40 Do roost type or sociality predict warming rate? A phylogenetic analysis of torpor arousal

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Abstract

Torpor arousal is energetically costly and many heterothermic endotherms rely on passive warming via ambient heat to reduce energy expenditure during the warming phase. However, species that live in stable microenvironments likely have little opportunity to exploit passive warming. These species may benefit from high warming rates because, when other factors are held equal, short-duration warming bouts cost less energy than long ones. Similarly, species that do not exploit social thermoregulation might face stronger selection pressure for rapid warming rates than social species if individuals of social species can share arousal costs with other group members. I analysed published and new data for 35 species of bats to test the hypothesis that species which roost in stable microenvironments and small colonies are characterised by faster warming rates than those living in variable microclimates and large colonies. After controlling for body mass and phylogeny, I found no influence of roost temperature stability or coloniality on arousal rates across all species or for 17 species from the family Vespertilionidae. However, when I analysed data for nine species from a largely tropical/subtropical clade, I found a strong influence of both roost temperature stability and colony size on warming rates. Species from this group that roost in stable microenvironments and in small colonies had significantly higher warming rates than other species. These findings complement recent work that highlights the influence of torpor arousal, and its energetic costs, on the lives of heterothermic endotherms.

Introduction

The energy required to warm up from torpor is widely viewed as a major cost of heterothermy for endothermic animals (e.g. Geiser & Drury 2003; Geiser et al. 2004; McKechnie & Wolf 2004). Recent work points to the importance of passive warming as a behavioural mechanism to mitigate this cost and it is clear that a range of endotherms gain energetic benefits from passive warming and/or basking during arousal from torpor (e.g. Geiser & Drury 2003; Geiser & Pavey 2007; Warnecke et al. 2008; Woods & Brigham 2004). However, many heterothermic endotherms nest or roost in sites where daily temperature variation may be insufficient to

allow for passive warming (e.g. underground burrows, well-insulated tree hollows, caves). When these species employ torpor they must depend on energetically expensive, active warming through shivering and/or non-shivering thermogenesis.

Rapid warming rates are less expensive in terms of energetic costs than slow warming rates (McKechnie & Wolf 2004; Stone & Willmer 1989). For example, McKechnie and Wolf's (2004) model of the energetic costs of warming predicts that, for a 15-g endotherm, increasing body temperature (T_b) from 21.5°C to 37°C, warming at a rapid rate of 1.5°C min^{-1} requires 44% less energy than slow warming at a rate of 0.2°C min^{-1}. For endotherms that regularly rely on active arousal from torpor, the accumulated costs of slow warming rates could quickly become significant for long-term energy budgets. Therefore, heterothermic endotherms that experience little variation in natural T_a in their burrows, nests or roosts may face selection pressure that favours rapid warming rates to reduce energetic costs.

Social thermoregulation may also influence warming rate. Species that rely heavily on huddling and social thermoregulation may be less likely to use torpor than those that tend to be solitary (e.g. Hwang *et al.* 2007). When individuals of these group-living species do use torpor, they may be able to rewarm at a reduced individual cost because the energy spent on warming can be shared by the group. Individuals of species that do not rely on social thermoregulation and huddling may need to use torpor more frequently and rely more heavily on endogenous heat production for active warming. Therefore, like species living in stable microclimates, solitary species or those in small groups may also face heightened selection pressure for rapid warming rates.

Intuitively, the rate at which heterothermic endotherms can warm up from torpor should correlate positively with metabolic power output because of the likely importance of metabolic performance during rapid warming (Geiser & Baudinette 1990; Stone & Purvis 1992). Surprisingly, Stone and Purvis (1992) found that for mammals ranging in size from 2.4–230 g, after controlling for phylogenetic influence, basal metabolic rate (BMR) was negatively correlated with warming rate. They suggested that rapid warming rates and low BMR are correlated because both represent strategies for energy conservation in heterothermic mammals. However, it is not clear how BMR may relate to warming rates across smaller ranges of body size or in specific taxonomic groups where body mass appears to have little influence on warming rate (Geiser & Baudinette 1990; this study).

