The Journal of Experimental Biology 207, 723-733
Published by The Company of Biologists 2004
doi:10.1242/jeb.00807

Temperature regulation in burying beetles (*Nicrophorus* spp.: Coleoptera: Silphidae): effects of body size, morphology and environmental temperature

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Accepted 17 November 2003

Summary

This study compares the thermoregulatory ability of three species of burying beetle (Coleoptera: Silphidae: *Nicrophorus hybridus*, *Nicrophorus guttula* and *Nicrophorus investigator*) that vary significantly in body size. It also explores possible mechanisms for temperature regulation in burying beetles, including physiological and behavioral thermoregulatory strategies, and the influence of environmental temperatures on body temperature and activity times. We measured beetle thoracic and abdominal temperatures before and after short (<5 s) flights, and thoracic temperature during sustained, tethered flights and following flight in the field. We calculated two measures of thermoregulatory ability: the slope of post-flight thoracic temperature against ambient air temperature and the slope of post-flight thoracic temperature against operative flight temperature. Thoracic temperatures following flight were significantly higher than abdominal temperatures, and the largest species, *N. hybridus*, was determined to be the better thermoregulator, with regression slopes closer to zero (0.315–0.370) than *N. guttula* (0.636–0.771) or *N. investigator* (0.575–0.610). We also examined the roles that insulation, wing loading, physiological heat transfer, basking and perceived environmental temperature play on temperature regulation and activity times in *Nicrophorus*. This study shows that body size, morphological features, such as wing loading and insulation, and perceived environmental temperatures affect thermoregulation and activity times in burying beetles.

Key words: thermoregulation, body size, body temperature, burying beetle, operative temperature, flight temperature, *Nicrophorus* spp., Coleoptera.

Introduction

The ability of insects to regulate body temperature and warm the body endogenously has been extensively studied in bees, flies and moths (Heinrich, 1993, 1996). Endothermy was first noted in the Coleoptera in 1945 (Krogh and Zeuthen, 1941) but received little attention for 30 years (Bartholomew and Heinrich, 1978; Heinrich and Bartholomew, 1979; Chappell, 1984; Morgan, 1987; Oertli, 1989; Oertli and Oertli, 1990; Chown and Scholtz, 1993; Schultz, 1998). Additionally, despite the enormous number of beetle species (nearly half of all known animal species), the thermal biology and thermoregulatory ability of only a handful of taxa have been studied (Oertli and Oertli, 1990), and not all of the findings agree. For example, studies on large, tropical ground beetles (Bartholomew and Casey, 1977a,b) and on large, African dung beetles (Bartholomew and Heinrich, 1978) suggest that only beetles of ≥2 g are capable of maintaining a thoracic temperature independent of ambient temperature, whereas smaller beetles (<2 g) are unable to regulate thoracic temperature due to a high surface area to volume ratio. By contrast, studies on beetles that are neither large (≤1 g) nor tropical (Chappell, 1984; Morgan, 1987; Oertli, 1989; Oertli and Oertli, 1990; Chown and Scholtz, 1993) indicate that mass is not always a reliable indicator of thermoregulatory ability and that wing loading and wing beat frequency may also play a critical role (Oertli, 1989; Chown and Scholtz, 1993). There is a need for more data on the thermal biology of flying beetles from different groups (Chown and Scholtz, 1993).

The ecology and reproductive behavior of burying beetles (Coleoptera: Silphidae: *Nicrophorus*) are well studied (Eggert and Müller, 1997; Scott, 1998; Smith and Merrick, 2001); however, little is known about the thermal ecology of this genus. Burying beetles must secure an ephemeral resource (in this case, the carcass of a small vertebrate) to complete their life cycle. Body size and the potential for increased thermal stability in larger species may play important roles in securing these resources from both conspecifics and heterospecifics. The ability to regulate and maintain a thoracic temperature independent of ambient conditions during and after flight may provide competitive benefits, both in terms of carcass defense and speed of burial and the ability to search for carcasses and mates over a wider temperature range, as demonstrated for *Plecoma* spp. (Morgan, 1987). There is also evidence to suggest that there are differential tolerances to environmental temperatures among *Nicrophorus* species (Wilson et al., 1984;

Trumbo, 1990; Sikes, 1996; Scott, 1998), which may be related to factors such as body size, pigmentation or evolutionary history and may play a role in species distributions and coexistence. Sympatric species that utilize different thermal and temporal windows for activity have been shown to coexist in the same habitat types without much direct contact (Wilson et al., 1984), and larger species in northern Europe and northeastern North America have been shown to be nocturnal (Scott, 1998).

Regulation of body temperature in *Nicrophorus* could be accomplished by behaviors such as basking, posturing and seeking shade (Casey, 1981, 1992; Heinrich, 1996), by regulating (conserving or losing) heat generated endogenously by flight muscles in the thorax (Kammer, 1981; Heinrich, 1993, 1996), altering metabolic rate or wing beat frequency or a combination of both behavioral and physiological thermoregulation (Coelho, 2001). *Nicrophorus* have been described as “good, persistent fliers that are capable of covering large distances in a short period of time” (Eggert and Müller, 1997), and members of this genus fall within the size class of smaller beetles known to regulate their body temperatures during flight (0.003–1.8 g; Chappell, 1984; Morgan, 1987; Oertli, 1989; Chown and Scholtz, 1993). Smaller beetles like *Nicrophorus* may rely on high wing loading and wing beat frequencies, insulation and morphology to counteract the amount of body heat lost to convection during flight (Chown and Scholtz, 1993), as opposed to passive heat retention as a result of a large body.

We tested whether three *Nicrophorus* species (*N. hybridus*, *N. guttula* and *N. investigator*) are able to (1) warm up before flight *via* endogenous heat production and (2) regulate body temperature during and following flight. We further investigated whether wing loading or body mass affected thermoregulatory ability, as well as whether the thermal environment influences the daily activity patterns of burying beetles. We assess thermoregulatory ability using two measures: (1) the relationship between thoracic temperature during flight and ambient temperature and (2) the relationship between thoracic temperature during flight and the effective (operative) temperature of a dead beetle in the flight position (index of thermoregulatory performance; Bishop and Armbruster, 1999). Additionally, we describe daily activity patterns for the three species over two 24-h observation periods and investigate how these patterns could be explained in part by the thermal environment that *Nicrophorus* experiences and by differential thermoregulatory abilities among species.

