Journal of Mammalogy, 95(6):1230–1239, 2014

Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents

Cory T. Williams,* Kathryn Wilsterman, Amanda D. Kelley, André R. Breton, Herbert Stark, Murray M. Humphries, Andrew G. McAdam, Brian M. Barnes, Stan Boutin, and C. Loren Buck

Department of Biological Sciences, University of Alaska Anchorage, Anchorage, AK 99508, USA (CTW, CLB)
Department of Biology, Bucknell University, Lewisburg, PA 17837, USA (KW)
Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2R3, Canada (ADK, SB)
Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523, USA (ARB)
Swiss Ornithological Institute, Sempach, CH-6204, Switzerland (HS)
Department of Natural Resource Sciences, Macdonald Campus, McGill University, Ste-Anne-de-Bellevue, Quebec H9X 3V9, Canada (MMH)
Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada (AGM)
Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA (BMB)

* *Correspondent: ctwilliams@uaa.alaska.edu*

Measuring daily and seasonal patterns of activity is useful for understanding the ecological and evolutionary drivers of behavior. We used collar-mounted light loggers to examine how nest attendance in arboreal squirrels and aboveground activity in semifossorial ground squirrels are affected by weather-driven changes in thermoregulatory conditions. Activity of lactating red squirrels (*Tamiasciurus hudsonicus*) had a diurnal pattern showing 3 daily peaks of activity with time spent outside the nest increasing with increasing ambient temperature, but decreasing with increasing relative humidity and wind. Despite the persistence of daylight during midsummer in the arctic environment, female arctic ground squirrels (*Urocitellus parryii*) also exhibited diurnal activity patterns with time spent above ground each day decreasing in response to precipitation but increasing with increasing ambient temperature and incident solar radiation. On cooler days, ground squirrels exhibited a unimodal activity pattern. However, on warm days, ground squirrels spent less time above ground when solar radiation and ambient temperature were both at their daily maxima, which resulted in a bimodal activity pattern. Our results highlight the utility of light loggers as a cost-effective means of addressing questions related to foraging behavior, parental care, thermoregulation, energetics, and timing of activity in arboreal and semifossorial small mammals.

Key words: arctic ground squirrel, circadian rhythms, environmental conditions, foraging behavior, geolocation tag, North American red squirrel, reproductive behavior

DOI: 10.1644/14-MAMM-A-062

Determining how daily patterns of activity are affected by changing environmental conditions is central for understanding the ecological and evolutionary drivers of behavior. Although most organisms time their daily activities and physiological processes using an endogenous circadian clock synchronized to the 24-h day by external timing cues (zeitgeber), short-term patterns of activity also can be affected by a broad range of abiotic and biotic factors, including weather and thermal exchange conditions, reproductive status, predation, parasites, and resource availability (Stephan and Zucker 1972; Kenagy 1973; Erickson and West 2002). Observed patterns of daily activity also are influenced by complex trade-offs between fitness costs and benefits associated with these factors; for example, the trade-off between rate of energy acquisition and predation risk can be a major determinant of daily activity patterns (Werner and Anholt 1993; Metcalfe et al. 1999; Wolff and Horn 2003).

Small endotherms are likely to be particularly sensitive to the direct effects of thermal exchange conditions because ambient conditions are often more likely to be below their critical temperature and thereby require active thermoregulation (McNab 1980; Aschoff 1981). Low ambient temperatures, for example, can promote the use of daily torpor in small birds and mammals (Vogt and Lynch 1982). However, in species that do not utilize daily torpor, mitigation of changing thermoregulatory costs often occurs through behavioral mechanisms, such as huddling, adjustment of nest insulation, changes in energy intake, reductions in activity, or a combination of these (Guillemette et al. 2009; Batavia et al. 2010; Gilbert et al. 2010; Williams et al. 2013).

Understanding how environmental conditions affect behavior in free-living animals requires high-resolution observations on activity patterns, although these data can be difficult to obtain, particularly in small mammals for which visibility is often limited by vegetation and topography. Observing events directly also can disturb animals, potentially biasing results. High-resolution observational data on the activity patterns of free-living small mammals can sometimes be obtained (e.g., Raveh et al. 2010), but it requires substantial effort and can be prohibitively expensive. Collecting observational data on many animals simultaneously is particularly difficult, such that many studies are forced to ignore variation at the level of the individual (e.g., Everts et al. 2004; Viera et al. 2010). This is problematic, because physiology and "personality" can vary substantially among individuals, potentially resulting in multiple strategies within a population to cope with the same environmental factors (Dall et al. 2004; Williams 2008).

Methodologies that provide high-resolution data on the behavior of individuals are needed to elucidate how individual variation in physiological performance constrains behavior in nature (e.g., Sears et al. 2006), as well as to better understand the adaptive function of consistent individual differences in behavior (i.e., animal "personalities"—Boon et al. 2007). When these types of data are available, they can be combined with recently developed quantitative methodologies that allow ecologists to explore variance partitioning across hierarchical levels (Dingemanse and Dochtermann 2013). Given the major challenges for observing animal movement and behavior, biologists are increasingly reliant on animal-attached tags for logging or relaying data, or both (i.e., biologging—Rutz and Hayes 2009). For example, accelerometer-based loggers can provide high-resolution data on activity patterns in larger fish, birds, and mammals (van Oort et al. 2005; Sakamoto et al. 2009; Whitney et al. 2010) although the size and weight of many movement-logging devices makes them unsuitable for smaller animals.

Here, we demonstrate that small loggers that record ambient lighting conditions, originally developed for geolocation of migrating birds based on the timing of dawn and dusk, provide a cost-effective means of measuring patterns of activity in arboreal and semifossorial squirrels. Using light loggers affixed to collars, we measured patterns of nest attendance in an arboreal rodent, the North American red squirrel (*Tamiasciurus hudsonicus*), and determined daily patterns of aboveground activity in a semifossorial hibernator, the arctic ground squirrel (*Urocitellus parryii*). We hypothesized that patterns of activity, as determined by light loggers, would be influenced by thermal exchange conditions, with squirrels decreasing activity outside the nest or burrow with decreasing ambient temperature and with increasing wind speeds and precipitation. Finally, we highlight the potential applicability of the light-logging approach to a variety of research questions.