My objective was to address potential ecological and physiological influences on the evolution of warming rates in heterothermic endotherms. Bats (Chiroptera) are good model organisms for examining these issues because of the diversity of their roosting habitats – from caves with high thermal stability to exposed roosts in foliage; their wide range of social patterns – from completely solitary to highly gregarious; and their propensity to rely heavily on torpor (Kunz & Lumsden 2003; Speakman & Thomas 2003). I used a phylogenetically informed analysis to test three specific hypotheses: 1) warming rates are positively correlated with the stability of roost temperature (T_{roost}) possibly because species that live in stable roost micro-environments face reduced opportunity to exploit passive warming; 2) warming rates are negatively correlated with colony size, possibly because social–thermoregulatory benefits of large colonies allow for less frequent use of torpor and shared arousal costs when needed; and 3) warming rate is positively correlated with BMR in bats because of potential functional links between metabolic performance and rapid warming.

Table 1. Data for warming rate (Rate), body mass, basal metabolic rate (BMR), maximum known or estimated colony size (Max. col. size) and roost temperature stability (T_{roost} score). The latter variable was quantified on a three-point scale from 0 for highly stable T_{roost} (e.g. large caves) to 2 for highly unstable T_{roost} (foliage, exfoliating bark, rock crevices). Sources for warming rate, BMR and body mass are reported in Materials and Methods.

Species	Mass (g)	Rate (°C/min)	Mass (g)	BMR (ml O$_2$/h)	Max col. size	T_{roost} score	Source for colony size and roost type
Pteropodidae							
Macroglossus minimus	16.0	0.31	16.3	21.00	1	2	Winkelmann *et al.* 2003
Nyctimene albiventer	28.0	0.60	30.9	26.30	1	2	Churchill 1998
Emballonuridae							
Taphozous australis	22.0	0.57	-	-	100	0	Churchill 1998
T. melanopogon	26.0	0.15	-	-	4000	0	Lekagul & McNeely 1998
Rhinopomatidae							
Rhinopoma hardwickei	10.0	0.50	-	-	5000	0	Qumsiyeh & Knox Jones 1986
R. microphyllum	19.0	0.30	-	-	5000	0	Schlitter & Qumsiyeh 1996
Rhinolophus hipposideros	6.0	1.05	-	-	100	1	Schober & Grimmberger 1997
R. ferremequinum	18.0	0.75	28.0	46.50	300	0	Schober & Grimmberger 1997
R. megaphyllus	8.0	0.84	10.6	25.84	2000	0	Churchill 1998
Hipposideridae							
Asellia tridens	15.0	0.42	-	-	5000	0	Nowak 1999
Hipposideros speoris	9.0	0.32	-	-	1200	1	Pavey *et al.* 2001
Phyllostomidae							
Glossophaga soricina	9.5	0.35	9.6	21.60	1000	1	Nowak 1999
Molossidae							
Mormopterus loriae	8.5	0.90	-	-	300	2	Churchill 1998
M. planiceps	9.5	1.40	-	-	150	2	Richards 1995a
Tadarida brasiliensis	12.0	0.73	11.0	15.30	20000000	0	Nowak 1999
T. teniotis	30.0	0.78	-	-	100	2	Arlettaz *et al.* 2000
Chaerephon pumilus	18.0	1.05	-	-	300	2	Bouchard 1998
Mops condylurus	36.0	0.80	23.20	31.09	700	2	Maloney *et al.* 1999
Vespertilionidae							
Miniopterus schreibersii	15.0	1.40	11.1	25.42	10000	0	Churchill 1998
Antrozous pallidus	28.0	1.00	22.0	21.20	139	2	Hermanson & O'Shea 1983
Pipistrellus hesperus	4.0	1.20	-	-	12	2	Reid 2006
P. pipistrellus	6.0	0.95	6.6	12.10	300	1	Gerell & Lundberg 1985
Chalinolobus gouldii	12.0	1.40	17.5	25.20	40	2	Churchill 1998
C. picatus	6.0	1.40	-	-	15	0	Churchill 1998; Richards 1995b
Eptesicus fuscus	16.0	1.50	15.0	17.00	700	2	Nagorsen & Brigham 1993
E. serotinus	25.0	1.30	27.0	43.10	20	2	Petrželková & Zukal 2001
Nyctalus noctula	27.0	1.58	-	-	234	2	Boonman 2000
Corynorhinus townsendii	10.5	1.52	-	-	300	0	Nagorsen & Brigham 1993
Plecotus auritus	12.0	0.70	10.3	11.20	30	1	Entwistle *et al.* 1997
Myotis lucifugus	7.6	0.80	6.5	9.30	3000	1	Nagorsen & Brigham 1993
M. adversus	8.0	1.20	-	-	300	2	Churchill 1998
M. californicus	5.0	1.29	-	-	52	2	Brigham *et al.* 1997
M. myotis	25.0	1.50	25.0	25.00	1000	0	Schneider & Hammer 2006
M. nattereri	8.0	1.05	-	-	200	2	Greenaway & Hutson 1990
M. thysanodes	6.5	0.91	8.1	17.40	300	1	Nagorsen & Brigham 1993

