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# Microclimatic characteristics of blue grouse *Dendragapus obscurus* roost-sites: influence on energy expenditure

Peter J. Pekins, James A. Gessaman & Frederick G. Lindzey

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Energetic models which incorporate environmental measures have demonstrated that significant thermoregulatory savings are accrued from nocturnal winter roost-sites, usually from reduced wind speed and radiated heat loss. Because blue grouse *Dendragapus obscurus* occupy high elevation, snow-bound coniferous stands in the Rocky Mountains during winter, selection of a favourable microhabitat is likely their primary thermoregulatory behaviour. Therefore, we measured the microclimatic conditions at diurnal and nocturnal roost-sites of blue grouse to determine whether their choice of roost-sites reflects thermoregulatory behaviour. Temperature, wind speed, and solar radiation were measured at 17 diurnal Douglas-fir *Pseudotsuga menziesii* and 17 nocturnal subalpine fir *Abies lasiocarpa* roost-sites and compared to those of an open control site in Logan, Utah, 1985-1986. Temperature varied  $<2^{\circ}\text{C}$  between the roost-sites and the control site. Wind speed was significantly lower in 15 of 17 diurnal ( $\bar{x} = 0.71$  m/sec) and all nocturnal roost-sites ( $\bar{x} = 0.24$  m/sec) than in the control site ( $\bar{x} = 1.75$  m/sec). Wind speed was reduced  $>75\%$  at all but one nocturnal roost-site. Solar radiation at the diurnal roost-sites ( $\bar{x} = 51$  W/m $^2$ ) was significantly lower than at the control site (201 W/m $^2$ ); however, five roost-sites had maximum values  $>90\%$  of the control maximum. Douglas-fir roost-sites had significantly greater solar radiation, diurnal, and nocturnal wind speed than subalpine fir roost-sites. Reduction of convective heat loss was the major thermoregulatory contribution of both diurnal and nocturnal roost-sites. Diurnal roost-sites also afforded measurable radiant energy and, presumably, grouse could track the sun in roost trees to maximize such heat input. Daily energy costs predicted from metabolic equations incorporating temperature and wind speed were below the metabolizable energy intake of captive blue grouse. Application of the average microclimatic conditions from both roost trees to an energetic model revealed that a blue grouse would realize a 50% greater reduction in convective heat loss, and a 10% greater net energy savings, by roosting overnight in a subalpine fir rather than a Douglas-fir. This difference may explain why blue grouse show affinity to subalpine firs for nocturnal roosting, and points to the energetic importance of specific coniferous habitats to wintering blue grouse.

*Key words:* blue grouse, *Dendragapus obscurus*, energy, habitat, microclimate, roost-site, winter

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Energy flow is the basic exchange between an animal and its environment, with survival dependent upon thermodynamic balance (Porter & Gates 1969). The maintenance of a favourable energy balance in the face of dynamic environmental factors such as ambient temperature, radiation, wind, and humidity is a major determinant of the abundance and distribution of birds (Weathers 1979). Therefore, the energy and activity budgets of birds relative to the energy demands of their environment is an important denominator in explaining avian adaptive strategies (King 1974). The primary, specific thermoregulatory behaviour of birds is likely the selection of a favourable microhabitat.

Avian use of energy-saving microhabitats has been reported in many studies (for review see Lustick 1980). Energetic models which incorporate environmental measures have demonstrated that significant thermoregulatory savings are accrued from nocturnal winter roosts (e.g. Calder 1974, Kelty & Lustick 1977, Lustick 1980, Walsberg & King 1980, Stalmaster & Gessaman 1984, Keister, Anthony & Holbo 1985, Thompson & Fritzell 1988). Decreased wind speed and a reduction in radiated heat loss, particularly in coniferous habitats, were the primary energy reducing factors identified in these studies.

