Winter activity patterns of northern flying squirrels in sub-boreal forests

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Abstract: We described autumn–winter activity patterns of northern flying squirrels (Glaucomys sabrinus) in northwestern British Columbia during 1996–1997 and 1997–1998. Nineteen flying squirrels (12 males and 7 females) were fitted with temperature-sensitive radio collars. We located animals in 82 daytime nests using radiotelemetry techniques and monitored 268 nights of activity using data-logging receivers placed at the base of nest trees. The average temperature of the animals, as determined by the collar sensors while the animals were in nests, was 39.2 ± 0.1°C, with no significant differences among animals, tree species, or tree sizes. Activity periods in a mild field season followed a dusk- and dawn-activity pattern, but activities in harsh winter conditions shifted towards a shorter single activity bout or two very short activity bouts in the middle of the night. No long activity bouts (>1.9 h) were observed at temperatures below –20°C. This reduction in time spent active and adjustment of the timing of activity during extremely low temperatures likely serve as an energy-conservation strategy.

Introduction

The northern flying squirrel (Glaucomys sabrinus) is endemic to coniferous forests over a wide range in North America, from Alaska to California, across Canada, and extending to North Carolina (Wells-Gosling and Heaney 1984). As a cavity nester that is generally mycophagous, its habitat requirements are specific. In winter, northern flying squirrels subsist primarily on arboreal lichens (Bryoria spp.) and cached mushrooms or truffles (e.g., Rhizopogon spp.; Laurance and Reynolds 1984; Maser et al. 1986; Hall 1991; Zabel and Waters 1997). Flying squirrels use tree cavities and witches’ brooms year-round for nesting, and typically do not augment arboreal nests with subnivean resting sites (unlike red squirrels (Tamiasciurus hudsonicus); Pruitt and Lucier 1958). These specific requirements make flying squirrels vulnerable in areas in which the availability of forested habitats is being reduced, as is seen in the endangered populations in the southeastern United States (Urban 1988).

Northern flying squirrels encounter extremely low winter temperatures in much of their range, yet they do not hibernate or enter torpor (Wells-Gosling and Heaney 1984). Their continual activity throughout winter, coupled with small mass (~150 g) and nocturnal habits, likely necessitates physiological and (or) behavioural strategies that are directly related to thermal conditions and energy conservation. These adaptations may be especially important in winter, when the difference between body and ambient temperatures is greatest, and when energy may be critically limiting. Only a few studies of flying squirrels have collected information throughout the year (Mowrey and Zasada 1984; McDonald 1995; Gerrow 1996) and none have specifically examined their activity patterns during winter.

We examined the activity patterns of northern flying squirrels as part of a study investigating their winter habitat and nest-tree characteristics in the sub-boreal forests of British Columbia (Cotton 1999). Our specific objectives were to determine the temperatures of nests used by northern flying squirrels, to describe their autumn–winter activity patterns, and to characterize those patterns in relation to ambient conditions (temperature and photoperiod).

Methods

The study was conducted at two sites in northwestern British Columbia: the Smithers site, where most data collection occurred,
and the Houston site, which was used to supplement our sample size during the first field season when rates of trapping flying squirrels were low at the Smithers site. The Smithers site was located in the Smithers Community Forest (54°43’N, 127°15’W), 10 km west of Smithers, British Columbia. The Houston site (54°27’N, 126°40’W), near Houston, British Columbia, was ~26 km south-east of the Smithers site. Both sites are in the Sub-Boreal Spruce (SBS) biogeoclimatic zone, which is characterized by a cold continental humid climate, with severe snowy winters (Pojar et al. 1984, 1987). Mean annual precipitation exceeds 512 mm; snowfall averages ~200 cm (Environment Canada 1980).

The Smithers Community Forest (~4620 ha in size) is a patchwork of stand types resulting from fire disturbance in the 1930s and 1940s. The research site was located on the lower slope of Hudson Bay Mountain at an average elevation of 850 m. Dominant species included hybrid white spruce (Picea engelmannii × Picea glauca), subalpine fir (Abies lasiocarpa), lodgepole pine (Pinus contorta), and some trembling aspen (Populus tremuloides) and cottonwood (Populus balsamifera). The Houston site, with an average elevation of 585 m, had a similar composition of trees, with the addition of paper birch (Betula papyrifera), and was surrounded by extensive clearcuts produced during the last 20 years. Witches’ broom rusts (Chrysomyxa spp.) occurred on conifers at both sites.