Materials and methods

I obtained data on warming rates, BMR, maximum known colony size and roosting habitat from the literature (Table 1). Most warming rates were the maximum rate (i.e. the steepest section of the T_b trace during arousal) and were taken from Geiser and Baudinette (1990). A few published warming rate data points may not have reflected maximum rates, but this likely had little influence on my results because maximum and overall warming rates appear to be closely correlated in mammals (Geiser & Baudinette 1990). I obtained additional data for *Glossophaga soricina* and *Macroglossus minimus* by digitising the T_b time-course plots presented by Kelm and von Helversen (2007) and Bartels *et al.* (1998), respectively, and then using Techdig 2.0 (Jones 1998) to pinpoint data points from each curve for calculation of maximum warming rates. I also added data for *Eptesicus fuscus* from Willis *et al.* (2005a). To ensure that the magnitude of warming was similar for all species, I only included warming rates for bats emerging from torpor at ambient temperature = $20° \pm 1.5°$ C. I only used data for T_b as opposed to skin temperature (T_{sk}) because T_{sk} warming rates can differ considerably from those for T_b in bats (Willis & Brigham 2003). Most data for BMR were taken from Speakman and Thomas (2003) and Willis *et al.* (2005b) but I added published data for *Mops condylurus* (Maloney *et al.* 1999) and *E. fuscus* (Willis *et al.* 2005a), as well as new data for *Rhinolophus megaphyllus* (Willis & Geiser unpubl. data). Direct measurements of T_{roost} are only available for very few bat species but certain types of roosts are likely to be much more variable than others in terms of microclimate (e.g. Baudinette *et al.* 2000; Kunz & Lumsden 2003; Willis & Brigham 2007). Owing to a lack of data on roost temperature in the literature, for each species I quantified the likely stability of T_{roost} on a three-point scale from highly stable = 0 to highly unstable = 2. Species known to roost exclusively in caves, which tend to have highly stable microclimates (i.e. Kunz & Lumsden 2003, Baudinette *et al.* 2000), were scored as 0. Species known to roost in caves some of the time but which also roost in trees, rock crevices or other structures with less stable microclimates, were scored as 1, along with species which roost mainly in well-insulated tree hollows and buildings. Species were scored as 2 if they are known to roost only in thermally unstable sites such as shallow rock crevices or tree hollows, under shedding bark, in foliage, under corrugated iron roofs, or in other sites that are likely characterised by substantial daily fluctuations in microclimate.