Materials and Methods

Red squirrels.—Red squirrels are small (150–250 g), diurnal, semiarboreal rodents that do not use torpor (Brigham and Geiser 2012). In the boreal forests of North America, red squirrels defend exclusive year-round territories and rely on cones from an intermittently masting conifer, white spruce (*Picea glauca*), for much of their nutrition (Fletcher et al. 2013; LaMontagne et al. 2013). Recruitment varies substantially in response to mast seeding and, consequently, population density exhibits pronounced annual fluctuations (Dantzer et al. 2013; Williams et al. 2014). This classic consumer–resource pulse system has proved useful for examining behavioral responses to fluctuations in population density and resource availability (e.g., Boutin et al. 2006; Dantzer et al. 2013).

We studied red squirrels in the boreal forest of the southwestern Yukon, Canada (61°N, 138°W), in 2012. Squirrels on study plots were marked with alphanumeric ear tags and given a unique color combination of wires for visual identification. All offspring born in the population were counted, sexed, and ear-notched within days of birth; nests were accessed again to ear-tag pups when they were approximately 25 days of age, prior to 1st emergence from the nest. We equipped 21 female red squirrels with a 5-g collar that included a 4-g radiotransmitter (model PD-2C; Holohil Systems Limited, Carp, Ontario, Canada) and a ~1-g logger that recorded light intensity each 2 min (20 SOI-GDL1.0; Swiss Ornithological Institute, Sempach, Switzerland).

We set a light intensity threshold (25 lux) for out of nest activity that was well above the baseline value of all loggers (range of baselines: 0–9 lux). We assumed that low light levels (< 25 lux) indicated that females were sequestered within their nests. Although this intensity threshold was somewhat arbitrary results were not sensitive to the chosen threshold (i.e., a doubling of the threshold had little effect on parameter estimates and no effect on significance levels). Based on exposure to light, we calculated the total amount of time squirrels spent out of the nest each day, the number of activity bouts during the day, as well as timing of 1st emergence in the morning and final return to the nest at night. When calculating the number of activity bouts and timing of initial daily emergence and final nightly immergence, we only recorded transitions between states (out of nest versus in nest) if there were 10 consecutive minutes for the same state (i.e., 5 consecutive light readings or 5 consecutive dark readings). Collars were deployed between 29 April and 3 July, immediately prior to or immediately following parturition in individual females. We removed collars from females immediately after tagging their offspring at age ~25 days. In 1 case, we removed a collar from a female after 14 days due to excessive wear around her neck (loss of fur and irritated and inflamed skin); wear appeared to be caused by the collar, rather than the logger itself. This research conformed to the guidelines of the American Society of Mammalogists (Sikes et al. 2011); red squirrel research was approved by the University of Alberta Animal Care and Use Committee.

Arctic ground squirrels.—As the farthest north hibernating small (400–1,000 g) mammal in North America, the arctic ground squirrel is exposed to profound seasonal changes in photoperiod and ambient temperature. The annual cycle of these ground squirrels includes a brief active season with individuals limiting aboveground activity to 3–5 months during which they reproduce, molt, and fatten, and males cache food in preparation for hibernation (Buck and Barnes 1999). Animals spend the remainder of the year sequestered in frozen burrow systems (hibernacula), alternating between long (2–3 weeks) bouts of continuous torpor interrupted by short (10–20 h) intervals of euthermia during interbout arousal episodes. Although arctic ground squirrels spend most of the year torpid, they do not utilize daily torpor during the active season. During the active seasons, ground squirrels nest (rear pups) and sleep underground. During the day these burrow systems also are used to evade predators and for thermoregulation (Long et al. 2005).

We studied arctic ground squirrels near Toolik Field Station (68°N, 149°W) on the North Slope of Alaska. In 2013, we equipped 16 adult females with light loggers; 14 females were equipped with BAS model MK7290 light loggers (1 g; Biotrack Ltd., Dorset, United Kingdom), which record light levels every 2 min, and 2 females were equipped with Intigeo-C65 light loggers (1 g; Migrate Technology Ltd., Cambridge, United Kingdom), which record light every minute and then save the highest value per 5-min interval. Similar to the red squirrel study, we selected a light-level threshold (MK7290 threshold: 2 units; C65 threshold: 5 lux) for "above ground" that was well above the baseline recorded in dark conditions (0 units or 0 lux for all devices); results were not sensitive to changes in thresholds. All collars were made of inline zip ties surrounded by plastic tubing; light loggers were wired and epoxied to the tubing. We collected environmental data (incident solar radiation, wind speed, ambient temperature, and rainfall) at our study site using a Hobo U30-NRC weather station (Onset Computer Corporation, Bourne, Massachusetts). Light loggers were deployed between 7 May and 30 June. However, only 3 devices deployed in May were recovered and therefore all results and analyses are restricted to data collected in June.

We obtained records of light exposure from 13 of the 16 adult females equipped with light loggers. During the study, 3 females lost their collars due to zip-tie failure; 2 of these females were outfitted with new collars and we subsequently used epoxy resin to prevent zip ties from opening. Two females were never recaptured and a 3rd was found dead (partially eaten and decomposed). In 1 case we removed a logger early due to excessive fur loss; this animal subsequently regrew its fur within 5 days. Additionally, 3 other ground squirrels had signs of collar irritation (inflamed and broken skin) when their collars were removed; 1 of these squirrels was recaptured 6 days later and its neck appeared to be mostly healed, although some scabbing was evident. In all cases, wear appeared to be caused by the collar rather than the logger itself. Arctic ground squirrel research was approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee.

Statistical analyses.—Summary statistics are means ± *SE* of individual averages, unless otherwise noted. We used a linear mixed model (LMM) in SAS statistical software (SAS Institute, Cary, North Carolina) to determine the effects of environmental conditions on total time red squirrels spent outside of their nest each day. We included animal identification as a random effect, and ambient temperature, wind speed (log-transformed), and relative humidity as fixed effects. Litter age also was included as a fixed effect based on previous findings that red squirrels spent less time in the nest with older litters (Studd 2012). We included data on 12 lactating females in our analyses (mean length of individual data sets: 24.7 ± 1.6 days); females that lost their litter within the first 25 days of lactation were excluded. We used weather data (ambient temperature, relative humidity, and wind speed) collected hourly at Environment Canada's Burwash weather station, located 50 km from the study site (Environment Canada 2013) in our analysis.

