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RELATIONS OF FOREST COVER AND CONDITION OF ELK: A TEST OF THE THERMAL COVER HYPOTHESIS IN SUMMER AND WINTER

by

JOHN G. COOK, LARRY L. IRWIN, LARRY D. BRYANT, ROBERT A. RIGGS, AND JACK WARD THOMAS

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FRONTISPIECE. Use of tractable animals provides considerable opportunities to test a variety of specific hypotheses that can be generated, but not easily assessed, from studies of free-ranging wildlife (photo by Dan Hengel).

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RELATIONS OF FOREST COVER AND CONDITION OF ELK: A TEST OF THE THERMAL COVER HYPOTHESIS IN SUMMER AND WINTER

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Abstract: Many biologists have accepted the concept that the weather-sheltering effect of dense forest cover (i.e., thermal cover) reduces energy expenditure of large ungulates and therefore enhances survival and reproduction. Providing thermal cover for ungulates has become a key habitat objective for western elk ranges. However, it remains uncertain that thermal cover significantly influences the nutritional condition, survival, or productivity of wild ungulates.

During 1991–95, we tested the hypothesis that the sheltering effect of thermal cover is of sufficient magnitude to enhance condition of elk (*Cervus elaphus nelsoni*) during summer and winter. Relative condition of captive young cows was monitored during 4 winter and 2 summer season-long experiments. These elk were placed in pens (2–3 elk per pen, n = 12 pens) at the center of 2.3-ha treatment units, each unit providing 1 of 4 levels of cover: (1) dense cover (≥70% forest canopy closure), (2) moderate cover (40–69% canopy closure), (3) zero cover (complete clearcuts), and (4) a combination of dense cover and zero cover. Controlled diets were set to induce moderate mass loss (5–10%) in winter and moderate growth in summer. Solar and net hemispherical radiation flux, windspeed, temperature, and relative humidity also were measured in the treatment units.

We found no significant, positive effect of thermal cover on condition of elk during any of the 6 experiments. In contrast, dense cover provided a costly energetic environment, resulting in significantly greater overwinter mass loss, fat catabolism, and (in 1 winter) mortality. These results were consistent in all 4 winters despite variable temperature regimes ranging from mild to relatively severe. In summer, we found no significant effects of forest cover on condition or growth of yearlings, although elk in dense forest cover generally consumed less water than those in the zero or moderate cover treatments. Our data indicated that (1) the enhanced performance of elk with little or no thermal cover in winter was due to the greater levels of solar radiation flux and (2) potential energetic benefits of thermal cover (from reduced windspeed, elevated nocturnal temperature, and nocturnal long-wave radiation flux during winter, and shading from solar radiation in summer) were negligible in respect to the thermoregulatory capabilities of elk.

We conclude that (1) thermal cover does not appreciably enhance the energetic status and productive performance of elk in climatological settings similar to those of our study, (2) providing thermal cover is not a suitable solution for inadequate forage conditions, and (3) habitat management based on the perceived value of thermal cover should be re-evaluated. Elk biologists should refocus their attention to the influences of forest management on (1) forage resources and related production potential of forest successional stages and (2) vulnerability of ungulates to harvest and harassment. Because the majority of empirical support for the thermal cover hypothesis is derived from observational studies of habitat selection, our findings amplify the difficulty associated with determining need or requirement, relevant in the context of population productivity, from empirical observations of habitat use.

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Key words: activity, bioenergetics, *Cervus elaphus*, condition, elk, forest management, nutrition, Oregon, survival, thermal cover.

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INTRODUCTION

The idea that vegetative cover, particularly that provided by dense coniferous forests, enhances survival of wild ungulates by conferring energetic benefits has become a fundamental paradigm in wildlife habitat management over the past 50 years. Thermal cover has been credited widely with moderating the effects of harsh weather and, therefore, may improve overall performance of populations (i.e., survival and reproduction) by reducing energy expenditures required for thermostasis. During winter, temperature can be several degrees warmer under forest canopies at night (Reifsnyder and Lull 1965, Bunnell et al. 1986) due to long-wave radiation emitted from the forest canopy (Moen 1968, Beall 1974, Grace and Easterbee 1979). As a result, forest canopies have been described as thermal blankets that retain warmer air masses near the ground (Nyberg et al. 1986). Because ungulates readily absorb long-wave radiation, these radiation fluxes also may directly contribute to energy balance of animals (Grace and Easterbee 1979). Forest canopies can reduce windspeed (Grace and Easterbee 1979, Bunnell et al. 1986) and therefore reduce convective heat loss. During summer, shade provided by forest cover reduces diurnal ambient temperature fluctuations and reduces absorption of solar radiation by the animal (Demarchi and Bunnell 1993). Thermal cover also may provide some shelter from precipitation and therefore, under some circumstances, may reduce heat loss due to reduced wetting of pelage.

Numerous studies have demonstrated that free-ranging ungulates use dense forest stands disproportionately to their availability (e.g., Irwin and Peek 1983, Leckenby 1984, Edge et al. 1987), ostensibly in part to take advantage of the potential energetic benefits of thermal cover (e.g., Beall 1976, Armstrong et al. 1983, Leckenby 1984, Zahn 1985, Ockenfels and Brooks 1994). Such intuitive interpretation is reasonable in light of the moderating effects of cover on weather and is supported by modeling efforts based on energy balance equations (e.g., Grace and Easterbee 1979, Parker and Gillingham 1990, De-

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marchi and Bunnell 1993). This has led to the belief that thermal cover can enhance animal performance and perhaps productivity of free-ranging herds (e.g., Christensen et al. 1993).

Since the late 1970s, the widespread belief that thermal cover constitutes a key component of ungulate habitat has resulted in its widespread application. In the case of elk (*Cervus elaphus*), variables that provide measures of the abundance and, in some cases, quality of thermal cover are incorporated into virtually all elk habitat evaluation procedures currently used in the Pacific Northwest (e.g., Wisdom et al. 1986, Thomas et al. 1988) and many other regions in the western United States (e.g., Christensen et al. 1993). These habitat evaluation procedures are used extensively in development of national forest plans (Edge et al. 1990). Management agencies also make site-specific, case-by-case decisions regarding timber harvest or prescribed fire based on thermal cover requirements of ungulates.

Nevertheless, the concept of thermal cover remains a poorly tested hypothesis. Peek et al. (1982) argued that descriptive studies of habitat use by ungulates inherently provide weak tests of (1) why animals select certain habitats and (2) the long-term consequences of observed selection patterns (i.e., need versus preference). Use of habitats that ostensibly provide thermal cover may be more related to other needs (e.g., security or forage). Swift et al. (1980) and Hobbs (1989) concluded that thermal cover had negligible influences on ungulates during winter, based on simulation modeling. Hobbs (1989) indicated that forage conditions, either during winter or prior to winter, exerted greater effects on overwinter survival of mule deer (*Odocoileus hemionus*) than did thermal cover.

The biological relevance of thermal cover depends on several conditions and assumptions. First, weather moderation by cover must be sufficiently large to invoke significant energetic benefits. For example, the warming effects of long-wave radiation from forest canopies on ambient temperatures and its absorption by animals may be too small to provide a biologically relevant benefit (Riggs et al. 1993). Second, such energetic benefits of thermal cover must overshadow, or at least significantly supplement, an animal's natural adaptations. Species such as elk possess numerous adaptations to winter weather, including a highly insulative pelage (Scholander et al. 1950*a,b*; Jacobsen 1980); autonomic regulation of vascular circulation in extremities and other tissues (Crawshaw 1980, Parker and Robbins 1984); seasonally reduced metabolism, activity, and energy requirements; and reliance on endogenous energy (Silver et al. 1971, McMillin et al. 1980). In summer, elk dissipate heat via sweating (Parker and Robbins 1984). Such adaptations may cause thermal cover to have a negligible role in energetics of ungulates (Freddy 1984).

Second, if the magnitude of thermal cover effects on weather is sufficiently large to provide significant energetic benefits at various times, then the biological importance of thermal cover depends upon the frequency and duration of weather events that cause standard operative temperature (i.e., air temperature adjusted to reflect wind and radiation flux; *see* Parker and Gillingham 1990) to range above or below thermoneutrality. Such events must increase cumulative expenditures of energy reserves such that survival and/or reproductive rates are reduced. If such events do not occur, then thermal cover has little practical relevance (Riggs et al. 1993).

Widespread acceptance and application of the paradigm risks reducing a variety of management options. For example, the inverse relation between forage production and forest overstory canopy cover is well documented (e.g., Young et al. 1967, McConnell and Smith 1970). Providing relatively large areas of thermal cover therefore could reduce nutritional carrying capacity and herbivore performance. Current definitions of thermal cover also may unnecessarily restrict timber harvest or any other management activity that reduc-

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es forest overstory density. Smith and Long (1987) noted that relaxing the criteria used to define thermal cover would increase silvicultural options significantly. If thermal cover has little practical relevance, then land management aimed at providing thermal cover is unnecessary and even counterproductive from the standpoint of long-term management (Riggs et al. 1993). The complex biophysical relationships, the widespread acceptance and application of the thermal cover paradigm despite lack of scientific testing, and its implications for forest management necessitate rigorous experimental evaluation.

Here we report results of a 4-year evaluation of thermal cover effects on elk during summer and winter. Our goal was to examine the effects of overstory cover on elk condition, with explicit emphasis on thermal-energetic effects of cover. We emphasized condition because it is the primary mechanism through which the effects of thermal cover might influence the likelihood of winter survival and successful reproduction. Condition was used in a relative context and is defined for the purposes of this study as the amount of fat and catabolizable lean muscle mass contained within the animal. Indices of condition were monitored in female elk held in small pens with varying levels of cover during season-long experiments (4 in winter and 2 in summer) to test predictions of the thermal cover hypothesis.

Acknowledgments.—We are indebted for the assistance of L. M. Kemp, L. J. Erickson, and B. K. Johnson of the Oregon Department of Fish and Wildlife for logistical support; R. C. Messinger and J. L. Spicer (deceased) of Boise Cascade Corporation; B. L. Dick, J. C. Nothwang, and R. O. Kennedy of the U.S. Forest Service for assistance with facility construction and moving animals; and others who volunteered their time. B. R., J. M., and K. S. Bobowski, C. W. Bowers, K. A. Brenner, K. A. Brown, M. L. Buhler, S. Cerini, S. E. Clark, K. L. Crane, M. Dial, D. A. and J. L. Hengel, R. Melegari, G. D. and M. Jacobs, J. E. Lee, M. E. Messaros, M. Morrissey, M. O'Leary, L. J. Quinlan, T. W. Stutzman, V. L. Walker, and K. A. Worden served as field assistants. Drs. T. M. McCoy and S. M. Parish treated sick elk. C. T. Robbins provided valuable guidance on raising and training elk calves. K. A. Nagy provided assistance with body composition assessments and deuterium assays. B. B. Davitt provided analysis of elk food. We thank J. Bohne, T. Easterly, L. Erickson, T. Hershey, R. Johnson, R. Kahn, L. Kuck, R. Lanka, R. Lee, B. Welch, D. Zalunargo, and others for assistance with selecting suitable weather stations for various elk winter ranges across the west. This research was conducted in accordance with approved animal welfare protocol (Wisdom et al. 1993).

STUDY AREA

The study site was about 30 km west of La Grande and 8 km southeast of Meacham in the Blue Mountains of northeastern Oregon (Fig. 1). It was considerably higher, colder, and more mesic than winter ranges typically used by elk in the Blue Mountains Ecoregion to help assure a conservative test of predictions of the thermal cover hypothesis (i.e., we included the most severe winter weather conditions as reasonably possible). The site was within the grand fir (*Abies grandis*) zone and primarily supported grand fir–western larch (*Larix occidentalis*) forests. Small stands of Engelmann spruce (*Picea engelmannii*)–lodgepole pine (*Pinus contorta*) and subclimax stands of Douglas-fir (*Pseudotsuga menziesii*) grew on concave and convex sites, respectively. Selective harvesting 50–70 years ago and subsequent growth and regeneration resulted in an uneven-aged, mature forest with a dense overstory canopy about 30 m in height. The study site was located on a gentle (10–20% slope) northeast-facing aspect and ranged from 1,300 to 1,350 m in elevation.

Annual precipitation averaged 87 cm/year. Average minimum and maximum January temperatures were −5.8 and 0.1 C° and minimum and maximum July temperatures were 11.0 and 24.7 C°, based on climatological data (National Oceanic and

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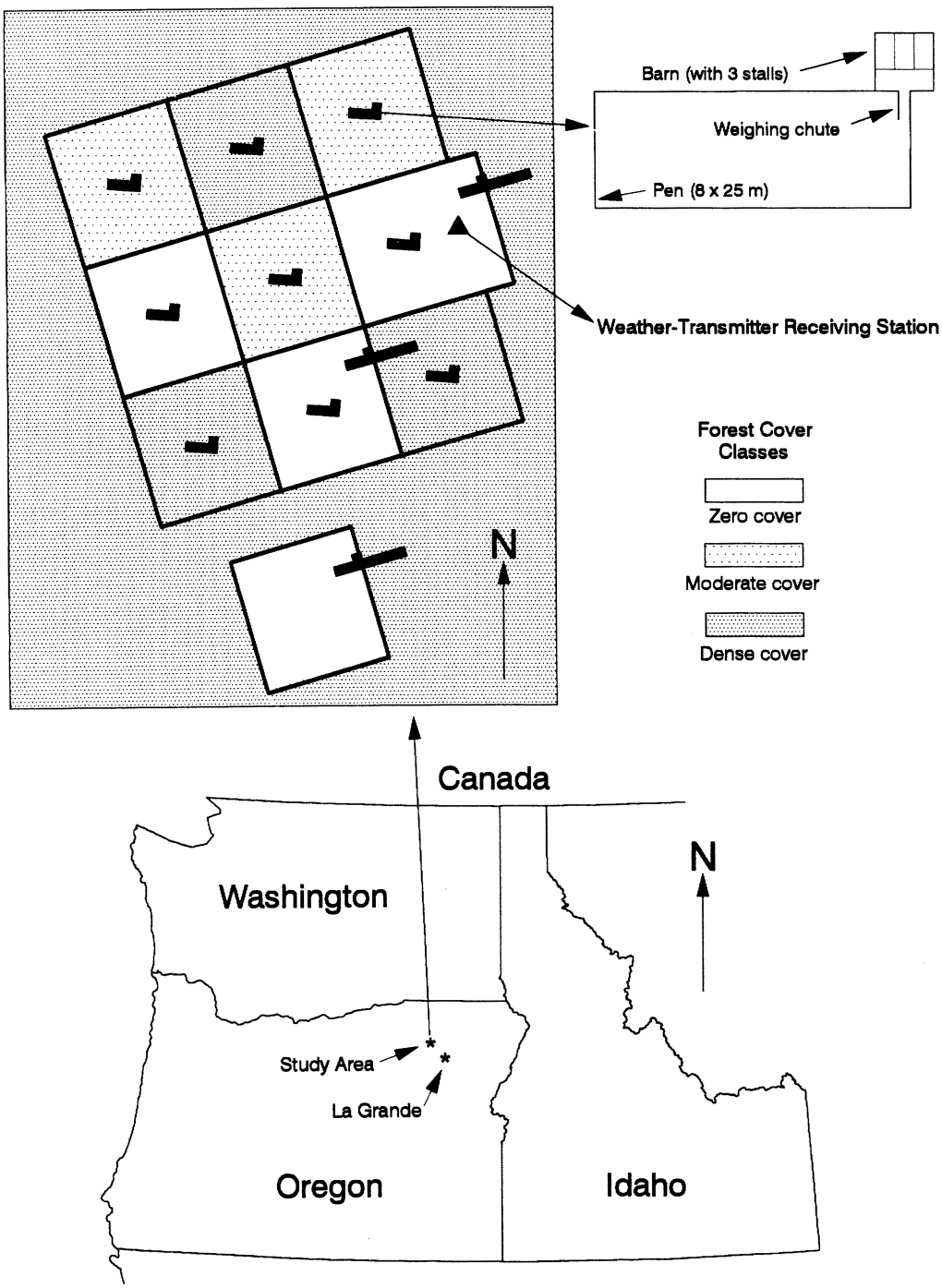

Fig. 1. Layout of 2.3-ha treatment units and holding pens on the study site used for thermal cover studies in northeastern Oregon, 1991–95 (the eastern-most clearcut was 3 ha in size). The 3 elongated pens represent the combination cover treatment units, where elk had access to both the zero cover and dense cover treatments.

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Table 1. Average canopy cover and tree height in each dense, moderate, and combination cover treatment unit in northeastern Oregon. Canopy cover was determined using a concave densiometer (with Strickler's [1959] modifications) and a moosehorn during winter 1992. Detailed descriptions of sampling protocol were presented by Cook et al. (1995).

		Canopy cover (%)					
		Densiometer		Moosehorn		Tree height (m)[a]	
Treatment	Unit[b]	Mean	SE	Mean	SE	Mean	SE
Dense cover	T	88.7	3.16	68.4	5.41	12.5	0.60
Dense cover	M	89.5	3.91	75.8	6.38	16.3	1.37
Dense cover	L	90.8	4.50	66.3	5.82	15.1	0.82
Moderate cover	T	58.8	2.73	28.6	2.23	15.0	1.08
Moderate cover	M	68.3	6.52	29.4	4.88	14.0	0.88
Moderate cover	L	63.7	4.25	30.0	5.10	14.5	1.85
Combination cover	T	91.1	4.43	72.2	6.93	23.4	1.34
Combination cover	M	85.3	8.41	61.7	10.42	15.1	3.31
Combination cover	L	92.6	3.69	61.5	1.00	13.0	1.57

[a] Trees <1 m in height were excluded from the sample.
[b] Unit refers to the individual replicate within treatments, and T, M, and L simply are arbitrary designations.

Atmospheric Administration 1966–75) collected at Meacham over the last 10 years that this station was in operation (the Meacham station was 8 km from the study site at approximately the same elevation). In the Blue Mountains Ecoregion, elk winter at lower and warmer elevations in vegetative mosaics of bluebunch wheatgrass–Idaho fescue (*Agropyron spicatum–Festuca idahoensis*) grasslands and xeric forest of Ponderosa pine (*Pinus ponderosa*)–Douglas-fir that typically range from 500 to 1,000 m in elevation.

The study site was partitioned into 9 2.3-ha square treatment units. Three of these units were clearcut, 3 were selectively cut, and 3 were left uncut (Fig. 1) by random assignment. All forest cover in the clearcut units was removed. This treatment is hereafter referred to as "zero cover." The selectively cut units were harvested to provide 40–69% canopy closure. Postlogging basal area and tree density ranged from 14 to 17 m^2/ha and 115 to 190 trees/ha, respectively, among the 3 units in this treatment. They were harvested as per the definition of "marginal cover" of Thomas et al. (1988) in the habitat evaluation model developed for elk winter ranges in the Blue Mountains. This treatment is hereafter referred to as "moderate cover." Unharvested units had ≥70% canopy closure, ≥12-m-high trees, multilayered canopies, and met the definition of "satisfactory cover" in the habitat evaluation model of Thomas et al. (1988). Basal area and tree density ranged from 23 to 46 m^2/ha and 300 to 520 trees/ha. This treatment is hereafter referred to as "dense cover."

We used a concave densiometer (Lemmon 1956) to estimate canopy cover in the treatment units after harvest (Table 1). Because densiometers significantly overestimate cover (Bunnell and Vales 1990, Cook et al. 1995), cover also was measured using an ocular sighting tube often referred to as a moosehorn (Garrison 1949), a relatively unbiased instrument (Bunnell and Vales 1990, Cook et al. 1995). Even though cover estimated using a moosehorn in several of the units failed to meet criteria of moderate and dense cover (Table 1), concave densiometers generally are used as a primary tool for estimating canopy closure in Pacific Northwest forests (Cook et al. 1995), and elk habitat selection studies upon which current habitat models are based typically used densiometers (e.g., Irwin and Peek 1983, Leckenby 1984). Thus, estimates from the densiometer apparently are appropriate for characterizing cover in our treatment units with respect to definitions of marginal and satisfactory cover presented by Thomas et al. (1988).