I log-transformed all variables prior to analysis and calculated Felsenstein's independent contrasts (Felsenstein 1985) using the PDAP:PDTREE module (Version 1.09, Midford *et al.* 2007) of Mesquite (Version 2.0, Maddison & Maddison 2007). I used a phylogeny based on the bat supertree (Jones *et al.* 2002) combined with more detailed molecular phylogenies for the Vespertilionidae (Hoofer & Van Den Bussche 2003) and *Myotis* (Stadelman *et al.* 2007; Figure 1). I performed three sets of analyses. The first was based on the entire dataset to identify general trends. The second focused on the Vespertilionidae because this family is by far the best studied in terms of use of torpor; previous work suggests that vespertilionids may differ from other bats for some energetic traits, including use of torpor and BMR (Speakman & Thomas 2003; Willis *et al.* 2005b). The third focused on a monophyletic group of non-vespertilionid bats that are thought to be largely tropical/subtropical in origin and are much less studied in terms of use of torpor compared to temperate vespertilionids (Nowak 1999; Speakman & Thomas 2003). This group (hereafter the non-vespertilionid clade) included representatives from four families (i.e. Emballonuridae, Hipposideridae, Rhinolophidae and Rhinopomatidae).
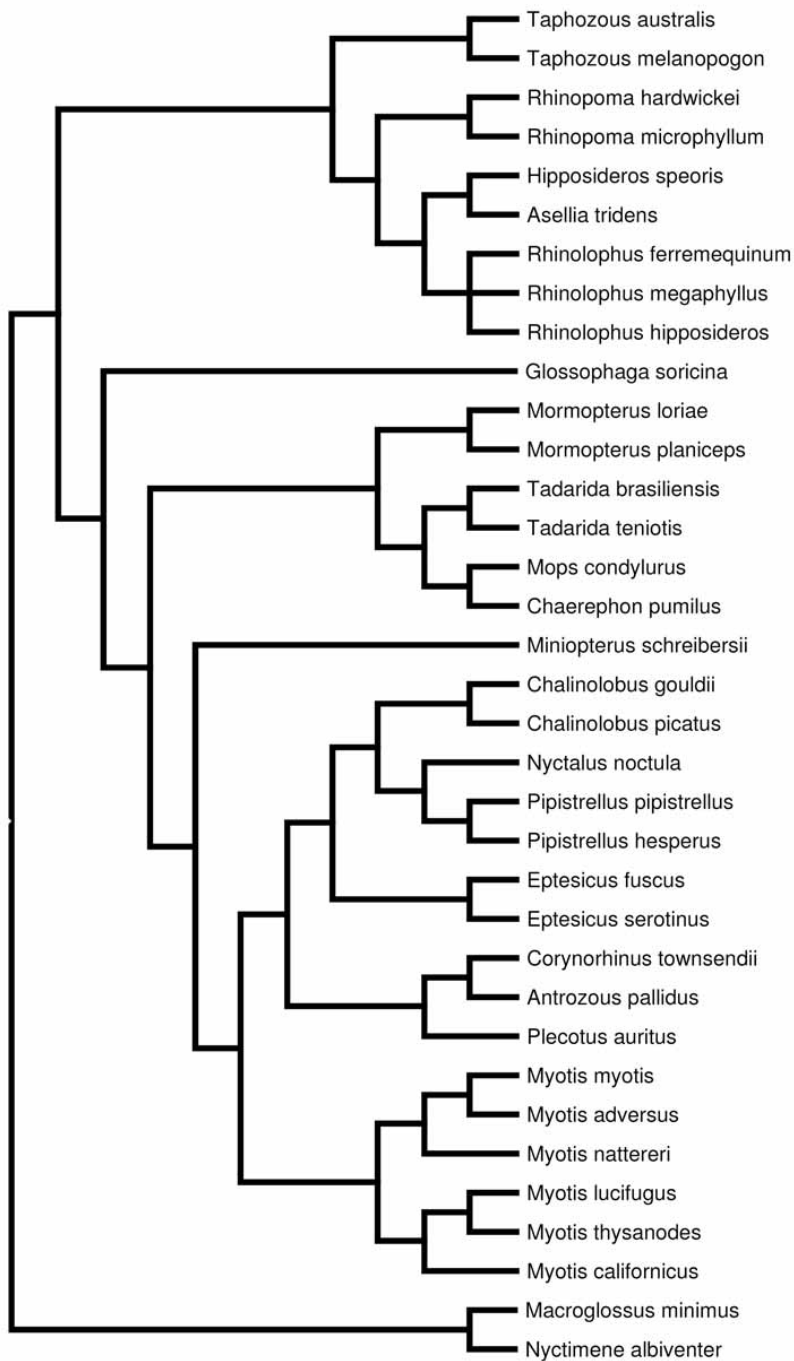
Figure 1. Phylogenetic tree used to calculate Felsenstein's independent contrasts for analysis of warming rates in bats. Topology from Jones *et al.* (2002), Hoofer and Van Den Bussche (2003) and Stadelmann *et al.* (2007).

