Joseph F. Merritt* and David A. Zegers

Social thermoregulation in least shrews, Cryptotis parva

Abstract: Cryptotis parva exhibits a geographic range and ecological requirements unique among North American soricines: it possesses a latitudinal distribution, metabolism and communal nesting pattern more like the crocidurines of the eastern hemisphere. We utilized oxygen consumption (VO2) techniques to examine metabolic shifts and video to document activity patterns and dynamics of solitary and group nesting C. parva. Between ambient temperatures of 4°C and 34°C, solitary C. parva demonstrated an inverse relationship between ambient temperature (T_a) and resting metabolic rate (RMR); thermal neutral zone (TNZ) was very narrow, between a T_a of 34°C and 36°C. VO2 was measured in groups ranging in size from one to eight at T_a of 4°C, 14°C, 24°C and 34°C. The group size had a significant effect on the median RMR and median predicted Kleiber value and was more effective at reducing metabolic cost at a lower T_a. In a second experiment designed to assess the effects of huddling group size and incubator T_a on the T_a of the nest chamber, both had significant effects. Group size had significant effects on the T_a of the nest chamber at incubator temperatures of 5°C, 10°C, 15°C and 32°C, but not at 25°C. We found no behavioral or physiologic evidence of heterothermy.

Keywords: Crocidurinae; Cryptotis; huddling; resting metabolic rate; social thermoregulation.

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Introduction

Winter-active small mammals employ many different behavioral, anatomical and physiological mechanisms to cope with cold. These mechanisms can be classified into two broad categories (Merritt 2010): 1) resistance to and 2) avoidance of cold. Resistance involves energy expenditure that increases thermogenic capacity through an elevated resting metabolism rate (RMR), nonshivering thermogenesis (NST) and/or shivering. Avoidance involves energy conservation and can be accomplished via a number of tactics, including heterothermy, seasonal reduction in body mass (Dehnel Effect), reduction in level of activity, changes in microclimatic regime (e.g., communal huddling or construction of elaborate nests), adjustment in foraging zone, food hoarding, or adaptation in body size, insulation, appendages or coloration (Merritt 2010). Small mammal species rarely depend upon a single mechanism to survive cold but exhibit a suite of adaptive strategies, a metabolic-behavioral profile, that has evolved in response to the specific habitat, basic attributes and lifestyle of the species (Merritt and Zegers 2002).

The metabolic-behavioral profiles of the two soricid subfamilies tend to differ in profound ways. Members of subfamily Crocidurinae, the white-toothed shrews of the southern Old World, tend to have lower metabolic rates (Vogel 1976, Nagel 1991), perform heterothermy and nest communally. In contrast, members of subfamily Soricinae, the red-toothed shrews of the northern Nearctic and Palearctic, are likely to have higher metabolisms, practice euthermy and nest solitarily. For example, Blarina brevicauda (Say 1823) and Sorex cinereus (Kerr 1792) exhibit northern geographic range limits of 54°N and 65°N latitude and exhibit basal metabolic rate (BMR) values 39% and 71% higher than those predicted by the Kleiber equation, respectively (Haysen and Lacy 1985). The Crocidurinae and the Soricinae have evolved separately since the Oligocene in the Paleotropical and the Holarctic regions, respectively (McKenna and Bell 1997). The Crocidurinae evolved in response to warm tropical climates; whereas, the elevated metabolism of the Soricinae may be an evolutionary response to maintain homeothermy in environments typified by seasonally low ambient temperatures. A departure from this trend has been noted in a New World soricine shrew, the desert shrew Notiosorex crawfordi (Coues 1877), which shows convergence with the Crocidurinae (Genoud 1988).