Flying squirrels were captured using Tomahawk live traps (Model 201, Tomahawk, Wis.) in September and October of 1996 and August and September of 1997, using the protocol outlined in Cotton and Parker (2000). They were fitted with radio collars that weighed 3 g and consisted of a temperature-sensitive radio transmitter (Model PD-2CT, Hollohill Systems, Ltd., Woodlawn, Ont.) attached to plastic-cable ties and encased in heat-shrink tubing. The transmitter antenna was folded back on itself and placed inside the tubing with the last 2.5 cm of the antenna protruding.

Flying squirrels were located in nest trees during the day, using a Lotek receiver (Model SRX_400 A, Lotek Engineering Inc., Newmarket, Ont.) with a visual display of signal strength that was used to distinguish the nest tree from other trees surrounding it. We also selected two or three animals each day for continuous monitoring, and ensured that all animals were monitored every 1–2 weeks. The data-logging receivers, powered by 12-V sealed rechargeable external batteries (Model PS-12150, Power Sonic, Redwood City, Calif.), were placed in Styrofoam-lined storage bins at the base of the nest trees occupied by these animals. The pulse rate of the radio signal (beats/min received from the collars) was directly related to the temperature of the collar. Consequently, when the subject animal left the nest tree, the pulse rate of the radio signal declined markedly. Flying squirrels were monitored until death or loss of signal (from 2 to 6 months). The 1996 field season (referred to as 1996) lasted from September 1996 to March 1997; the 1997 field season (referred to as 1997) was from August 1997 to February 1998.

At all nest trees, we recorded whether the tree had a visible nest (cavity, witches’ broom, or dray, which is a constructed nest). We also recorded tree species, height, diameter at breast height (DBH), and other surrounding-habitat measurements (see Cotton and Parker 2000). Measurements of air temperature (from a shaded protected thermistor), wind speed (using a cup anemometer), and solar radiation (obtained with a short-wave Li-cor sensor) were recorded continuously and averaged every 15 min, using a CR-21X Micrologger mounted on a CM10 tripod weather station (Campbell Scientific, Edmonton, Alta.) in a representative stand at the Smithers site. Dusk was defined as the time at which the Li-cor sensor reading declined to <0.1 W/m² at the end of daylight hours. Conversely, dawn was defined as the time at which the sensor reading increased to >0.1 W/m² following a period of complete darkness. Phases of the moon and the time of moon rise were obtained from U.S. Navy astronomical data, using Ketchikan, Alaska, as an approximation for Smithers, British Columbia (<http://aa.usno.navy.mil/AA/data/>).

An α level of 0.05 was assigned for all analyses. Unless otherwise stated, all means are presented as mean ± SE. We used ANOVA to test for differences in animal temperature (i.e., temperature of the radio collar on a flying squirrel in the nest) by individual (n = 19) among nest trees and to test for differences in animal temperature in cavities versus outside nests (witches’ brooms and drays) for those animals (n = 8) that used both. We ran correlations (Moore and McCabe 1993) between animal temperature in the nest and each of the following variables separately: ambient temperature, tree height, and DBH. We then used multiple regression (Sokal and Rohlf 1995) to examine the combined influence of ambient temperature and nest-tree DBH on the temperature of animals in the nest, using all data, by sex and within each species of nest tree. Because of the strong correlation between DBH and tree height (r = 0.71, P < 0.001), tree height was not used in the regression model. For each animal, a separate ANOVA was run for each nest tree that was used for aggregations of flying squirrels, to determine if there were differences in animal temperature prior to and during aggregation (nest sharing) with other radio-collared animals. Pearson’s χ² contingency analysis (Everitt 1977) was used to test if the distributions of time spent away from nest trees differed between years. We tested whether the timing of activity by flying squirrels was correlated with moon phase or the time of moon rise. Correlation analysis was also used to examine the relationship between the duration of activity and ambient temperature in each winter. Because our data may have been confounded by differences in the number of observations for each animal, we ran correlations for individuals. Descriptive statistics, ANOVAs, correlations, multiple regressions, Pearson’s χ² analysis, and graphical representations were completed using STATISTICA (StatSoft, Inc. 1997).