For analyses of all bats and the non-vespertilionid clade, I assumed an evolutionary model based on equivalent branch lengths set to 1. More data are available for vespertilionids so for the analysis of this family I used published branch lengths (Hoofer & Van Den Bussche 2003).

For each variable I ensured that Felsenstein's contrasts were appropriately standardised by using Mesquite to test for significant relationships between the absolute value of each standardised independent contrast against its standard deviation (Garland *et al.* 1992). I natural-log transformed branch lengths for vespertilionids to achieve this standardisation of contrasts; contrasts for the other two analyses met standardisation assumptions without transformation. I tested for univariate relationships between contrasts for each independent variable (T_{roost} stability, colony size and BMR) and contrasts for warming rates using least squares regression analyses through the origin. Even though body mass did not necessarily exert significant effects on warming rates (see Results), all variables had the potential to be influenced by body mass and non-statistically significant influence of body mass could still have contributed to variation in the dataset. Therefore, I made sure to control for effects of body mass by calculating independent contrasts for all variables in Mesquite and then performing regression analyses through the origin for each variable's contrasts against body mass (Garland *et al.* 1992). Subsequent multiple linear regression analyses were then performed on the mass-independent residuals of phylogenetically independent contrasts (see Garland *et al.* 1992 for a full description of this approach). All regression analyses were conducted through the origin using Systat (Version 11.0, Systat Software Inc., San Jose, CA).

Results

All bats

There was no significant relationship between log body mass and log warming rate for the entire subset of bats either before (Figure 2A, $F_{1,33} = 1.5$, $p = 0.23$, $r^2 = 0.04$) or after accounting for phylogeny (Figure 2B, $F_{1,33} = 0.03$, $p = 0.80$, $r^2 > 0.002$). Based on the smaller subset of bats for which both warming rate and BMR data were available, there was a significant
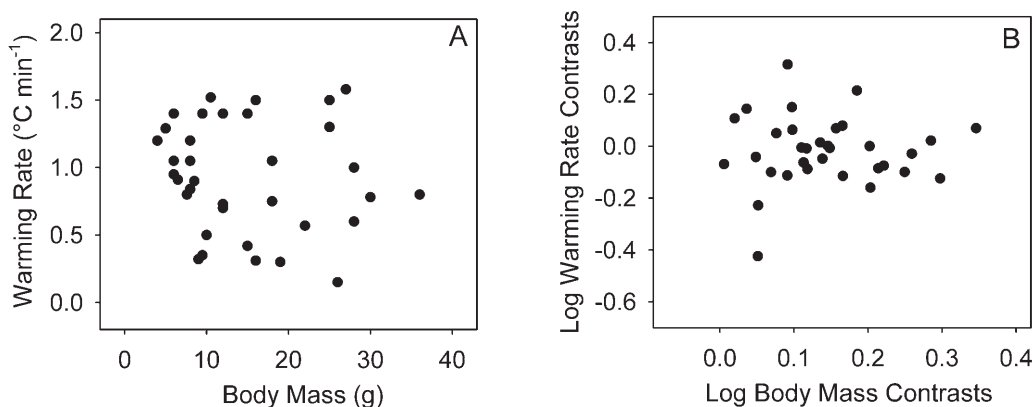

Figure 2. Plots of (A) body mass against warming rate and (B) Felsenstein's independent contrasts for log body mass against contrasts for log warming rate for 35 species of bats.

relationship between contrasts for body mass and BMR ($F_{1,15} = 27.0$, $p < 0.001$, $r^2 = 0.64$, scaling exponent = 0.68) but no relationship between contrasts for BMR and warming rates ($F_{1,15} = 1.9$, $p = 0.19$, $r^2 = 0.11$). Similarly, neither contrasts for colony size ($F_{1,33} = 1.11$, $p = 0.30$, $r^2 = 0.03$) nor roost temperature stability ($F_{1,33} = 0.12$, $p = 0.91$, $r^2 = 0.0003$) were correlated with contrasts for arousal rate. When I excluded the influence of body mass by calculating mass-independent residuals of all variables, residual contrasts for colony size and roost stability were significantly correlated ($r^2 = 0.33$, $p < 0.001$). I therefore excluded roost stability from the overall multivariate model. Warming rates were not significantly related to colony size or BMR ($F_{2,14} = 0.63$, $p = 0.55$, $r^2 = 0.08$).