Another soricine shrew, the least shrew, Cryptotis parva (Say 1823), ranges from 8.8°N to 44°N latitude in warm, dry weedy fields (Figure 1) and has been shown to nest communally (Davis and Joeris 1945, McCarley 1959, Whitaker 1974). Although metabolic rates of C. parva reported by Pfeiffer and Gass (1962) and Mock (2005) ranged from 7.0 to 13.1 ml O2 g⁻¹ h⁻¹ for individuals below thermoneutrality, McNab (1991) recorded a mean BMR of 3.06 for animals at...
thermoneutrality. This is only 13% above that predicted by the Kleiber equation and more similar to the BMR for crocidurines than soricine shrews. These data plus the small body mass of *C. parva*, its unusually long life span and its tendency to exhibit social thermoregulation (Mock 2005) caused us to reexamine the metabolic-behavioral profile of this species. We hypothesized that *C. parva* would demonstrate huddling behavior at a low Ta and experience energy conservation (avoidance) related to the total mass of the group and the difference between Ta and normothermic body temperature. We also hypothesized that huddling would influence the temperature of the nest chamber at low ambient temperatures.

**Materials and methods**

**Resting metabolic rate**

The RMR was measured in the laboratory by means of a positive-pressure pull-through assembly with an Applied Electrochemistry oxygen analyzer (S-2A Applied Electrochemistry, AEI Technologies, Inc, Pittsburgh, PA, USA). The analyzer was calibrated to an upper value in dry air (20.94% O₂) prior to the measurement of each animal or group of animals. Air flowed through columns of soda lime and Drierite for removal of CO₂ and H₂O before entering the oxygen analyzer (Condition B of Hill 1972). The rate of flow (500 cm³/min) was measured by Sho-rate 150, model 1355D-V flowmeters (Brooks Instruments, Hatfield, PA, USA) calibrated both at the factory and with an RT-100 calibration analyzer (Timeter Instrument Corporation, Lancaster, PA, USA). Shrews were tested in a 3800-ml glass jar, equipped with air inlet and outlet ports, containing an empty wooden nest box and placed in a low temperature incubator (Fisher Scientific, Inc., Pittsburgh, PA, USA, Model 146E, uniformity ±0.5°C). All metabolic trials were conducted between 0700 and 1800 h. Before and after testing, each shrew was weighed and its body temperature (Tb) recorded by inserting a thermometer sensor (Type PT-6, YSI, Inc., Yellow Springs, OH, USA) 6 mm into the rectum. The sensor was held in place for 10 s, and the body temperature was recorded on a Digi-Sense thermocouple thermometer (Cole Parmer, Chicago, IL, USA).
The RMR was measured at temperatures ranging from 4°C to 36°C and was interpreted to be the lowest oxygen consumption rate sustained for at least 5 min by a quiescent (but not necessarily post-absorptive), unanaesthetized shrew during the first 60 min in the respirometer. The RMR was calculated according to the methods of Depocas and Hart (1957) and Hill (1972), expressed as ml of O₂ per g per h and corrected for standard temperature and pressure conditions. We calculated Kleiber values as the metabolic rates predicted by body mass (Kleiber 1961), using the equation \( MR = 3.8 \times \text{body mass (in g)}^{0.75} \) and expressed as ml O₂ g⁻¹ h⁻¹. We compared these values to the empirically determined RMR. Mean minimal thermal conductance was calculated for solitary individuals at \( T_a = 31°C \) to 36°C using the technique of McNab (1980).

**Experimental animals**

Least shrews, *Cryptotis parva*, were obtained from a self-replenishing, closed laboratory colony established in 1966 and maintained in the Animal Care Facility housed at Kirksville College of Osteopathic Medicine (KCOM), Kirksville, MO, USA (Mock 1982, 1994, 2005). The original 32 animals in the colony were captured in Boone County, MO and augmented with animals captured during the 1970s from Adair County, MO. At KCOM, every effort to preserve the outbreed nature of the colony was heeded. Animals were transferred to the mammal laboratory facility adjacent to the residence of the first author in Oakwood, Illinois on February 22, 2010. A total of 40 shrews were procured for metabolic experiments and housed in plastic tubs (60×60×60 cm) connected with a plastic tube to permit movement between tubs. Tubs were provided with watering devices (60 cm³ bottles attached to a Neoprene rubber stopper with a sipper tube affixed to a polycarbonate frame). The opening of the sipper tube possessed an inside diameter of 3.3 mm and was placed a minimum of 2 cm above the floor of the tub. Shrews were fed a mixture of wet cat food and water (Laboratory Feline Diet, Purina 5003, Purina, Inc., St. Louis, MO, USA), provided *ad libitum*. Mealworms were provided once every other day as a dietary supplement. Typical food containers were a 6.7-cm watch glass for wet diet and a 3.5-cm diameter culture dish for mealworms. Four nest boxes (7.5×5.0×6.0 cm) were provided in each tub. Nest boxes were constructed from pine, Philippine mahogany plywood and stainless steel or brass nails. Each nest box was provided with dried grass clippings as nesting material. The entrance to the nest box was 2 cm in diameter and located approximately 1 cm above the floor. The floor of each tub was provided with potting soil. Animal housing and care is described by Mock (2005). This research was conducted according to the guidelines approved for animal care and use by the American Society of Mammalogists (Sikes et al. 2011).