**Results**

Nineteen adult northern flying squirrels were fitted with radio collars over the two field seasons: eight males and four females in 1996 (725 trap-nights) and four males and three females in 1997 (832 trap-nights). No individual was fitted with a collar in both field seasons. The average mass of the animals at the time they were fitted with a collar was 145.3 ± 2.4 g. We located individuals 1–3 times per week, although three animals located in a remote area of the Houston site were located only 3–4 times monthly after snowfall. In the 1996 field season, animals were located in nest trees in the daytime 303 times, with 7–82 locations per animal; in the 1997 field season, animals were located 265 times (29–50 locations per animal).

Temperature extremes and snowfall were considerably harsher in 1996 than in 1997. In the 1996 field season, there were many periods of extremely cold weather (below –20°C), with a minimum temperature of –35.8°C (25 January). The snowfall (>10 cm) that occurred on 9 November persisted with a minimum temperature of –35.8°C (25 January). In 1997, temperatures were milder, with –16.8°C (18 December) the lowest recorded temperature, and the first persistent snowfall did not occur until 24 November. Snow depth at the weather station in the 1996 field season (1.12 m in mid-January) was approximately twice that of the 1997 field season (0.56 m in mid-January).

**Nest use**

On 280 occasions, individual flying squirrels were relocated on consecutive days. For 92% of these observations, animals stayed in the same nest tree the second day. Only 14 nests in trees were visible from the ground: 11 witches’ brooms, 2 drays, and 1 cavity. All other nests (n = 68) were
presumed to be in cavities. The average temperature of northern flying squirrels in nest trees, as determined from the temperature-sensitive radio collars, was 39.2 ± 0.1°C (n = 529), ranging from 30.9 to 43.0°C. Only one temperature for an individual was used per 24-h period in these calculations. There were no differences in temperatures recorded for individual animals among nest trees (all P > 0.308) or between outside nests and cavities (P = 0.459). Animals used confirmed outside nests and other types of nests over the same range of lowest nightly temperatures (~35.8 to 5.0°C). The temperatures of animals in nest trees were not correlated with ambient temperature, tree height (which ranged from 11.2 to 32.7 m), or tree DBH (16.7–79.0 cm) (all P > 0.05).

Because there were no differences among animals and no correlations with individual nest tree attributes, we included all data in the multiple-regression model. Using all data, air temperature and tree DBH were not good predictors of animal temperature (R² = 0.052), even though the multiple regression was significant (P < 0.001); similar results were obtained for analyses within males (R² = 0.084, P < 0.001) and within females (R² = 0.080, P < 0.015). Within nest trees of the same species, only hybrid white spruce and lodgepole pine showed a significant relationship among animal temperature, air temperature, and tree DBH, although again, with little predictive value (spruce, R² = 0.124, P < 0.001; lodgepole pine, R² = 0.073, P < 0.004). Further, there was no difference between the average temperature of individual animals prior to or during times of aggregation with other radio-collared animals (all P > 0.178).

We observed three separate cases of aggregation by radio-collared animals, each involving two or three animals and beginning in October or early November. The lowest nightly temperatures at the onset of aggregation ranged from ~1.6°C to ~6.5°C. The animals in each aggregation used three or four nest trees during the aggregation periods, which lasted from 3 weeks to 2 months and ended following the death of one of the partners or when the radio signal ceased (see Cotton 1999 for details). In addition to aggregations, two nest trees were used by two animals, although not nesting together.

Activity patterns

We recorded 268 days and nights of activity patterns using the data-logging receivers placed at the base of nest trees. Radio-collared flying squirrels never left their nests during daylight hours. During nighttime activity periods, the amount of time that animals were away from nest trees, as recorded by each observation of leaving and reentering the nest, ranged from 0.52 to 13.7 h. The distributions of time periods away from nest trees significantly differed between years (Fig. 1; Pearson’s χ² = 76.797, df = 6, P < 0.001). More than 70% of all time periods away from the nest tree showed that flying squirrels returned to the tree within 6 h. Given these distribution patterns (Fig. 1), coupled with the likelihood that greater times spent away from the nest included time spent at other nest trees (Weigl and Osgood 1974), we set 6 h as a conservative maximum amount of time for a single activity period. Fifteen of our study animals met this criterion.