Blue grouse *Dendragapus obscurus* in the Rocky Mountains typically occupy high elevation, snow-bound coniferous stands during the winter (Marshall 1946, Caswell 1954, Stauffer & Peterson 1985, Cade & Hoffman 1990). They are very sedentary during winter, seldom leaving a feeding tree during the day, often moving to a different tree for the night, and seldom snow roosting (Cade & Hoffman 1990, Pekins 1988b, Remington 1990, Pekins, Lindzey & Gessaman 1991). In Utah, Douglas-firs and subalpine firs were selectively chosen as diurnal and nocturnal roosting trees, respectively (Pekins et al. 1991). Blue grouse activity patterns apparently revolve around diurnal and nocturnal roost trees which presumably provide favourable microhabitats based on their physical characteristics (Pekins et al. 1991). The objective of this study was to measure the actual winter microclimatic conditions that blue grouse experi-

ence at roost-sites during winter, and to determine whether their choice of roost-sites reflects thermoregulatory behaviour.

## Material and methods

### Study area

The study area was located on the Cache National Forest in the Bear River Range of the Wasatch Mountains in northeastern Utah. The primary study area was centrally located on a north-south ridge 2.5 km east of Logan Peak (USGS, Logan Peak, Utah, 7.5 min quadrangle, 1969) and encompassed approximately 700 ha. The forest is a subalpine-fir/Douglas-fir mix with a shrubby undergrowth classified as the *Abies lasiocarpa* climax series *Pseudotsuga menziesii* phase (Mauk & Henderson 1984). Topography varied from flat ridgetops to steep canyon faces and included all aspects. Elevations ranged from 2,500 to 2,950 m, and regional mean January temperature was -10°C. Mean annual precipitation is 102 cm, with 85% occurring from September through April, the majority as snow (Mauk & Henderson 1984). Snow depth on the study area ranged from 2 to 3 m during 1987. The area is characterized by strong winter temperature inversions which result in 5-10°C higher temperatures at high elevations than those in valley bottoms (Wilson, Olsen, Hutching, Southard & Erickson 1975).

### Roost and control site selection

Diurnal roost-sites were located by visual observation of both radio-collared and non-collared blue grouse. Radio-collared birds were captured during winter with a telescopic noose pole (Zwickel & Bendell 1967) and fitted with a 25-30 g (<3% body weight) poncho-mounted radio (Amstrup 1980, Pekins 1988a). A site was identified as a roost only if a roosting (vs standing) bird was observed in a non-alarmed state (e.g. crown feathers were not raised). Diurnal roost-sites were located after 09:00 hrs.

Nocturnal roost-sites were identified from visual sighting of radio-collared birds. The general area



within a tree in which a grouse roosted was determined by homing with a portable receiver and antenna. The tree was then searched with flashlights to locate the bird. The tree was flagged and the grouse left undisturbed.

Microclimatic conditions at selected roost-sites were measured during the winters of 1984-85 and 1985-86. Choice of roost-sites for microclimatic evaluation was based on: 1) location, to provide an adequate sample of topographic range; 2) branching characteristics at the roost-site which allowed instruments to be attached without disturbing the site.

A permanent, weather control site was situated centrally in the study area in a flat opening at 2,650 m (minimal treeless radius of 50 m) to provide comparative data for measurements at roost-sites. The unit was placed on a platform  $2.0 \pm 0.3$  m high in the middle of the opening and oriented to eliminate interference among instruments.

### Microclimatic measurements

A microclimatic monitoring unit consisted of the following three instruments mounted on a white, aluminum assembly: a thermistor (Yellow Springs Instrument Thermoliner Component - US144203), a cup anemometer (Model No 6101 from R.M. Young Co.) with average starting threshold speed of 0.28 m/sec, and an Eppley Black and White Pyranometer (Model 8-48 from Climatronics Corporation) that measured air temperature, wind speed, and solar radiation, respectively. The unit was attached and leveled at a roost-site with adjustable lag screw mounts. Voltage signals from the instruments were carried through a Belden (No 8778) 6-pair, shielded cable to a Campbell Scientific CR5 data logger at the base of the roost tree. The CR5 was powered by a Gates, 12 volt, rechargeable battery. Weatherproof connectors wrapped with duct tape were used at all connections to provide moisture protection. Instrument signals were modified by a circuit board in the CR5 recorder to insure that all voltages were within the range of the recorder. An integrator within each recorder took a 0.3 sec sample of an instrument's voltage every 2.4 sec, accumulated averages, and printed these averages in millivolts every 15 minutes. The effective area monitored was approximately  $50 \times 30 \times 15$  cm. Data were excluded when instruments were snow-covered. Prior to the study all units were placed in proximity in an open area for three days to ensure that the individual instruments performed similarly.