**Group nesting**

We examined the metabolic requirements of 1) solitary shrews for ambient temperatures of 4°C, 10°C, 14°C, 18°C, 24°C, 28°C, 34°C and 36°C, and 2) shrews in nesting groups of one, two, three, four, five, six, seven and eight shrews for ambient temperatures of 4°C, 14°C, 24°C and 34°C. We employed small nest boxes (8.5×5.0×6.0 cm) when running from one to five animals and large nest boxes (9.0×7.0×6.0 cm) when running from 6 to 10 animals. No replication of individuals took place (i.e., if an individual shrew was employed in a measurement for a group size of two, it was not used again for any group size). Groups were placed in the respirometer chamber for a given temperature for 15 min prior to the metabolic trial. Typically animals would acclimate and settle into communal groups in <30 min. During the metabolic trial, oxygen consumption was continually tracked, and the lowest oxygen consumption was accepted for purposes of the calculation of group metabolic rate. This value was divided by the total mass of the huddling group to give oxygen consumption in ml O₂ g⁻¹ h⁻¹. Shrews were observed during each trial by employing an infrared video camera and DVR (Supercircuits, Inc., Austin, TX, USA). The video camera was placed inside the incubator and directed at the entrance of the nest boxes. This device permitted us to determine the number of shrews occupying the nest boxes at a given time.

**Nest box temperatures**

To assess the effect of huddling on nest box ambient temperature, we measured the difference between the temperatures inside an occupied wooden nest box compared to the ambient temperature of the incubator housing the nest box. Experiments were conducted at five different incubator temperatures (5°C, 10°C, 15°C, 25°C and 32°C). Small nest boxes (8.5×5.0×6.0 cm) were used to sequence from one to five shrews; larger boxes (9.0×7.0×6.0 cm) were employed to sequence from six to ten shrews. Each nest box was provided with a small amount of dried grass and contained a single entry hole measuring 2.0 cm in diameter. The temperature of the occupied nest chamber was measured by inserting the thermister probe of a YSI
2100 tele-thermometer (YSI, Inc., Yellow Springs, OH, USA) 2.5 cm into the nest box through the lid. This nest temperature was compared to the temperature in the incubator. We used a weatherproof infrared camera (equipped with DVR and motion detector Supercircuits, Inc., Austin, TX, USA) positioned 30 cm above the nest box to monitor movements of shrews in and out of the nest box during the trials. The camera and motion detector were used during each metabolic experiment to assess activity levels and positions of the shrews.

**Statistical analysis**

Because our data did not always meet the assumptions of parametric tests concerning normality, nonparametric tests were used (Sokal and Rohlf 1981). The Kruskal-Wallis one-way analysis of variance (ANOVA) and the Wilcoxon matched-pairs signed-rank tests were used to assess a central tendency around the median RMR, predicted Kleiber values and nest box temperatures. Spearman's rho and Kendall's tau were used to evaluate the relationship between group size and $T_a$ of the occupied nest box and to assess the relationship between group size and the difference in RMR of huddling and solitary individuals at the same $T_a$. Pearson's correlation coefficient ($r$) was employed to determine the correlation between $T_b$ and $T_a$. Metabolic values, body temperatures and masses are expressed as means ±1 SE. Statistical significance was accepted at $p<0.05$, all tests were two-tailed and were conducted using MINITAB 16.1.1 (Minitab, Inc., State College, PA, USA).