Vespertilionidae

For vespertilionids alone, there was no relationship between contrasts for body mass and warming rate ($F_{1,15} = 1,10$, $p = 0.31$, $r^2 = 0.07$) and there was a significant relationship between contrasts for body mass and BMR ($F_{1,8} = 16.8$, $p = 0.003$, $r^2 = 0.68$, scaling exponent = 0.79). There was no relationship between contrasts for warming rate and either colony size ($F_{1,15} = 0.0007$, $p = 0.99$, $r^2 = 0.00006$) or roost stability ($F_{1,15} = 0.43$, $p = 0.52$, $r^2 = 0.03$) but, interestingly, there was a significant positive relationship between contrasts for BMR and warming rate ($F_{1,8} = 5.8$, $p = 0.04$, $r^2 = 0.42$). In other words, before correcting for the influence of body mass, species with high BMR had high warming rates. As above, I controlled for potential influence of body mass by calculating mass-independent residuals and, this time excluded colony size from the analysis because there was a strong trend for a relationship between residual BMR and colony size ($F_{1,7} = 5.5$, $p = 0.051$, $r^2 = 0.44$). Again the overall model was not significant ($F_{2,7} = 1.7$, $p = 0.24$, $r^2 = 0.33$) and the trend for a BMR vs warming rate effect was no longer significant after removing the influence of body mass ($p = 0.10$).

Figure 3. Relationship between mass-independent residuals of phylogenetic contrasts for log colony size vs log warming rate for 9 species (i.e. 8 contrasts) of non-vespertilionid microchiropterans (i.e. the non-vespertilionid clade). A multivariate linear model that included these variables plus mass-independent contrasts for roost temperature (T_{roost}) stability (scored between 0 for highly stable and 2 for highly unstable) was significant (see Results). The regression equation, through the origin, for the residual contrasts was Warming Rate = 0.304 x colony size + 0.457 x T_{roost} Stability. The solid line represents values for this equation plotted based on the mean residual contrast value for T_{roost} stability in these species (0.18). The lower and upper dashed lines represent values for the equation based on the maximum (1.10) and minimum (-0.76) values for T_{roost} stability score residual contrasts. In other words, the upper dashed line represents predicted values for species that roost in the most thermally stable microenvironments and the lower dashed line represents predicted values for species in the most thermally unstable microenvironments.
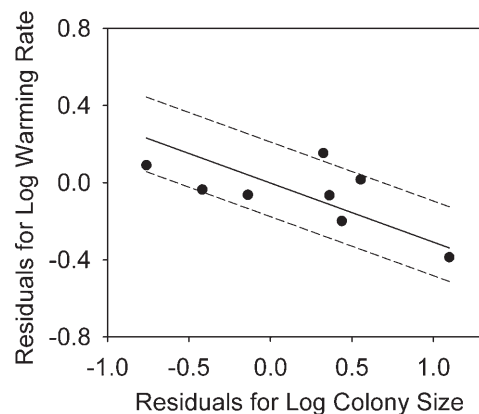
Non-vespertilionid bats

I performed a third set of analyses on the monophyletic, non-vespertilionid clade. Data on BMR were only available for two species in this group so I could not include BMR in the analysis. Again, there was no significant relationship between contrasts for body mass and warming rate ($F_{1,7} = 1.48$, $p = 0.26$, $r^2 = 0.18$). There was no univariate relationship between T_{roost} stability and warming rate ($F_{1,7} = 0.03$, $p = 0.87$, $r^2 = 0.004$), but this time there was a significant trend for a relationship between contrasts for colony size and warming rate ($F_{1,7} = 5.7$, $p = 0.048$, $r^2 = 0.45$). When I removed potential effects of body mass on all variables by analysing residuals as described above, the multivariate model was highly significant (Figure 3, $F_{2,6} = 46.5$, $p < 0.001$, $r^2 = 0.93$) and both colony size ($t = -8.8$, $p < 0.001$) and roost stability ($t = -6.7$, $p = 0.001$) contributed significant effects. In this clade, after controlling for body size and phylogeny, bats which roost in large colonies and/or in unstable roost microclimates tend to have low warming rates, while species that roost in smaller colonies and/or stable microclimates tend to have high warming rates.