For statistical analysis of daily aboveground activity in arctic ground squirrels, data sets were truncated to contain only dates where we also had concurrent environmental data from our Hobo U30-NRC weather station, reducing the data set to 12 animals with 6–27 days of data (median: 21 days). We then used a linear mixed model with individual (animal identification) included as a random effect to determine the effects of environmental conditions on total time ground squirrels were active (above ground based on light readings) each day. Time spent above ground each day was normalized using an inverse-root transformation (time spent above ground was normally distributed for red squirrels). We included animal identification as a random effect. Fixed effects in the model included day of the year, rain (as a class variable; 0 mm/day, 0–3 mm/day, or $>$ 3 mm/day), average daily wind speed, incident solar radiation, and ambient temperature. Solar radiation and temperature were weakly correlated ($r = 0.3199$).

Results

Red squirrels.—Based on light-logger data, the average time lactating female red squirrels spent outside the nest each hour exhibited a trimodal pattern across the day (Fig. 1); individuals averaged 6.0 ± 0.6 activity bouts each day and cumulatively spent 10 h 5 min ± 37 min outside of the nest each day. Excluding bouts of $<$ 10 min, red squirrels first left the nest at 0611 h ± 10 min each morning and last entered the nest at 2135 h ± 38 min each night. Red squirrels first left the nest in

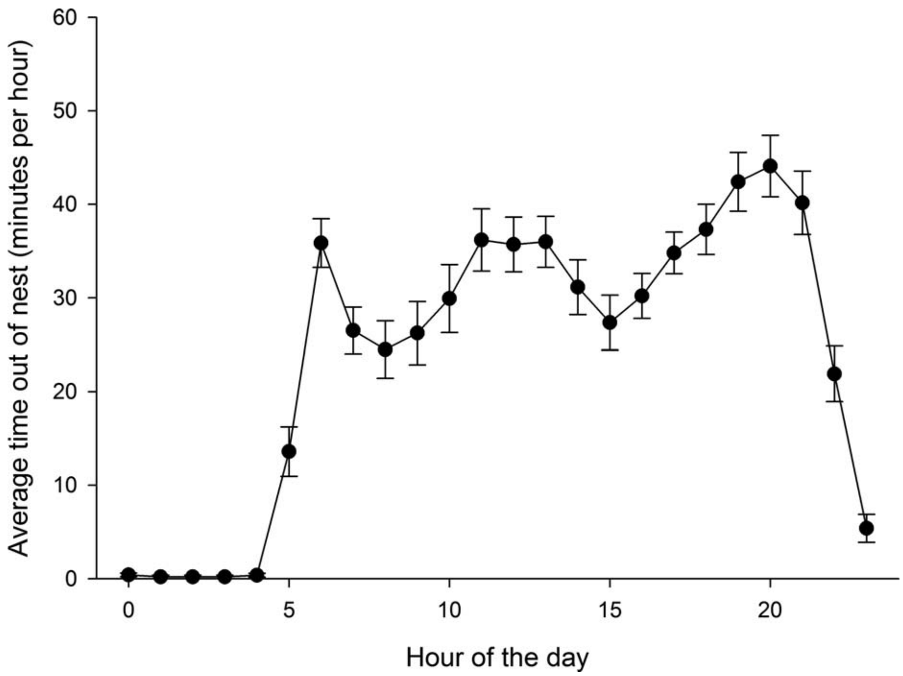

Fig. 1.—Average time female red squirrels (*Tamiasciurus hudsonicus*) spent out of the nest each hour ($\bar{X} \pm SE$) during the first 25 days of lactation ($n = 12$).

the morning 2 h 7 min ± 11 min after sunrise and last returned to the nest 14 ± 11 min after sunset. The total amount of time spent active each day (i.e., outside of the nest) increased with age of the litter and was affected by environmental conditions, with squirrels increasing time in the nest with decreasing temperature, increasing wind speed, and higher relative humidity (Table 1). For example, red squirrels spent 40–48% less time outside on a cool (mean temperature: 8.6°C), humid (88% relative humidity) day relative to the preceding day, which was warmer (11.5°C) and drier (44% relative humidity; see Fig. 2). Only 1 red squirrel exhibited noticeable signs of collar irritation.

Arctic ground squirrels.—During the month of June, during which time the sun is constantly above the horizon at our study site, aboveground activity in female arctic ground squirrels occurred almost exclusively between 0600 and 2300 h each day; squirrels emerged at 0751 h ± 11 min each morning and immerged at 2029 h ± 10 min each evening. On average, female arctic ground squirrels had 3.3 ± 0.3 aboveground activity bouts and cumulatively spent 10 h 44 min ± 49 min above ground each day. The total amount of time spent above ground each day was affected by environmental conditions and increased across the study period (Table 2). Individual activity decreased when daily precipitation exceeded 3 mm, and increased with warmer temperatures and higher levels of incident solar radiation (e.g., Fig. 3). For example, female ground squirrels spent an average of 6 h 50 min above ground on days with > 3 mm of precipitation compared to 10 h 52 min on days with < 3 mm of precipitation. Females averaged 11 h 27 min above ground on rain-free days when average daily temperature exceeded 10°C compared to 10 h 32 min above ground on rain-free days with average temperatures below 10°C.

Although temperature and solar radiation positively affected daily aboveground activity, individual activity near midday tended to drop on days that were both very warm and very sunny (Fig. 3; day 4) compared to cooler days (Fig. 3; day 3). Noticeably, transitions between below- and aboveground activity increased on warm days when incident solar radiation and temperature were both near their daily maxima (Fig. 3). During cold weeks, peak aboveground activity coincided with the daily maxima in ambient temperature (Fig. 4A). However, during the warmest weeks, aboveground activity of female arctic ground squirrels was slightly reduced when incident solar radiation and ambient temperature were both high (Fig. 4B). Thus, depending on ambient conditions, the amount of time active (above ground) across the day exhibited either a unimodal or bimodal pattern.

Table 1.—Solutions for fixed effects from a linear mixed-effects model that examined the influence of mean daily weather conditions on the total amount of time (hours) female red squirrels (*Tamiasciurus hudsonicus*) spent outside of the nest each day during the first 25 days of lactation. Individual identification was included as a random effect in the model. 95% CI = 95% confidence interval.