**Results**

**Resistance**

The inverse relationship between $T_a$ and RMR for solitary Cryptotis parva is illustrated in Figure 2A and described by the equation $\text{RMR}=13.237 -0.2714 \ (T_a) \ (r^2=0.8094)$ between ambient temperatures of 4°C and 34°C. The presumptive thermal neutral zone appeared very narrow, between 34°C and 36°C, although because RMR values were not necessarily basal, the TNZ may be truncated. At $T_a=36°C$, individuals dissipated heat via panting and flattening. Solitary individuals maintained a mean body temperature of 36.6±0.86°C (n=130) between ambient temperatures of 4°C–32°C. The mean minimal thermal conductance of solitary individuals at $T_a$ from 4°C to 32°C was 0.54±0.14 ml O₂ g⁻¹ h⁻¹ (n=130), which is 1.25 times the value expected based upon body mass (McNab 1991).

**Avoidance**

Although heterothermy has been reported in some North American Soricinae, we did not observe lethargic behavior or obvious reductions in visible breathing rates during the course of our experiments. Metabolic rates for individuals exposed to temperatures below thermoneutrality (Figures 2A and 3) are not consistent with those of individuals experiencing spontaneous or induced heterothermy. Moreover, the correlation of $T_b$ and $T_a$ is negative ($r=-0.24$, $p=0.004$), and only 6% of the total variation in $T_b$ and $T_a$ is due to covariation between them ($r^2=0.06$). Both of these findings are inconsistent with heterothermy.
Thus, we conclude that Cryptotis parva in our experiments did not experience heterothermy.

The relationships between group size and RMR and predicted metabolic rate based upon the Kleiber equation were determined for incubator temperatures of 4°C, 14°C, 24°C and 34°C (Figures 3 and 4). Note that trials were not conducted for all group sizes for each of these four temperatures (Table 1).

Overall, group size had a significant effect on median RMR (Kruskal-Wallis H = 18.85, df=6, p=0.004). This relationship was significant for T_a of 4°C, 14°C and 24°C, but not for 34°C (Table 2). Generally, group size appeared to become more effective at reducing metabolic cost as the ambient temperature declined (Figure 3). The percent reduction in mean RMR of

![Image of Figure 3](Unauthenticated/Download Date | 5/27/19 11:02 PM)

Figure 3  Relationship of RMR (ml O_2 g\(^{-1}\) h\(^{-1}\)), with group size and ambient temperature for Cryptotis parva.

Circles represent mean values; + indicates medians.

![Image of Figure 4](Unauthenticated/Download Date | 5/27/19 11:02 PM)

Figure 4  Percent reduction in RMR (ml O_2 g\(^{-1}\) h\(^{-1}\)) of huddling Cryptotis parva compared to solitary individuals at the same ambient temperature.

### Table 1

<table>
<thead>
<tr>
<th>Group size</th>
<th>Mean RMR</th>
<th>Mean mass</th>
<th>Median RMR</th>
<th>Median mass</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>11.75</td>
<td>5.97</td>
<td>11.65</td>
<td>5.87</td>
</tr>
<tr>
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<td>5.55</td>
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<td>7</td>
<td>4.25</td>
<td>4.85</td>
<td>4.25</td>
<td>4.95</td>
</tr>
<tr>
<td>8</td>
<td>4.12</td>
<td>4.75</td>
<td>4.12</td>
<td>4.85</td>
</tr>
</tbody>
</table>

Units for median and mean RMR are ml O_2 g\(^{-1}\) h\(^{-1}\) ± SE. Units for body mass are g ± SE.
and that of solitary individuals at Ta and the difference in mean RMR of individuals in groups significant correlations between group size (two to eight) and Kendall’s tau confirmed significance of p<0.05. Note that there was only one category tested for group size seven, making comparisons impossible.

The effect of incubator ambient temperature on resting metabolic rate (RMR) and predicted Kleiber MR for group sizes of one to six and eight Cryptotis parva.