Materials and methods

Study sites

Laboratory studies were conducted on the campus of Idaho State University, Pocatello, ID, USA, and the majority of field studies were carried out along the South Fork of Mink Creek drainage, Bannock County, ID, USA, during the spring and summer of 2001, near the South Fork of Mink Creek in the Caribou National Forest. Additional field measurements of field activity and flight temperatures for *N. investigator* were made at the Rocky Mountain Biological Laboratory along the East River drainage, Gunnison County, CO, USA. In Idaho, two sites were established: South Bench and South Fork. South Bench is located at 2133 m on the lower slopes of Scout Mountain and consists of a mixed Douglas fir/shrub stand including chokecherry (*Prunus virginiana)*, snowberry (*Symphoricarpos oreophilus*), serviceberry (*Amelanchier alnifolia*) and snowbrush (*Ceanothus velutinus*). South Fork is located at 1828 m in a clearing at the edge of a sage-steppe riparian area, dominated by aspen (*Populus tremuloides*), willows (*Salix* spp.) and mixed forbs. In Colorado, two established sites were used for beetle collection and observation: Kettle Ponds and Bellview (see Smith and Merrick, 2001 for site descriptions).

Capture techniques

Beetles were captured in traps consisting of metal cans (17 cm deep, 15.5 cm in diameter) pierced to allow drainage, half-filled with soil and covered with wire screening formed into a funnel. Each trap was suspended approximately 40 cm above the ground and baited with fresh chicken and water added to the soil (Smith and Merrick, 2001).

Body temperature before, after and during flight

To determine the thermoregulatory ability of *Nicrophorus* before and after flight, we conducted a series of flight trials in a 2.44 m×3 m Weatherport® or in a 1.2 m×1.2m screen tent throughout the season and over a range of ambient temperatures. Field-caught beetles were used within 24 h of capture or held in the laboratory and used within two weeks of capture. We tested a total of 137 beetles, including individuals of both sexes, of *N. hybridus* Hatch and Angell (N=53), *N. guttula* Motschulsky (N=28) and *N. investigator* Zetterstedt (Idaho N=7, Colorado N=49). Although *N. defodiens* were collected, no flight information was obtained from this species.

For each flight trial we randomly selected a beetle from a holding container and immediately measured both its abdominal and thoracic temperatures using a 29-gauge hypodermic temperature probe (Model HYPO-33-1-T-G-60-SMP-M; Omega Engineering Inc., Stamford, CT, USA) and a digital microprocessor thermometer (Omega Model HH23). Abdominal temperatures (T_{ab}) were taken by inserting the probe between two abdominal sclerites, and thoracic temperatures (T_{thx}) were taken by inserting the probe into the ventral metathorax. After measuring the temperatures, a beetle was then placed on the middle of a stick (8–10 cm diameter, 0.5 m length) secured at a 45° angle, where it would walk to the end of the stick and make preparations to fly. After take-off and flights of 2–4 s duration, the beetle’s thoracic and abdominal temperatures were measured again. We wore gloves while handling the beetles and measurements were made within 2–3 s after landing. Because *Nicrophorus* have the ability to raise T_{thx} to a temperature adequate for flight (≈25–30°C) even on cooler days by basking (M. J. Merrick and R. J. Smith, personal observation), every captive flight took place in the absence of direct sunlight, in addition to being sheltered from wind.

The time between the preflight T_{thx} measurement and actual flight was frequently long, often taking more than 5–10 min. We were therefore unable to determine when the warming occurred or if the temperature immediately prior to flight was different from the post-flight temperatures, although continuous flight measurements indicate that during flight in the shade, thoracic temperatures remain near the initial flight temperature. We assume that a beetle's T_{thx} immediately before flight and T_{thx} measured post-flight were similar since each captive flight was short (<4 s.). During the time prior to flight, we did not observe any shivering, wing vibrations or outward signs of muscle contraction. Beetles spent this time cleaning foretarsae and antennae clubs, in addition to extending and retracting wings from below the elytra.

We recorded the ambient temperature using both a bare thermocouple and the effective environmental temperature (T_{e}) of a null temperature model in the flight position (T_{e} flight); a dead, dry beetle equipped with thermocouples, wings and elytra raised, and suspended approximately 0.75 m above the ground (Hertz et al., 1993) after each short flight. We also measured hourly the operative temperatures of null temperature models placed in positions that represented other behaviors a beetle could adopt in response to its thermal environment: (1) on bare ground, 1–2 cm below the ground surface, and (2) beneath foliage (at the base of short grasses or under fresh leaves resting upon a soil substrate). Operative temperatures, also known as T_{e}, take into account the effects of radiative and convective heat gain and loss in addition to ambient temperatures on the body temperature of a non-thermoregulating organism (Bakken, 1992; Heinrich, 1993) and more closely approximate the thermal environment that beetles actually experience (Bakken, 1992; Bishop and Armbruster, 1999). Differences between T_{e} and actual body temperature (T_{b}) can indicate some form of thermoregulation by the animal (i.e. $T_{\mathrm{b}}>T_{\mathrm{e}}$ indicates endogenous heat production or basking).

To address the point raised by Stone and Willmer (1989a) that some insects actually warm up upon cessation of flight, which could cause overestimation of post-flight T_{thx} measurements, we measured T_{thx} continuously for 10–12 min after 24 successful flight trials for *N. hybridus* (N=4), *N. guttula* (N=3) and *N. investigator* (N=17) individuals to determine whether beetles are able to regulate an elevated thoracic temperature after flight. We recorded T_{thx} in four tethered *N. hybridus* individuals during continuous (12–39 min) flights and subsequent cooling to determine whether T_{thx} is regulated during longer flights.

Indices of thermoregulation

A regression of post-flight thoracic temperature against ambient temperature was used as an index of thermoregulatory precision (Oertli, 1989). Additionally, we calculated a thermoregulatory performance index for each species. Bishop and Armbruster (1999) define this index as the slope of T_{thx} against T_{e}, which indicates how a real beetle regulates its thoracic temperature in flight compared with a non-regulating, metabolically inactive one. Differences between T_{thx} and T_{e} would then be the result of physiological or behavioral control of body temperature (Casey, 1992). A slope equal to or close to one ($T_{\mathrm{thx}}=T_{\mathrm{a}}$) is considered evidence for thermal conformity, whereas slopes close to or approaching zero are evidence of thermoregulation.

Possible mechanisms for thermoregulation

Cooling rates and body size

Cooling rates (deg. min^{-1}) were calculated for beetles representing three species and ranging in mass from 0.11 g to 0.62 g. Beetles were observed cooling after short flights (N=24) and after artificial heating (N=13), where live beetles were heated to a T_{thx} of 40°C and then allowed to cool. Differences in cooling rates between size classes indicate the amount of heat retention that is a result of body size alone. Based on physiological properties alone, larger beetles should cool more slowly because of a decreased surface area to volume ratio and higher thermal inertia. Three body size classes were assigned for all species based on the median body mass ± 25th and 75th percentiles (small ≤25th percentile; large ≥75th percentile; medium 25th–75th percentile). Cooling rates of live, artificially heated beetles (N=13) were determined by placing the 29-gauge hypodermic thermocouple probe into the lateral metathorax of a beetle that had been cross-pinned to a Styrofoam block. The beetle was then placed inside a 28 cm×18 cm×18 cm Styrofoam box and heated to 40°C with an incandescent lamp, then allowed to cool to within 1–2° of ambient air temperature while its thoracic temperature was recorded every 30 s. Cooling rates of live beetles after flight (N=24) were also measured for 10–12 min following flight (see previous section), and the differences in cooling rates between size classes for post-flight and artificially heated beetles were compared in a one-way analysis of variance (ANOVA). For comparisons, cooling rates for artificially heated beetles were also calculated between the approximate average ambient temperature recorded for outdoor flights and ambient laboratory temperature.