Effect	Parameter estimate (95% CI)	P
Intercept	13.4 (10.9, 15.9)	< 0.0001
Litter age	0.12 (0.09, 0.14)	< 0.0001
Temperature	0.25 (0.17, 0.33)	< 0.0001
Wind speed	−1.35 (−1.74, −0.96)	< 0.0001
Relative humidity	−0.055 (−0.076, −0.035)	< 0.0001

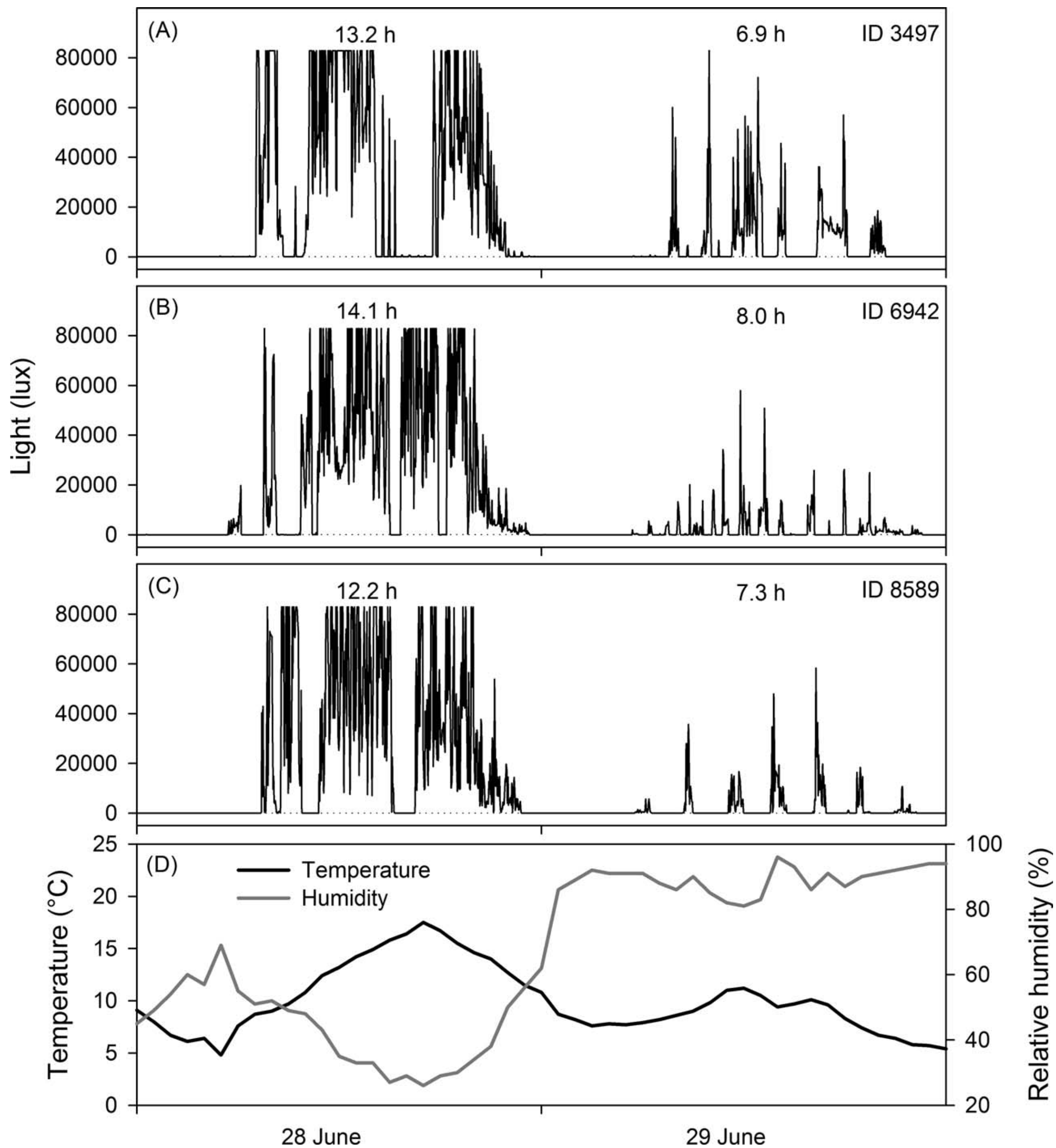

Fig. 2.—A–C) Light levels recorded from collars affixed to 3 lactating female red squirrels (*Tamiasciurus hudsonicus*) during D) a warmer, less-humid day (28 June) and a cooler day with high humidity (29 June). There was no precipitation on 28 June at our study site, whereas it rained intermittently on 29 June. Numbers in panels A–C denote total time spent out of the nest (light level > 25 lux; hashed lines) each day.

Discussion

Endogenous circadian systems are fundamentally responsible for the daily organization of physiology and behavior in most organisms, although activity patterns within each day also are altered in response to other physiological and environmental attributes (Vogt and Lynch 1982; Prendergast et al. 2012). Based on light-logger data, we show that the thermal environment affects the length and pattern of daily activity in free-living red squirrels and arctic ground squirrels. We suggest light loggers have the potential to make important contributions to our understanding of small mammal behavior and ecology although we encourage future studies directed at measuring effects of long-term collar deployment.

Daily activity patterns.—We found that lactating red squirrels exhibited a diurnal trimodal activity pattern with time spent outside the nest each day being reduced in response to low temperatures, high winds, high relative humidity, or a combination of these. In contrast, we found that female arctic

TABLE 2.—Solutions for fixed effects from a linear mixed-effects model that examined the influence of mean daily weather conditions on the total time female arctic ground squirrels (*Urocitellus parryii*; inverse-root transformed hours) spent above ground each day. Individual identification was included as a random effect in the model. Aboveground activity was inverse-root transformed such that data are reflected; positive parameter estimates denote a negative effect on activity, whereas negative parameter estimates indicate a positive effect. 95% *CI* = 95% confidence interval.

Effect	Parameter estimate (95% *CI*)	*P*
Intercept	1.13 (0.68, 1.58)	< 0.0001
Day of year	−0.004 (−0.006, −0.001)	0.005
Temperature	−0.005 (−0.009, −0.002)	0.005
Solar radiation	−0.0004 (−0.0006, −0.0002)	0.0002
Wind speed	0.0002 (−0.02, 0.019)	0.979
Precipitation		
(0 mm)	0	—
(0–3 mm)	0.008 (−0.03, 0.04)	0.669
(> 3 mm)	0.12 (0.07, 0.16)	< 0.0001

ground squirrels exhibited a diurnal activity rhythm with a unimodal or bimodal distribution across the day. In arctic ground squirrels, the amount of time spent above ground each day decreased in response to rain (> 3 mm) but increased with increasing mean daily ambient temperature and incident solar radiation.