<table>
<thead>
<tr>
<th>Group size</th>
<th>RMR</th>
<th>Kleiber</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>H</td>
<td>df</td>
</tr>
<tr>
<td>1</td>
<td>43.42</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>20.64</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>10.27</td>
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</tr>
<tr>
<td>4</td>
<td>9.62</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>5.00</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>8.73</td>
<td>2</td>
</tr>
<tr>
<td>8</td>
<td>7.94</td>
<td>3</td>
</tr>
</tbody>
</table>

Discussion

Crocidurinae and Soricinae

White-toothed shrews (subfamily Crocidurinae) likely evolved in warmer, more southern latitudes of the eastern hemisphere, and some have exhibited the ability to enter daily torpor and exhibit huddling as a form of energy conservation. Red-toothed shrews (subfamily Soricinae) evolved in the more northerly latitudes of the Palearctic and Nearctic regions and are not known to enter torpor and typically do not aggregate under natural conditions. Our data confirm that the metabolic-behavioral profile of Cryptotis parva is indeed intermediate between the profiles typical of the two subfamilies.

Effect of group size on the difference in ambient temperature (T_a) between the nest box and incubator; this relationship was not significant at 25°C (Table 4, see Figure 5).

<table>
<thead>
<tr>
<th>T_a of environmental chamber</th>
<th>Spearman’s rho</th>
<th>Kendall’s tau</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>0.966</td>
<td>0.899</td>
</tr>
<tr>
<td>10</td>
<td>0.830</td>
<td>0.733</td>
</tr>
<tr>
<td>15</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>25</td>
<td>-0.17</td>
<td>-0.17</td>
</tr>
<tr>
<td>32</td>
<td>0.652</td>
<td>0.535</td>
</tr>
</tbody>
</table>

aSignificance of p=0.001; bsignificance of p=0.005; and csignificance of p=0.05.
Resistance to cold

Our values for mean RMR are lower than those reported by Mock (2005) at 19°C–20°C and Pfeiffer and Gass (1962) at 25°C–27°C. Our minimal RMR values for solitary individuals at thermoneutrality (3.97±0.29) are slightly higher than the basal rate of 3.06±0.10 in the only other study of the effect of Th on metabolic rates of this species (McNab 1991). This may be the result of the slightly lower mean body mass (6.06 vs. 6.2 g) in our study, or to differences in methodology. Th was slightly lower in our study (36.6°C vs. 37.0°C) than in McNab’s. Mean thermal conductance in our study was 1.13 times that conveyed by McNab (1991). In sum, RMR in our study is not equivalent to BMR as...
measured by McNab (1991), but still accurately reflects the metabolic response of Cryptotis parva to cold.

Torpidity

Although daily torpor is reported for Soricidae (Taylor 1998, Table 11.2), red-toothed shrews (subfamily Soricinae) are not known to enter torpor – most likely related to their evolution in more northerly latitudes and comparatively higher metabolic rate (Churchfield 1990, Taylor 1998). In contrast, researchers working in Palearctic regions have elucidated intriguing patterns of heterothermy in white-toothed shrews. Torpor may result in a savings of approximately 15% of the daily energy expenditure of the greater white-toothed (Crocidura) and Etruscan (Suncus) shrews, and it appears that these shrews employ torpor as a short-term tactic in coping with emergencies in the form of food shortages (Frey and Vogel 1979, Frey 1980). In such studies, torpor was generally induced at various ambient temperatures by reducing the food of captive animals, although torpidity in Crocidura russula and Crocidura flavescentes I. (Geoffroy 1827) was elicited spontaneously in the presence of food (Baxter et al. 1979, Frey 1980, Genoud 1985, Baxter 1996). Torpidity has also been reported for free-ranging Crocidura (Nagel 1977, 1991, Vogel and Genoud 1981). Myosorex varius (Smuts 1832), a crocidurine trapped in Kwa-Zulu-Natal, South Africa, showed contrasting behavior to most crocidurines, in that M. varius did not enter torpor (Brown et al. 1997). In contrast to crocidurine shrews, soricine shrews are not reported to undergo torpidity, and attempts to elicit heterothermy by means of food deprivation have been unsuccessful (Gębczyńska 1977, Genoud 1985, Merritt and Adamerovich 1991), with two exceptions. Torpor-like behavior was observed in the Suisun shrew (Sorex ornatus) from northern California maintained in the laboratory (Newman and Rudd 1978). During metabolic experiments, animals became inactive, with slowed breathing rates and a 63%–88% drop in metabolic rates. In addition, the desert shrew (Notiosorex crawfordi) was reported to exhibit long bouts of torpor (Armstrong and Jones 1972, Lindstedt 1980a,b). For N. crawfordi, an inhabitant of desert scrub habitats of southwestern North America, torpidity combined with a reduction in BMR is thought to represent an adaptation for coping with heat, aridity and fluctuating food supply. To our knowledge, only McNab (1991) has experimentally tested the capacity of Cryptotis parva to undergo heterothermy and found no evidence of reduced Tc when individuals were exposed to a low Tη. Layne and Redmond (1959) demonstrated some lability in Tη, ranging from 31.9°C to 39°C. Based on this information, McNab (1991) predicted that daily torpor may be found in this species. Our metabolic, behavioral and body temperature data (Figure 2, Table 1), however, do not support the hypothesis of heterothermy in C. parva. It appears that concerning this parameter, C. parva is more like other soricines than some crocidurines.