Insulation

To understand the role that wings, elytra and thoracic pile play in insulation and maintenance of body temperature, we divided 28 beetles (representing three species; *N. hybridus*, *N. investigator* and *N. guttula*) into three groups: (1) no treatment, (2) thoracic pile removed with a scalpel and (3) wings and elytra removed (Chown and Scholtz, 1993). We determined cooling rates for live beetles in the three treatments as above and compared cooling rates using a one-way ANOVA.

Physiological heat transfer

We employed methods similar to Chown and Scholtz (1993) and Coelho (2001) to determine whether or not *Nicrophorus* have the ability to transfer heat produced in the thorax to the abdomen to regulate T_{thx}. A live beetle was cross-pinned to a Styrofoam block, and one thermocouple probe was inserted into the lateral thorax and another into the abdomen. The head and thorax were heated with an incandescent lamp while the abdomen was shielded with Styrofoam wrapped with aluminum foil. Measurements of T_{thx} and T_{ab} were taken simultaneously every 30 s until a thoracic temperature of 40°C was attained. The beetle was then euthanized with an injection of ethyl acetate and allowed to cool. Once the T_{thx} had returned to within 1°C of T_a, the procedure was repeated for the same individual, now dead. A total of 12 *N. hybridus* individuals were used in this investigation. We used paired *t*-tests to compare the rates of warm-up between alive and dead T_{thx} and T_{ab}, between alive T_{thx} and T_{ab} and between dead T_{thx} and T_{ab}. If physiologically mediated heat transfer to the abdomen were occurring, one would expect the rate of abdominal heating to be higher in the living beetle than the dead beetle.

Wing loading

We measured wing loading to quantify differences in the amount of power output required for flight between the species. Species with a higher average wing loading may produce more excess heat in flight. To calculate wing loading, one wing was removed at its base from each beetle that flew successfully (N=137). Each beetle was weighed to the nearest milligram following flight and temperature measurements. Wing area was determined in the lab by scanning (Epson 636U scanner) wings taped to graph paper (five squares per centimeter) into NIH image® software, where we measured the area of each wing in mm^2. Wing loading was calculated in mg mm^{-2} for each beetle.

Influence of thermal environment on daily activity patterns

To see how daily activity patterns were affected by temperature, two 24-h field observations were carried out on 28 June and 28 July at the South Bench site in Idaho. During each 24-h observation period, traps were checked every 2–3 h during the day and twice during the night (after midnight), and the number of beetles and species of each was recorded. During daylight hours, the number of beetles seen flying in the vicinity of the traps was also recorded. These observations allowed us to estimate the relative beetle activity at different times of the day.

We measured the T_{thx} and T_{ab} of beetles caught flying into a trap, recorded their weight and removed one wing to calculate wing loading (see previous section). Each time that traps were checked or a beetle was seen flying overhead, we recorded the T_a and T_e of a beetle in a flight position. Measurements from the other T_e models (on bare ground, 1–2 cm below ground, under foliage) were taken every 2–3 h during a 24-h observation period.

We also developed a model to predict T_{thx} for beetles throughout the day. We measured T_e throughout an entire day in late July 2001 and then applied these values to the regression equation of T_{thx} against T_e for each species to predict post-flight thoracic temperatures at each T_e value. We then used the range of post-flight T_{thx} actually measured for the three species in flight trials and in the field and compared these ranges to the predicted T_{thx} throughout the day to estimate windows of possible flight times.

Statistical analyses

All statistical tests were carried out using StatView® 5.0 for Macintosh. ANOVAs were followed by Fisher's PLSD *post-hoc* multiple comparison tests. Paired *t*-tests were used to determine significant differences between pairs of measurements taken for individuals and to test if there were significant differences in T_{thx} pre- and post-flight, between T_{thx} and T_{ab} and in cooling/warming rates for living *vs* dead individuals. Simple, linear regression was used to test whether the relationship between T_b and T_{te} or T_a was significantly different from zero. Mean values, unless otherwise specified, are reported ±1 S.E.M.

Results

Body temperature before, after and during flight

Beetles warmed themselves on average 4.7±0.3°C before initiating flight, which represents a significant increase in T_{thx} prior to flight (paired t=18.852, mean difference=4.663, P<0.0001, N=136). The mean post-flight thoracic temperature (across species and sites) was 30.0±0.2°C (N=136) during flight trials. Post-flight T_{thx} was significantly higher than T_a (paired t=19.358, mean difference=5.3°C, P<0.0001, d.f.=135). After flight, T_{thx} was also significantly higher than T_{ab} (paired t=11.852, mean difference=1.692, P<0.0001, d.f.=128). Among species, there was a significant difference in

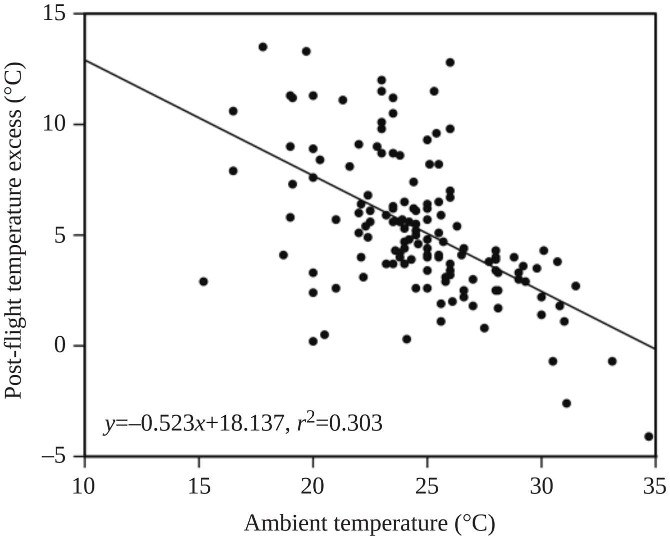

Fig. 1. The relationship between temperature excess (post-flight T_{thx}–T_a) and ambient air temperatures. As ambient temperature increases, the temperature differential between the thorax and the environment decreases, finally becoming negative at ambient temperatures above approximately 30°C. T_{thx}, thoracic temperature; T_a, ambient air temperature.

post-flight temperature excess (T_{thx}–T_a), with *N. investigator* having the highest mean excess (7.3±0.5°C), followed by *N. guttula* (4.5±0.3°C) and *N. hybridus* (3.7±0.4°C) (one-way ANOVA F=24.746, d.f.=2, P<0.0001). Most beetles went through a series of behaviors before actually attempting flight; these consisted of abdominal pumping, unfolding and extending both wings, elevation of elytra and grooming of antennae clubs and foretarsae. Some individuals would repeat these behaviors many times before flight. All flight trials took place in the shade and so the increase in T_{thx} between the initial pre-flight measurement and the measurement directly following short flight is most likely due to endogenous heat production prior to flight.