The data were analyzed with three-way factorial

analysis. Factors were treatments (roost-sites and the control), blocks (15-minute periods), and days. Days were a repeated measure. Balanced data sets were compared with an analysis of variance and F-tests ( $P < 0.05$ ). Planned comparisons were employed to test for differences ( $P < 0.05$ ) between each roost-site and the control.

## Results

### Diurnal roost-sites

The microclimate of 17 diurnal, Douglas-fir roost-sites was measured during six time periods of 7-10 days from 06:00 to 18:00 hrs (Table 1). Time periods varied because of snow-covered instruments.

Air temperature was different ( $P < 0.05$ ) between most roost-sites and the control, but absolute difference was  $\leq 2.1^\circ\text{C}$  (see Table 1). The mean minimum and maximum roost-site temperatures for all periods were  $-10.4$  and  $-4.2^\circ\text{C}$ , respectively. The individual minimum and maximum diurnal temperatures recorded were  $-26.4$  and  $6.3^\circ\text{C}$ , respectively. The average diurnal temperature for all periods was  $-7.2^\circ\text{C}$ .

Insolation at roost-sites was less ( $P < 0.05$ ) than that at the control site in all periods (see Table 1). Maximum solar radiation at nine (53%) roosts was  $\geq 60\%$  of the corresponding maximum control; five had maximums within 10% of the control maximum. The mean solar radiation at the roost-sites was one-fourth of that at the control site. Between 10:00 and 15:00 hrs, when insolation was greatest, roosts and the control site averaged 85.2 and 370.6  $\text{W/m}^2$ , respectively. Solar flux density increased as winter progressed.

Wind speed was less ( $P < 0.05$ ) at 15 (88%) diurnal roost-sites than at the control site (see Table 1); two of these roost-sites had lower average wind speeds than the minimum threshold speed of the anemometer. Subsequent correction of these observations to the threshold speed affected the overall wind speed average at roost-sites by  $<2\%$ . Wind speeds were 2 and 9% higher than control values at the other two roost-sites. The average wind speed at the control site was 2.65 times that at the roost-sites ( $0.71 \pm 0.62$  m/sec). Only three roost-sites had average diurnal wind speeds greater than 1.0 m/sec. The maximum wind speed at all diurnal roost-sites averaged 51% of the corresponding maximum wind speed at the control site. The maximum recorded wind speeds at diurnal roost-sites and the control site were 7.5 and 8.7 m/sec, respectively.



Table 1. Microclimatic measurements (mean  $\pm$  SE) at 17 diurnal, Douglas-fir roost-sites of blue grouse, and a control site, Logan Peak, Utah.