Discussion

These analyses provide evidence that roosting habitat selection and social behaviour are related to warming rate in small heterothermic endotherms, at least for some species. After controlling for phylogeny and body mass, the effects of both colony size and T_{roost} stability were significant for the non-vespertilionid clade but there was no relationship between warming rate and colony size or T_{roost} stability for bats on the whole, or for the Vespertilionidae. Based on the available data, it is not yet possible to determine if this difference between clades reflects biogeography and adaptation to regional climate (e.g. Lovegrove 2000), an effect of different roosting behaviours, or differences in the seasonality of thermoregulation in the different groups. Most of the vespertilionids for which data are available are temperate-zone species that roost in thermally unstable tree roosts during summer (mean T_{roost} stability score = 1.3) and hibernate during winter. Most of the non-vespertilionid clade are tropical/subtropical or warm-temperate species which roost in thermally stable sites (mean T_{roost} stability score = 0.2) and may or may not hibernate (Nowak 1999). Thus, comparisons between the two groups are confounded for these variables and more data are needed, especially for tropical/sub-tropical vespertilionids. It is also important to note that my analyses include only small proportions of total species within each clade and should therefore be interpreted cautiously until more data are available.

Despite limitations of the data, my findings are consistent with the hypothesis that heavy reliance on torpor among temperate-zone vespertilionids, in general, results in consistently strong selection pressure for high rates of active warming. Potentially more variable and lesser reliance on torpor in the tropical/subtropical, non-vespertilionid clade results in more variable and weaker selection pressure for rapid warming rates in this group. In relatively warm climates it is likely much easier for bats to balance their energy budgets without using torpor by roosting in large colonies, or by using torpor occasionally while roosting in sites with unstable microclimates that facilitate passive warming. Thus, species that form large colonies or roost in sites with variable microclimates that allow for passive warming might face relatively weak selection pressure for rapid warming rates. Living in large colonies can provide thermoregulatory benefits (and other benefits, e.g. information transfer and predator avoidance if group living reduces individual risk of predation) but may also increase risk of parasite or pathogen

infection, cause local competition for food, and perhaps elevate risk of predation if nightly emergence events of large colonies are conspicuous to potential predators (Kunz & Lumsden 2003). Therefore, some tropical/subtropical species may form smaller groups and use torpor more regularly, even in warm climates (e.g. Kelm & von Helversen 2007; Stawksi *et al*. 2008; Turbill *et al*. 2003b). These species would be predicted to face stronger selection pressure for rapid warming rates, especially if they roost in sites with stable microclimates where there is little opportunity for passive warming. I only found evidence for this relationship within the non-vespertilionid clade and not for vespertilionids but, again, this may reflect limitations of the dataset and the relationship could apply to other phylogenetic groups.

In contrast to most species in my analysis from the non-vespertilionid clade, virtually all species of temperate-zone vespertilionids may need to rely on torpor much more heavily to balance their energy budgets, regardless of colony size or roosting habitat (e.g. Lausen & Barclay 2003; Turbill *et al*. 2003a; Willis 2006). They are also much more likely to exhibit marked seasonality of thermoregulation. Importantly, most of the vespertilionids for which data are available are seasonal hibernators. Hibernators almost certainly face intense pressure to reduce energy costs during their frequent periodic arousals throughout hibernation. Short bouts of warming cost less energy than longer bouts (McKechnie & Wolf 2004; Stone & Willmer 1989), so seasonal hibernators that must periodically arouse while roosting in cold microenvironments should benefit enormously from rapid warming rates. These species may retain the ability for rapid warming during summer because it provides additional energetic benefits with little added cost. This scenario is further supported by an overall comparison of warming rates between vespertilionids vs the non-vespertilionid clade. Mass-independent residuals of warming rate contrasts for vespertilionid nodes in the phylogeny (Figure 1) are significantly greater than those for the non-vespertilionid clade (*t*-test, t = -3.6, p = 0.002, d.f. = 22). In other words, after removing the influence of body mass and phylogeny, the temperate-zone vespertilionids in my analysis are capable of significantly faster warming rates than the non-vespertilionid clade. A physiological mechanism underlying the apparent difference between clades could be relative amounts of, and thermogenic capacity of, brown adipose tissue (BAT). Mammalian hibernators, including vespertilionid bats, often possess significant deposits of BAT and rely heavily on BAT during torpor arousal (e.g. Hirshfeld & O'Farrell 1976; Kronfeld-Schor *et al*. 2000).