Post-flight temperature excess in the thorax decreased significantly with increasing ambient temperature (slope=–0.523, r^2=0.303, N=135, P<0.0001). Above approximately 30°C, the temperature excess between T_{thx} and T_a becomes negative, indicating that beetles lost heat before or during flight, and no energy for warming up is required (Fig. 1). Post-flight T_{thx} did not differ significantly among species (for all Idaho and Colorado sites; one-way ANOVA, F=0.803, d.f.=2, P=0.4502), and *post-hoc* comparisons show that there were no significant differences between species.

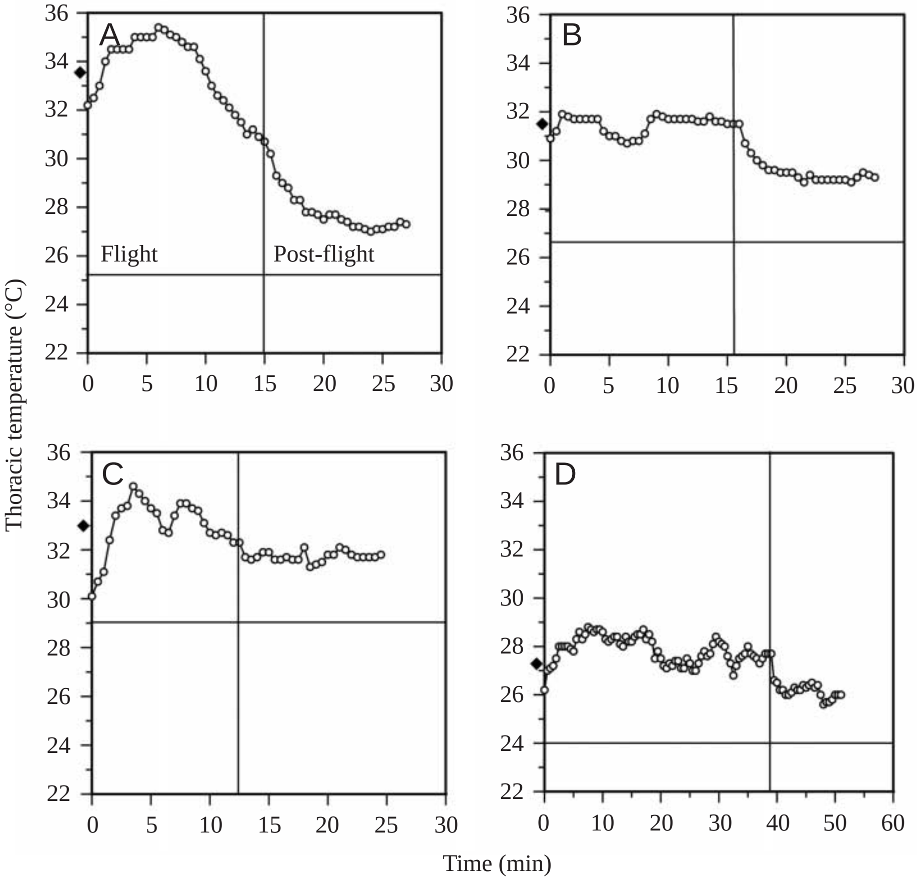

Fig. 2. Four examples of sustained, continuous flight (flight time 12–39 min) for four *N. hybridus* individuals and subsequent post-flight cooling (12 min). The horizontal line represents T_{thx}=T_a and the vertical line denotes cessation of flight. The filled diamond indicates the mean thoracic temperature measured during the flight. Mean flight temperatures were 33.5°C (A), 31.5°C (B), 33.01°C (C) and 27.83°C (D). Mean flight temperature for post-flight T_{thx} taken *via* the ‘grab and stab’ method was 29.9±3.1°C. T_{thx}, thoracic temperature; T_a, ambient air temperature.

Recordings of continuous T_{thx} measurements for four sustained (>5 min), tethered flights (Fig. 2) show that *N. hybridus* has the ability to sustain and regulate thoracic temperatures to some degree during long flights and that the length of the flight may be dependent upon ambient temperature, as the longest flight occurred at the lowest T_a. Mean T_{thx} for the four sustained flights was 31.5±2.6°C compared with a mean T_a of 26.13°C.

Indices of thermoregulation

Nicrophorus hybridus is significantly larger than *N. guttula* (t=5.364, P<0.0001, d.f.=79) and *N. investigator*: *N. hybridus* mean mass=500±20 mg, *N. guttula* mean mass=340±20 mg and *N. investigator* mean mass=293±10 mg. The slopes of T_{thx} *vs* T_a and T_{thx} *vs* T_e of an operative model (thermoregulatory performance index) indicate that *N. hybridus* is better able to regulate body temperature prior to and during short flights compared with *N. guttula* and *N. investigator*. The slope of the regression of T_{thx} against T_a for *N. hybridus* (0.315; r^2=0.227) is much closer to zero than the slopes calculated for *N. guttula* (0.771; r^2=0.784) and *N. investigator* (0.610; r^2=0.221) and is also significantly different from the slopes for these smaller species (*N. hybridus vs N. guttula* t=33.853, P<0.0001, d.f.=77; *N. hybridus vs N. investigator* t=14.7795, P<0.0001, d.f.=107). The slopes for T_{thx} *vs* T_e (thermoregulatory performance index) were similar to those comparing T_{thx} and T_a, and, again, the regression slope for *N. hybridus* (0.370; r^2=0.411) is closer to zero than the slopes calculated for *N. guttula* (0.636; r^2=0.679) and *N. investigator* (0.575; r^2=0.327) and is also significantly different from the other two (*N. hybridus vs N. guttula* t=19.777, P<0.0001, d.f.=77; *N. hybridus vs N. investigator* t=12.059, P<0.0001, d.f.=107) (Fig. 3).

Mechanisms for thermoregulation

Cooling rates and body size

Beetles cooling after short flights (mean post-flight T_{thx}=30.4°C) cooled at the same rate as beetles that were artificially heated when artificial cooling rates were calculated from 30.4°C (t=0.275, d.f.=35, P=0.7847). No beetles warmed up following flight unless flight was initiated while the post-flight temperatures were being measured, in which case the trial was omitted from the analysis of cooling rates. Post-flight and artificial cooling rates (from 30.4°C) were then combined, and cooling rates among size classes were compared. As expected, based on surface area to volume ratios, large beetles cooled more slowly than small individuals and significantly slower than medium-sized individuals (one-way ANOVA, F=4.081, d.f.=2 P=0.0261; Fisher's PLSD, large *vs* medium mean difference=–0.745 deg. min^{-1}, P=0.0074). Beetles in the large size class (N=10) had a mean cooling rate of –1.062±0.121 deg. min^{-1}, beetles in the medium size class (N=21) had a mean cooling rate of –1.807±0.166 deg. min^{-1}, and beetles in the small size class (N=5) had a mean cooling rate of –1.610±0.341 deg. min^{-1}. Cooling rates for the three species following short flights are summarized in Table 1. Artificial cooling was only measured for *N. investigator* and *N. guttula*.