An 8 × 25-m elk holding pen was constructed at the center of each treatment

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unit (Fig. 1). All understory vegetation was eliminated from the pens before any of the experiments were conducted. The long axis of each pen was oriented west–east. Pen size was relatively small to minimize dietary confounding from lichen and arboreal vegetation falling into the pens during winter (but the pens were adequately large for running and playing). A small barn (3 × 4 m) with 3 stalls was placed on the north side of each pen, so that the barn provided no shade inside the pen and was connected to the pen with a weighing chute (Fig. 1). The barn was used for weighing, feeding, collecting physiological samples, and treating sick animals. A hay manger for feeding was attached on the outside of the barn, inside the pen.

A fourth treatment called "combination cover" provided elk with dense cover and zero cover habitats within the same pen. Because the decision to include this treatment was made after the original treatment units were harvested, 3 replicates of this new treatment could not be randomly assigned to the study area. Instead, site selection of these pens was based on 2 criteria. First, we required that solar radiation be available in the clearcut portion of the pen most of the day. Second, we deemed that obtaining as much interspersion of the new combination units as possible among the other treatment units was desirable (Hurlbert 1984) because randomization was not possible. Two of the 3 pens for this combination treatment were constructed within the study area on the west side of 2 dense cover units. An additional clearcut was harvested immediately adjacent to the study site for placement of the third pen (Fig. 1). The 3 pens for this treatment were rectangular and measured 7 × 70 m, with 50 m extending into dense cover and 20 m extending into clearcuts. Distance into dense cover was based on selection patterns of free-ranging elk in relation to distance into forests from the forest edge (Leckenby 1984). The barn for each of these combination treatment pens was constructed at the forest–clearcut edge on the north side of the pen.

Each of the 12 pens and barns held 3 elk; thus the facilities accommodated 36 elk. A small house trailer and feed storage facilities were located on the site. The house trailer provided room-temperature conditions for handling physiological samples and a freezer for storing the samples until they could be moved to more permanent storage.

ELK HERD

Two cohorts of female elk were bottle-raised for this study, the first during summer 1991 and the second in summer 1993. The elk were captured when 1–4 days old from a 70-ha enclosure on the winter feeding grounds of the Starkey Experimental Forest and Range or from areas outside the Starkey Experimental area in northeast Oregon. Calves were raised in a calf-rearing barn at the Starkey Experimental Forest and Range using protocol described by Cook et al. (1994, 1996). The 1991 cohort, consisting of 30 calves, was moved from Starkey to the thermal cover study area in October 1991 and the 1993 cohort, consisting of 39 calves, was moved in late July 1993. Calves were weaned in early November and in mid-October in 1991 and 1993, respectively, about 6 weeks before thermal cover experiments began.

METHODS

The experiments were primarily designed to test the null hypothesis that forest cover does not affect condition of elk. Response variables included 2 sets of measures of condition: body mass and body composition (Harder and Kirkpatrick 1994). If thermal cover has a significant positive effect on condition, we would expect a gradient of reduced condition among elk held in the combination, dense, moderate, and zero cover treatments. We monitored 24-hour activity budgets to determine if elk compensated for lack of thermal cover by altering activity patterns (Gilbert and Bateman 1983). Water consumption also was measured during summer to assess thermal cover effects on water requirements.

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Each of the 4 thermal cover treatments were replicated 3 times. Pens, rather than elk, were designated the experimental unit and data from elk in each pen were pooled to provide a single estimate per pen. Four winter and 2 summer experiments were conducted over the 4 years of the study. Each experiment lasted 3.5–4 months, generally from early December through mid-March during winter and from late May through mid-September during summer. The measures of relative condition were monitored across the experiments. The 1991 cohort of elk was used in the 1991–92 winter experiment as calves and in the 1992 summer and 1992–93 winter experiments as yearlings. Similarly, the 1993 cohort was used in the winter 1993–94, summer 1994, and winter 1994–95 experiments.

Weather data were collected at the study site during the experiments primarily for 3 purposes: (1) to assess the effects of forest cover on microclimate at elk height, (2) to compare weather conditions among experiments, and (3) to provide a basis for assessing the general applicability of study results across different climatological settings. Long-term weather records collected by the National Oceanic and Atmospheric Administration were used to compare the relative severity of weather during the experiments to that typically occurring in the northeast Oregon region.

Weather

An automated weather station was located in the eastern-most clearcut (Fig. 1). This station was used to monitor weather conditions during the entire study. The station included probes to measure windspeed (Met-one 014A windspeed sensor), relative humidity and temperature (HMP 356 temperature–relative humidity probe), solar radiation (LI-COR 200S pyranometer), and net hemispherical radiation (Q-6 net radiometer [Fritschen]). A CR10 control module accumulated and stored data on a SM192/716 storage module in PC compatible format. All equipment was obtained from Campbell Scientifics, Inc., Logan, Utah, USA. This system provided estimates of each weather variable averaged over 15-minute intervals.

A second, equivalently equipped station was rotated weekly among each of the pens beginning the third year of the study. Data from this station were used to assess the effects of varying levels of forest cover on microclimate in the zero cover, moderate cover, and dense cover treatment units. This mobile station was rotated among pens at 1-week intervals providing 2 weeks of data per experiment at each pen. It was placed on the south side of, outside of, and at the center of the pens. Data from the permanent and mobile station were used to develop prediction equations, such that weather at each pen site could be predicted from weather data recorded from the permanent station across the entire experiment. We calibrated the weather probes of the 2 stations to account for inherent differences among them. Both stations were placed adjacent to each other for 4 1-week periods from December 1993 to April 1995, and weather measurements from them were used to develop correction equations that adjusted the mobile station's estimates to match estimates from the permanent station.

Ancillary data were collected on general weather conditions to aid development of the prediction equations. Personnel recorded cloud conditions, timing of precipitation, and times that the solar- and net-radiation probes were covered with water, ice, frost, dew, or snow. Data collected from the radiation probes could not be used when covered (one of the first activities during the day was to clean the probes). Because no personnel worked at night, decisions about cloud conditions at night were based on observations at the end of the work day and the beginning of the next work day. Identification of precipitation during the night was based on measurement each morning of snow deposited on a protected platform or rain in a rain gauge.

We used weather data collected by National Oceanic and Atmospheric Administration (1991–95) at La Grande, located 30

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km east of the study site at 850 m in elevation, to assess how weather conditions during the experiments compared to long-term, 30-year averages. Because weather data collected at the study area were not directly comparable to those collected in La Grande, the comparisons were based entirely on data collected at La Grande. This analysis was limited to average temperature and precipitation; no other relevant long-term weather data were available for the La Grande station.

Handling and Feeding

Elk were fed twice daily (typically at 0800 and 1400 hr) throughout the study. Each morning, elk were brought into the barn and fed pelleted food individually. Alfalfa hay was fed communally in the afternoon in hay managers located inside the pen. Elk were held in the barns 30–60 minutes in winter and about 2 hours in summer, providing only enough time for consumption of pellets offered. Hay composed about 40% of the total amount of food offered. We initially attempted to feed hay at 20%, but had problems with chronic enteritis due to insufficient dietary fiber. Feeding higher proportions of hay solved this problem, but the enteritis delayed the winter 1991–92 experiment by 2 weeks.

The winter feeding regime was designed to provide submaintenance digestible energy and to induce average body-mass losses of about 5% in calves and 10% in yearling cows. These levels enhanced susceptibility of elk to their energetic environment (i.e., well-fed animals might not be sensitive to differences in thermal environments from the forest cover treatments) and induced mass loss typical in winter, without unduly risking death. Animal-specific feeding levels were set at the beginning of each winter trial and held constant through winter. Individual feeding levels were based on each animal's metabolic mass (kg body mass$^{0.75}$).

The feeding regime was more complicated in summer. Our objective was to support high growth rates unrestricted by nutritional level while maintaining equal daily intake among individual elk, thereby removing the confounding effect of dietary variation. This was not strictly possible, however, because mass-specific daily food intake of about 10% of the elk was markedly lower than that of the other elk. Feeding at the intake level of the least thrifty elk would ensure equal intake, but would have reduced growth of the others. We compromised by feeding at a level in which all elk except the 3 or 4 least thrifty consumed all food offered each day. Because daily intake of yearling elk increased as they grew, feeding levels were adjusted at 2-week intervals to account for temporal changes in intake. As in winter, the amount of food offered to each elk was based on metabolic mass.

Elk were fed a moderate quality pellet that met or slightly exceeded protein and digestible energy requirements for maintenance during winter (Table 2). They were fed a higher quality pellet that exceeded requirements of crude protein and digestible energy for growth during spring through fall. Vitamin and mineral supplements were added to each pelleted ration at a level that met requirements published by the National Research Council (1984, 1985) for domestic livestock, and mineral blocks were provided in each pen. No effort was made to feed hay of different quality in winter versus summer. Protein content of hay exceeded requirements in all seasons; digestible energy content generally met or exceeded requirements for maintenance in winter and was slightly below requirements for growth in summer (Table 2). The submaintainence diet in winter was therefore induced by restricting quantity of food offered more so than by restricting quality.

Each elk's pellet ration was weighed daily before elk were brought into the barns, and orts were weighed soon after elk were released from the barns. Virtually all hay was consumed each day, so weighing hay orts was rarely necessary. Composite samples of pellets and hay were collected for nutritional analyses over the duration of each experiment. The Habitat Analyses

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Table 2. Crude protein (CP), gross energy (GE), in vitro digestible dry matter (DDM), digestible energy (DE), and primary ingredients of rations fed to elk during thermal cover experiments in northeastern Oregon. All nutritional values are expressed on a dry-matter basis. The pelleted rations were manufactured by Pendleton Grain Growers (Hermiston, Oregon, USA).

Season	Year	Ration	CP (%)	GE (kcal/g)	DDM (%)	DE (kcal/g)	Primary ingredients
Winter	1991–92	Pellets	12.3	4.341	63.5	2.76	Oats, ryegrass screenings
		Hay	18.1	4.476	63.0	2.82	Alfalfa
Winter	1992–93	Pellets	10.5	4.420	61.8	2.73	Oats, oat hulls[a]
		Hay	17.9	4.504	59.1	2.66	Alfalfa
Winter	1993–94	Pellets	11.5	4.265	59.7	2.55	Oats, ryegrass screenings
		Hay	17.2	4.496	58.7	2.64	Alfalfa
Winter	1994–95	Pellets	12.1	4.350	62.2	2.71	Oats, ryegrass screenings
		Hay	18.2	4.397	57.9	2.56	Alfalfa
Summer	1992	Pellets	15.5	4.412	72.2	3.19	Oats, wheat, alfalfa hay
		Hay	17.0	4.325	56.8	2.46	Alfalfa
Summer	1994	Pellets	13.9	4.314	74.0	3.19	Oats, wheat, alfalfa hay
		Hay	18.7	4.458	57.0	2.54	Alfalfa

[a] Ryegrass screenings were commercially unavailable when this ration was produced, and oat hulls were used as a substitute.

Laboratory, Washington State University, Pullman, Washington, USA, estimated crude protein by macro-kjeldahl analysis, gross energy by bomb calorimetry, and dry matter digestibility by 2-stage in vitro trials (Association of Official Analytical Chemists 1980). Digestible energy content was estimated as the product of gross energy and in vitro digestibility (Hobbs et al. 1982).

Elk were assigned to pens randomly for every experiment, with the constraint that each pen contained elk of approximately the same distribution in body mass. This was accomplished by ranking each elk by body mass and subdividing the population into 3 size categories (i.e., small, medium, and large), with each category containing about the same number of elk. For each pen, 1 elk was randomly selected from each category. For experiments in which the number of elk was insufficient to fill all pens, elk were divided into 2 body-size categories. After randomly selecting pens that would receive 2 instead of 3 elk, an elk from each of the 2 categories was assigned to the pen. When these pens were filled, the remaining elk were restratified into 3 categories, and elk were assigned to unfilled pens as described above.

Ten to 14 days prior to the beginning of each experiment, elk were moved to their randomly assigned pen. This time period was selected to minimize the effects of thermal cover influences of the new pen on our condition indicators measured at the beginning of the experiment and to provide sufficient time for elk to habituate to their new pens prior to the beginning of the experiment.

Body Mass

Elk were weighed twice weekly as they entered the barn for the morning feeding during the first 3 years of the study and as they exited the barn, after eating, during the last year of the study. This change was initiated because several elk would not enter if weighing gear was set up. Portable electronic scales were placed underneath a floating floor in each chute to obtain mass. Doors on the chute held the elk stationary until a reliable mass estimate was obtained.

Body Composition

Water, fat, protein, ash, and total gross energy of the ingesta-free body were determined in vivo using isotope dilution techniques (Robbins et al. 1974, Torbit 1985*a*) at the beginning and end of each seasonal experiment. Technical problems precluded usable results for the winter 1991–92 and summer 1992 experiments. A number of modifications of our protocol after summer 1992 largely eliminated technical problems.

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Deuterium oxide (D_2O: VWR Scientific, Seattle, Washington, USA) (Rumpler et al. 1987, Watkins et al. 1990) was used in the body composition determinations. We used the single-point equilibrium approach (Watkins et al. 1990) rather the multisample regression approach of Torbit (1985*a*) and Knox et al. (1969). Watkins et al. (1990) indicated, however, that the single-point approach may overestimate body water ≤20% compared to the multisample approach, for reasons that are not completely understood. We evaluated the extent of this potentially important bias using 12 elk calves during February 1994. We collected the 5-hour equilibrium sample using our standard protocol described below, and sampled serially at 1, 2, 3, and 6 days after injection. We used the approach of Knox et al. (1969) and Torbit (1985*a*) to estimate isotope concentration at equilibrium for the serial samples. The multisample approach underestimated D_2O concentration by 3.6 ppm compared to the single-point approach ($P = 0.003$; df = 11; paired t test), thereby resulting in higher (by 3–4 percentage points), rather than lower, estimates of body water than that obtained using the single-point approach. We therefore concluded that the potential bias of the single-point approach discussed by Watkins et al. (1990) was unimportant in our data and used the single-point approach to reduce costs and handling of elk. These data do suggest, however, that our estimates of body water content were slightly overestimated (by ≈3–4 percentage points), probably because we sampled slightly before equilibrium actually occurred.

Body composition trials began by bringing elk into the barns in the morning and sedating them with carfentanil citrate (6–10 μg/kg body mass). A blood sample was taken to determine naturally occurring (background) D_2O levels, D_2O was injected via a syringe into the elk's left jugular vein, and the immobilization effects were immediately reversed with naltrexon hydrochloride (0.6–1.0 mg/kg body mass). Carfentanil was used for immobilization, rather than xylazine hydrochloride, to avoid potentially confounding diuretic effects of xylazine (Green and Thurmon 1988). The injected solution contained 99.98% D_2O; amount of solution infused was 0.9 g/kg body mass. Upon injection, the blood was drawn back into the syringe several times to ensure that all isotope was injected. The solution was weighed in the syringes using electronic scales in the early morning (0500–0700 hr) just prior to the beginning of the body composition determinations.

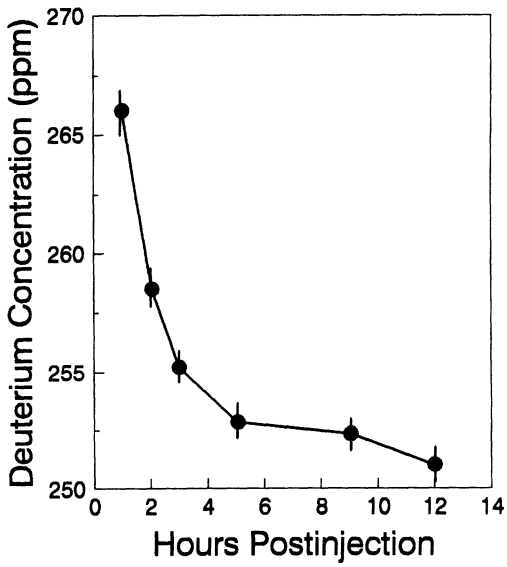

Fig. 2. Relation between deuterium oxide concentration in body water of 6 elk calves and time after deuterium injection determined during November 1991 in northeastern Oregon (J. G. Cook, unpubl. data). Vertical lines are SEs. About 5 hours were required for deuterium to reach equilibrium in these elk calves.

Five hours after D_2O injection, elk were manually restrained and a second blood sample was obtained from the right jugular vein. This sample provided estimates of isotopic concentration at equilibrium with body water. Five hours were required for equilibration based on trials conducted in November 1991 (Fig. 2). Although 1–2 hours were considered sufficient in several deer studies (DelGiudice et al. 1990, Watkins et al. 1990), Nagy (1983) and Nagy and Costa (1980) indicated that 5–10 hours are required for isotope equilibrium in large ruminants.

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Elk were held in their stalls and provided no food or water during the equilibration period. The background and equilibrium samples were transferred from syringes to heparinized microhematocrit tubes and were flame sealed using a small butane torch immediately after collection. The sample tubes were held in storage >3 months so that unsealed tubes could be identified and discarded. Sealed samples were then submitted to the Laboratory of Biomedical and Environmental Sciences (University of California, Los Angeles, USA) for D_2O concentration assays using a Finnigan-MAT delta E gas isotope ratio mass spectrometer (Finnigan Corporation, San Jose, California, USA).

Total amount of body water (TBW) was calculated based on the ratio between equilibrium D_2O minus the background D_2O levels and the amount of injected D_2O. Because estimates of TBW typically exceed true TBW by 3–7% for tritium and D_2O (Watkins et al. 1990), we reduced our estimates of TBW by 4% (e.g., Torbit 1985*a*). We used the formula of Robbins et al. (1974) to estimate ingesta-free body mass (IFBM = $e^{(-0.0771 + 0.9928 \ln x)}$; where x = live body mass. Ingesta mass (IM) was then calculated as the difference between live body mass and IFBM, and ingesta water (IW) was estimated as IM × 0.87 (0.87 was based on proportional water content of ingesta determined by Torbit [1985*a*] for mule deer in winter). Water content of the ingesta-free body was calculated as IFBW = TBW − IW.

Comparison of body composition estimates among seasons potentially was confounded by differences in feeding rates and, therefore, ingesta content between summer and winter. We assessed the effects of changing intake rates on ingesta contents and developed a correction for higher summer food intake using data collected in another study with 6 yearling and 6 3-year-old elk during spring 1995. In that study, feeding levels were changed dramatically (≤90%) at 2-week intervals over a period of 8 weeks. We calculated the percent change in body mass based on body mass 1–2 days prior to and 4–5 days after feeding levels were changed. Percent body-mass change was regressed on percent change in intake to estimate the effect of intake on ingesta content (Fig. 3). The amount of ingesta resulting from the higher intake levels in summer was added to the amount of ingesta calculated for IM described above. We again assumed that amount of ingesta water was 87% of total ingesta mass.