Our finding that red squirrels and arctic ground squirrels significantly altered their activity patterns in response to changing thermoregulatory conditions is consistent with previous small mammal studies, although much of this earlier work focused on population-level responses (versus individuals) or examined individual responses in captive or semicaptive populations (e.g., Pauls 1978; Bacigalupe et al. 2003; Vieira et al. 2010; Wan et al. 2013). In a study of individual arctic ground squirrels and using taxidermic mannequins containing temperature loggers, Long et al. (2005) estimated operative temperature, which combines the effects of convective and radiant heat transfer, and found that conditions at our study site in the Arctic typically reach into the thermoneutral zone of arctic ground squirrels (17–37°C) only between 6 AM and 9 PM. Thus, we hypothesize the persistence of diurnal rhythms of behavior and physiology in this species, organized to include aboveground activity between approximately 8 AM and 9 PM despite the seasonal absence of a light–dark cycle, functions to reduce thermoregulatory costs (Long et al. 2005; Williams et al. 2012a). In addition to adjusting behavior in response to ambient temperature conditions, we found that arctic ground squirrels were less active on days with precipitation > 3 mm. Avoidance of rain is not surprising given that wet fur can greatly increase heat loss through evaporation and, to a lesser extent, convection (Gebremedhin and Wu 2001; Cuyler and Øritsland 2004). Although we lacked precipitation data for our red squirrel study, the observed negative effect of relative humidity may have been due to the fact that high humidity is associated with precipitation events. Interestingly, we found strong effects of environmental conditions on daily activity in red squirrels even though the weather station was 50 km away from our study site. However, we anticipate the relationship between weather and activity would be stronger if environmental conditions were measured locally within the microhabitat red squirrels occupy.

Despite our finding that both solar radiation and ambient temperature have a positive effect on total daily aboveground activity, we found that arctic ground squirrels reduce aboveground activity when incident solar radiation and ambient temperature are at their daily maxima, resulting in a bimodal activity pattern (Fig. 3). Solar radiation can significantly affect operative temperatures, with contributions up to 10°C in small rodents, depending on coat composition (Chappell 1980; Walsburg and Wolf 1995). Thus, on cool days, incident solar radiation can push operative temperatures into the thermoneutral zone of a small mammal. However, on days when ambient temperatures are high, incident solar radiation may cause operative temperatures to exceed thermoneutrality. Although arctic ground squirrels are supremely adapted to cold conditions (Karpovich et al. 2009), they are less well adapted to coping with conditions of heat gain due to solar radiation and locomotor activity because they are unable to sweat or pant. Thus, high midday solar radiation in combination with high ambient temperatures may force ground squirrels to move below ground to dissipate heat through behavioral thermoregulation. Long et al. (2005) found that ground squirrels will increase the frequency of short belowground forays when midday operative temperatures exceed thermoneutrality, although the percentage of time spent above ground was still highest at midday. The difference in results between the present study and that of Long et al. (2005) is likely attributable to the timescale of analysis; Long et al. (2005) examined activity across months whereas we examined activity on a weekly basis within one of the warmest months of the year.

In contrast to arctic ground squirrels and to previous studies of red squirrels, we found that red squirrels exhibited a trimodal activity pattern (Fig. 1). Free-living European red squirrels (*Sciurus vulgaris*) studied using radiotelemetry exhibited a bimodal distribution in the summer and a unimodal or bimodal distribution in the winter, depending on habitat type (Wauters et al. 1992). Similarly, Pauls (1978) found that captive North American red squirrels living in seminatural conditions exhibited a bimodal distribution in summer and a more unimodal pattern in winter. Transitions from a unimodal to a bimodal activity pattern associated with avoidance of exposure to heat also have been observed in free-living degus (*Octodon degus*—Bacigalupe et al. 2003). However, we are not aware of another study reporting a trimodal activity pattern such as the one we observed in red squirrels. We speculate this pattern may be due to the fact that we studied lactating females at a northern study site where exposure to cold conditions may be a much more important factor than exposure to warm conditions. In addition to a midday peak in activity, female red squirrels in our study may have increased early morning and late evening activity in order to meet the energetic costs of lactation. However, further study of activity patterns in other