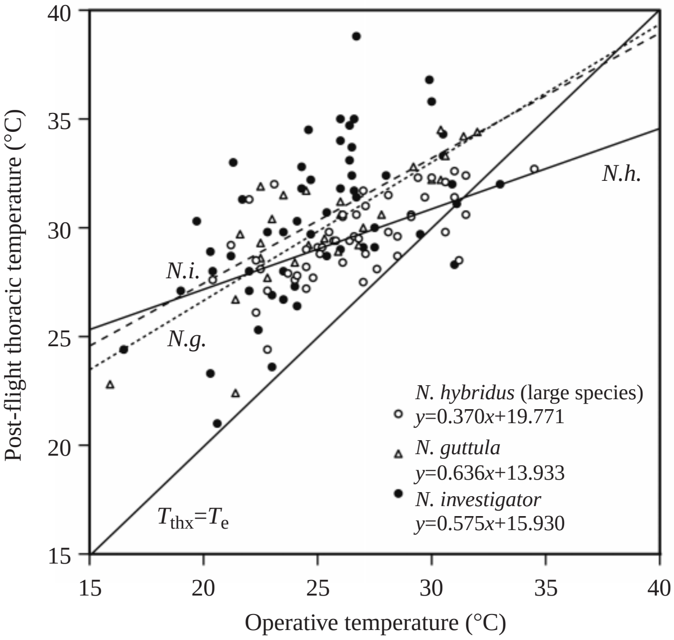

Fig. 3. The relationship between post-flight thoracic temperature (T_{thx}) and operative flight temperature (T_e) for the three species. Slopes from the regression of T_{thx} on T_e were used as an index of thermoregulatory performance.

Insulation

To determine the importance of the wings, elytra and thoracic pile as insulation for burying beetles, we compared the cooling rate of individuals assigned to one of three treatments: intact (I), wings and elytra removed (WER), and thoracic pile removed (TPR). There was a significant effect of treatment (F=4.332, P=0.0248, d.f.=2, power=0.696); beetles with elytra removed cooled significantly faster (mean=–0.145 deg. min^{-1}) than intact beetles (mean=–0.098 deg. min^{-1}) (Fisher's PLSD, P=0.0110). Beetles with thoracic pile removed also cooled faster than intact beetles, but only marginally (Fisher's PLSD, P=0.0655). Because of the small sample size in each treatment (I, N=14; WER, N=7; TPR, N=7), we increased the power of the test (α=0.10, power=0.816), which resulted in a significant difference between the cooling rates of intact beetles compared with those with insulation removed.

Table 1. *Summary of morphological and thermal data for the three species*

Measured variable	*N. hybridus*	*N. guttula*	*N. investigator*
Elytra (mm)			
Mean ± S.E.M.	10.33±0.13	8.71±0.13	9.28±0.15
(min.–max., *N*)	(8.36–13.23, 53)	(7.31–10.51, 28)	(7.0–11.84, 52)
Body mass (mg)			
Mean ± S.E.M.	500±20	340±20	290±10
(min.–max., *N*)	(280–880, 53)	(200–620, 28)	(110–550, 53)
Wing loading (mg mm^{-2})			
Mean ± S.E.M.	4.61±0.08	4.55±0.13	3.37±0.09
(min.–max., *N*)	(3.56–5.86, 53)	(3.04–5.86, 28)	(1.96–4.32, 44)
Conductance (deg. min^{-1})			
Mean ± S.E.M.	–1.0±0.34	–1.65±0.35	–1.69±0.23
(min.–max., *N*)	(–1.66 to –0.54, 3)	(–2.0 to –1.3, 2)	(–3.92 to –0.18, 18)
Post-flight T_{thx} (°C)			
Mean ± S.E.M.	29.6±0.2	30.2±0.6	30.3±0.5
(min.–max., *N*)	(24.4–32.7, 53)	(22.4–34.5, 28)	(21.0–38.8, 55)
Post-flight T_{ab} (°C)			
Mean ± S.E.M.	27.4±0.4	28.4±0.5	28.9±0.6
(min.–max., *N*)	(23.3–32.3, 50)	(24.6–34.0, 28)	(20.7–35.7, 51)

The data are reported as means ± S.E.M. (range, *N*). Conductance values are for cooling rates measured for 10–12 min following short flights only and do not include cooling rates following artificial heating or cooling rates following longer, continuous flights.

Physiological heat transfer

The rate of abdominal warming between living and freshly killed individuals was not different (paired t=0.989, P=0.3461, d.f.=10), indicating that living beetles do not actively shunt heat from the thorax to the abdomen. Live beetle $T_{\rm thx}$ increased on average 0.451 deg. min^{-1} faster than in dead beetles, but the difference was not significant (paired t=1.898, P=0.0869, d.f.=10).

Wing loading

Wing loading was significantly different among species, with *N. hybridus* (mean=4.61±0.08 mg mm^{-2}) and *N. guttula* (mean=4.55±0.13 mg mm^{-2}) exhibiting significantly higher levels of wing loading than those calculated for *N. investigator* (mean=3.37±0.09 mg mm^{-2}) (one-way ANOVA, F=58.617, d.f.=2, P<0.0001; Fisher's PLSD, *N. guttula vs N. investigator* mean difference=1.182 mg mm^{-2}, P<0.0001; *N. hybridus vs N. investigator* mean difference=1.244 mg mm^{-2}, P<0.0001). There was also a positive relationship between the post-flight temperature excess (post-flight $T_{\rm thx}$–$T_{\rm a}$) and wing loading in *N. hybridus* (slope=1.189, r^2=0.066, P=0.06) and *N. investigator* (slope=0.868, r^2=0.026, P=0.292) but not for *N. guttula* (slope=–0.04, r^2<0.0001, P=0.924). Wing loading measurements for each species are summarized in Table 1.