Aggregation

Aggregation, or social thermoregulation, is an important avoidance mechanism for the enhancement of survival in cold and is widespread among Mammalia (Feldhamer et al. 2007). For rodents, aggregation is an effective form of heat conservation during winter, when food supplies are scarce (Vogt and Lynch 1982, Madison 1984, Andrews and Belknap 1986, Hayes et al. 1992, Feldhamer et al. 2007, Kotze et al. 2008, Merritt 2010). In northern regions, nonhibernating small mammals, particularly those of the rodent families Cricetidae and Sciuridae, reduce the differential of body surface to ambient air temperature by constructing elaborate nests and engaging in communal nesting (Merritt 2010). The greatest gain from huddling should logically accrue for small mammals that possess a large surface-area-to-mass ratio and a limited capacity for increasing the insulation value of their pelage. Huddling reduces each individual’s exposed surface, thus reducing the cold stress and the metabolic requirement for heat production. For example, southern flying squirrels (Glaucomys volans Linnaeus 1758) form “huddles” of up to 20 individuals (but groups fewer than 10 are more common) in hollow trees to conserve energy during winter; a group of six southern flying squirrels in New Hampshire, huddling within a wooden nest box and surrounded by temperatures of 6°C, reduced their energy expenditure by 36% (Stapp et al. 1991). Both G. volans and Glaucomys sabrinus (Shaw 1801) supplement huddling with periodic bouts of torpor during extended periods of food shortage and low temperature in winter (Muul 1968, Weigl et al. 1999). This behavioral strategy, augmented by a nearby supply of hoarded nuts, enhanced survival during winter (Merritt et al. 2001).

The classic work of Sealander (1952) showed that for Peromyscus at low temperatures, individuals at the bottom of a “communal” nest group enjoyed temperatures well above ambient levels, but by continually shifting position, each mouse in the huddle was periodically rewarmed and thus avoided hypothermia. In our experiments, huddling Cryptotis parva at low ambient temperatures demonstrated considerable movement and shifting of position, suggesting that a similar process occurs in this species.

Researchers in Palearctic regions have compared the influence of nest utilization of shrews. When compared with resting rates at low ambient temperatures, the four species tested [Crocidura russula, Sorex coronatus (Millet 1828), Sorex minutus (Linnaeus 1766) and Suncus murinus (Linnaeus 1766)] all demonstrated a 10%–30% reduction in metabolic rates (Dryden et al. 1974, Genoud 1985, McDevitt and Andrews 1995). Several authors have shown that C. russula exhibits social behavior (Martin 1910, Vogel 1969), and the occurrence of communal nesting has been occasionally documented (Vogel 1969). Nest sharing has been documented by several individuals using radioactively tagged shrews (Genoud and Hausser 1979, Vogel and Genoud 1981, Ricci and Vogel 1984), and winter nests have been found in the bicolored shrew Crocidura leucodon (Hermann 1780, Frank 1984). Genoud (1985) found a negative correlation between the degree of insulation of nests of Crocidura russula and S. coronatus live-trapped in western Switzerland. Sharing a common nest occurred regularly each winter, and all individuals within a certain area took part (Cantoni and Vogel 1989); however, it is unclear if the members of such groups were related.