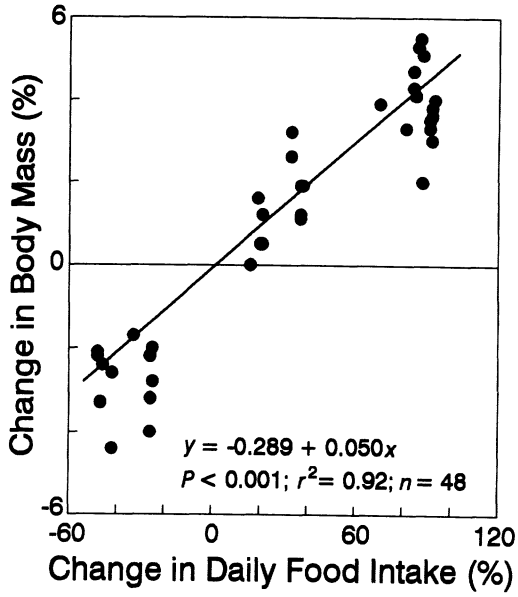

Fig. 3. Relation between percent change in daily food intake and short-term (i.e., 1 week) percent change in body mass, assumed to be due to changes in mass of alimentary tract contents. Data were collected from 6 yearling and 6 3-year-old captive cows in spring 1995 in northeastern Oregon (J. G. Cook, unpubl. data).

Subsequent estimation of various body-composition variables of the ingesta-free body followed calculations of Torbit (1985*a*), which were originally developed by Robbins et al. (1974) for white-tailed deer (*Odocoileus virginianus*).

1. Percent body water was calculated as IFBW% = IFBW ÷ IFBM × 100.
2. Percent body fat was calculated as IFBF% = 80 − (1.083 × IFBW%).
3. Body fat (kg) was calculated as IFBF = (IFBF% ÷ 100) × IFBM.
4. Ash (kg) was calculated as IFASH = $e^{-2.9 + (0.95 \times \ln \text{IFBM})}$.

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5. Percent ash content was calculated as IFASH% = IFASH ÷ IFBM × 100.
6. Protein (kg) was calculated as IFPR = IFBM − (IFBW + IFBF + IFASH).
7. Percent protein content was calculated as IFPR% = IFPR ÷ IFBM × 100.
8. Gross energy content (Mcal) of the ingesta-free body was estimated by IFMCAL = (IFBF × 9.49) + (IFPR × 5.41) (Robbins et al. 1974).
9. Concentration (Mcal/kg BM) was estimated by IFMCALC = IFMCAL ÷ IFBM.

A substantial proportion (about 25%) of D_2O concentration estimates, either background or equilibrium blood samples, produced unrealistic estimates of body water content, e.g., estimates of body water that exceeded body mass. This was due to difficulties with flame-sealing the hematocrit tubes. Unrealistic estimates of background D_2O concentrations were easily identified, because naturally occurring D_2O concentration is approximately constant among animals (±3–4 ppm). Deviant background D_2O values were simply replaced by the average of nondeviant values. Duplicates of equilibrium samples that were unrealistic were resubmitted for laboratory analysis. In most cases, results of the second analysis produced realistic estimates of body water; if not, these data were excluded from body-composition analyses.

Estimation of ingesta content, fat, protein, and ash rely on data and equations developed from deer. Therefore we caution that our body-composition estimates should be considered a relative, rather than an absolute, estimate of composition.

Activity

Activity budgets were monitored on a 24-hour basis using an activity recording system described by Riggs et al. (1990). This system used motion-sensitive transmitters (MOD-400, Telonics, Inc., Mesa, Arizona, USA) attached to the shank of the right-front leg. Identification of activity was based on differences in pulse rate diagnostic of different activities. Transmitter signals were received at a station located on the study area. This station consisted of an omnidirectional antenna and a programmable scanning receiver coupled to a digital data processor (TDP-II, Telonics, Inc.) and datalogger (CR10, Campbell Scientific, Inc., Logan, Utah, USA). Data recorded and stored with this system were downloaded to an office-based microcomputer.

One transmitter was deployed per pen and was rotated among elk in each pen at 2-week intervals. Data storage media typically were filled to capacity (roughly 1.5 megabytes) after 48 hours of operation, requiring downloading to computers at 48-hour intervals. The standard routine for data collection was 48 hours on-line and 24 hours off-line throughout each experimental period. No activity data were collected on days that elk were sedated for changing transmitters or collecting physiological samples. The scanner was programmed to dwell 30 seconds on each of the 12 transmitter frequencies, resulting in about 120 minutes of data collected during 240 scans per elk per 24-hour period. Activity was sampled approximately 16 days each month during each experiment.

We identified 5 levels of activity with this system: (1) bedded, (2) standing with little or no walking (defined as 0–5 steps per 30-sec scan period), (3) slow walk (defined as 6–9 steps per scan period), (4) pacing (a deliberate, moderate to rapid walk defined as 10–20 steps per scan), and (5) running (defined as ≥30 steps per scan). Identification of activity was based on several features of the transmitter. When the transmitter is horizontal (e.g., the animal is bedded), the interpulse period (IPP) (i.e., time between transmitted pulses) of the animal is short (800 msec between pulses) and nearly constant. When the animal is standing, IPPs are longer (about 1,400 msec between pulses) and again are roughly constant. When the animal takes a step, IPPs during the step vary between the bedded and standing IPPs (referred to as walking IPPs). The slower the walking rate, the fewer the walking IPPs per scan and vice versa. The

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system was programmed to sample the IPPs every 650 msec, thereby producing 45 estimates per 30-second scan. These estimates were stored as a line of data along with the time and date of the scan and transmitter number.

Correct identification of activity when elk were bedded is virtually 100% accurate (Riggs et al. 1990) because the IPPs for this activity are distinct and stable. Accurate identification of the different activities when elk were nonbedded was more difficult and required considerable field sampling to develop and validate the computer programs designed to differentiate among them. Leading elk by hand to induce different rates of walking, we first generated data sets to identify various attributes of the IPP data (e.g., mean, standard deviation, skewness, and others) that were best correlated to the number of steps taken during the scan. We collected a second data set using a different transmitter to confirm our findings of the first and to develop regression models to predict the number of steps per scan. Finally, we developed 3 more data sets using 3 different transmitters to test the accuracy of the prediction model.

Skewness of IPPs and number of walking IPP values, per 30-second scan, most accurately and consistently (i.e., among transmitters) predicted nonbedded activity levels. Both were nonlinearly correlated with number of steps taken ($r^2 = 0.83$ and 0.88, $n = 242$, $P < 0.001$). We developed a regression model that included both variables and their quadratic (nonlinear) terms to predict number of steps ($r^2 = 0.90$, $n = 242$, $P < 0.001$). Predicted number of steps was converted to one of the 4 nonbedded activity categories and compared to observed activity using the 3 validation data sets ($n = 261$). Accuracy of prediction of all nonbedded activities was 92% (Fig. 4). The regression model was as follows.

$$y = 7.7757 - 0.17432(W) + 0.0128127(W^2) + 2.39635(S) + 0.2230298(S^2)$$

where

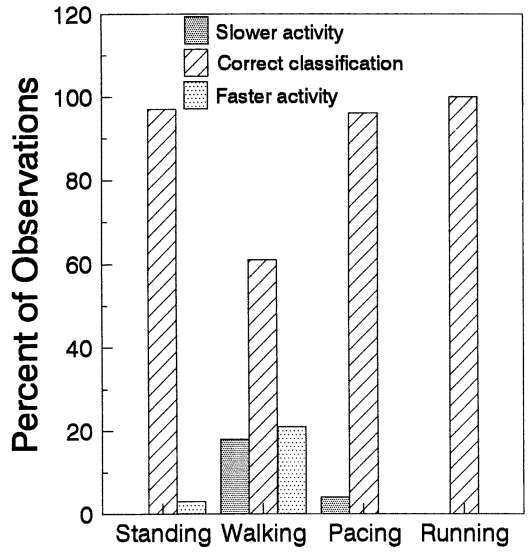

Fig. 4. Within-activity classification accuracy of prediction equation using pulse-rate data from leg-mounted transmitters on captive elk during spring 1995 in northeastern Oregon. Activity definitions were as follows: standing = 0–5 steps, walking = 6–9 steps, pacing = 10–20 steps, and running = ≥30 steps per 30-second observation.

y = number of steps per 30 second scan,
W = number of walking IPP values per scan, and
S = skewness of IPP values per scan.

Problems occasionally were encountered with performance of the system caused by transmitter malfunctions and, rarely, problems with the receiving equipment. The computer program that was written to identify activity of elk therefore included a set of diagnostics that identified and flagged any lines with anomalous data. Lines containing anomalous data were manually checked and excluded from analysis if deemed unreliable.

Distribution of Elk in Combination Cover Pens

We assessed elk use of different portions of the pens in the combination treatment at night during winter by recording the location of elk beds in snow. These data were used to assess selection for the 2 major cover types in the pens. The pens

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were stratified into 5 portions: (1) clearcut, (2) forest edge (underneath the canopy on the clearcut side to 6 m within the forest from the forest edge), (3) first half of the forested side (beginning at 6 m from the forest edge), (4) the second half of the forested side (ending at 4 m from the end of the pen), and (5) the last 4 m of the pen on the forested side. The number of beds in each portion of the combination pens was counted each morning of the winter trials when the elk were brought into the barn. Beds were not counted when snow conditions were unsuitable for identifying bed sites. Near the end of the work day, snow was shoveled into the beds so that reuse of beds would be readily apparent the following day.

Summer Water Consumption

The amount of water consumed during summer was measured each day in each pen. Water was provided in 80-liter tubs placed in pen corners; barriers were placed in front of the tubs so that elk could not easily splash water or overturn the tubs. Water consumption was measured by filling the tubs to a mark in the tub each day. We used a measuring bucket to measure the amount of water to refill the tubs in 1992. In 1994, we developed a system with an in-line water meter connected by hose to a water tank mounted on the back of a pickup truck. The water-meter system was less cumbersome and more accurate.

We accounted for water lost through evaporation and differential evaporative water loss among treatments by measuring water loss in tubs (1 in each treatment) placed in the zero cover, moderate cover, and dense cover treatments (the tubs were placed outside the pens and were covered with a wire mesh to exclude free-ranging wildlife). Water loss was measured on 35 days lacking precipitation from early August through mid-September 1994. We developed 3 regression equations, one for each cover treatment, that predicted evaporative water loss based on average daily temperature. Water lost through evaporation (estimated using the regression equations) was subtracted from measured water loss to estimate water consumption.

Data Analyses

Weather.—We used daily maximum and minimum ambient temperatures and average daily windspeed collected on the study area to assess differences in weather conditions among each experiment. We tested for differences in each of the 3 weather variables for each month of the experiment and across the entire experiment using 2-factor, fixed-effects ANOVA (PROC GLM, SAS Institute 1988). Month and year (i.e., experiment) composed the factors. The least significant difference multiple comparison technique was used to identify significant differences among years.

We developed equations to predict weather at each pen based on weather data collected at the permanent station using stepwise multiple regression (PROC REG, SAS Institute 1988). Prediction equations were developed for each of the 5 weather variables for each pen site. Independent variables included in regression analysis for prediction of temperature and relative humidity included temperature, windspeed, and relative humidity recorded at the permanent station. Squared and $\log_e$ transformations of each variable also were included as independent terms to account for nonlinear effects of each of the independent variables. Solar- and net-radiation data were not used to predict temperature because these were occasionally unusable due to water or snow that collected on the probes. Independent variables used to predict windspeed included only windspeed at the permanent station. Independent variables used to predict solar and net radiation at the pens included solar and net radiation, temperature, windspeed, relative humidity at the permanent station, and squared and $\log_e$ transformations of these variables. Weather data collected from the mobile station were adjusted to correct for inherent differences between the mobile and permanent station before

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stepwise regression analyses were conducted.

Because specific relations between weather variables at the permanent station and those at the pens often changed from day to night or among cloud–precipitation conditions, we calculated prediction equations for each combination of day–night and cloud–precipitation conditions. Cloud–precipitation conditions were separated into 3 categories: (1) clear to partly cloudy (0–50% cloud cover, no precipitation), (2) partly cloudy to cloudy (50–100% cloud cover, with virtually no precipitation), and (3) cloudy (>90% cloud cover) with at least occasional precipitation. Day–night periods were based on solar radiation data: solar-radiation values of 0.0 occurred during night; solar radiation values >0.0 occurred during the day (this approach was operational even when the solar-radiation probe was covered with precipitation, because light nevertheless penetrated to the probe).

The regression analysis was set to select independent variables to maximize the adjusted coefficient of multiple determination (adjusted r^2). The number of variables was limited to the 3 that best accounted for the variation in the dependent variable. However, any variables that were included in the best set of 3, but were not significant or did not improve the adjusted $r^2 \geq 1\%$, were eliminated from the equation. In addition, we used separate equations for each diurnal period and each cloud–precipitation category if regression coefficients for independent variables changed substantially among categories and/or if r^2 values were improved by developing unique equations for each category. Weather data collected in the winters of 1993–94 and 1994–95 were combined and used to develop equations for winter. Weather data collected in summer 1994 were used to develop equations for summer. This approach required generation and assessment of about 1,200 equations for each seasonal period.

A program was written that estimated weather data every 15 minutes at each pen site using the selected regression equations, weather data collected at the permanent station, and the day–night and cloud–precipitation categories. We then calculated hourly means for each weather variable using the estimate taken 15 minutes before the hour, the estimate taken on the hour, and the estimate taken 15 minutes after the hour. Thus, the weather data set was simplified to 24 estimates of each weather variable, rather than 96, per 24-hour period.

Differences among the treatments were calculated using the zero cover treatment as the basis for comparison; we subtracted the estimates of each weather variable predicted at each pen from the average calculated across the 3 zero cover pens. Thus, difference estimates always equaled 0.0 for the zero cover treatment. Positive difference estimates for the moderate and dense cover treatments indicated they were greater than that in the zero cover treatment, and negative estimates for the 2 treatments indicated they were less than that in the zero cover treatment. We then calculated the average difference for each weather variable in each treatment for each hour across all days in each seasonal period (2 winters combined and 1 summer).

Because this was a modeling exercise and all data values were predicted from equations of varying accuracy, we believed that statistical testing for significant differences among treatments was unwarranted. We did, however, calculate 95% confidence intervals around the zero cover mean (based on 3 estimates, 1 per zero cover pen, at each hour). This provided some indication whether or not the magnitude of differences between the moderate or dense cover treatments and the zero cover treatment were relevant given the amount of variation among the 3 zero cover treatment units.

Body Mass.—Body mass was converted to percent change in mass for analysis. The 2 estimates of mass collected per week were averaged into a single estimate for the week. Percent change in mass was calculated as the difference between the mass at the beginning of the experiment

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and mass during each week of the experiment, divided by the beginning mass and multiplied by 100. Beginning mass was calculated by averaging estimates from 4 weighings: the second body-mass estimate from the previous week, both estimates during the first week, and the first estimate of the second week of the experiment. Using 4 rather than 2 mass estimates provided a more reliable estimate of beginning mass.

The effect of thermal cover on percent change in mass was analyzed with fixed-effects, 1-way repeated measures ANOVA using the multivariate mode of PROC GLM in SAS (SAS Institute 1988). The 4 levels of the single factor (i.e., forest cover) with 3 replications of each level were included in this analysis. The test statistic for this analyses was the time × treatment interaction effect, because the treatment effects would appear after the experiment began and increase through time if thermal cover influenced body mass. Differences among treatments each week were assessed using the least significant difference multiple comparison procedure. Data from each experiment (4 during winter and 2 during summer) were analyzed separately. The assumption of sphericity (SAS Institute 1988:605) was routinely violated in these analyses; we therefore used the Huynh-Feldt adjustment to the numerator degrees of freedom for the time × treatment interaction to account for this violation (SAS Institute 1988:605).

Despite our randomization efforts to ensure similar average body mass of elk among pens, there remained some possibility that differences in body mass confounded relations between elk performance and treatments (i.e., smaller elk may have been more susceptible to the treatments). We assessed the possibility of this confounding influence by initially conducting the repeated measures ANOVA with average beginning body mass in each pen (experimental unit) as a covariate. There was no effect (nor any tendency of an effect) of average body mass in the pens on body-mass dynamics over any of the winter or summer experiments (P always > 0.43 and usually > 0.75 for the body mass, time × body mass, and time × body mass × treatment effects across all winter and summer experiments). This indicates that our randomization procedure successfully eliminated this potentially confounding effect, and we therefore excluded beginning body mass as a covariate in all ANOVAs conducted.

All data from calves that died or were removed from the experiments for various reasons were excluded from the repeated measures ANOVA. This removal of data was insignificant during all experiments except the winter experiment of 1993–94. In it, 3 calves died and 6 were removed from the study to prevent death due to unusually severe body mass loss rates. The decision to remove calves from the study to prevent death was based on distinct behavioral attributes. Such calves were unable to stand and acutely hypoglycemic (glucose levels ranging around 40 mg/dL compared to normal levels of 90–120 mg/dL). This experiment was terminated in late February to avoid any further mortality.

For this winter experiment, we conducted 2 analyses. First, we tested the hypothesis that the 9 "deaths" were randomly distributed among the 4 cover treatments using Fisher's Exact Test (rather than Chi-square, because a large proportion of the cell counts were <5; Zar 1974). Thus, we treated attrition as a response variable for this experiment. Second, using body-mass data collected through 21 February 1994, during which all calves except 6 remained in the study, we conducted the normal repeated measures ANOVA (data from the 6 "dead" calves were excluded). All elk from one of the pens were removed, such that the ANOVA was unbalanced ($n = 11$ rather than the usual 12).

Winter Weather Effects on Body Mass.—We used weather and elk body-mass data to more specifically assess what features of weather contributed most to observed body-mass dynamics of the elk over the 4 winters of study. Three of the 5 weather variables measured (windspeed, solar radiation, and temperature) were se-

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lected for this analysis because they are considered key determinants of energy balance (Parker and Gillingham 1990). Percent daily mass change (calculated using simple linear regression over 6-week subunits of each winter period) was included as the dependent variable, and average daily solar radiation, average minimum temperature, and average daily windspeed during the 6-week period were included as independent variables in multiple regression analysis (PROC REG, SAS Institute 1988). Solar radiation was converted from watts/m^2 to kcal/m^2/day such that cumulative daily solar radiation could be used in these analyses, an approach that would better account for seasonal change in day length. In addition, it might be expected that as winter proceeded, elk would become more acclimated to winter weather and the submaintenance diet, such that the tendency to lose body mass at any point during winter might depend upon the amount of prior mass change. This might result primarily because energy intake on a metabolic mass basis would increase as the elk lost mass through catabolism of fat and muscle even though total feeding level remained constant. Thus, percent change in mass, calculated from the beginning of the experiment to the beginning of the 6-week period, also was included as an independent variable in the multiple regression analysis. This variable is hereafter referred to as beginning percent change in mass (BPCM).

There were 2 6-week periods each winter extending from 15 December to 31 January and from 1 February to 15 March. Weather and mass dynamics data during the 6-week periods estimated for each pen (excluding the combination treatment pens) composed the experimental unit for this analysis. Pens that lost elk during the 1993–94 winter experiment were excluded from this analysis beginning at the time elk were removed from the pen. This approach risks lack of independence of error terms due to within-pen autocorrelation among sequential (early to late winter) estimates of change in body mass. But including percent change in mass at the beginning of the time period as a regressor variable accounted for a key source of this potential autocorrelation.

The specific contribution of each independent variable on percent mass change also was examined with the effects of the other variables controlled. Each independent variable was regressed on the residuals (observed percent daily-mass change minus predicted percent daily-mass change) calculated from the multiple regression equation with the term for the independent variable being examined removed from the equation. Thus, positive residuals for solar radiation, for example, would indicate that observed percent mass change was greater than that predicted based on the other variables in the regression equation. The resulting r^2 for each variable using this approach is identical to the partial r^2 for each variable in the full regression model.

Body Composition.—Changes in body water, fat, protein, ash, and gross energy content of the ingesta-free body were calculated by difference between estimates at the beginning and end of each experiment. Forest cover effects on each of these components were assessed using 1-way ANOVA. Least significant difference multiple comparisons were used to identify differences among treatments pending F tests with $P \leq 0.10$ (we allowed a greater P value because of the key relevance of this data).