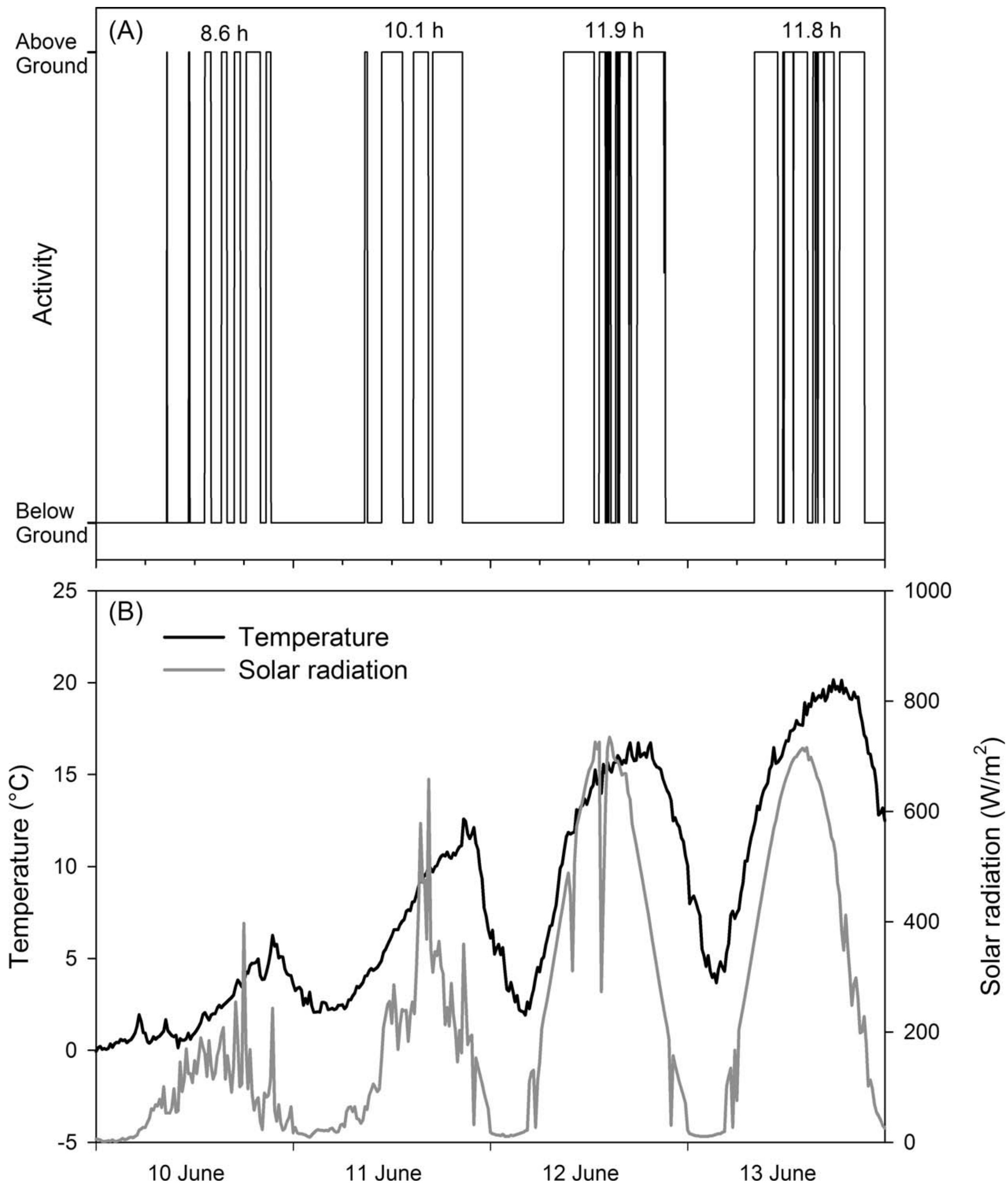

Fig. 3.—A) Aboveground activity of a female arctic ground squirrel (*Urocitellus parryii*) in relation to B) ambient temperature and incident solar radiation from 10 to 14 June. Numbers in panel A) denote total time spent above ground each day in hours, based on light-logger data.

groups is needed to establish whether lactation costs play a significant role in determining patterns of activity. For both species, time spent in nests was similar and longer than that of time spent active each day, despite the availability of additional hours of daylight at both study sites. This emphasizes the daily importance of nest-bound behaviors including sleep and care of young in these free-living animals.

Biologging in small mammals.—Biologging, which involves the use of animal-borne tags for logging or transmitting data, or both, regarding an animal's behavior, movements, physiology, or environment, or a combination of these, has undergone considerable development in recent years, particularly with respect to the miniaturization of devices, which has led to more widespread use (Rutz and Hayes 2009). Although light-sensitive

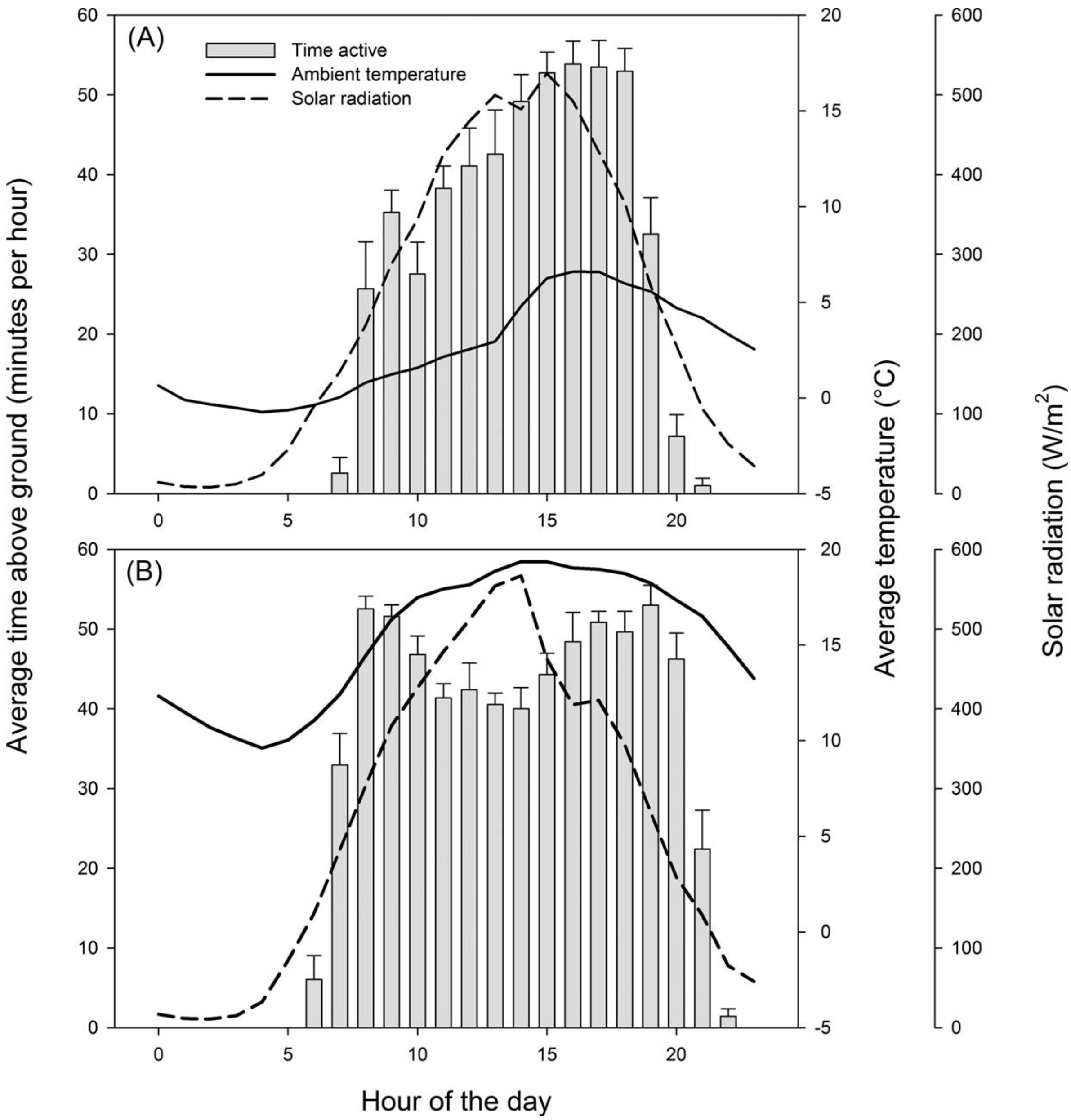

Fig. 4.—Average hourly aboveground activity ($\bar{X} \pm SE$) of female arctic ground squirrels (*Urocitellus parryii*), ambient temperature (solid line), and solar radiation (dashed line) from A) one cold week and B) one hot week in June. During cold weather, aboveground activity peaks with ambient temperature. However, in hotter weeks, aboveground activity decreases when both solar radiation and temperature peak ($n = 7$). Activity remains constrained to approximately 0700–2100 h when temperatures are cold, but broadens to 0600–2200 h when average daily temperature increases.