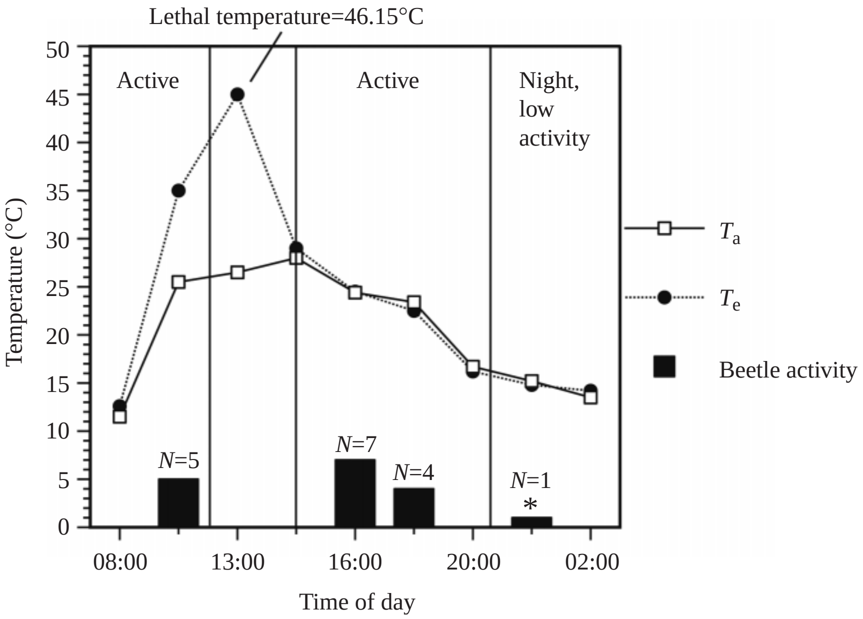

Fig. 4. An example of a 24-h observation period, illustrating the thermal environment a beetle may experience throughout the day and how beetle activity corresponds to operative temperatures. Beetle activity is defined as the number of beetles caught while flying into a trap in addition to beetles seen flying in the vicinity of the traps but not landing. An asterisk indicates one observation where an *N. investigator* individual was found walking on the ground near a can.

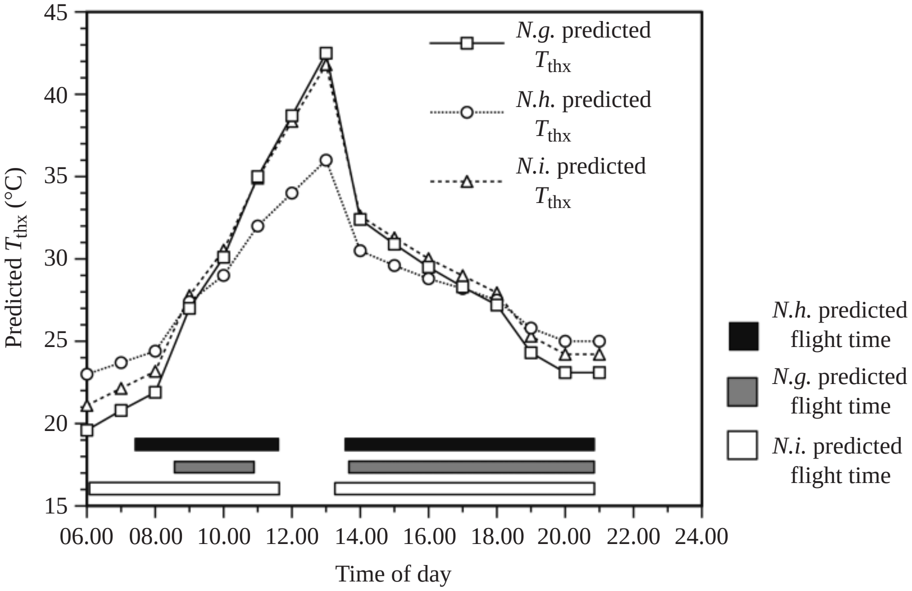

Fig. 5. Predicted thoracic temperature ($T_{\rm thx}$) during flight for *N. hybridus*, the largest species, *N. guttula* and *N. investigator*. Operative temperatures ($T_{\rm e}$) measured throughout an entire day in late July 2001 were then used to predict the flight $T_{\rm thx}$ for the three species using the regression of post-flight $T_{\rm thx}$ against the $T_{\rm e}$ developed for each species. The bars represent possible flight times throughout the day for the three species. Flight times were estimated based on the minimum and maximum thoracic temperatures recorded for each species following a flight trial.

Influence of thermal environment on daily activity patterns

We found four species of burying beetle co-occurring at the two Idaho study sites: *N. hybridis*, *N. guttula*, *N. investigator* and *N. defodiens*. During a 24-h period, beetle activity began in mid-morning and then peaked in the late afternoon/early evening, when ambient temperatures were ~20–30°C. Around mid-day, ambient temperatures ranged from 25°C to 30°C. Although this temperature range is moderate, the temperature of operative models on the ground surface and suspended approximately 1 m above the ground in a flight posture often approached lethal temperatures, especially during periods of full sun (mean lethal temperature from previous cooling experiments=

46.15±0.6°C, N=8; M. J. Merrick and R. J. Smith, unpublished data; Fig. 4).

The windows of activity time available for flight throughout the day differed among the three species. Based on the amount of time throughout the day that the post-flight T_{thx} ranges for the three species (*N. hybridus*, 24.4–32.7°C; *N. guttula*, 22.4–34.5°C; *N. investigator*, 21–38°C) fell within the predicted thoracic flight temperatures (based on the species-specific regression of T_{thx} *vs* T_{e}), it appears that *N. investigator* would have the largest potential window of activity time, followed by *N. hybridus* and then *N. guttula* (Fig. 5). This assumes that the post-flight T_{thx} measured for each species following short flights approximates actual T_{thx} in the field and that the range of ambient air temperatures within which we collected flight data reflects the range of ambient air temperatures in which these species are active under field conditions.

Discussion

Elevation and regulation of thoracic temperature

Following short flights, the T_{thx} was significantly higher than the T_{thx} measured prior to flight, and significantly higher than ambient air temperatures. This indicates that each species considered here has the ability to elevate T_{thx} above T_{a} either prior to short flights or during them. Because the captive flights were short (≤5 s), it is more likely that T_{thx} is elevated prior to taking off. The mean post-flight T_{thx} excess was significantly different among the three species, and the degree to which post-flight T_{thx} is elevated above T_{a} does not appear to be related to body mass, and only very weakly related to wing loading, in *N. hybridus* and *N. investigator*. However, the ability to *regulate* thoracic temperature independent of T_{a} or T_{e} appears to be directly related to the mean body mass of a species. The difference between T_{thx} and T_{a} or, more accurately, T_{e} is attained by temperature regulation on the part of the organism, and in this study *N. hybridus*, the species with the largest mean mass, was better able to regulate T_{thx} in short flights independent of T_{e} or T_{a} (Fig. 3). Both the slope of T_{thx} on T_{a} and the index of thermoregulatory precision for *N. hybridus* are similar to published values for insects considered to be good thermoregulators (Table 2). The slope of T_{thx} on T_{e} (index of thermoregulatory performance) is considered more useful here as it provides a better, more realistic measure of the degree to which an organism regulates its T_{b} (Hertz et al., 1993; Bishop and Armbruster, 1999).