Activity Budgets.—Proportion of time spent in each of the 5 activity categories was calculated for each pen every 2 weeks. Estimates of activity were assessed separately during the day from 1100 to 1700 hours and at night from 1700 to 0700 hours. All data collected between 0700–1100 hours were excluded from analysis because elk activity was inordinately influenced by the morning feeding. Repeated measures ANOVA and least significant difference multiple comparisons were used to identify among-treatment differences in each activity category. We normalized activity data for analysis using an arcsine transformation (Zar 1974) for the ANOVA.

Collection of activity data generally be-

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gan 1–2 weeks after the beginning of each trial. It is possible that thermal cover effects influenced activity profiles during this 1–2 week period, and therefore the treatment effect could be as relevant as the treatment × time interaction effect. Thus, we also presented the treatment effect in the analysis of cover effects on elk activity.

Summer Food and Water Consumption.—Daily intake of dry matter, digestible energy, and crude protein were calculated for each month. Average daily water intake per 100 kg of body mass was calculated for 2-week intervals. Differences in food and water intake among treatments were tested with repeated measures ANOVA and least significant difference multiple comparisons.

RESULTS

Cover Effects on Microclimate

Regression equations used to calibrate weather variable estimates from the permanent and mobile stations generally had high correlation coefficients (Appendix A). Correlation coefficients for windspeed declined in fall 1994, however, because the mobile station anemometer occasionally malfunctioned. Therefore, all windspeed prediction equations (Appendix B) were calculated using 9 months of data collected in winter and summer 1994.

Coefficients of multiple determination were high, usually >0.95, for equations to predict temperature and relative humidity at the pens from weather data collected at the permanent station (Appendices C, D). On clear nights with no wind, temperature was usually variable across the study site, mostly due to cold air drainage from higher to lower areas (the lower areas cooled faster than higher areas). Temperature tended to be homogenous across the study site whenever breezes of even slight windspeed occurred and during periods of dense cloud cover. Such patterns also held for relative humidity. Predicting temperature and relative humidity under these variable conditions was enhanced by using separate prediction equations for the day–night and cloud–precipitation categories.

Coefficients of determination were more variable for equations used to predict windspeed, solar radiation, and net radiation (Appendices C, D). Moderate r^2s for windspeed apparently were due to variation in wind direction. The northeast-facing hillside of the study site apparently introduced different airflow patterns across the site that varied as wind direction varied. Solar- and net-radiation r^2 values for moderate and dense cover equations typically were low to moderate during the day, because openings in the forest canopy caused dramatic changes in radiation flux to the radiation probes of the mobile station as the sun moved across the sky. Coefficients of determination usually were quite high for net radiation at night.

Several patterns were evident regarding forest cover effects on microclimate that were mostly consistent between winter and summer (Figs. 5, 6). Ambient temperature and relative humidity varied little among treatments at night across all weather conditions and during the day during cloudy periods with at least occasional precipitation. During clear to mostly cloudy days with no precipitation, temperature averaged about 2 C° cooler and relative humidity 5–10 percentage units higher in the dense cover pens than in the zero cover pens. Temperature and relative humidity in the moderate cover treatment deviated little from that in the zero cover treatment.

Although forest cover had substantial effects on windspeed (Fig. 7), differences in windspeed among treatments largely depended on prevailing wind patterns. Windspeed and differences in windspeed among treatments tended to be minimal at night and during the day under cloudy periods with at least occasional precipitation and moderate during the day under clear to mostly cloudy conditions without precipitation. On days with clear to mostly cloudy skies without precipitation, windspeed averaged up to 2 m/sec slower in the dense cover treatments compared to the zero cover treatments. Windspeed in the

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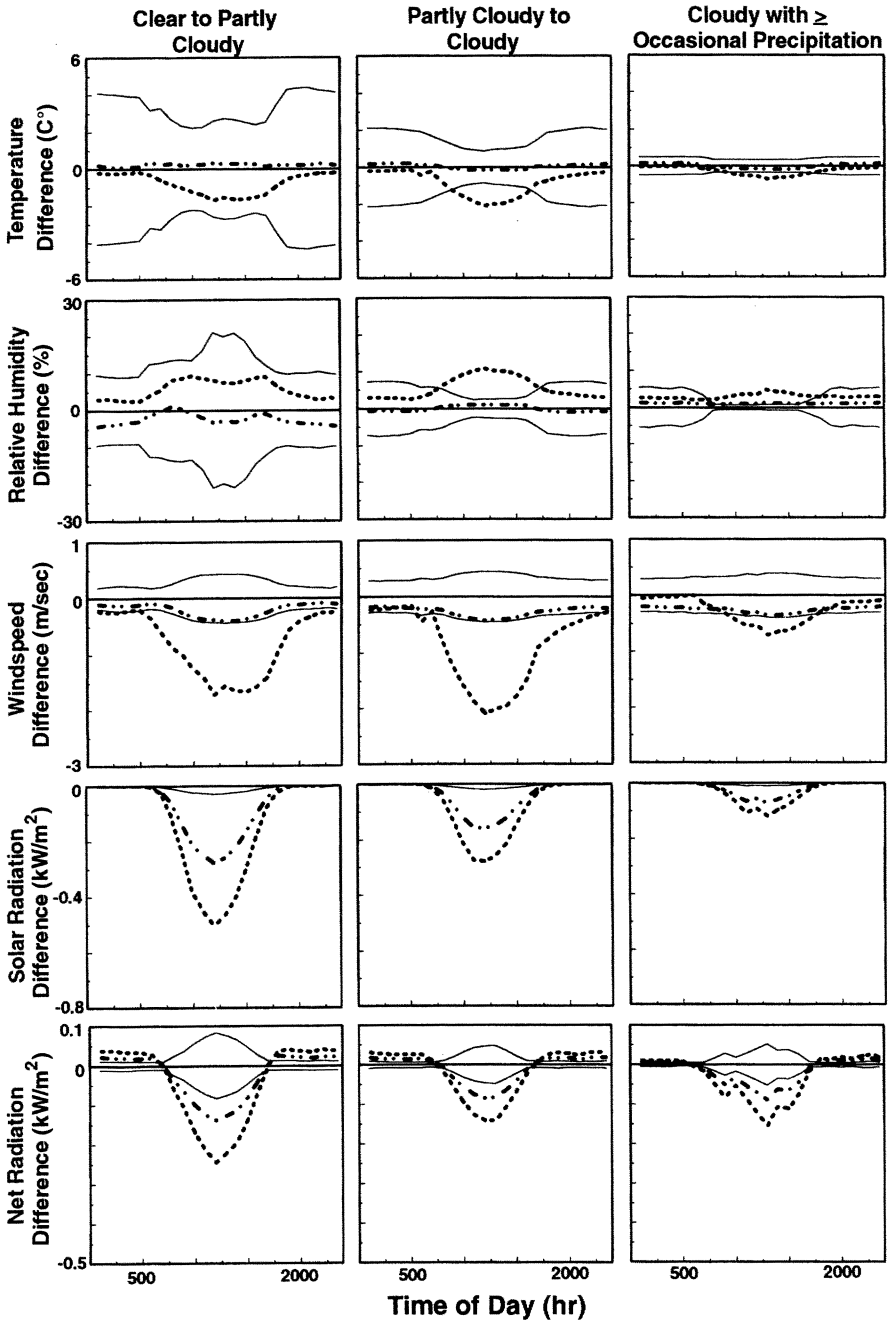

Fig. 5. Difference in winter weather characteristics among zero (heavy solid lines), moderate (dash-dotted lines), and dense (dashed lines) cover treatment units using data collected during winters of 1993–94 and 1994–95 in northeastern Oregon. Data from zero cover units were used as a base for comparison (i.e., the average for the zero cover units was subtracted from values for the moderate and dense cover units) and thus always equaled 0.0. Narrow, solid lines indicate 95% confidence intervals of the zero cover data. Positive values for either the moderate or dense cover treatments indicate greater values than that measured at the zero cover units and vice versa.

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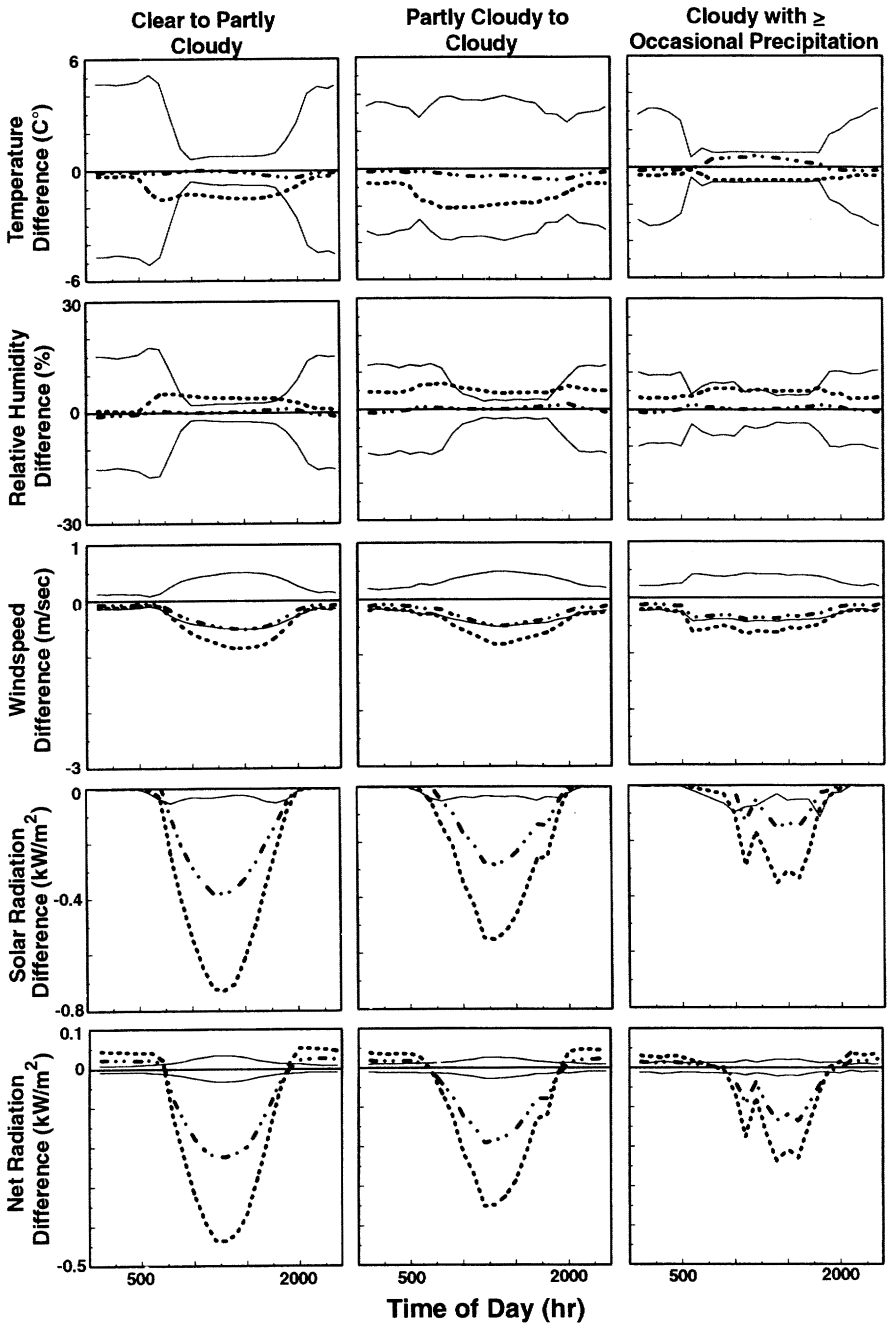

Fig. 6. Difference in summer weather characteristics among the zero (heavy solid lines), moderate (dash-dotted lines), and dense (dashed lines) cover treatment units using data collected during summer 1994 in northeastern Oregon. Data from zero cover units were used as a base for comparison (i.e., the average for the zero cover units was subtracted from values for the moderate and dense cover units) and thus always equaled 0.0. Narrow, solid lines indicate 95% confidence intervals of the zero cover data. Positive values for either the moderate or dense cover treatments indicate greater values than that measured at the zero cover units and vice versa.

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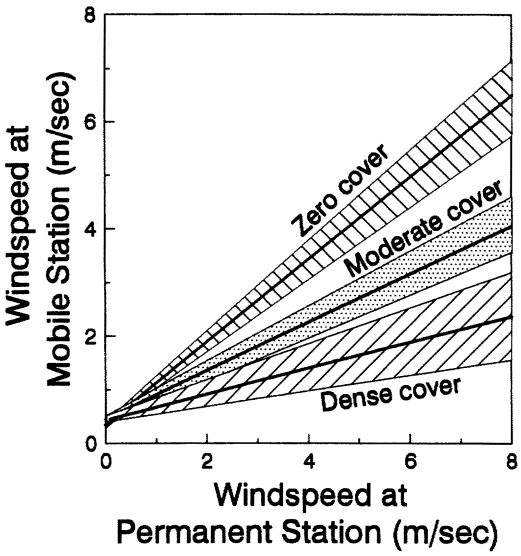

Fig. 7. Windspeed in the 3 cover treatments estimated from windspeed measured at the permanent station (*see* Fig. 1) using prediction equations in Appendix B during 1993–95 in northeastern Oregon. Upper and lower bounds for each forest cover type were based on the treatment units with the greatest and least windspeed, respectively.

moderate cover treatment did not differ substantially from that in the zero cover treatment (Figs. 5, 6).

Forest cover markedly affected solar and net radiation during the day. These differences diminished as cloud cover increased, such that the magnitude of the forest cover effect was about 50% less on cloudy days with precipitation compared to that on clear to partly cloudy days. Differences among treatments were likely overestimated during cloudy periods with occasional precipitation, because the radiometer data could not be used when precipitation collected on the radiometer probes. Daytime differences in net radiation among treatments were substantially greater in summer than in winter. This undoubtedly was due to reflection of sunlight from snow (Parker and Gillingham 1990) to the underneath side of the net radiometer probe in winter. At night, net radiation flux in the moderate and dense treatments tended to be higher than that in the zero cover treatment particularly during clear to partly cloudy conditions, but the magnitude of difference was quite low, particularly compared to differences that occurred during the day (Figs. 5, 6). Differences in net radiation among the treatments at night are a measure of long-wave irradiance from forest canopies, assuming that long-wave radiation from the ground was similar among treatments. This assumption is reasonable in winter when snow covered the ground but is questionable in summer due to solar heating of substrates in areas without forest cover (Zahn 1985).

Weather Conditions during Winter Experiments

Ambient temperature varied significantly among the 4 winter experiments ($P < 0.001$) (Table 3). The first winter of the study was the mildest, with minimum and maximum daily temperatures averaging −2.4 and 6.3 C°. Daily minimum temperatures virtually never fell below −10 C° and nearly 80% were above −5 C°. The second winter was the harshest. Minimum and maximum temperatures averaged −7.1° and 0.8 C° across winter; nearly 30% of the days had minimum temperatures below −10 C°. Ambient temperature was similar during the last 2 winters—significantly cooler than during the first winter and significantly warmer than during the second winter (Table 3). Eight and 15% of the days had minimum temperatures below −10 C° in 1993–94 and 1994–95.

Average daily windspeed was similar ($P = 0.145$) among winter experiments and averaged about 1.4 m/sec (1 m/sec = 3.6 km/hr) (Table 3). Relatively windy conditions (>2 m/sec) occurred on about 12% of days across all winters. The percent of days with little or no wind (≤1 m/sec) was lowest the second winter of the study (20% versus 27–37% in the other 3 winters).

The first winter of the study was mild, based on long-term (30-yr) temperature and precipitation averages collected at La Grande, Oregon. Temperature averaged 3.2 C° warmer and precipitation averaged 2.7 cm less than normal across winter (Ta-

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Table 3. Average monthly and winter-long minimum and maximum temperature (C°) and windspeed (m/sec) during winter thermal cover experiments in northeastern Oregon from 1991 to 1995. Within months, means with different letters are significantly different ($P \leq 0.05$).

Variable and year	December		January		February		March		Winter	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Minimum temperature										
1991–92	−2.7A	0.9	−3.9A	0.7	−2.1A	0.6	−0.3A	0.4	−2.4A	0.4
1992–93	−7.6B	0.7	−9.6B	0.8	−8.3B	1.1	−2.3BC	0.6	−7.1B	0.5
1993–94	−4.7AC	0.6	−3.3A	0.6	−6.6B	1.0	−3.4B	0.8	−4.6C	0.4
1994–95	−6.3BC	0.9	−4.1A	0.8	−3.4A	1.1	−0.8AC	1.2	−4.2C	0.5
Maximum temperature										
1991–92	3.9A	0.4	3.1A	0.6	8.0A	0.8	10.8A	1.0	6.3A	0.5
1992–93	−1.0B	0.6	−2.5B	0.8	1.1B	0.8	6.3B	0.6	0.8B	0.5
1993–94	1.8AC	0.6	4.2A	0.7	2.9B	0.5	8.2AB	1.1	3.9C	0.4
1994–95	0.5BC	0.9	4.1A	0.8	6.0A	1.1	7.9AB	1.2	3.6C	0.6
Windspeed										
1991–92	1.6	0.2	1.5	0.1	1.2	0.1	1.2A	0.1	1.4AB	0.1
1992–93	1.6	0.1	1.4	0.1	1.4	0.1	1.3AB	0.1	1.4A	0.1
1993–94	1.4	0.1	1.3	0.1	1.3	0.1	1.1A	0.1	1.3B	0.1
1994–95	1.4	0.1	1.5	0.1	1.1	0.1	1.6B	0.2	1.3AB	0.1

ble 4). The second winter, in contrast, was substantially cooler than normal, averaging about 4.5 C° below normal during January and February and 3.2 C° cooler across the entire winter. The last 2 winters of the study were slightly warmer than normal. Precipitation across the last 3 winters was similar to the long-term average (Table 4). Our study area occurred at substantially higher elevation than the La Grande weather station and winter ranges of elk in the Blue Mountains. Temperature and moisture conditions during the study therefore should have simulated "normal" to "severe" weather conditions typically found at elevations used by elk during winter in this region.

Elk Response to Thermal Cover during Winter Experiments

Characteristics of elk at the beginning of each experiment and feeding regimes of each experiment are presented in Table 5. Calves tended to be small (relative to free-ranging calves in late fall) due to the effects of several gastrointestinal diseases when the calves were neonates (Cook et al. 1994). The smaller size of the second calf cohort was due to the effects of neonatal disease and a nutrition study conducted during early autumn 1993 (Cook et al. 1996). The small size of calves should have enhanced the probability of finding a significant thermal cover effect on energy

Table 4. Average temperature (temp) (C°) and precipitation (precip.) (cm) by month during each winter experiment and long-term (30 yrs from 1960 to 1990) means from weather records collected at La Grande, Oregon, USA (National Oceanic and Atmospheric Administration 1991–95).

Year	December		January		February		March		Winter	
	Temp	Precip.	Temp	Precip.	Temp	Precip.	Temp	Precip.	Temp	Precip.
1991–92	2.3	1.6	2.2	0.8	5.4	2.8	7.7	2.2	4.4	1.9
1992–93	−3.6	6.6	−5.1	3.8	−3.0	0.9	4.2	4.7	−1.9	4.0
1993–94	0.9	4.3	2.6	5.8	0.2	7.8	6.4	1.5	2.5	4.9
1994–95	0.2	2.9	1.3	3.9	4.5	3.0	5.1	7.2	2.8	4.3
30-yr mean	−0.3	5.0	−1.1	5.5	1.7	3.8	4.6	3.9	1.2	4.6

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Table 5. Body mass, number of elk in each thermal cover treatment, and daily dietary intake levels at the beginning of each winter experiment in northeastern Oregon.