Nest sharing does indeed occur in crocidurines; however, it is noteworthy that energy savings from social thermoregulation have been determined only in Crocidura russula. For two huddling individuals at 2°C, the reduction in metabolic rates amounted to 21% of the resting rates of isolated individuals (Genoud 1985), which is similar to the 26% reduction in RMR exhibited by groups of two Cryptotis parva compared to solitary individuals at 4°C in our study. Below thermoneutrality, huddling appears to be an important energy-saving tactic for C. parva, but at thermoneutrality that savings is negated (Figure 4). At T_b=34°C, the RMR of huddling individuals appeared to have been slightly elevated compared to that of solitary individuals, which may be the result of body heat elevating the T_b of the nest box above thermoneutrality.

Social organization in some crocidurines is reportedly strongly influenced by season, e.g., Crocidura russula (Cantoni and Vogel 1989). In contrast Sorex species, due to their mutually antagonistic behavior and strict territoriality, especially in winter (Rychlik 1998), are territorial throughout the year. Thus, social thermoregulation appears atypical among soricines; reports of aggregation in North American shrews are rare and limited to two species, Sorex ornatus (Hays and Lidicker 2000) and Cryptotis parva. These species are well known to undergo aggregation under natural conditions. Unlike most North American shrews, C. parva is not commonly associated with mesic habitats; rather, they reside in dry successional communities, such as grassy, weedy and brushy fields, abandoned pasturelands and prairies of bluegrass and orchard grass (Whitaker 1974).

Least shrews are well known to be gregarious and colonial (Whitaker 1974). Hamilton (1934) noted two groups (of three and five individuals each) huddled in a group in a nest of dry grass about 100 mm below ground. Davis and Joeris (1945) found a nest in December in east-central Texas occupied by 12 individuals. This species is reported to inhabit nests of 31 and 25 individuals sharing a single nest in the wild in eastern Texas (McCrary 1959) and southern Virginia (Jackson 1961). This tendency is common during winter months and reported to function as a heat conservation measure (McCrary 1959). In our study, reductions in RMR of 52% and 53%, compared to solitary individuals, were exhibited for huddling groups of five and eight individuals at 4°C. Further, as with northern short-tailed shrews (Blarina brevicauda), least shrews are well known to establish latrine sites (Whitaker 1974, Merritt 1987). Broadbooks (1952) noted the presence of a toilet approximately 75 mm in diameter located at the edge of a nest. In our study, latrine sites adjacent to nest boxes and bedding of shrews maintained in plastic tubs of the laboratory was commonly noted.

When confined to nest boxes of varying numbers of shrews, there was an impressive difference in temperature inside the nest compared to ambient temperatures outside the nest boxes (Table 4, Figure 5). Based on metabolic tests, we believe that aggregation in nests confers a significant advantage to individual Cryptotis parva combating cold. This is especially true for shrews residing in prairie environments with microhabitats of sparse understory and vegetative complexity that experience cold winter temperatures commonly reaching minimum temperatures in winter of -20°C. It is not known, however, if the individuals in such huddling groups are related, and thus it is unclear if the metabolic advantage of huddling was sufficient alone to overcome the mutually antagonistic behavior and territoriality typical of soricines or if kin selection also played a role in the evolution of this behavior.

In sum, our data indicate that, like most other soricines, Cryptotis parva does not undergo torpor, but that huddling can be an important energy conservation...
mechanism in winter. In this regard, its metabolic-behavioral profile is more similar to the pattern of crocidurines than its fellow soricines. It may be that this is the result of the evolution of *C. parva* in a climate more similar to that of the crocidurines (Vogel 1976, Genoud 1985). Future directions for research should involve both laboratory and field studies designed to determine 1) if food deprivation and/or photoperiod changes will induce heterothermy in *C. parva* and 2) the genetic relationships of the coinhabitants of nests.

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**References**