Animals returned to the same nest tree within 6 h of first leaving in 179 of the recorded nights of activity patterns; in the remaining cases (n = 89), animals either did not return to the nest tree or returned just before dawn (>6 h since leaving). Of these 179 observations, 42.4% showed two activity periods per night: one beginning within the 2 h after dusk and another commencing later in the night and ending within the 2 h before dawn. Another 49.7% of the observations showed an activity period or periods during the middle of the night. The remaining nighttime observations were composed of a combination of dusk, mid-night, and (or) dawn activity periods. When analyzed separately, yearly differences in the number of activity bouts away from the nest were evident. During the 1996 field season, 72.4% of the observations contained only one period away from the nest, whereas 76.3% of the observations in the 1997 field season consisted of two periods away from the nest. The two field seasons also differed in the timing of nightly activity. The time of departure and the time of return to nest trees were much more variable and often later in the night in the 1996 than in the 1997 field season (Fig. 2). The latter was characterized by a predominantly dusk–dawn activity pattern. In both field seasons, deviations from a dusk–dawn activity pattern were observed only after the temperature dropped sharply and was below ~12°C. This occurred in early November in 1996 but not until early December in 1997. The timing of activity was not correlated with moon phase or the time of moonrise (both P > 0.05).

The duration of activity bouts (<6 h in duration) away from the nest was positively correlated with air temperature in 1996 but not in 1997 for those animals for which we had observations over the entire temperature range of the field season (1996, all P < 0.005, n = 3; 1997, all P > 0.054, n = 4). Data for all animals were not obtained across all temperatures, because of animal movements to unmonitored trees, animal mortalities, and (or) because our experimental protocol was designed to sample animals evenly across time and could not control for different weather conditions. Because of the relatively consistent responses to temperature of those animals for which we did have data over wide temperature ranges, and to conservatively show the variation in responses, we present the data for all animals (Fig. 3). At very low temperatures (below ~20°C) in 1996, there were no long activity
bouts (maximum bout length = 1.9 h), whereas at higher temperatures, time spent away from a nest tree was generally more variable. When we summed all active bouts per night to examine overall nightly activity strategies in relation to air temperature, we observed a similar pattern (Fig. 4). At temperatures below –20°C, the total time absent from the nest ranged from 1.4 to 1.9 h, regardless of whether the animal had one \((n = 3)\) or two \((n = 3)\) nightly activity bouts. Three activity bouts during a single night were only observed in the 1997 field season and occurred at temperatures above –10°C \((n = 5)\). The total time spent away from the nest tree per night at temperatures above –10°C was highly variable and ranged from 1.3 to 11.0 h \(\text{Fig. 4; males, 1.3–10.2 h; females, 4.0–11.0 h.}\)

**Discussion**

**Nest use**

Northern flying squirrels were capable of sustaining high temperatures over a variety of nest-tree characteristics. We expected that trees of larger diameter with thicker bark and wood would minimize temperature fluctuations, that tall trees in exposed conditions would cause greater temperature fluctuations, and that tree species with potentially different thermal properties would affect temperatures of animals inside nests. We were unable to detect temperature differences resulting from any of these factors. Instead, we suggest that the sustained high temperatures recorded in nests were caused primarily by the sleeping position of the animals. We observed that, when a flying squirrel was sedated or arousing from sedation, it tended to curl into a ball with its tail wrapped over its head. Because the temperature sensor of the radio collar was positioned under the chin of the animals, temperature readings of squirrels inside nests were likely close to body temperature. For example, the body temperature of the closely related southern flying squirrel \((Glaucomys volans)\) was recorded at 39°C \((\text{Neumann 1967)}\).

Similarly, Weigl and Osgood \((1974)\) reported that nest temperatures, as determined by temperature-sensitive radio collars, varied only 1–3°C regardless of air temperature. In our study, animals were able to maintain high temperatures in all nest types, although they may have augmented the thermal.
value of nests by lining them with mosses and lichens or by aggregating (Stapp et al. 1991).

Our observations of aggregating flying squirrels were limited to radio-collared animals. There may have been additional animals without radio collars nesting with our subject animals. Each aggregation began after the minimum nightly temperature was below freezing but before temperatures were extremely low, which is similar to observations from interior Alaska (Mowrey and Zasadzka 1984) and western Oregon (Carey et al. 1997). Using captive animals, Stapp et al. (1991) found that aggregations of southern flying squirrels were correlated with temperature and that aggregation reduced energy expenditures by 26–33%. Aggregations of northern flying squirrels have been observed year-round, however, in New Brunswick (Gerrow 1996). Therefore, while aggregating may be adaptive for cold weather, it is not necessarily confined to winter months and may also serve a social role (Gerrow 1996). Our observations show that nest trees can be shared concurrently, used by more than one animal within a season, and used across years by different animals.