		Body mass (kg)		No. elk/treatment[a]					Daily intake[b]			
Year	Age class	Mean	Range	ZC	MC	DC	CC	Total[c]	Pellets	Hay	CP	DE
1991–92	calf	86.6	68–113	8	7	8	7	30	41.1	13.9	7.6	152.9
1993–94	calf	74.0	62–92	9	9	9	9	36	34.0	24.7	8.2	151.9
1992–93	yearling	146.5	115–168	6	7	6	6	25	36.0	20.1	7.4	151.8
1994–95	yearling	153.0	134–170	9	9	8	8	34	31.2	27.5	8.8	154.7

[a] Thermal cover treatment codes are ZC = zero cover, MC = moderate cover, DC = dense cover, and CC = combination cover.
[b] Units of intake are g/kg body mass$^{0.75}$ for pellets, hay, and crude protein (CP) and kcal/kg BM$^{0.75}$ for digestible energy (DE). All dietary attributes are expressed on a dry-matter basis.
[c] Total number of elk at the beginning of the experiment. Three elk either died or were removed from the 1991–92 experiment due to disease, and 9 elk either died or were removed from the 1993–94 experiment due to severely reduced body condition.

balance, due to their relatively greater surface area:body-mass ratio, compared to larger animals (Parker and Robbins 1984).

Of the 30 calves available at the beginning of the first winter (1991–92) experiment, 2 died from clostridiosis (based on necropsy results) and a third was removed from the study after developing polioencephalomalasia, apparently due to a thiamine deficiency (National Research Council 1985). All body-mass data from these elk were excluded from analyses. Of the 36 calves available for the second-winter calf experiment (1993–94), 3 died and 6 were removed to prevent death due to severely reduced condition over the course of the experiment. The experiment was terminated 3 weeks earlier than planned because risk of mortality for many of the remaining calves was high.

Twenty-five and 34 yearling cows were used in the second and last winter experiments (1992–93 and 1994–95), respectively. All were retained for the entire experiment.

Body Mass of Calves.—In the first winter experiment (1991–92), body-mass dynamics exhibited 2 phases: an initial phase of mass loss until midwinter and a period of mass recovery in late winter (Fig. 8), despite no changes in feeding rate or food quality. Body-mass dynamics differed among treatments over the winter (P = 0.006 for the treatment × time interaction effect). Body-mass loss of elk calves held in the dense cover treatment (DCT) was significantly greater than that for calves in the zero cover treatment (ZCT) from late January through mid-February and was significantly greater than that for calves in both the ZCT and moderate cover treatment (MCT) through the rest of winter (Fig. 8B). Mass dynamics among the ZCT, MCT, and the combination cover treatment (CCT) did not differ significantly at any point during the experiment.

In 1993–94, 5, 3, 1, and 0 calves died or were removed in the DCT, MCT, ZCT, and CCT, respectively, a significantly nonrandom distribution of attrition (P = 0.037). Moreover, timing of attrition tended to be earlier in the DCT: all calves in the DCT were removed between the week of 10 January and 3 February. In the MCT, 1 calf was removed during the week of 10 January, whereas the other 2 were removed the week of 24 February. Loss of the calf from ZCT occurred the week of 24 February.

Removal of data from calves that died or were removed from the ANOVA of body-mass data provided for a conservative test, because the calves that were removed had lost the most mass at the time they were removed and most of these calves were in the DCT. Nevertheless, effects of treatment on body-mass dynamics was significant (P = 0.026 for the treatment × time interaction effect). Significant differences among treatments within weekly time periods was limited to the CCT and DCT during mid-February (Fig. 8D). Among-treatment mass-loss patterns closely paralleled those of calves during

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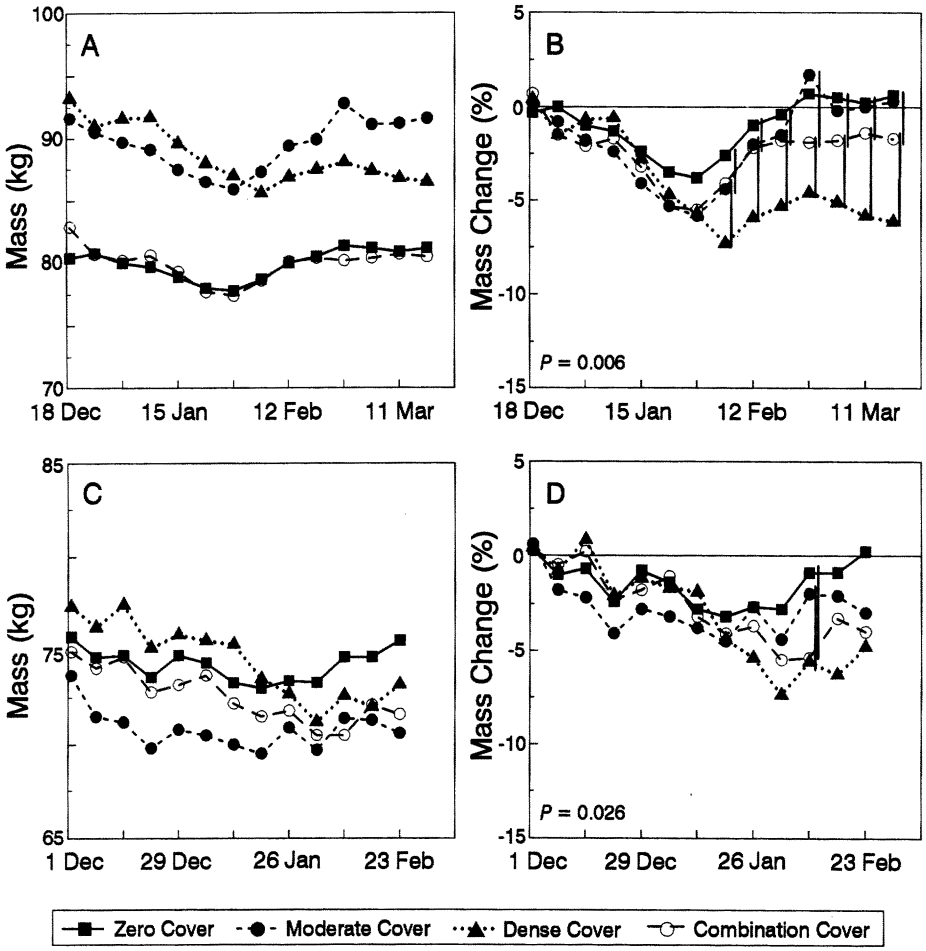

Fig. 8. Body-mass dynamics of female elk calves during winter 1991–92 (A, B) and winter 1993–94 (C, D) in northeastern Oregon. In graphs B and D, data values not connected by vertical lines differ significantly ($P \leq 0.05$) within weekly periods. The P values in B and D are the significance levels of the time × treatment interaction effect.

the first winter experiment of 1991–92 (Fig. 8B vs. 8D).

Body Mass of Yearlings.—In 1992–93, all elk lost mass relatively rapidly until mid-February; most elk then tended to increase in mass during the first several weeks of March (Fig. 9). Mass dynamics among cover treatments began to differ relatively early in the experiment ($P = 0.002$ for the treatment × time interaction effect). Loss of mass for elk in the DCT was significantly greater than that of elk in the ZCT by early January and remained so through the remainder of the experiment (Fig. 9B). Mass loss of elk in the DCT was greater than that of elk in the MCT at the end of the experiment. Mass loss of elk in the CCT was greater than that of elk in the ZCT during 3 weeks of this experiment.

Mass loss in winter of 1994–95 was more gradual, and lost mass was not regained in late winter, compared with that of yearlings in the 1992–93 winter experiment (Fig. 9). Differences in mass dynamics among treatments ($P = 0.018$) first appeared in late December. From late December through mid-January, elk in the ZCT lost significantly less mass than elk in the other treatments (Fig. 9D). Although this trend continued across the rest of winter, significant differences within weeks existed only between the ZCT and DCT. Mass loss of elk in the MCT and

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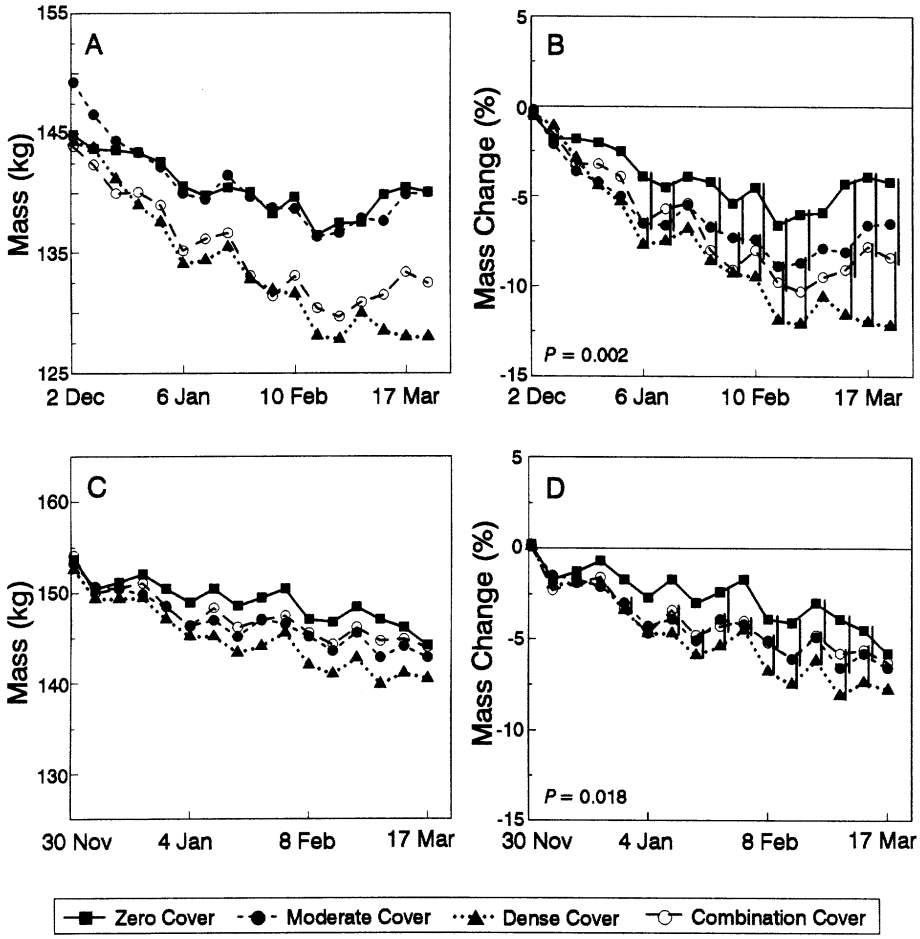

Fig. 9. Body-mass dynamics of yearling cow elk during winter 1992–93 (A, B) and winter 1994–95 (C, D) in northeastern Oregon. In graphs B and D, data values not connected by the narrow vertical lines differ significantly ($P \leq 0.05$) within weekly periods, and P values are the significance levels for the time × treatment interaction effect.

CCT generally tracked midway between those in the ZCT and DCT.

Winter Weather Effects on Body Mass.—Solar radiation, minimum temperature, and beginning percent change in mass (BPCM, *see* variable descriptions below) accounted for a substantial portion of the variation in daily mass change across 6-week time intervals (adjusted $r^2 = 0.73$, $P \leq 0.001$, $n = 45$). Solar radiation had the greatest effect, minimum temperature had the least effect of these 3 variables, and windspeed was uncorrelated to daily mass change (Table 6). Excluding windspeed from the regression equation increased the adjusted r^2 to 0.74 and resulted in the following equation:

$$y = -0.135 + 0.0000876(\mathrm{SR}) + 0.0102(\mathrm{MNTMP}) - 0.0133(\mathrm{BPCM})$$

where

y = daily percent mass change over the 6-week analysis period,

SR = average cumulative irradiance of solar radiation (kcal/m^2/day),

MNTMP = average minimum daily temperature (C°), and

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Table 6. Effects of weather on 6-week body-mass changes during 4 winters from 1991–92 through 1994–95 in northeastern Oregon based on multiple regression analysis.

Independent variable[a]	Regression coefficient	SE	Standardized regression coefficient	Partial r^2	p[b]
Solar radiation	0.0000876	0.0000130	0.6761	0.534	0.0001
Windspeed	−0.0000474	0.0384	−0.0001	0.000	0.9990
Minimum temperature	0.0102	0.0030	0.2747	0.222	0.0016
Beginning mass	−0.0133	0.0027	−0.4048	0.377	0.0001
Intercept	−0.1352	0.0308			0.0001

[a] Solar radiation was average cumulative irradiance in kcal/m^2/day; windspeed was average daily windspeed in m/sec; minimum temperature was average daily minimum temperature in C°; and beginning mass was the percent change in mass from the beginning of the experiment to the beginning of the 6-week time period. These variables were regressed on average daily percent change in mass over the 6-week periods.
[b] Significance level of variables included in the regression equation.

BPCM = beginning percent change in mass, calculated from the beginning of the experiment to the beginning of the 6-week analysis period.

Our partial correlation analysis using the above equation indicated the effects of each of the 3 significant independent variables were linear when the effects of the other independent variables were controlled (Fig. 10) under the weather conditions encountered during this study.

Yearly variations in patterns of temperature and flux of solar radiation apparently accounted for differences in body-mass dynamics among years. In all years, temperature (Table 3) and solar radiation (Fig. 11) generally increased after midwinter. Cumulative daily solar radiation was approximately 2 times higher in late February and early March than in December and early January, providing markedly greater radiation energy inputs for elk with access to sunshine after midwinter. Increased solar radiation and warming temperatures probably accounted for the late-winter mass recovery of calves in 1991–92 and yearlings in 1992–93 (Figs. 8D, 9B), and, to a lesser extent, calves during 1993–94 (Fig. 8D). Mass recovery by calves during February 1994 was less pronounced than that in the previous 2 winters, perhaps due to relatively low temperatures during the month (Table 3) and relatively low flux of solar radiation during the last 2 weeks of the month (Fig. 11). If the experiment had not been terminated early (late Feb), mass gains may have been greater, because March temperatures warmed considerably and flux of solar radiation increased to relatively high levels. The lack of recovery of yearlings after midwinter during the 1994–95 experiment may have been due to relatively low levels of solar radiation in March combined with minimal mass loss in early winter (i.e., 3–5%, Fig. 9D). Finally, yearlings during early winter in 1992–93 lost mass at roughly twice the rate of elk in the other 3 experiments. We attribute this to the considerably colder temperatures during the early part of this experiment (Table 3).

Body Composition of Calves.—In 1991–92, body composition estimates were unusable due to problems with sealing hematocrit tubes and other technical problems. In 1993–94, all data from calves that were removed from the study were excluded from analysis (including all data from 1 pen in the DCT). Catabolism of fat, protein, and endogenous energy during this winter was similar among elk in the ZCT, MCT, and CCT, whereas elk in the DCT tended to lose more fat and lost significantly more endogenous energy than elk in the other treatments (Table 7, Fig. 12). The minimal losses of protein across all treatments (Table 7) may be misleading; the recovery of body mass of many calves near the end of the trial (Fig. 9D) may have masked lower body protein levels during the middle of the experiment (particularly if recovered mass was primarily due to anabolism of protein rather than fat).

Body Composition of Yearlings.—In

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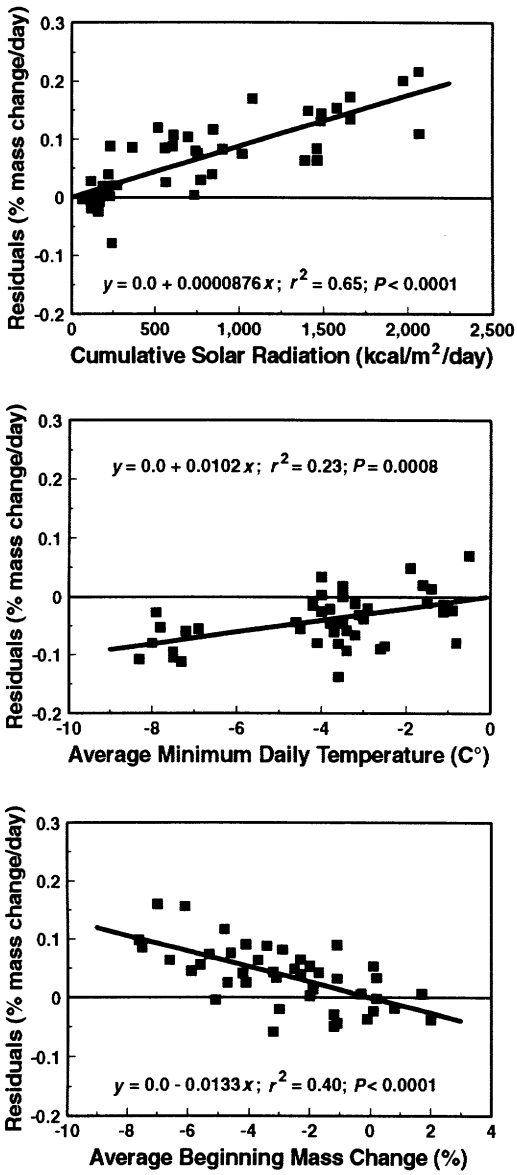

Fig. 10. Relations between 6-week percent mass change residuals and solar radiation, minimum temperature, and percent mass change (the latter calculated from the beginning of the experiment to the beginning of the 6-week period of data analysis) during winters from 1991 to 1995 in northeastern Oregon. Residuals were calculated as observed percent mass change minus predicted percent mass change where predicted was based on the regression equation on page 30, with the term for the independent variable being examined removed from the prediction equation. This analysis allowed assessment of the effect of each independent variable on mass change over 6-week periods while simultaneously accounting for the effects of the other independent variables.

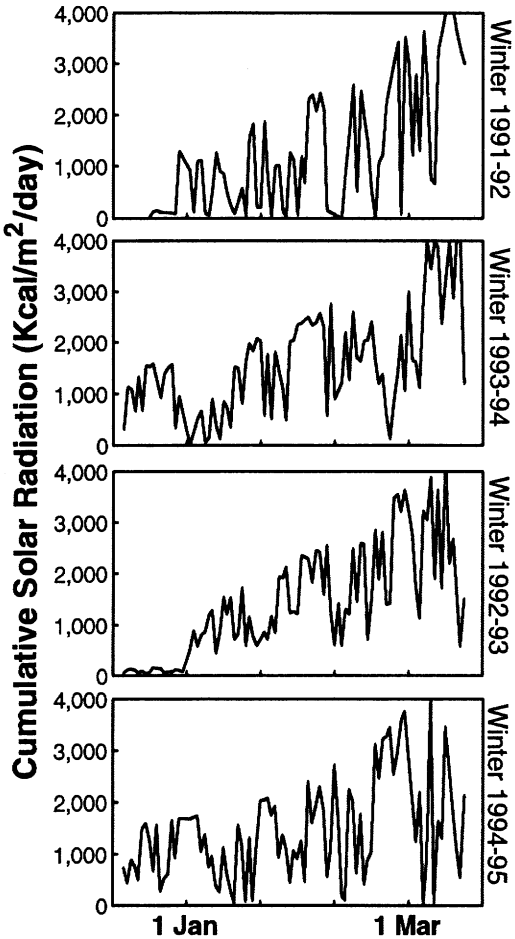

Fig. 11. Cumulative daily solar radiation flux during 4 winter experiments from 1991 to 1995 in northeastern Oregon.

1992–93, catabolism patterns of ingesta-free body fat and protein and loss of endogenous energy followed a pattern analogous to body-mass loss patterns (Table 8, Fig. 13). Loss of these body components generally was greatest in elk in the DCT and least in elk in the ZCT.

In 1994–95, total catabolic loss of fat, protein, and endogenous energy was relatively mild (Table 9, Fig. 14) compared to that during the yearling experiment of 1992–93. Differences among treatments approached significance (P = 0.087–0.153). Elk in the DCT again tended to lose more fat and endogenous energy than elk in the other treatments.

