, correct classification was significantly higher when there was little variation in T_b (79.3%, $N = 116$; one-tailed paired t test versus no T_b in the model: $t_5 = 2.07$, $P = 0.033$). Overall prior probability would have been 16.7%.

DISCUSSION

As in some birds and mammals (e.g. Whittow & Tazawa 1991; MacArthur & Humphries 1999; Holloway & Geiser 2000), including some other bats (Noll 1979), young *E. fuscus* initially are unable to regulate their T_b at adult normothermic levels. They regularly enter torpor at night when their mothers leave to forage and the roost cools (Hollis 2004). If torpor prevented young from producing i-calls, or had a major effect on their structure, as it does for some vocalizations of adult bats (Barclay et al. 1979), the ability of a female to locate her offspring among

Table 1. Results from analyses of covariance testing for the effect of body temperature on various parameters of *E. fuscus* i-calls

Variable	Model	T_b	Individual	$T_b \times$ Individual	Partial regression
Min 1	6.79***	3.43	5.77***	5.78***	
Max 1	14.71***	22.50***	16.26***	9.95***	−176.8
Initial 1	13.85***	23.31***	17.11***	11.18***	−188.5
Final 1	15.77***	4.44*	20.08***	26.45***	−38.8
Min 2	17.07***	4.64*	10.05***	13.77***	−89.4
Max 2	23.80***	7.09**	14.66***	6.34***	−141.8
Duration	11.46***	6.89**	5.15**	4.54***	0.001
Interval	128.7***	72.62***	83.12***	90.25***	−0.009

The overall model contained individual as a main effect, body temperature (T_b) as a covariate, and the interaction between individual and T_b . F values are presented, as well as the partial regression coefficients, which reflect the effect of T_b on call parameters. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

dozens or hundreds of pups in a maternity colony might be compromised. This might be especially true early in lactation, because mothers would have had little time to learn the variable nature of their offspring's calls. However, not only did young *E. fuscus* produce i-calls at body temperatures as low as 11°C, but the calls also had the general features typical of the i-calls of this species (Gould 1971; Moss 1988). We suggest that selection for this ability is strong, not only in this species, but in other colonial mammals and birds in which reunions with parents are necessary, and young experience variable ambient temperatures and are essentially poikilothermic.

Although at a general level, the structure of *E. fuscus* i-calls was consistent regardless of body temperature, details of the calls did change with T_b , as they do in some poikilotherms (e.g. Gerhardt 1978; Ritchie et al. 2001). This variation may occur for several reasons. Changes in pup call structure might be adaptive in that they convey information to the mother regarding the pup's level of stress, as occurs in some other mammals (Haskins 1979; Weary & Fraser 1995; Weary et al. 1996). Hunger levels may also have increased during the recording sessions, adding further stress to the pups. Any stressful stimulus may result in changes to i-calls, and these changes may be used by the mothers to gauge the status of their offspring. However, if temperature had this effect, one might expect more consistent changes to call structure with changes in temperature than those that we found.

Changes in the structure of i-calls may also result from the physiological responses of muscles to temperature. For example, call interval may be a function of the rate of muscle contraction and relaxation, features that decline at low T_b (Bennett 1984), potentially resulting in longer intervals between calls. Interval might also increase if call production is tied to respiratory rate, as is the case for the echolocation calls of bats (Speakman & Racey 1991).

In contrast to the rate of muscle contraction, the amount of muscle tension is influenced relatively little by temperature (Bennett 1984; Choi et al. 1998). This difference may help to explain why i-call frequencies did not consistently decline with lower T_b . Indeed, the pattern was for frequencies to increase.

To a certain degree, the i-calls of *E. fuscus* are individually distinctive even when body temperature varies, as indicated by the finding that a higher proportion of calls were correctly identified than expected by random assignment. Although the number of individuals that we recorded was relatively small, colonies in this species are also relatively small (dozens to a few hundred individuals; e.g. Davis et al. 1968), especially in natural roosts (C. Lausen, personal communication), and pups are generally found in clusters of fewer than 10 (Hollis 2004). Thus, a mother might typically have to discriminate among fewer than 10 pups, as our analysis did. We found that correct classification rate was significantly higher when there was no T_b variation, indicating that, even with small groups of pups, mothers would be better able to recognize the calls of their offspring if T_b did not vary.

Not only did calls vary with T_b , but the changes were also inconsistent among individuals, unlike the relatively predictable changes in poikilotherms (e.g. Ritchie et al.

2001; Lüddecke & Sánchez 2002). This inconsistency is indicated by the finding that there was a significant interaction between T_b and individual in the univariate analyses, and that assignment did not improve when T_b was included as a covariate in the analyses. Thus, even if a mother could estimate the body temperature of her offspring, such as from roost temperature, the unpredictability of the changes to i-calls would preclude better call recognition, at least until she had learned the individual pattern of changes for her pup.

Several behaviours may assist female bats in identifying their pups, despite variation in calls caused by variation in T_b . Pups are frequently found in clusters when they are separated from their mothers (Hollis 2004), and this may increase their ability to maintain T_b and therefore decrease within-individual variation in isolation calls. A mother may also use spatial memory to locate her pup, and can confirm pup identity using olfactory cues (Turner et al. 1972; Brown 1976; de Fanis & Jones 1995). These behaviours may help to compensate for any reduction in acoustic recognition resulting from variation in body temperature. If vocalizations of poikilothermic young in other colonial mammals and birds also vary with body temperature, such alternative identification cues may be widely important.

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