Date	Roost site	Temperature ( $^{\circ}$ C)	Solar radiation (W/m $^2$ )	Wind speed (m/sec)
24 Dec, 1984 - 5 Jan, 1985	1	-7.7 $\pm$ 0.1*	7.1 $\pm$ 0.4*	0.63 $\pm$ 0.03*
	2	-6.8 $\pm$ 0.2*	17.2 $\pm$ 0.7*	0.60 $\pm$ 0.02*
	Control	-6.1 $\pm$ 0.2	126.8 $\pm$ 7.4	2.25 $\pm$ 0.05
10-21 Jan. 1985	3	-6.4 $\pm$ 0.2*	17.6 $\pm$ 0.7*	2.24 $\pm$ 0.08
	4	-6.0 $\pm$ 0.2*	19.6 $\pm$ 1.6*	0.98 $\pm$ 0.05*
	5	-6.1 $\pm$ 0.2*	54.1 $\pm$ 3.5*	0.91 $\pm$ 0.03*
	Control	-5.0 $\pm$ 0.2	187.1 $\pm$ 9.3	2.05 $\pm$ 0.07
21 Jan. - 1 Feb. 1995	6	-10.2 $\pm$ 0.3*	64.7 $\pm$ 5.9*	0.22 $\pm$ 0.01*
	7	-10.4 $\pm$ 0.9	23.8 $\pm$ 1.2*	0.41 $\pm$ 0.03*
	8	-10.4 $\pm$ 2.8	25.7 $\pm$ 1.0*	0.82 $\pm$ 0.04*
	Control	-9.5 $\pm$ 0.3	198.1 $\pm$ 10.4	1.24 $\pm$ 0.04
16 Feb. - 1 Mar. 1995	9	-7.9 $\pm$ 0.2*	25.2 $\pm$ 1.0*	0.70 $\pm$ 0.03*
	10	-6.8 $\pm$ 0.2	105.9 $\pm$ 7.8*	0.37 $\pm$ 0.02*
	11	-6.8 $\pm$ 0.3	122.9 $\pm$ 9.0*	0.35 $\pm$ 0.03*
	Control	-6.6 $\pm$ 0.2	253.0 $\pm$ 12.4	2.32 $\pm$ 0.07
1-15 Mar. 1995	12	-8.6 $\pm$ 0.3*	53.8 $\pm$ 1.9*	0.11 $\pm$ 0.003*
	13	-7.3 $\pm$ 0.3	101.3 $\pm$ 8.6*	0.57 $\pm$ 0.03*
	14	-7.9 $\pm$ 0.3*	76.8 $\pm$ 6.7*	0.83 $\pm$ 0.05*
	Control	-6.5 $\pm$ 0.3	241.5 $\pm$ 11.0	2.40 $\pm$ 0.06
20-31 Dec. 1995	15	-4.3 $\pm$ 0.1*	93.7 $\pm$ 5.8*	0.28 $\pm$ 0.01*
	16	-4.2 $\pm$ 0.1*	33.3 $\pm$ 2.4*	1.59 $\pm$ 0.03*
	17	-4.3 $\pm$ 0.1*	18.8 $\pm$ 1.5*	2.09 $\pm$ 0.04
	Control	-3.4 $\pm$ 0.2	150.4 $\pm$ 7.6	2.05 $\pm$ 0.03

\* = significantly different from the control ( $P < 0.05$ ).

### Nocturnal roost-sites

The microclimate of 17 nocturnal, subalpine fir roost-sites was measured during seven time periods of 9-11 days from 18:00 to 06:00 hrs (Table 2). Time periods varied because of snow-covered instruments. Solar

radiation was typically absent during this interval.

Nocturnal temperatures varied less than 1 $^{\circ}$ C between roost-sites and the control site (see Table 2). The mean minimum and maximum roost-site temperatures were -8.8 and -0.8 $^{\circ}$ C, respectively. The indi-

Table 2. Microclimatic measurements (mean  $\pm$  SE) at 17 nocturnal, subalpine-fir roost-sites of blue grouse, and a control site, Logan Peak, Utah.