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Table 7. Average change in amount of water, fat, protein, and total caloric content of the ingesta-free body of elk calves across the 1993–94 winter thermal cover experiment in northeastern Oregon. Within rows, means with different letters differ significantly ($P \leq 0.05$).

	Thermal cover treatment								
	Zero		Moderate		Dense		Combination		
Component[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	P[b]
Water	1.1	0.85	2.2	1.30	0.6	0.57	−0.5	0.90	0.555
Fat	−1.5	0.57A	−1.9	0.44A	−3.8	0.48B	−1.5	0.45A	0.062
Protein	0.0	0.18	0.3	0.37	−0.6	0.26	−0.2	0.08	0.247
Energy	−13.7	5.10A	−16.5	4.77A	−39.1	5.96B	−15.4	4.30A	0.043

[a] Units of water, fat, and protein are kg and energy is Mcal.
[b] Significance level of thermal cover treatment effects on each body component based on single-factor ANOVA. (One of the pens in the dense cover treatment could not be used in this analysis because all calves in the pen were removed from the study; thus, $n = 11$ rather than the usual n of 12.)

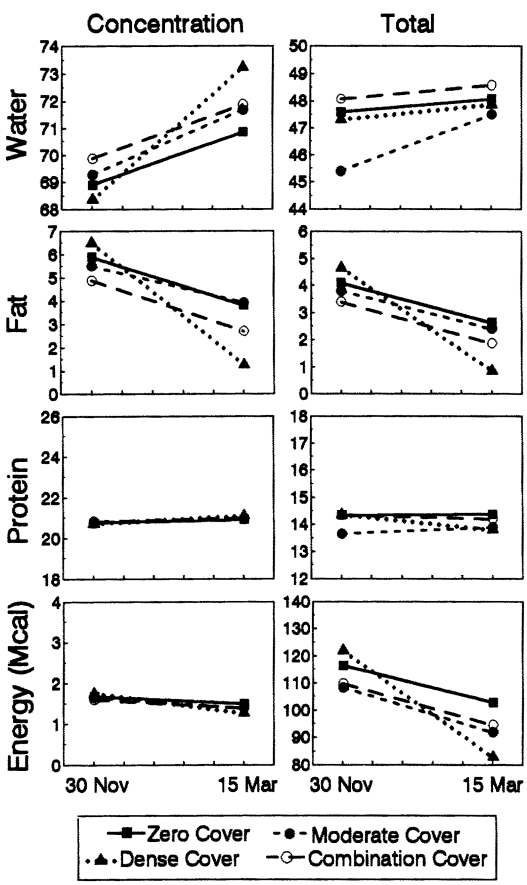

Fig. 12. Body composition dynamics of female elk calves during winter 1993–94 in northeastern Oregon. Units for the Concentration graphs are percent of ingesta-free body mass for water, fat, and protein, and Mcal/kg of ingesta-free body mass for energy. Units for the Total graphs are kg of water, fat, and protein and Mcal of energy in the ingesta-free body.

Activity of Calves.—Several marked patterns existed in elk activity profiles. Elk tended to spend most of their time either bedded or standing and were more active during the day than at night (Fig. 15). Running was rarely observed (≤0.5% of time during any of the experiments); this activity was omitted from graphs and data analysis. Pacing largely occurred during the afternoon, probably in anticipation of the second feeding.

In 1991–92, there were no significant treatment effects on activity during either the diurnal or nocturnal periods (Fig. 15), except for pacing at night. Elk in the DCT paced more by 2–3 percentage points than elk in the other treatments; the small extent of difference seems biologically irrelevant, however.

Difficulties with the telemetry receiving equipment complicated activity data collection during the 1993–94 winter experiment. Primarily during the first half of January and extending intermittently to late January, a rapid beeping that originated from an unknown source confounded interpretation of pulses from all of the transmitters. We excluded those files that were substantially affected. Moreover, no elk were left in 1 of the DCT pens by late January due to attrition. The ANOVA on this winter's activity data did not include any data collected from the DCT pen in which all elk were removed, nor any data collected during the first 2 weeks of January, nor any data collected in March (because the experiment was terminated ear-

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Table 8. Average change in amount of water, fat, protein, and total caloric content of the ingesta-free body of yearling elk across the 1992–93 winter thermal cover experiment in northeastern Oregon. Within rows, means with different letters differ significantly ($P \leq 0.05$).

	Thermal cover treatment								
	Zero		Moderate		Dense		Combination		
Component[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	P[b]
Water	1.1	0.48	0.6	0.95	−1.7	0.79	−0.4	0.25	0.082
Fat	−4.6	1.11A	−6.8	0.51AB	−10.4	1.91AB	−7.5	0.82AB	0.054
Protein	−0.6	0.35A	−1.2	0.37A	−2.5	0.53B	−1.6	0.20AB	0.039
Energy	−47.1	12.43A	−70.7	6.76AB	−112.4	20.88B	−80.1	8.84AB	0.049

[a] Units of water, fat, and protein are kg and energy is Mcal.
[b] Significance level of thermal cover treatment effects on each body component based on single-factor ANOVA.

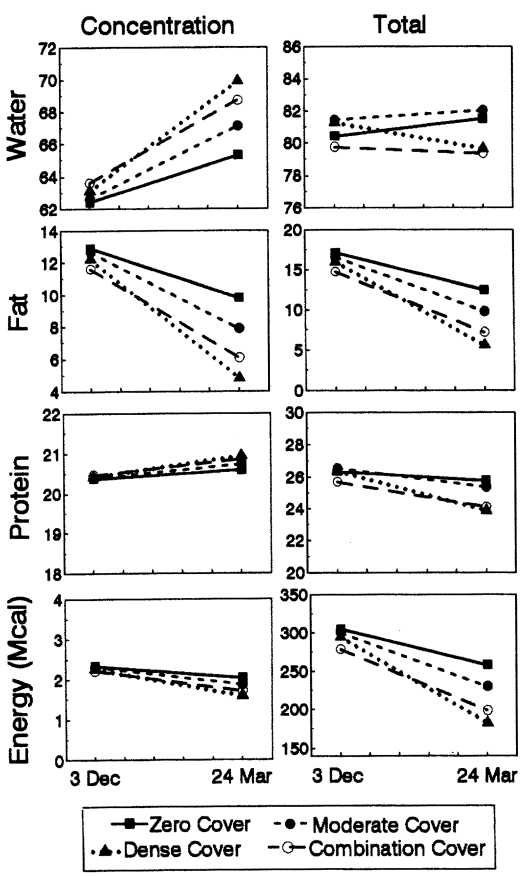

Fig. 13. Body composition dynamics of yearling elk cows during winter 1992–93 in northeastern Oregon. Units for the Concentration graphs are percent of ingesta-free body mass for water, fat, and protein, and Mcal/kg of ingesta-free body mass for energy. Units for the Total graphs are kg of water, fat, and protein and Mcal of energy in the ingesta-free body.

ly). With these constraints, none of the activity levels differed significantly among treatments during day or night during this winter (Fig. 15).

Activity of Yearlings.—Three activity transmitters malfunctioned during part of the winter 1992–93 experiment—1 in each thermal cover treatment except in the MCT. ANOVA tests using 9 instead of the usual 12 transmitters indicated minimal differences in activity among treatments, except that elk in the DCT apparently bedded more and stood less during the first 2 weeks of March compared to elk in the other treatments (Fig. 16).

All activity transmitters and the receiving equipment worked well throughout the 1994–95 winter experiment. No treatment × time interaction was significant for any activity category during day or night (Fig. 16); however, the treatment effect was significant for bedded and standing at night (P = 0.048 and 0.023, respectively). Elk in the MCT tended to spend more time bedded and less time standing at night than did elk in the other treatments.

Distribution of Elk in Combination Cover Pens.—Based on our bed-site data, elk exhibited mostly consistent patterns of use of various portions of the CCT pens across years within pens, but different patterns of use among pens (Fig. 17). In Pen I, elk typically bedded at night in the clearcut or near the forest edge. In Pen II, elk usually bedded from the middle of the forested side to the end of the pen on the forested side, except during winter 1993–94. In Pen III, use of various portions of the pen

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Table 9. Average change in amount of water, fat, protein, and total caloric content of the ingesta-free body of yearling elk across the 1994–95 winter thermal cover experiment in northeastern Oregon. Within rows, means with different letters differ significantly ($P \leq 0.05$).

	Thermal cover treatment								
	Zero		Moderate		Dense		Combination		
Component[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	P[b]
Water	0.3	0.40	−0.3	0.22	−0.4	0.56	−0.4	0.57	0.709
Fat	−6.1	0.45A	−5.9	1.47A	−9.0	0.56B	−7.6	0.26AB	0.087
Protein	−1.1	0.16	−1.2	0.32	−1.9	0.21	−1.6	0.21	0.153
Energy	−63.3	4.95A	−62.9	15.64A	−95.9	6.05B	−80.2	3.45AB	0.088

[a] Units of water, fat, and protein are kg and energy is Mcal.
[b] Significance level of thermal cover treatment effects on each body component based on single-factor ANOVA.

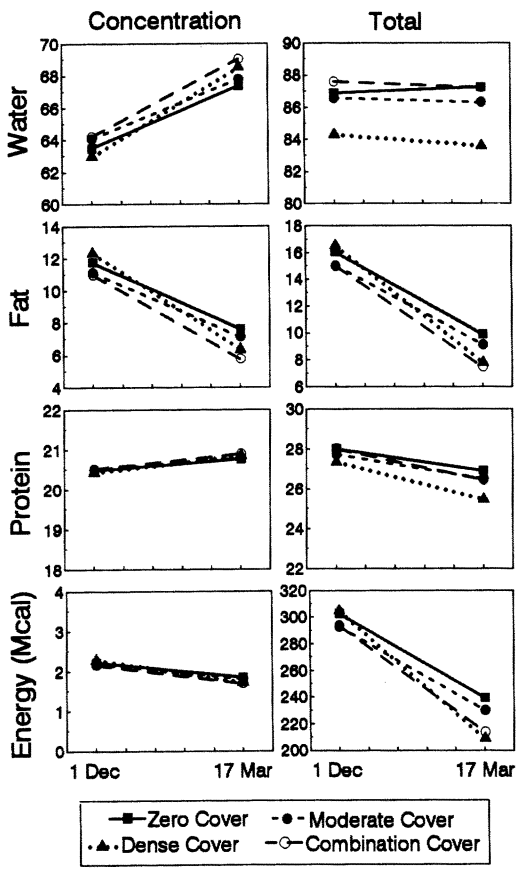

Fig. 14. Body composition dynamics of yearling elk cows during winter 1994–95 in northeastern Oregon. Units for the Concentration graphs are percent of ingesta-free body mass for water, fat, and protein, and Mcal/kg of ingesta-free body mass for energy. Units for the Total graphs are kg of water, fat, and protein and Mcal of energy in the ingesta-free body.

were variable within winters and, in particular, among winters (Fig. 17). Such among-pen inconsistencies are difficult to explain, but suggest that elk had little preference for either of the 2 forest overstory conditions that existed in the pens. Because elk spent 70–80% of each night bedded, our bed-site location data provides a reasonable indication of where elk occurred in the pens during most of the night in winter.

Weather Conditions during Summer Experiments

Ambient temperature was similar across both summer experiments ($P = 0.25$ for both minimum and maximum temperatures), although temperature was generally warmer early and cooler late across the summer season during the 1992 experiment (Table 10). Temperatures tended to be more extreme during the first summer experiment, with 4% of the days with minimum temperatures falling below 0 C° and 14% with maximum temperatures above 30 C° versus 0% and 5% during the second summer. Average daily windspeed also was similar ($P = 0.479$) during both experiments. Significant differences between years occurred only during September (Table 10).

Temperature at La Grande during the summer experiments was moderately warmer than 30-year normals (Table 11). Greatest temperature departures from normal occurred during July–September in 1994. August and September were sub-

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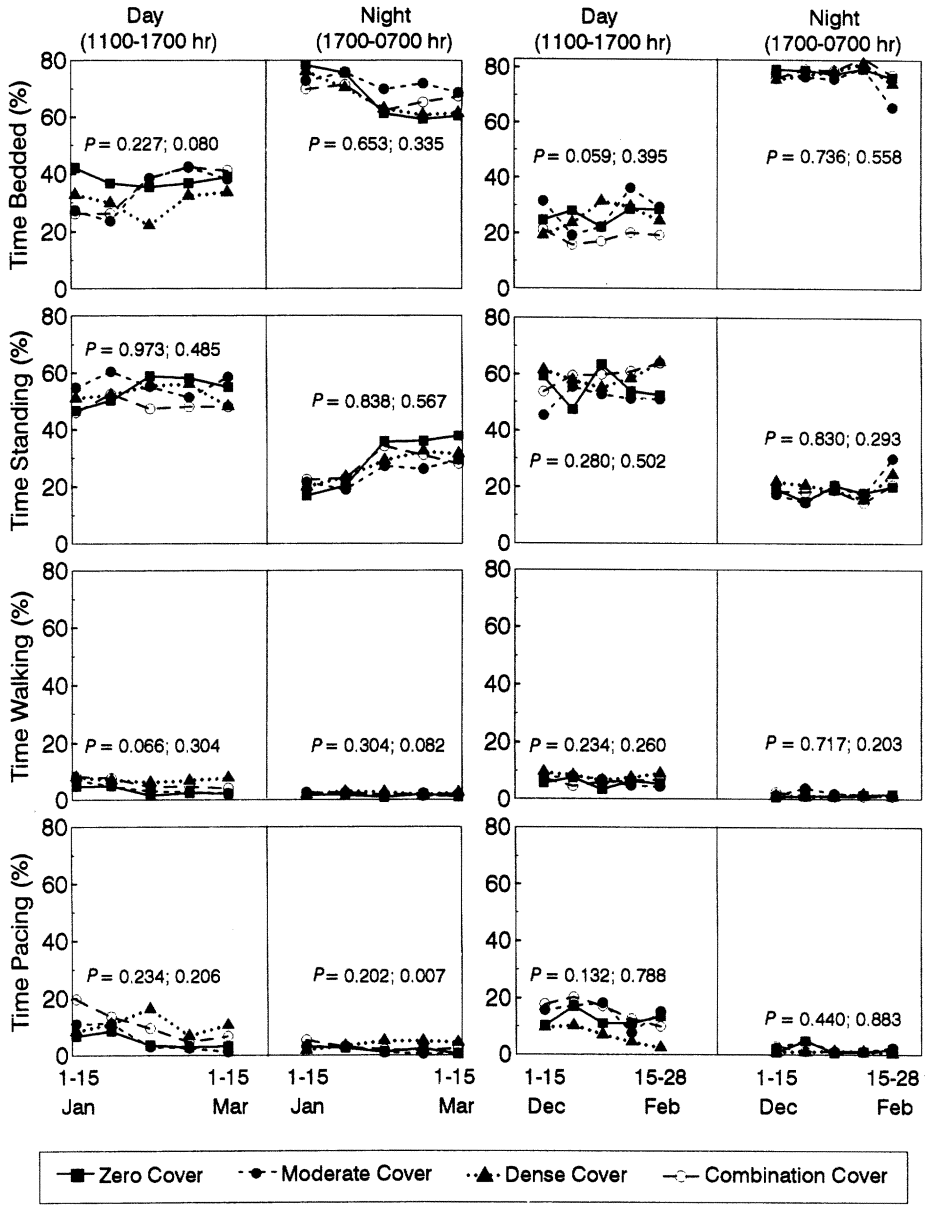

Fig. 15. Activity of female elk calves during winter 1991–92 (the first double-column of graphs) and winter 1993–94 (the second double-column of graphs) in northeastern Oregon. The first *P* value is for the treatment main effect; the second *P* value is for the time × treatment interaction effect.

stantially drier than normal during this second experiment as well.

Elk Response to Thermal Cover during Summer Experiments

Twenty-six and 31 elk were used during the first and second summer experiments. At the beginning of the summer experiments, yearling cows averaged nearly 5 kg heavier during the first experiment compared to the second (Table 12). Over the course of the experiments, daily intake of crude protein and digestible energy averaged about 8% higher during the second

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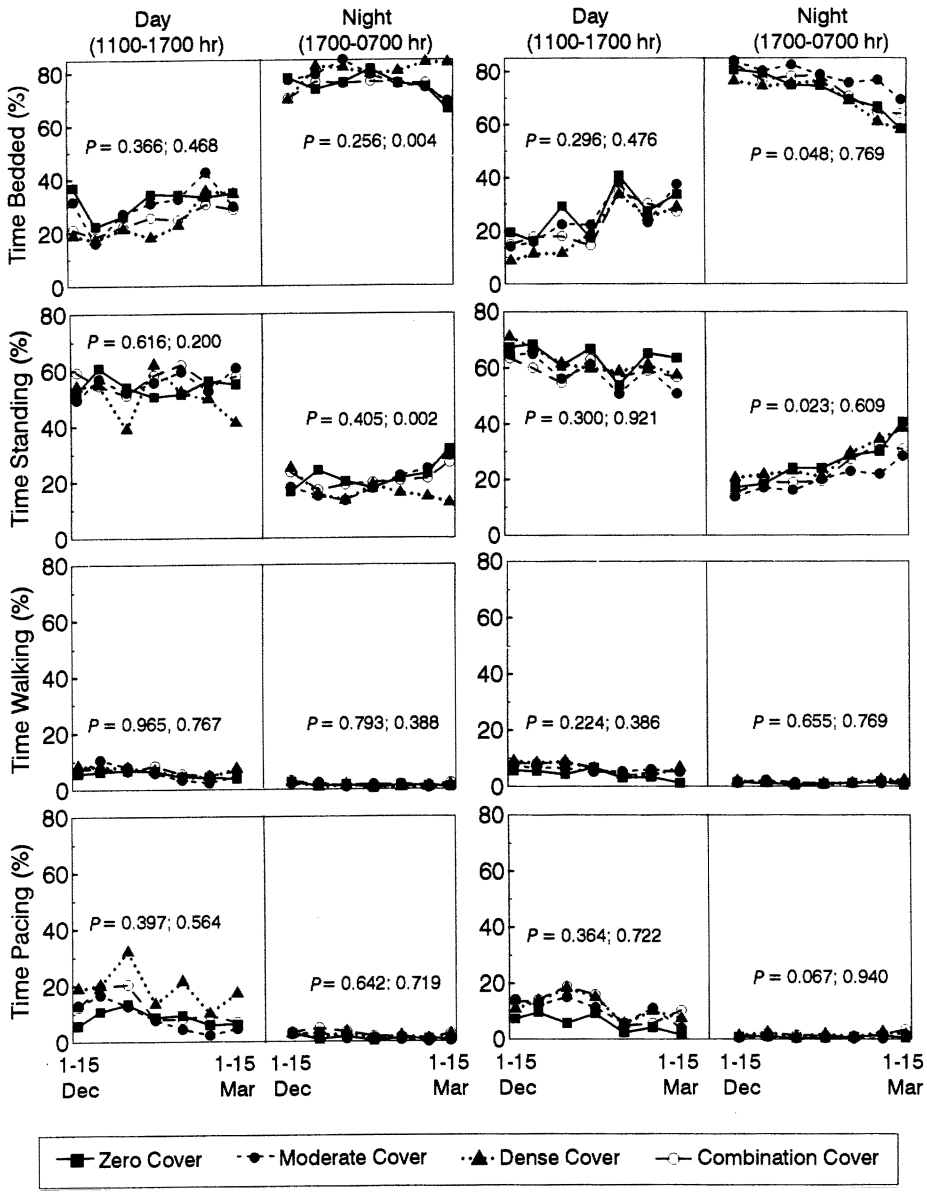

Fig. 16. Activity of yearling elk cows during winter 1992–93 (the first double-column of graphs) and winter 1994–95 (the second double-column of graphs) in northeastern Oregon. The first *P* value is for the treatment main effect; the second *P* value is for the time × treatment interaction effect.