Data from four continuous, sustained flights (Fig. 2) show that *N. hybridus* can maintain elevated T_{thx} over long periods of flight. Longer flights may be possible at cooler T_{a}s, suggested by the fact that the longest flight occurred at 28°C, the coolest T_{a} measured for any of the continuous flights. It is possible that smaller species also regulate T_{thx} during sustained flight, based on results from Oertli (1989) where small beetles (7–93 mg, *Nicrophorus* size range=110–880 mg) regulated T_{thx} during short flights (≤5 s) *via* temperature-dependent changes in wing beat frequency. Further studies of continuous flights, including measurements of wingbeat frequencies for the smaller species (*N. guttula*, *N. investigator*) are warranted. Although continuous flight data obtained for *N. hybridus* indicate that this species is able to maintain a relatively constant T_{thx} during longer flights, one caveat is that these results do not fully represent actual flight conditions. Continuous flight data were taken from individuals flying while supported by a thermocouple probe, and so the T_{thx} measurements may not take into account effects of generating lift and thrust that would occur in free flight. During free flight, lift and thrust, in addition to heat generated from muscle contractions, may increase T_{thx} during longer flights above measurements of T_{thx} made in this study, especially at low wind speeds where less heat is lost *via* forced convection (Church, 1960; Casey, 1992). Tethered flights also do not allow an animal to carry out normal flight behavior and do not consider the effects of solar radiation during flight (Casey, 1992). Field data indicate that flight activity ceases when solar radiation is most intense (Fig. 4), and T_{e} models confirm that activity during these times could potentially be lethal, so wind speed and solar radiation may limit the degree to which a beetle can regulate T_{thx} during actual flights in the field.

Mechanisms for thermoregulation

Cooling and body size

Because of an inherently lower surface area to volume ratio,

Table 2. *Comparison of thermoregulatory indices documented for different species with those measured for* N. hybridus

Species	Order	Reference study	Body mass (mg)	Slope T_{thx} *vs* T_{a}	Index of thermoregulatory performance
Popilla japonica	Coleoptera	Oertli (1989)	93.20±19.9	0.27±0.27 (S.E.M.)	
Pidonia ruficolis	Coleoptera	Oertli (1989)	6.03±2.71	0.29±0.14 (S.E.M.)	
Cotinus texana	Coleoptera	Chappell (1984)	1,2902	0.469	
Dorsiana bonaerensis	Homoptera	Sandborn (1995)	1890±62	0.417	
Bombus sylvicola	Hymenoptera	Bishop and Armbruster (1999)	277.1		0.370 (0.03–0.58; 95% CI)
Bombus occidentalis	Hymenoptera	Bishop and Armbruster (1999)	211.6		0.430 (0.05–0.72; 95% CI)
Anthophora bomboides	Hymenoptera	Bishop and Armbruster (1999)	170.5		0.410 (0.24–0.58; 95% CI)
Nicrophorus hybridus	Coleoptera	Present study	495±20	0.315±0.071 (S.E.M.)	0.370±0.062 (S.E.M.)

Values reported from other studies are for insects that are considered good thermoregulators during flight by the authors.

larger insects should be able to regulate and maintain higher temperature excesses because they cool more slowly and have a higher thermal inertia (Bartholomew, 1981; Stone and Willmer, 1989b). This is true for *Nicrophorus* and is evident in the marked difference in mass and subsequent thermoregulatory ability between *N. hybridus*, *N. investigator* and *N. guttula*. Similar results have been shown for other beetles much larger than *Nicrophorus* (Bartholomew and Casey, 1977a,b; Bartholomew and Heinrich, 1978) and for other insects such as desert robber flies (Morgan and Shelly, 1988), where larger species were better thermoregulators.

Data from beetles cooling from flight or from artificial heating provide evidence that larger beetles may be able to maintain elevated T_{thx} longer after flight, which may confer a competitive advantage once a carcass is located. Because of slower cooling rates, larger beetles stay warmer longer, which may be one reason why larger beetles tend to be more successful in competitive interactions (Otronen, 1988; Trumbo, 1990). This would need to be tested with a series of carcasses in the field, where body temperatures of individuals arriving at the carcass and later competing for the carcass were measured, as was done previously for dung beetles arriving at dung piles (Bartholomew and Heinrich, 1978). Controlled laboratory experiments in which an individual beetle is warmed to a temperature that approximates an after-flight T_{thx} and is then placed in an arena with a carcass and other beetles (potential competitors) may be a way to approach this question. The use of infrared thermocouples is an appealing, non-invasive approach for obtaining field temperature measurements, allowing for more natural behavior.

Insulation, wing loading and heat transfer

Wings, elytra and thoracic pile all played a role in slowing heat loss, and beetles with both wings and elytra removed cooled significantly faster. Removal of thoracic pile also resulted in faster cooling rates. Other studies have reported that thoracic pile had no effect on the cooling rates of beetles (Nicolson and Louw, 1980; Morgan, 1987; Chown and Scholtz, 1993), but this does not seem to be the case in *Nicrophorus* as the cooling rates of beetles with and without pubescence differed. A difference in cooling rates with and without pubescence is also the case for desert locusts (Church, 1960b), where the insulating ability of the pubescence was dependent upon its density, and potentially for *Colias* butterflies, where it was shown that fur thickness increased with elevation (Kingsolver, 1983). *Nicrophorus* species vary in the density of thoracic pile and the actual area covered by the pile (M. J. Merrick and R. J. Smith, personal observation). Studies to determine if this variation is related to a species' thermoregulatory ability and distribution would be of great interest.

During flight, *Nicrophorus* flies with the elytra elevated and wings extended. With these structures held away from the body, a beetle in flight probably loses a great deal of endogenous heat by forced convection (Church, 1960; Casey, 1992). Even without air movement, beetles cooled significantly faster with wings and elytra removed, which indicates that this is a substantial avenue for heat loss during flight.

The ability to regulate body temperatures in flight requires that heat be generated and maintained at cooler ambient air temperatures and dumped at higher air temperatures. One mechanism for dumping excess heat is to shunt it to the abdomen, where it dissipates faster because of the large surface area of the abdomen and increased airflow and convection during fast flight (Heinrich, 1993, 1996). This mechanism of heat transfer is common in large moths (Heinrich, 1993, 1996) but it has not been observed in beetles (Chown and Scholtz, 1993), *Nicrophorus* (present study), honeybees (which have counter-current heat exchangers in the petiole; Casey, 1992) or in cicada killer wasps (Coelho, 2001). Although there does not appear to be any physiological mechanism for control of heat transfer to and from the abdomen, the fact that the abdomen of *Nicrophorus* is significantly cooler than the thorax following short flights means heat can be lost to the abdomen by simple diffusion of hemolymph from the thorax to the abdomen. This is supported by the observation that abdomens of living and dead beetles, shielded from a heat source, heated up at the same rate. Because the abdomen is exposed during flight and contains large spiracles along its margins, the opportunity for heat to be lost by forced convection is great. This presents a problem for retaining heat during flights at cooler temperatures if no mechanism (such as counter-current heat exchangers) to prevent heat dissipation to the abdomen exists (Casey, 1992; Heinrich, 1996). Inability to control heat loss to the abdomen in cooler temperatures may limit the ambient temperatures at which flight is possible for *Nicrophorus*.