Date	Roost site	Temperature ( $^{\circ}$ C)	Wind speed (m/sec)
18 Mar. - 3 Apr. 1985	1	-5.9 $\pm$ 0.2*	0.47 $\pm$ 0.03*
	2	-5.2 $\pm$ 0.2	0.19 $\pm$ 0.01*
	3	-6.2 $\pm$ 0.2*	0.21 $\pm$ 0.01*
	Control	-5.2 $\pm$ 0.2	2.04 $\pm$ 0.06
2-14 Jan. 1986	4	-3.5 $\pm$ 0.3	0.07 $\pm$ 0.001*
	5	-3.2 $\pm$ 0.2*	0.08 $\pm$ 0.01*
	6	-3.5 $\pm$ 0.3	0.38 $\pm$ 0.03*
	Control	-3.9 $\pm$ 0.2	1.71 $\pm$ 0.06
14-26 Jan. 1986	7	-5.6 $\pm$ 0.2	0.27 $\pm$ 0.01*
	8	-5.3 $\pm$ 0.2	0.81 $\pm$ 0.03*
	9	-5.5 $\pm$ 0.2	0.30 $\pm$ 0.01*
	Control	-5.0 $\pm$ 0.2	2.53 $\pm$ 0.07
26 Jan. - 10 Feb. 1986	10	-8.8 $\pm$ 0.3	0.14 $\pm$ 0.01*
	11	-8.3 $\pm$ 0.3	0.33 $\pm$ 0.03*
	Control	-8.5 $\pm$ 0.3	1.53 $\pm$ 0.06
28 Feb. - 9 Mar. 1986	12	-1.6 $\pm$ 0.2	0.12 $\pm$ 0.01*
	13	-0.8 $\pm$ 0.2	0.07 $\pm$ 0.30*
	Control	-1.5 $\pm$ 1.1	1.00 $\pm$ 0.05
9-20 Mar. 1986	14	-6.5 $\pm$ 0.1	0.35 $\pm$ 0.02*
	15	-6.8 $\pm$ 0.1	0.00 $\pm$ 0.00*
	Control	-6.7 $\pm$ 0.1	1.37 $\pm$ 0.07
20 Mar. - 6 Apr 1986	16	-0.4 $\pm$ 0.2	0.06 $\pm$ 0.01*
	17	-0.3 $\pm$ 0.2	0.24 $\pm$ 0.02*
	Control	-0.2 $\pm$ 0.2	1.53 $\pm$ 0.03

\* = significantly different from control ( $P < 0.05$ ).



vidual minimum and maximum nocturnal temperatures were -20.4 and 9.4°C, respectively. The average nocturnal temperature for all periods was -4.4°C.

All nocturnal roost-sites had lower ( $P < 0.05$ ) wind speed than the control site (see Table 2). The average wind speed at roost-sites ( $0.24 \pm 0.20$  m/sec) was an 85% reduction from wind speed at the control site. All but one roost-site reduced wind speed more than 75%, one half reduced it more than 90%. The minimum and maximum mean wind speed at the roost-sites were  $<0.28$  and  $0.81$  m/sec, respectively. The individual maximum wind speeds at roost-sites and the control site were  $5.0$  and  $8.23$  m/sec, respectively. The mean maximum wind speed for all roost-sites was 69% of that at the control site.

### Diurnal vs nocturnal roost-sites

We compared the nocturnal microclimate (18:00-06:00 hrs) at the diurnal Douglas-fir roost-sites and the diurnal microclimate at the nocturnal subalpine fir roost-sites with the control site (Table 3). Blue grouse occasionally used these tree species during these periods. Nocturnal wind speed was lower ( $P < 0.05$ ) at 14 (82%) Douglas-fir roost-sites than at the control. Diurnal wind speed and solar radiation were lower ( $P < 0.05$ ) at subalpine fir roost-sites than at the control. Douglas-fir roost-sites had greater ( $P < 0.10$ ) solar radiation ( $51.1$  vs  $14.8$  W/m<sup>2</sup>), and diurnal ( $0.71$  vs  $0.25$  m/sec) and nocturnal wind speed ( $0.92$  vs  $0.24$  m/sec) than subalpine fir roost-sites. Temperature varied  $<2^\circ\text{C}$  between all roost-sites and the control site. The mean diurnal and nocturnal temperatures were  $-2.7$  and  $-7.9^\circ\text{C}$ , respectively. The lowest recorded temperature was  $-26.2^\circ\text{C}$ .

## Discussion

Roost-site selection was apparently not dictated by ambient temperature ( $T_a$ ) alone, because the mean  $T_a$  was above the lower critical temperature of fed blue grouse ( $-10^\circ\text{C}$ , Pekins, Gessaman & Lindzey 1992),

and  $T_a$  varied only  $1\text{--}2^\circ\text{C}$  between roost sites and the control site. A substantial reduction of  $T_a$  at roost-sites has been found only in situations where local effects or a temperature inversion was present (Gyllin, Kallander & Sylven 1977, Yom-tov, Imber & Otterman 1977). In a general sense, blue grouse occupy high elevations during winter and realize a thermal advantage because thermal inversions occur commonly relative to their summer habitat at lower elevations (Wilson et al. 1975). Significant elevation of  $T_a$  has been recorded in snow roosts that provide thermoneutral conditions for tetraonids (Korhonen 1980, 1989, Marjakangas, Rintamaki & Hissa 1984). No study has documented extensive snow roosting by blue grouse, although we occasionally found snow roosts ( $N = 53$  in 2 years). Most were used during or immediately after major snowstorms in windy or snowy conditions.