radiotransmitters have previously been used to measure above- versus belowground activity patterns in ground squirrels (Hut et al. 1999; Long et al. 2005, 2007), use of these devices never became widespread, perhaps because of their size (~10 g), manufacturing costs, or because of the challenges associated with the continuous collection of telemetry data in heavily vegetated or topographically complex environments. Light loggers, in contrast, are a smaller, more cost-effective, and user-friendly alternative, although animals must be recaptured to download data; devices in this study ranged in price from US$155 to US$210 each.

Although we are not aware of any studies to date that have used light loggers to examine daily activity patterns in mammals, we previously used these devices to determine when arctic ground squirrels first entered their hibernacula in late summer or fall and when they first emerged in spring (Williams et al. 2012b). Collar-mounted devices that measure both temperature and light can potentially provide information on the entire hibernation interval, including the timing and duration of torpor–arousal cycles and the belowground euthermic intervals that precede and follow this cycling. Because these devices provide high-resolution data on the activity patterns of individuals, the devices are likely to be particularly useful in exploring how much of the variance in a measured behavior occurs at the individual versus population level. Furthermore, we suggest the devices are likely to be invaluable in experimental studies of free-living populations where treatments occur at the level of the individual.

In the present study, collar-mounted light loggers provided high-resolution data on activity patterns in arboreal and semifossorial squirrels and we assumed these devices provided unbiased estimates of measured parameters. However, as with all biologging approaches, attachment of any device to an animal has the potential to influence behavior and can potentially affect reproductive output, survival, and other demographic parameters (e.g., Moorhouse and Macdonald 2005; Whidden et al. 2007). We did not test for effects of devices on survival or reproductive output in the present study as small sample sizes left us with insufficient power. However, we did observe excessive wear of fur or irritated or inflamed or broken skin caused by collars for 1 red squirrel and 4 ground squirrels. Subsequent examination of recaptured individuals suggests they healed quickly following the removal of collars, although the degree to which behavior was affected by this irritation is unknown. Although we anticipate that light loggers can provide important insight into the proximate and ultimate drivers of behavior, we encourage studies specifically designed to examine whether long-term deployment of collar-mounted devices affects behavior, physiology, survival, or reproductive output, or a combination of these.

Acknowledgments

Research was supported by grants from the National Science Foundation (United States) to CLB (EF-0732763 and IOS-1147187), CTW (IOS-1147187), and BMB (EF- 0732755 and IOS-1147232), and from the Natural Science and Engineering Research Council (Canada) to MMH, AGM, and SB. KW received summer support through the National Science Foundation Research Experience for Undergraduates program (UAA site award 1263415). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation or the Natural Science and Engineering Research Council. We are grateful to the many students and crew members for data collection and to A. Sykes and J. Moore for data and field management. This is contribution 76 of the Kluane Red Squirrel Project.

Literature Cited

Aschoff, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. Comparative Biochemistry and Physiology, A. Physiology 69:611–619.

Bacigalupe, L. D., E. L. Rezende, G. J. Kenagy, and F. Bozinovic. 2003. Activity and space use by degus: a trade-off between thermal conditions and food availability? Journal of Mammalogy 84:311–318.

Batavia, M., A. Matsushima, O. Eboigboden, and I. Zucker. 2010. Influence of pelage insulation and ambient temperature on energy intake and growth of juvenile Siberian hamsters. Physiology and Behavior 101:376–380.

Boon, A. K., D. Réale, and S. Boutin. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. Ecology Letters 10:1094–1104.

Boutin, S., L. A. Wauters, A. G. McAdam, M. M. Humphries, G. Tosi, and A. A. Dhondt. 2006. Anticipatory reproduction and population growth in seed predators. Science 314:1928–1930.

Brigham, R. M., and F. Geiser. 2012. Do red squirrels (*Tamiasciurus hudsonicus*) use daily torpor during winter? Ecoscience 19:127–132.

Buck, C. L., and B. M. Barnes. 1999. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. Journal of Mammalogy 80:430–442.

Chappell, M. A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. Journal of Mammalogy 61:278–291.

Cuyler, C., and N. A. Øritsland. 2004. Rain more important than windchill for insulation loss in Svalbard reindeer fur. Rangifer 24:7–14.

Dall, S. R., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters 7:734–739.

Dantzer, B., et al. 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. Science 340:1215–1217.

Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. Journal of Animal Ecology 82:39–54.

Environment Canada. 2013. Historical climate data—Burwash Landing weather station A. http://climate.weatheroffice.gc.ca. Accessed 26 September 2013.

Erickson, J. L., and S. D. West. 2002. The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropterologica 4:17–24.

Everts, L., A. Strijkstra, R. A. Hut, I. Hoffmann, and E. Millesi. 2004. Seasonal variation in daily activity patterns of free-ranging European ground squirrels (*Spermophilus citellus*). Chronobiology International 21:57–71.

Fletcher, Q. E., M. Landry-Cuerrier, S. Boutin, A. G. McAdam, J. R. Speakman, and M. M. Humphries. 2013. Reproductive timing and reliance on hoarded capital resources by lactating red squirrels. Oecologia 173:1203–1215.

Gebremedhin, K. G., and B. Wu. 2001. A model of evaporative cooling of wet skin surface and fur layer. Journal of Thermal Biology 26:537–545.

Gilbert, C., et al. 2010. One for all and all for one: the energetic benefits of huddling in endotherms. Biological Reviews 85:545–569.