Higher wing loading increases the amount of heat produced as the flight muscles do more work to beat faster and maintain lift. Wing loading increased with body size in *Nicrophorus*, and wing loading and body mass were also negatively correlated with the slope of T_{thx} against T_{a} and the index of thermoregulatory performance, indicating that better thermoregulators had higher wing loading and were heavier in general. These results are consistent with those found for other beetles (Oertli, 1989), noctuid moths (Casey and Joos, 1983) and bees (Stone and Willmer, 1989b; Bishop and Armbruster, 1999).

Another mechanism for thermoregulation that may be important in *Nicrophorus* includes heat dissipation from the head. Studies on thermal stability in honeybees (Roberts and Harrison, 1999), desert carpenter bees (Chappell, 1982), dragonflies (May, 1995) and cicada killer wasps (Coelho, 2001) indicate that cooling at high temperatures is facilitated by shunting warm hemolymph to the head, where heat is then dissipated over either a large surface area as in carpenter bees or *via* regurgitated fluid (see Heinrich, 1996, chapter 6 for a review). This mechanism for cooling is a possibility for *Nicrophorus*, as burying beetles regularly secrete fluid from the mouth and anus. Because of these secretions, however, water balance becomes important for burying beetles. Without access to water, beetles in captivity quickly die (M. J. Merrick and R.

J. Smith, personal observation), and *Nicrophorus* are not common in hot, dry habitats.

Influence of thermal environment on activity patterns

Nicrophorus species found in southeastern Idaho are highly influenced by the thermal environment they experience. Operative temperature models can be used to gauge the thermal environment that an organism is experiencing and how habitat features such as substrate, orientation and solar radiation affect body temperatures. High operative temperatures corresponded to times of inactivity for beetles in the field (Fig. 4) and, given the wide fluctuations in operative temperatures, it is clear that microhabitat choice could influence the body temperature of an individual. Solar radiation is likely to play a large role in limiting the activity of *Nicrophorus* not only in flight but also in terrestrial activity. *Nicrophorus* flies at a lower T_{thx} range (20–38°C) than other diurnal insects that can tolerate high heat loads, such as the hawkmoth *Macroglossum stellatarum* (Herrera, 1992; T_{thx} range 39–46°C) or cicada killers (*Sphecius speciosus*; Coelho, 2001; T_{thx} range 37–42°C). Members of *Nicrophorus* probably cannot tolerate high heat loads imposed by flying at midday on warm, calm and clear summer days. On windy days, the window of flight opportunity may widen, as high wind speeds and fast forward flight increase convective heat loss (Casey, 1992). Beetles left on the ground in direct sunlight quickly die (M. J. Merrick and R. J. Smith, personal observation) and a pair of beetles tending to a carcass left on bare soil (where T_{e} rapidly approaches lethal temperatures around 45–46°C) will quickly work together to move the carcass under vegetation (M. J. Merrick and R. J. Smith, personal observation).

Flight activity appears to be restricted to ambient temperatures between approximately 14°C and 36°C, which would, at higher elevations, restrict flight to primarily a diurnal activity. If thermal tolerances for flight and terrestrial activity are determined for a species, one might be able to predict areas where nocturnal flight is possible, based on the mean nighttime temperature for a given habitat and the thermoregulatory abilities of the species being studied. This information could also allow for predicting where a species is distributed geographically (in latitude and elevation) and what habitat types it might utilize. For example, *Nicrophorus nigrita* is a burying beetle that occurs along the Pacific coast of North America but lacks dorsal maculations on the elytra (i.e. it is completely black). Sikes (1996) found that this beetle is not active during the middle of the day and that it preferred to locate and bury carcasses in “moist, cool, redwood-forested canyons”. Perhaps because of its dark pigmentation, this species cannot tolerate high incident sunlight, or higher operative temperatures, leading one to predict that it would live in a shady habitat or have crepuscular or nocturnal activity patterns. Conversely, this species’ black pigmentation may be selectively advantageous for heating up faster in cooler environments.

Temperatures that are restrictive to flight are not necessarily restrictive to other activity, and temperatures restrictive to flight in one species may not restrict flight in another. In the present study, *N. investigator* flew over a wider range of ambient air temperatures than the other two species, and elevated T_{thx} on average 7.3°C above ambient. Since most of the *N. investigator* individuals documented in this study came from Colorado (higher elevations, cooler daily temperatures), this population may be able to tolerate a wider range of environmental temperatures. Beetles were also observed beneath carcasses and walking near them or in baited traps at night and at dawn (temperatures between 12°C and 15°C), with a mean T_{thx} excess of approximately 4.5°C.

Predictions of potential flight times for the three species (Fig. 5) show that the largest species (*N. hybridus*) and the species with the widest thermal tolerance (*N. investigator*) may be able to be active longer throughout the day compared with *N. guttula*. These predictions for activity times are based on the range of ambient temperatures recorded following each flight during flight trials but do not consider how well each species is able to regulate its body temperature during flights throughout the day. *N. investigator* may have the widest ‘window’ of possible activity times but may not be able to fly for very long before it becomes too cool or too hot to maintain flight. By contrast, because *N. hybridus* can regulate its body temperature better, it may be able to fly for longer periods throughout the day. For a beetle that must fly in search of carcasses for food and reproduction, the capability for sustained flights might increase an individual’s chances of finding the rare carcass resource and thus their subsequent fitness.

This study incorporates body temperature data, thermal profiles of various microhabitats and actual observations of animal activity in the field to show that (1) burying beetle activity is influenced by environmental temperatures, (2) burying beetles have the ability to elevate thoracic temperatures prior to flight and (3) thermoregulation during flight is influenced by body mass, morphological features such as wing loading and insulation. We provide a preliminary framework for predicting and testing hypotheses about burying beetle activity times and distributions based on thermal tolerances and thermoregulatory ability. Body size has been shown to influence competitive outcomes (Otronen, 1988; Trumbo, 1990), speed of carcass burial (Smith et. al. 2001) and reproductive success (Trumbo, 1990) in burying beetles and we show here that it also influences thermoregulatory ability, which may help to further explain these observed relationships between body size and fitness. We suggest that additional studies examining the relationships between body size, morphology and thermoregulatory ability and determining thermal tolerances and how these relate to distributions and activity times among different species of burying beetles will advance our current understanding of species distributions, niche partitioning among sympatric species and the relationship between body size and reproductive success.

We thank C. F. Williams, N. Huntly and an anonymous reviewer for providing critical reviews and suggestions that greatly improved this article. Partial support for this project was provided by the Idaho State University Graduate Research and Scholarship Committee, grant no. F00-06 to M.J.M. The work reported here was part of the work submitted to Idaho State University in partial fulfillment of the requirements for an M.Sc. degree.

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