Absorption of radiant energy not only reduces thermoregulatory costs at low  $T_a$ 's (Hamilton & Heppner 1967, Morton 1967, Lustick 1969, 1970, Ohmart & Lasiewski 1971, DeJong 1976), it also reduces these costs in wind because of the reduced rate of heat transfer from the bird's core to its surface. Although the insolation measured at diurnal roost-sites was reduced throughout the day, about  $1/3$  of the roost-sites had maximum solar radiation similar to that at the control site, indicating their potential to influence thermoregulation of blue grouse. A limitation of the microclimatic units was that they were not able to measure the radiative environment of a grouse which moved to stay in the sun. Therefore, the solar radiation values measured at identified roost-sites probably underestimated that available to blue grouse. Relatedly, we observed 71% of grouse roosting in sunlight (Pekins et al. 1991), further indicating that our measurements underestimated the insulative benefits of diurnal roost-sites. It is probable that blue grouse seek solar radiation to offset convective heat loss in Douglas-firs which are more open (Pekins et al. 1991) and have higher wind speed than subalpine firs. The choice of a roost site on a sunny day is likely dependent on a balance between the positive effects of solar radiation and the negative effects of exposure to wind.

The reduction of wind speed (63% diurnal, 85% nocturnal) was the primary thermoregulatory advantage provided by roost-sites. Wind speed reductions of 70-90% are common at nocturnal, coniferous roost-sites of many species of birds (Francis 1976, Kelty & Lustick 1977, Lustick 1980, Walsberg &

Table 3. Comparison of the mean microclimatic measures of diurnal and nocturnal blue grouse roost-sites in Douglas-firs and subalpine firs during winters 1985 and 1986, Logan Peak, Utah.

	Douglas-fir	Subalpine fir
Diurnal Wind Speed (m/sec)	$0.71 \pm 0.62$	$0.25 \pm 0.21^*$
Nocturnal Wind Speed (m/sec)	$0.92 \pm 0.83$	$0.24 \pm 0.20^*$
Solar Radiation (W/m <sup>2</sup> )	$51.10 \pm 37.10$	$14.80 \pm 10.60^*$

\* = significant difference between roost tree species ( $P < 0.10$ ).



King 1980, Keister et al. 1985). The average wind speeds measured at nocturnal roost-sites (<1.0 m/sec, see Table 2) were within the linear response of blue grouse metabolic rate (MR) to the square root of wind speed (0-2.75 m/sec) at  $T_a$ 's of 5 to -15°C (Pekins 1988b). Because metabolic response to wind speed is non-linear when plumage is penetrated by wind (Kelty & Lustick 1977, Hayes & Gessaman 1980, Walsberg 1985), the microclimate at roost-sites prevented such substantial convective heat loss.

The effect of wind speed and temperature on MR of blue grouse was measured in a related laboratory study (Pekins 1988b). The equation which described these effects was:

$$MR = 0.835 + 0.269u^{0.5} - 0.024T_a \quad (1)$$

where MR = metabolic rate (mL O<sub>2</sub>/hr<sup>-1</sup>/g<sup>-1</sup>),  $u^{0.5}$  = square root of wind speed (m/sec),  $T_a$  = ambient temperature (°C).