My results also provide modest evidence for a functional link between high BMR and rapid warming rate in vespertilionids. Intuitively, one expects a positive relationship between BMR and warming rate because warming requires intense metabolic output and BMR correlates with overall metabolic performance (e.g. Speakman *et al*. 2004). Surprisingly, Stone and Purvis (1992) found the opposite relationship for mammals on the whole and hypothesised that rapid warming rates are correlated with low BMR because both are adaptations that reduce overall energy costs. In contrast, my analysis for vespertilionids is suggestive of the expected positive relationship, at least before controlling for effects of body mass. The relationship was not significant after controlling for mass so it may be an artefact of the strong influence of body mass on BMR in bats (e.g. Willis *et al*. 2005b, Cruz-Neto & Jones 2006) or it could reflect low statistical power owing to a small sample size. Indeed, comparison of vespertilionids to other bats lends support to Stone and Purvis's (1992) hypothesis. Vespertilionids in my analysis had relatively high warming rates, as described above, and they are thought to have relatively low BMR compared to other bats (Willis *et al*. 2005b), especially compared to the families that make up the non-vespertilionid clade (Cruz-Neto & Jones 2006). More data on warming rates, BMR, thermal

conductance, and maximum metabolic rate during warming are needed to help resolve the relationship between metabolic rate and warming rate in bats and other mammals.

Across mammals there is a clear negative relationship between body mass and warming rate (Geiser & Baudinette 1990; Stone & Purvis 1992). Small species warm more quickly than large ones, which may reflect enhanced performance of thermogenic tissues in small species or greater allocation of overall body mass to thermogenic tissue (Geiser & Baudinette 1990; Stone & Purvis 1992). The absence of any relationship between body mass and warming rate in my analyses is intuitively perplexing, but consistent with previous work on bats (e.g. Geiser & Baudinette 1990). In part this likely reflects the small body mass range (4–36 g) of the species of bats for which data are available. However, mass-independent variability in thermal conductance may also play a role, as conductance should influence warming rates (Stone & Purvis 1992). Endotherms with high thermal conductance (e.g. poorly insulated species) should have difficulty maintaining high warming rates because the heat they generate will quickly be lost to the environment. Individual bats may be able to adjust thermal conductance to a greater extent than many other heterothermic endotherms because of their large un-insulated, vascularised flight membranes which can be tightly collapsed to reduce conductance or unfurled to increase it. Thus, postural adjustments may exert stronger influence on conductance, and therefore warming rate, for bats than for other mammals. This effect could have masked a body mass signal in my analysis and in previous studies. I was not able to control for this potential source of variation in my analyses and more data on the effects of postural changes on thermal conductance in bats would be useful, especially in conjunction with data on warming rates.

In general, my findings highlight the influence of costs associated with the warming phase of torpor bouts on the lives of heterothermic endotherms. Clearly, some species gain large energetic benefits from passive warming (e.g. Geiser & Drury 2003; Geiser *et al.* 2004), but other species, which have less opportunity to exploit passive warming, appear to have evolved more rapid warming rates as an alternative means to reduce energetic costs. The influence of habitat and coloniality on warming rates appears to be strongest for species that rely on torpor relatively infrequently, while there appears to be little influence of these factors on species that depend heavily on torpor and exhibit long-term seasonal hibernation. My analysis highlights the need for more data on warming rates, especially for tropical/subtropical vespertilionids, but for other species as well.

Acknowledgements

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