(1994) compared to the first experiment (1992).

Our efforts to feed elk at constant levels among treatments without unduly underfeeding were reasonably successful. There were significant differences ($P < 0.001$) in mass-specific intake levels of dry matter, crude protein, and digestible energy among cover treatments across both experiments, but these differences were limited to the last 7 weeks of the 1992 experiment and limited to the month of June during the 1994 experiment (Table 13). Moreover, evidence is lacking that cover treatments consistently influenced daily intake rates. For example, elk in the DCT

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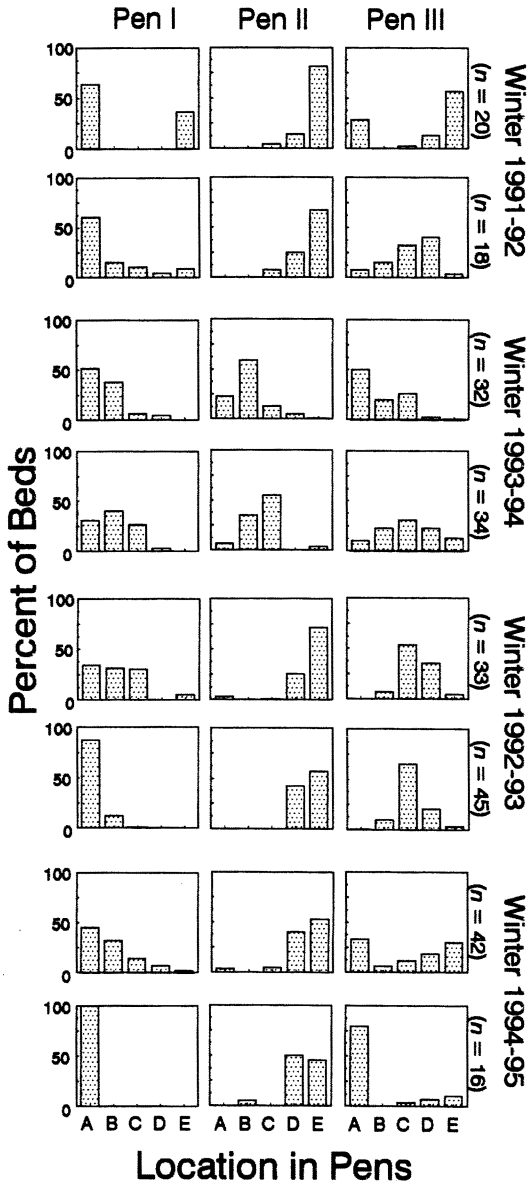

Fig. 17. Location of nocturnal beds of elk in the 3 pens of the combination treatment during 4 winters in northeastern Oregon. Location codes are A = clearcut, B = forest edge, C = 6 m from forest edge to center of forested portion of pen, D = middle of forested portion to 4 m from the end of the pen on the forested side, and E = last 4 m of pen on forested side. Sample sizes refer to the number of nights that bed-site data were collected. The first row of graphs within winters presents data for the first half of winter (Dec and Jan); the second row presents data for the second half of winter (Feb and Mar).

had the second lowest daily intake during the 1992 experiment, but the highest daily intake during the 1994 experiment. Thus, although some differences occurred in intake levels, they seemed inconsistent with respect to the cover treatments.

Body Mass of Yearlings.—Elk increased body mass 43% over the 16 weeks of the 1992 experiment (Fig. 18). There were no significant differences in mass dynamics among treatments ($P = 0.715$ for the treatment × time interaction effect), although gain of elk in the ZCT tended to be greater than that of elk in the other treatments (Fig. 18B).

Elk increased body mass 58% (Fig. 18) during the second summer (1994) experiment, a considerably greater gain than during the first. This likely was due to greater food intake. Again there were no significant differences in mass dynamics among treatments ($P = 0.300$). The tendency for elk in the CCT to gain mass more rapidly than elk in the other treatments (Fig. 18D) was principally due to the extraordinary growth rate of a single elk in this treatment. Percent increase in mass for this cow was 93% by the end of the trial, about 1.7 times that of the average of all other elk.

Body Composition of Yearlings.—Body composition data were unusable for the 1992 experiment. Anabolism of fat and protein and accumulation of endogenous energy was not different among treatments during the 1994 experiment (Table 14, Fig. 19).

Activity of Yearlings.—During the 1992 experiment, an activity transmitter in 1 of the CCT pens and a transmitter in 1 of the MCT pens occasionally failed to operate correctly. Based on ANOVA using 10 transmitters, activity patterns were not different among treatments; only the treatment × time interaction effect for bedded activity during the day was significant ($P = 0.024$) (Fig. 20). However, no differences among treatments within time periods were found based on least significant difference multiple comparisons, and no relevant, consistent trends among treatments across the experiment were apparent.

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Table 10. Average monthly and seasonal minimum and maximum temperatures (C°) and windspeed (m/sec) during the summer thermal cover experiments in 1992 and 1994 in northeastern Oregon. Within months, means with different letters are significantly different ($P \leq 0.05$).

	June		July		August		September		Summer	
Variable and year	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Minimum temperature										
1992	8.4A	0.8	9.4A	0.5	8.9	1.2	3.3A	0.9	8.0	0.43
1994	6.0B	0.9	11.9B	0.7	8.9	0.6	7.7B	0.6	8.1	0.38
Maximum temperature										
1992	21.7	1.2	23.1A	0.9	23.9A	1.2	17.1A	1.1	22.0	0.58
1994	18.8	1.0	26.9B	1.0	24.4B	0.6	22.1B	1.0	22.2	0.53
Windspeed										
1992	1.4	0.1	1.2	0.1	1.2	0.1	1.5A	0.2	1.3	0.04
1994	1.4	0.1	1.3	0.1	1.4	0.1	1.2B	0.1	1.4	0.04

Table 11. Average monthly temperature (temp) (C°) and precipitation (precip.) (cm) during each summer experiment and long-term (30-yr period from 1960 to 1990) means based on weather data collected at La Grande, Oregon 1991–95).

	June		July		August		September		Summer	
Year	Temp	Precip.	Temp	Precip.	Temp	Precip.	Temp	Precip.	Temp	Precip.
1992	19.7	4.0	19.7	1.9	21.1	2.0	14.4	1.6	18.7	2.4
1994	16.0	3.8	22.2	2.3	21.8	0.6	17.2	0.7	19.3	1.9
30-yr mean	16.9	3.6	20.8	1.5	20.4	2.3	15.4	2.4	18.4	2.5

Table 12. Body mass and number of elk in each thermal cover treatment at the beginning and average daily intake levels of each summer experiment in northeastern Oregon.

		Body mass (kg)		No. elk/treatment[a]					Daily intake[b]			
Year	Age class	Mean	Range	ZC	MC	DC	CC	Total[c]	Pellets	Hay	CP	DE
1992	Yearling	101.6	80–122	7	7	7	6	26	53.2	42.7	15.5	278.2
1994	Yearling	97.0	85–116	8	7	8	8	31	52.9	52.0	17.0	300.8

[a] Thermal cover treatment codes are ZC = zero cover; MC = moderate cover; DC = dense cover; and CC = combination cover.
[b] Units of intake are g/kg body mass$^{0.75}$ for pellets, hay, and crude protein (CP) and kcal/kg BM$^{0.75}$ for digestible energy (DE). All dietary attributes are expressed on a dry-matter basis.
[c] Total number of elk in the experiment.

All transmitters functioned reliably during the 1994 experiment, but the rapid beeping originating from an unknown source again confounded the collection of reliable data primarily during the first half of August and intermittently during September. Much of the activity data collected during these 2 time periods were excluded from ANOVA. No significant differences were found among the thermal cover treatments during either the day or night based on the remaining data (Fig. 20).

Water Consumption.—Prediction equations of water evaporation were moderately precise ($r^2 = 0.41$–0.49, $P < 0.001$, $n = 35$) and reflected differences in daily evaporation among the ZCT, MCT, and DCT units. These equations were used to adjust estimates of water intake based on average daily temperature and were as follows:

$$y = -0.21 + 0.036x \quad \text{for the DCT units,}$$

$$y = -0.20 + 0.043x \quad \text{for the MCT units,}$$

and

$$y = -0.34 + 0.066x \quad \text{for the ZCT units,}$$

where

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Table 13. Average daily intake of dry matter (DM), crude protein (CP), and digestible energy (DE) by month and entire summer for each cover treatment in northeastern Oregon.[a] Within time periods, means with different letters differ significantly ($P \leq 0.05$) and apply to all 3 dietary variables within each period.

Date and treatment	June			July			August			September			Summer		
	DM	CP	DE	DM	CP	DE	DM	CP	DE	DM	CP	DE	DM	CP	DE
Summer 1992															
Zero	91	14.8	265	105	17.0	305	107	17.2	310AB	109	17.8	311A	97	15.7	281A
Moderate	90	14.6	260	103	16.6	297	101	16.4	294B	102	16.7	292B	93	15.1	270B
Dense	92	14.8	266	106	17.2	308	103	16.6	298B	100	16.3	284B	94	15.2	272B
Combination	96	15.5	279	109	17.5	315	112	18.0	325A	105	17.1	299AB	100	16.1	289C
Summer 1994															
Zero	104	17.0	298A	108	17.5	308	103	16.6	293	103	16.7	294	104	16.9	297A
Moderate	104	16.9	298A	105	17.0	300	104	16.8	298	104	16.8	296	103	16.7	294A
Dense	109	17.7	314B	108	17.6	312	105	17.1	303	105	17.1	302	107	17.3	307B
Combination	107	17.4	307AB	108	17.5	310	105	17.0	300	106	17.2	303	106	17.2	305B

[a] Units for DM and CP are g/kg body mass$^{0.75}$ and DE is kcal/kg BM$^{0.75}$. All units are expressed on a dry-matter basis.

y = water lost via evaporation (L/day), and
x = average daily temperature (C°).

Water intake estimates collected during summer 1992 were highly variable and nonsensical, likely reflecting problems with accuracy of the bucket measuring system. These data were not analyzed. Water intake estimates collected during summer 1994 using the water-meter system differed significantly among treatments (P = 0.003 for the treatment × time interaction) (Fig. 21). Magnitude of differences among treatments increased as summer progressed and waned near the end of summer. Elk in the CCT and DCT generally used less water than elk in the other treatments during the hotter months of summer.

DISCUSSION

If thermal cover provides energetic benefits that enhance condition of elk, then (1) elk held in the CCT or DCT during winter should have lost condition more slowly than elk in the MCT or ZCT, and (2) elk held in the CCT or DCT during summer should have either grown more rapidly across summer or increased condition more rapidly than elk in the MCT or ZCT. None of our measures of condition or growth supported these predictions during any summer or winter experiment. Our results therefore refute the thermal cover hypothesis—that the weather-moderating effects of forest cover significantly enhance condition of elk in summer or winter.

This conclusion depends on our success at measuring relative condition, an attribute that is difficult to assess in large, live animals. Of our indicators of condition, body-mass dynamics provided the most useful insights regarding elk response to thermal cover. Under certain situations, however, body mass may be a poor measure of condition (Torbit 1985*b*). Changes in condition without concomitant changes in body mass may occur, particularly as animals progress through various anabolic

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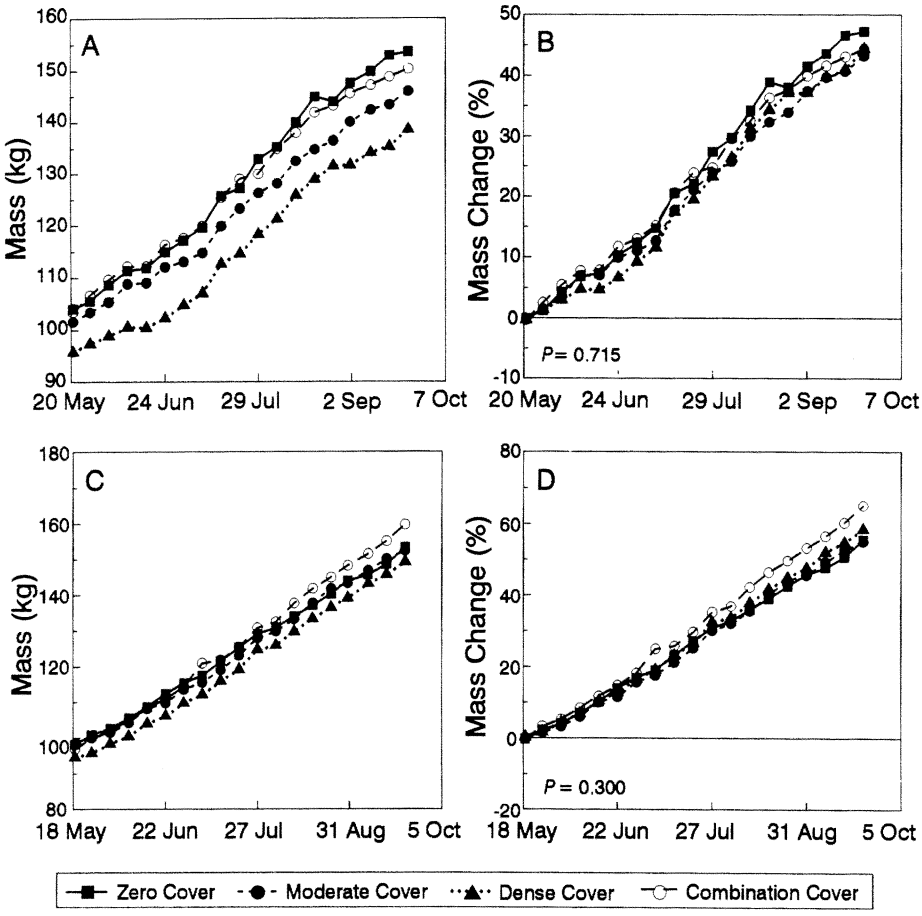

Fig. 18. Body-mass dynamics of yearling elk cows during summer 1992 (A, B) and summer 1994 (C, D) in northeastern Oregon. The *P* values in graphs B and D are the significance levels of the time × treatment interaction effect.

stages (Verme and Ozoga 1980, Bartle et al. 1983), and changes in body mass without concomitant changes in condition occur when food intake and gut fill change. For nonpregnant animals held on identical, submaintenance diets, and where mass change is predominantly due to catabolism of fat and lean muscle, there is little reason to suspect (1) that changes in body mass were not indicative of changes in relative

Table 14. Average change in amount of water, fat, protein, and total caloric content of the ingesta-free body of yearling elk across the 1994 summer thermal cover experiment in northeastern Oregon.

	Thermal cover treatment								
	Zero		Moderate		Dense		Combination		
Component[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	P^b
Water	28.9	0.74	30.2	1.09	30.4	1.56	34.1	3.91	0.324
Fat	6.3	0.64	6.2	1.02	6.6	0.98	5.5	0.43	0.788
Protein	9.6	0.34	9.9	0.42	10.1	0.57	10.9	1.01	0.539
Energy	111.7	7.86	112.4	11.43	117.3	11.76	111.1	9.54	0.587

[a] Units of water, fat, and protein are kg and energy is Mcal.
[b] Significance level of thermal cover treatment effects on each body component based on single-factor ANOVA.

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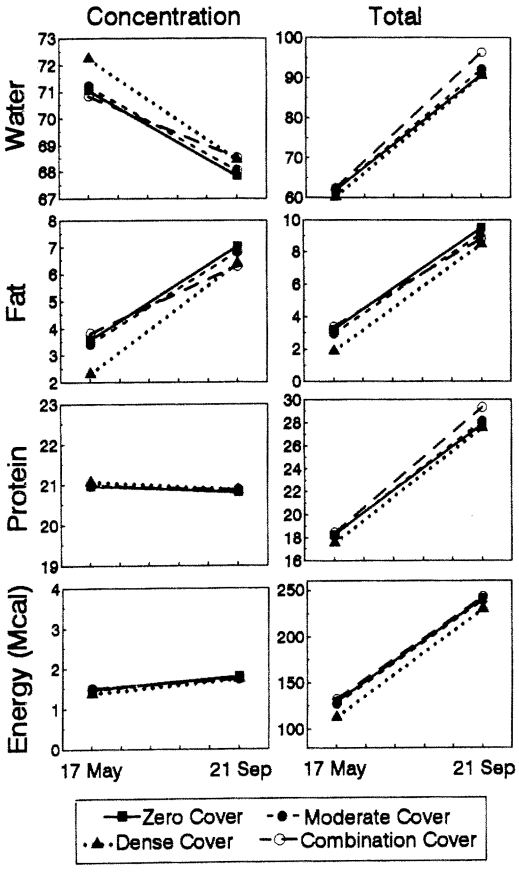

Fig. 19. Body composition dynamics of yearling elk cows during summer 1994 in northeastern Oregon. Units for the Concentration graphs are percent of ingesta-free body mass for water, fat, and protein, and Mcal/kg of ingesta-free body mass for energy. Units for the Total graphs are kg of water, fat, and protein and Mcal of energy in the ingesta-free body.

condition and (2) that relations between body mass and condition differed among elk held in the different cover treatments. Moreover, although much less frequently sampled, our body composition data (a more direct measure of condition) corroborate observed among-treatment body-mass patterns. Finally, the patterns of calf attrition among cover treatments during the third winter experiment inadvertently provided perhaps the ultimate test of thermal cover effects on elk and also corroborate the tenet that body mass provided a useful index of condition. The calves that died or had to be removed from the study to prevent death generally had the greatest percent mass loss (typically 18–20%) of any elk at the time they were removed from the study.

We monitored activity to identify behavioral strategies of elk that might allow them to compensate for differences in amount of thermal cover. Energy expenditures while standing or walking are considerably higher than that while bedded (e.g., about 25% higher [Renecker and Hudson 1986]); thus, we hypothesized that elk in treatments with little or no cover might attempt to compensate for lack of cover by altering activity if cover influenced condition. We found no evidence that elk attempted to compensate for cover influences via altering activity in summer or winter.

Winter

Given the widespread acceptance of the thermal cover hypothesis, our inability to find any significant benefit of thermal cover might seem surprising. However, this finding is consistent with those of 3 previous studies that aimed to test the thermal cover hypothesis under experimental conditions. These 3 studies, to our knowledge, represent the only other attempts to assess the effect of thermal cover on condition of large ungulates.

The first of these studies was conducted over 2 winters in Maine using white-tailed deer fawns (Robinson 1960). Three groups of 2 fawns in 1 winter and 3 groups of 5 fawns in a second winter were maintained on submaintenance rations in 3 0.5-ha pens—one with sparse (34%), a second with moderate (55%), and the third with dense (73%) closure of forest canopies. Relative estimates of condition were based on body mass, visual estimates of condition, and fat content of femur marrow. Minimum nocturnal temperatures were quite cold, occasionally falling to −30 C° during the 2 winters of the study. There was no evidence that deer in the sparse cover experienced greater declines in condition than those held in the moderate or dense cover.