Equation (1) was used to assess whether subalpine fir roost-sites have a thermoregulatory advantage over Douglas-fir roost-sites at night. We assumed that the effect of canopy cover was equivalent to that in the laboratory wind tunnel (i.e. complete) where MR measurements were made, and that  $T_a$  was -10°C. Canopy cover in Douglas-fir and subalpine fir roost-sites was 85 and 91%, respectively, in the study area (Pekins et al. 1991). Wind speed was set equal to the respective average recorded in each tree species (Douglas-fir = 0.92, subalpine fir = 0.24 m/sec). Calculations showed that a blue grouse would realize a 50% greater reduction in convective heat loss, and a 10% greater net energy savings, by roosting at night in a subalpine fir, the preferred nocturnal roost tree, rather than a Douglas-fir, the preferred diurnal roost tree. We recognize that this comparison was between diurnal, Douglas-fir roost-sites and nocturnal, subalpine fir roost-sites, but the extended measurements obtained at both tree species lends support to the conclusion that subalpine firs provided superior nocturnal shelter.

Similarly, we estimated daily energy expenditure or field metabolic rate (FMR) with equation (1) by summing the energy costs incurred during the average weather conditions measured at diurnal and nocturnal roost-sites. An inherent assumption of this exercise was that activity was minimal because of the sedentary nature of blue grouse during winter. Because no equation is available to determine the interactive effects of solar radiation, wind speed, and  $T_a$  on blue

grouse MR, we assumed diurnal conditions without solar radiation, and used equation (1) to calculate diurnal and nocturnal MR. The FMR of a 1,200 g blue grouse was estimated as  $655 \text{ kJ} \times \text{d}^{-1}$  ( $573 \text{ kJ} \times (\text{kg}^{-0.734})^{-1} \times \text{d}^{-1}$ ;  $1 \text{ L O}_2 = 19.7 \text{ kJ}$ ), or 1.5 times the standard metabolic rate of blue grouse ( $\text{SMR} = 0.814 \text{ mL O}_2 \times (\text{kg}^{0.734})^{-1} \times \text{hr}^{-1}$ , Pekins et al. 1992). This value is about 5% less than the energy assimilated by two male blue grouse maintained on Douglas-fir needles in captivity (683 kJ, Remington 1990), and 95% of the mean FMR measured with doubly labelled water ( $600 \pm 52 \text{ kJ} \times (\text{kg}^{-0.734})^{-1} \times \text{d}^{-1}$ , Pekins, Gessaman & Lindzey 1994). Presumably, the estimated FMR would be lower if a blue grouse received the benefit of solar radiation; a conservative estimate of 5% net savings was realized at a mean solar radiation of 250 W/m<sup>2</sup> (mean value in February-March) based on predictive equations developed with red-tailed hawks *Buteo jamaicensis* by Hayes & Gessaman (1980). The estimated FMR was further reduced 5% by increasing  $T_a$  by 3°C; such increase was realized between early (1 January - 15 February) and late winter (16 February - 1 April). Thus, slight microclimatic changes at roost-sites yield measurable daily and seasonal effects on the FMR of blue grouse.

Roosting in conifers during winter theoretically provides protection from avian predators (Bergerud & Gratson 1988), specifically goshawks *Accipiter gentilis* at the study site, and blue grouse probably realized this advantage, although overwinter predation is considered minor (Cade & Hoffman 1990). However, blue grouse also realized distinct thermoregulatory benefit at diurnal and nocturnal roost sites. This benefit, versus predator avoidance, was most evident when considering the affinity by blue grouse for nocturnal roost-sites in subalpine firs; presumably, switching roost trees each morning and evening increased exposure to predation.

This study provided evidence that microhabitat selection by blue grouse was advantageous to their winter energy balance. Douglas-firs provided exposure to solar radiation, wind protection, and a source of food during the day. Subalpine firs increased protection from wind, reducing or nearly eliminating convective heat loss at night. The application of microclimatic data to a MR predictive equation indicated that blue grouse probably experience a positive energy balance throughout winter as hypothesized previously (Pekins et al. 1994). Habitat selection by blue grouse, particularly microhabitat selection of roost-sites, reflects active choices which minimize



energy costs imposed by weather conditions in their wintering areas. Because blue grouse survival is implicitly related to the protection afforded by specific coniferous habitats, such habitats should be considered critical for survival and maintenance of blue grouse populations, and managed accordingly.

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