Activity patterns

Northern flying squirrels adjusted the duration and timing of nocturnal activity periods in response to the onset of darkness or light and air temperature. Few studies have quantified the duration of activity bouts for flying squirrels, and no values have been reported for animals in the northern regions of their geographic distribution. In Pennsylvania and North Carolina during summer, Weigl and Osgood (1974) noted that flying squirrels were absent from nests for an average of 118 min (range = 53–225 min) in the activity bout following dusk and for an average of 76 min (range = 38–110 min) in the activity bout before dawn. In our study, the duration of activity bouts was also variable at warm temperatures, but was reduced during periods of extreme cold. This trend was most pronounced in the 1996 field season, when there were no long activity bouts and the total time spent away from nests per night was less at extremely cold temperatures. Further, there was a shift towards shorter bout lengths during the harsh 1996 field season (Fig. 1). The high differential between body temperature and low ambient temperature likely reduces the time that animals can spend outside the nest. Nonetheless, flying squirrels were active each night to some extent throughout both winters, regardless of ambient temperature.

The timing of activity by flying squirrels in relation to photoperiod has been studied more extensively. In Oregon, northern flying squirrels, on average, became active 70 min after sunset in late summer (Witt 1992). In West Virginia, Urban (1988) reported two peaks in nightly activity: one at 1–3 h after sunset and another at 7–10 h after sunset. Captive animals also became active 35 min (range = 53–117) after sunset and ceased activity within an hour of sunrise (Radvanyi 1959). Our observations from the mild winter season of 1997 (typically with two active bouts/night) are similar to those reported from studies farther south. Deviations from the general biphasic pattern of nighttime activity (Wells-Gosling and Heaney 1984) have not been reported previously, although the timing of activity may be delayed by high winds, rain, or cold temperatures (Weigl and Osgood 1974; Urban 1988).

By comparison, during the harsh conditions of 1996, animals shifted towards a shorter single activity bout or two very short bouts in the middle of the night. Because nightly minimum temperature typically occurs in the predawn hours, a shift in the timing of activity to earlier in the night would potentially lessen energetic demands. We suggest that this shift, combined with a reduction in total activity outside the nest (Fig. 4), likely serves as an energy-conservation strategy during extremely cold temperatures. Further, if animals use lichens for nest materials (Hayward and Rosentreter 1994), they could consume lichens in the nest as a cached food instead of foraging outside the nest. Stapp (1992) suggested that the relatively low metabolic rate and rates of heat loss of southern flying squirrels were adaptive for reducing winter energetic costs, but similar studies have not been conducted on northern flying squirrels. Stapp (1992) also emphasized behavioural adaptations, such as reduced foraging activity at low temperatures, aggregating, and food caching, as additional means of reducing energetic costs.

Some nocturnal species exhibit decreased activity levels in relation to moonlight (e.g., Daly et al. 1992; Rogowitz 1997), potentially to avoid nocturnal predators that gain an advantage with increased nighttime illumination. Radvanyi (1959) found that the activity of captive northern flying squirrels followed the lunar cycle: animals decreased the amount of nightly activity during the brightest part of the lunar cycle, although the timing of activity was not affected. In our study, there was no detectable relationship between activity and lunar phase. Our observations, however, were only able to detect the timing, not the amount, of activity. Thick forest canopies may reduce the moonlight illumination reaching the ground by as much as 99% (Radvanyi 1959). If illumination was negligible due to canopy effects (>70% canopy closure in our study; Cotton and Parker 2000), animals in our study might not have exhibited the same reduction in activity that was observed in captive animals.

In summary, northern flying squirrels exhibit considerable flexibility in their ability to live across a wide range of environmental conditions. In the boreal forests of British Columbia, flying squirrels used behavioural strategies that likely contribute to winter survival. They sustained high temperatures in nest cavities and nest structures used for resting, regardless of tree size or species. Nocturnal activity away from nests varied with photoperiod and air temperature, presumably in response to high energetic costs. Physiological adaptations that allow animals to limit energetic costs, such as relatively low rates of heat loss, as in the southern flying squirrel, should be examined. We recommend that subsequent studies address the role of lichens in providing thermal protection in nests and the extent to which they serve as a cached food resource to help balance energy demands.

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