Guillemette, C. U., Q. E. Fletcher, S. Boutin, R. M. Hodges, A. G. McAdam, and M. M. Humphries. 2009. Lactating red squirrels experiencing high heat load occupy less insulated nests. Biology Letters 5:166–168.

Hut, R. A., B. E. van Oort, and S. Daan. 1999. Natural entrainment without dawn and dusk: the case of the European ground squirrel (*Spermophilus citellus*). Journal of Biological Rhythms 14:290–299.

Karpovich, S. A., Ø. Tien, C. L. Buck, and B. M. Barnes. 2009. Energetics of arousal episodes in hibernating arctic ground squirrels. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 179:691–700.

Kenagy, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201–1219.

LaMontagne, J. M., C. T. Williams, J. L. Donald, M. M. Humphries, A. G. McAdam, and S. Boutin. 2013. Linking intraspecific variation in territory size, cone supply, and survival of North American red squirrels. Journal of Mammalogy 94:1048–1058.

Long, R. A., R. A. Hut, and B. M. Barnes. 2007. Simultaneous collection of body temperature and activity data in burrowing mammals: a new technique. Journal of Wildlife Management 71:1375–1379.

Long, R. A., T. J. Martin, and B. M. Barnes. 2005. Body temperature and activity patterns in free-living arctic ground squirrels. Journal of Mammalogy 86:314–322.

McNab, B. K. 1980. On estimating thermal conductance in endotherms. Physiological Zoology 53:145–156.

Metcalfe, N. B., N. H. Fraser, and M. D. Burns. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology 68:371–381.

Moorhouse, T. P., and D. W. Macdonald. 2005. Indirect negative impacts of radio-collaring: sex ratio variation in water voles. Journal of Applied Ecology 42:91–98.

Pauls, R. W. 1978. Behavioural strategies relevant to the energy economy of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology 56:1519–1525.

Prendergast, B. J., A. K. Beery, M. J. Paul, and I. Zucker. 2012. Enhancement and suppression of ultradian and circadian rhythms across the female hamster reproductive cycle. Journal of Biological Rhythms 27:246–256.

Raveh, S., et al. 2010. Mating order and reproductive success in male Columbian ground squirrels (*Urocitellus columbianus*). Behavioral Ecology 21:537–547.

Rutz, C., and G. C. Hays. 2009. New frontiers in biologging science. Biology Letters 5:289–292.

Sakamoto, K. Q., et al. 2009. Can ethograms be automatically generated using body acceleration data from free-ranging birds? PLoS ONE 4:e5379.

Sears, M. W., J. P. Hayes, C. S. O'Connor, K. Geluso, and J. S. Sedinger. 2006. Individual variation in thermogenic capacity affects above-ground activity of high-altitude deer mice. Functional Ecology 20:97–104.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Stephan, F. K., and I. Zucker. 1972. Circadian rhythms in drinking behavior and locomotor activity of rats are eliminated by hypothalamic lesions. Proceedings of the National Academy of Sciences 69:1583–1586.

Studd, E. K. 2012. Environmental and biological correlates of maternal investment in red squirrels. M.S. thesis, McGill University, Montreal, Quebec, Canada.

van Oort, B. E., N. J. Tyler, M. P. Gerkema, L. Folkow, A. S. Blix, and K. A. Stokkan. 2005. Circadian organization in reindeer. Nature 438:1095–1096.

Vieira, E. M., L. C. Baumgarten, G. Paise, and R. G. Becker. 2010. Seasonal patterns and influence of temperature on the daily activity of the diurnal Neotropical rodent *Necromys lasiurus*. Canadian Journal of Zoology 88:259–265.

Vogt, F. D., and G. R. Lynch. 1982. Influence of ambient temperature, nest availability, huddling, and daily torpor on energy expenditure in the white-footed mouse *Peromyscus leucopus*. Physiological Zoology 55:56–63.

Walsberg, G. E., and B. O. Wolf. 1995. Effects of solar radiation and wind speed on metabolic heat production by two mammals with contrasting coat colours. Journal of Experimental Biology 198:1499–1507.

Wan, X., X. Zhang, Y. Huo, and G. Wang. 2013. Weather entrainment and multispectral diel activity rhythm of desert hamsters. Behavioural Processes 99:62–66.

Wauters, L., C. Swinnen, and A. A. Dhondt. 1992. Activity budget and foraging behaviour of red squirrels (*Sciurus vulgaris*) in coniferous and deciduous habitats. Journal of Zoology 227:71–86.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. American Naturalist 142:242–272.

Whidden, S. E., C. T. Williams, A. R. Breton, and C. L. Buck. 2007. Effects of transmitters on the reproductive success of tufted puffins. Journal of Field Ornithology 78:206–212.

Whitney, N. M., H. L. Pratt, Jr., T. C. Pratt, and J. C. Carrier. 2010. Identifying shark mating behaviour using three-dimensional acceleration loggers. Endangered Species Research 10:71–82.

Williams, C. T., B. M. Barnes, and C. L. Buck. 2012a. Daily body temperature rhythms persist under the midnight sun but are absent during hibernation in free-living arctic ground squirrels. Biology Letters 8:31–34.

Williams, C. T., B. M. Barnes, M. Richter, and C. L. Buck. 2012b. Hibernation and circadian rhythms of body temperature in free-living arctic ground squirrels. Physiological and Biochemical Zoology 85:397–404.

Williams, C. T., J. C. Gorrell, J. E. Lane, A. G. McAdam, M. M. Humphries, and S. Boutin. 2013. Communal nesting in an 'asocial' mammal: social thermoregulation among spatially dispersed kin. Behavioral Ecology and Sociobiology 67:757–763.

Williams, C. T., J. E. Lane, M. M. Humphries, A. G. McAdam, and S. Boutin. 2014. Reproductive phenology of a food-hoarding mast seed consumer: resource- and density-dependent benefits of early breeding in red squirrels. Oecologia 174:777–788.

Williams, T. D. 2008. Individual variation in endocrine systems: moving beyond the 'tyranny of the Golden Mean.' Philosophical Transactions of the Royal Society, B. Biological Sciences 363:1687–1698.

Wolff, J. O., and T. V. Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. Canadian Journal of Zoology 81:266–271.

Submitted 26 February 2014. Accepted 7 July 2014.

Associate Editor was Michael A. Steele.