In a second study also conducted in

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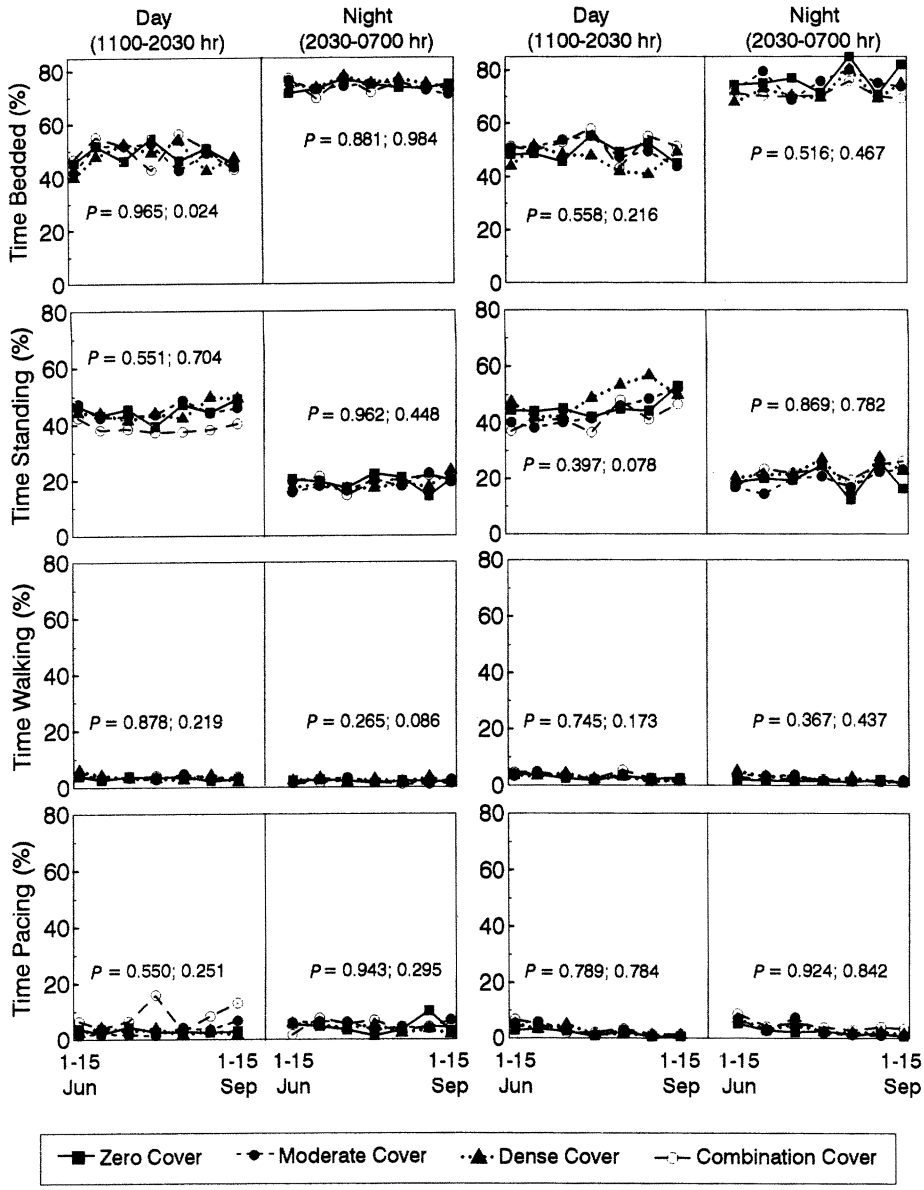

Fig. 20. Activity of yearling elk cows during summer 1992 (the first double-column of graphs) and summer 1994 (the second double-column of graphs) in northeastern Oregon. The first *P* value is for the treatment main effect; the second *P* value is for the time × treatment interaction effect.

Maine using white-tailed deer fawns (Gilbert and Bateman 1983), 1 deer was confined in each of 11 0.1-ha pens located in 3 cover treatments: clearcut, clearcut with artificial windbreaks, and uncut forest that averaged 72% canopy closure. Condition, based on body-mass change and kidney and bone marrow fat indices, feed intake, and activity patterns were used as response variables. Despite temperatures as low as −34 C°, forest cover was found to have little biologically relevant effect on those deer. The authors concluded that "increasing attention should be given to the quality of food available on winter range . . . and to physical condition of fawns in the au-

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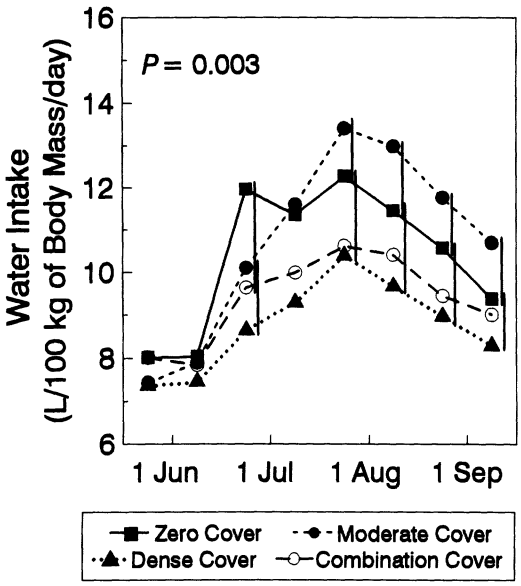

Fig. 21. Water consumption of yearling elk cows during summer 1994. The P value is for the time × treatment interaction effect. Values connected by vertical lines do not differ significantly ($P > 0.05$).

tumn . . ." (Gilbert and Bateman 1983: 397).

The third study was conducted over 3 winters using mule deer fawns and adults in Colorado and was reported in a series of Colorado Division of Wildlife reports (Freddy 1984, 1985, 1986). That study used small, 3-sided, covered sheds with windbreaks as thermal cover for the deer. Body-mass loss, food intake rate, and activity were measured. The second winter of the study was harsh, with average minimum temperatures occasionally dropping below −30 C°. Yet, no significant differences in body-mass dynamics or digestible energy intake were reported, and Freddy (1985) concluded that absence of thermal cover apparently did not reduce potential for deer to survive winter.

No study has established that thermal cover significantly enhances performance (i.e., condition, survival, and/or reproduction) of wild ungulates during winter, and thus the biological connection between thermal cover and winter performance of ungulates has not been demonstrated. The findings of this study and those of the 3 studies described above indicate the weather-moderating effects of forest cover are too small, occur too infrequently, or are too variable to have significant effects, at least in the ecological settings where thermal cover–condition relations have been assessed.

Perhaps the most surprising finding of this study was not that thermal cover provided no energetic benefit to elk, but that cover had detrimental effects. Our finding that clearcuts provided energetic environments that resulted in body condition at least as good or better than that of elk in any of the other treatments is, to our knowledge, without empirical precedent.

Yet, the influences of forest cover on microclimate observed in this study clarify these seemingly illogical results and have important implications not only regarding the role of thermal cover but also the effects of winter weather on bioenergetics of large ungulates in general. First, our data indicated that solar radiation had an inordinately positive effect on overwinter elk performance. Solar radiation provides a direct energy input that helps to warm the animal, thereby reducing the amount of food energy or endogenous energy required to maintain thermal homeostasis. Although noted by Parker and Gillingham (1990) and Parker and Robbins (1984), the importance of solar radiation is poorly recognized in much of the literature dealing with condition and survival of wild ungulates. For example, winter severity indices developed for western ungulate ranges typically do not include adjustments based on solar radiation (e.g., Picton 1979, Leckenby and Adams 1986) (although we recognize that relevant solar radiation estimates are generally unavailable). Moreover, elk habitat evaluation models typically used regionally in the Northwest (e.g., Wisdom et al. 1986, Thomas et al. 1988) did not recognize the importance of solar radiation or recognize that shading by thermal cover may induce negative consequences.

Second, results of our study indicate that wind had no measurable effect on elk performance. The effects of forest cover

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on wind are well established (Grace and Easterbee 1979, Bunnell et al. 1986) (and documented in this study; Fig. 7). Parker and Gillingham (1990) concluded that the magnitude of windspeed effects on heat loss via convection can be as great as the energetic inputs of solar radiation, based on standard operative temperature modeling. Windspeed was usually mild in our study, and the higher windspeeds usually occurred around midday. Windspeed therefore was greatest at the time of day when temperature stress was least likely to occur, i.e., when elk were well within thermoneutrality. Chappel and Hudson (1978) and Blaxter et al. (1963) reported that the effect of wind on metabolic rates (which increase to maintain body temperature) was most substantial when ambient temperatures are cold, near the animal's lower critical temperature (temperature at which metabolic rate and thus energy demands increase). Therefore, our finding that windspeed has little influence on elk must be considered in the context of the prevailing windspeeds of our study.

Third, the warming effect of long-wave radiation from forest canopies on nocturnal temperature basically did not occur to any appreciable extent, suggesting that the effect often may be too inconsistent and small to be relevant. For example, the warming effect of cover on temperature typically amounts to only 2–3 C° (Bunnell et al. 1986, Parker and Gillingham 1990). This effect is reduced or eliminated under cloudy conditions due to long-wave emittance from clouds (Reifsnyder and Lull 1965), or if air is mixed due to cold air drainage (Riggs et al. 1993) and/or wind. In our study, nocturnal breezes, sloping topography conducive to cold-air drainage, and cloudy conditions apparently accounted for our inability to show a warming effect of cover.

Fourth, our data also suggested that the direct effect (i.e., animal absorbance) of long-wave radiation on energy balance at night was insignificant, particularly when compared to that of solar radiation. The effect apparently was greatest on clear to partly cloudy nights and least on heavily overcast nights (Fig. 5) (Reifsnyder and Lull 1965). We cannot conclude with certainty that there was no net benefit of long-wave radiation emanating from forest canopies on elk condition. However, a primary purpose of the combination cover treatment was to assess this; we presumed that elk able to take advantage of long-wave radiation at night and solar radiation during the day should have performed better than elk without access to long-wave radiation from forest canopies. This failed to occur, supporting the contention that the long-wave radiation effect was minor.

Much of the empirical support for the thermal cover hypothesis during either summer or winter is derived from observational studies of habitat use (Peek et al. 1982). Evolved habitat preferences undoubtedly confer long-term fitness advantages (Ruggiero et al. 1988), but conclusions about relations between habitat components and fitness variables (i.e., survival, reproductive success) derived from such studies can be tenuous (Peek et al. 1982, Van Horne 1983, Hobbs and Hanley 1990). Moreover, our microclimate data (Fig. 5) illustrate that selection for cover provides little or no inferential support that animals are selecting for thermal energetic needs, unless the complex biophysical interactions between cover and prevailing weather are taken into account. If, in fact, elk select habitats primarily to optimize their thermal energetic environment, they should select for openings during the day to have access to solar-radiation flux and associated warmer temperatures even when skies are overcast. If windspeed is high, animals should nevertheless remain in openings but should occupy sites protected by topography from wind. At night during overcast periods with or without slight wind, there is virtually no thermal energetic advantage for selecting thermal cover. Elk would most likely benefit from forest cover during nights when temperature is cold and windspeed is high. The extent of the primary benefit (i.e., protection from wind), however, would depend on whether or not animals spend an appreciable portion of the

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night bedded, because windspeed is markedly reduced at ground level (Campbell 1986). Free-ranging animals obviously have a number of options to avoid high winds that do not require forest cover.

Moreover, animals select habitats for various reasons, further reducing the value of habitat selection studies to assess the importance of thermal cover. These habitat selection studies include those that compare changes in habitat use as weather conditions vary (e.g., Burcham et al. 1993). Conclusions of such studies depend upon the assumption that relatively greater preference for habitats providing thermal cover during harsh weather does in fact indicate bioenergetic benefits of cover. This may not be true if security needs, for example, ultimately drive the selection of habitats providing cover. If weather conditions are sufficiently harsh such that net energetic gains of feeding are negligible, then animals may not feed in psychologically insecure areas, in preference for bedding in secure areas.

Our finding that temperature significantly and linearly affected body-mass dynamics (Fig. 10) at relatively moderate nocturnal temperatures seems inconsistent with concepts of thermoneutrality and critical temperature thresholds. Empirical estimates of lower critical temperature (LCT) averaged about −20 to −30 C° for deer and bighorn sheep (*Ovis canadensis*) (Stevens 1972, Chappel and Hudson 1978, Parker and Robbins 1984, Mautz et al. 1985) and below −30 C° for moose (*Alces alces*) (Renecker and Hudson 1986). Parker and Robbins (1984) reported a distinct threshold (LCT) of about −20 C° (operative temperature) in elk calves and showed that metabolism markedly increased due to shivering thermogenesis as temperatures fell below LCT. But our data indicated a gradual, linear effect, rather than a threshold effect, of temperature on loss of body mass. Moreover, the effect of temperature on mass loss occurred at moderate temperatures (>−10 C°), well within the zone of thermoneutrality of elk (Parker and Robbins 1984). Therefore, elk in our study theoretically should rarely have been temperature stressed, and there should have been little need for them to adjust metabolic rates to compensate for differing microclimates among treatments. The fact that there were consistent and significant differences in mass loss among cover treatments indicates that our elk were temperature stressed, despite apparently thermoneutral temperatures. (We should mention that Parker and Robbins [1984] measured operative, rather than ambient temperature effects on elk and deer, calling into question the equivalency of nocturnal ambient temperature estimates of our study and operative temperature estimates of their study. During the night in our study, however, windspeed was generally quite low; under conditions of no solar radiation and slight wind, standard operative temperature, operative temperature, and ambient temperature are similar [*see* Parker and Gillingham 1990]).

These findings call into question the applicability of empirical LCT study results to wintering animals in free-ranging conditions. Most of these studies evaluated temperature–metabolic rate relations over short periods of time (usually a few hours). Although useful for identifying changes in metabolic rate due to shivering thermogenesis, they may not adequately account for changes in metabolic rate due to nonshivering thermogenesis or other physiological adaptations requiring several weeks of acclimation (Landsberg and Young 1983, Hudson and Christopherson 1985). Results of these studies also may not be applicable for animals that consume a submaintenance or starvation diet (e.g., *see* Moen 1968 and Wesley et al. 1973), animals frequently subjected to coat wetting from rain or melted snow (Parker 1987), or animals in poor condition.

The extrapolability of results of ecological studies conducted in a single study area, such as our study, typically is unknown, and caution is warranted when such results are used for management purposes. But there are several reasons for expecting that our rejection of the thermal cover hypothesis is robust across a variety of climatic settings. First, patterns of elk

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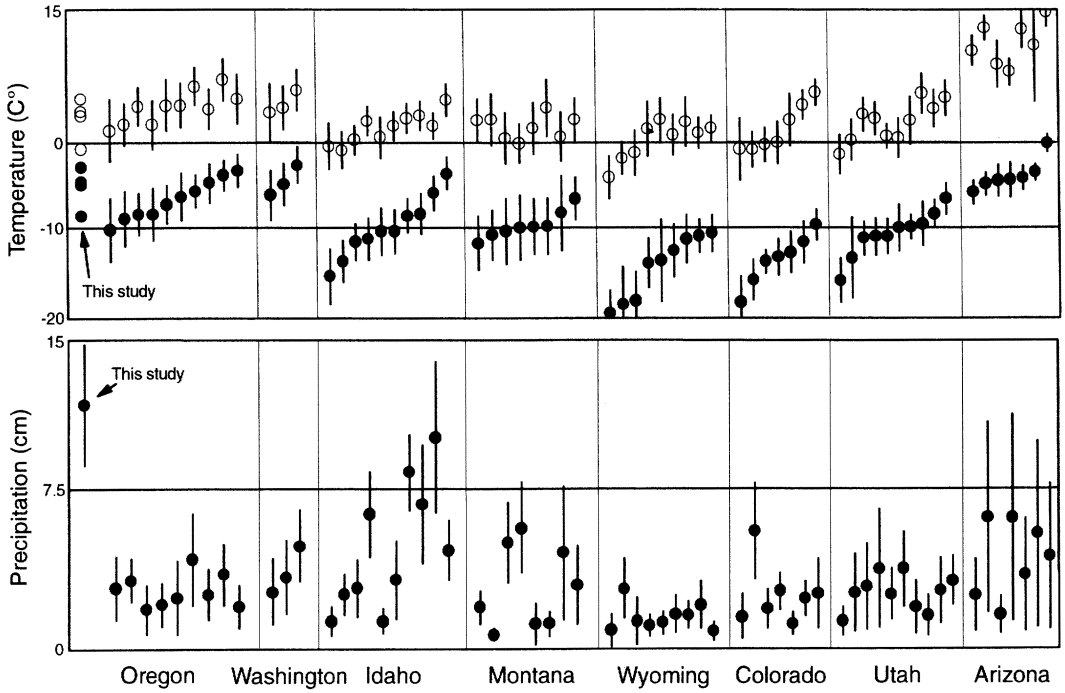

Fig. 22. Estimates of minimum (solid circles) and maximum (open circles) daily temperature and average monthly precipitation in December–February on elk winter ranges in selected western states. Estimates are means of 15 years of data from 1980 through 1994 from National Oceanic and Atmospheric Administration (1980–94). Vertical lines are ±1 SD. For temperature at our study site, December–February averages are presented for each year of the study. Total precipitation was not measured at our study site; thus we calculated the mean ±1 SD from 10 years of weather data collected at the Meacham Oregon weather station (located 8 km from our study site at similar elevation) to represent precipitation levels that occurred during the study. Weather stations selected for each wintering area are presented in Appendix E.

response among treatments were similar each winter, despite significantly different weather among the 4 winters—a relatively warm, dry winter; an atypically cold winter with roughly normal precipitation; and a slightly warmer-than-normal winter that included periods with considerable rain and wet snow (e.g., 2.5 cm of rain over 3 days in the first week of Dec and 7.5 cm of rain over 7 days in the first 2 weeks of Jan). It was during this rainy winter that much of the "mortality" occurred; this attrition was greatest in the dense cover treatments, suggesting that thermal cover provided little relevant benefit during rainy weather. During the coldest winter, the magnitude of difference in body-mass loss between animals in the zero cover and dense cover treatments was the greatest of any of the winter experiments, suggesting that the negative effects of forest cover actually increase as temperatures decline, because the relative value of solar radiation increases as temperatures decline. Finally, similar studies with deer (Robinson 1960; Gilbert and Bateman 1983; Freddy 1984, 1985, 1986) failed to find positive thermal cover effects, despite being conducted during colder winters using smaller, and thus more susceptible (Parker and Robbins 1984), experimental animals.

To further assess the robustness of our findings, we compared temperature and precipitation data during our study to 15-year averages based on National Oceanic and Atmospheric Administration (1980–94) records at interior (east of the coastal maritime climates) elk winter ranges across much of the West, particularly where Rocky Mountain elk populations are well established (Fig. 22, Appendix E). These data indicate that minimum and

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maximum temperatures during our coldest winter were equivalent to or substantially colder than that found in most wintering areas in the Pacific Northwest (i.e., Washington and Oregon). In the Rocky Mountain states, average minimum temperature during our coldest winter was colder, equivalent to, or fell within 1 standard deviation of all winter ranges in Arizona and about half of those in Idaho, Montana, and Utah, but was warmer than most winter ranges in Wyoming and Colorado. Average maximum (daytime) temperature during our coldest winter was as cold or colder than that on nearly every winter range for which we had data. Our study area also was markedly wetter than virtually every other winter range included in this analysis (Fig. 22). The precipitation levels and temperature regimes particularly during our coldest winter suggest weather patterns equivalent to or considerably harsher than that on many western winter ranges and nearly all winter ranges in the Pacific Northwest for which we had data.

The lack of solar radiation and windspeed data for winter ranges hindered our ability to assess applicability of our results to many wintering areas, particularly those in Wyoming and Colorado and other areas with cooler temperatures. But we offer several predictions. First, in wintering areas where daily cumulative solar radiation fluxes are less than those in our study, the negative effects of thermal cover would be reduced. Given the high precipitation levels at our study area (Fig. 22), however, this seems unlikely; our study may have underestimated the negative effects of thermal cover for many interior winter ranges. Second, assuming a positive relation between temperature and cloud cover (Reifsnyder and Lull 1965), areas that tend to be quite cold also may provide greater solar radiation flux, which may compensate to some extent for the colder temperatures. Thus, colder temperatures do not necessarily indicate more severe thermal energetic environments, and the potentially beneficial effects of thermal cover may be lowest in some of the coldest regions. Third, the value of thermal cover may be greater than our study would indicate in areas with considerably more wind, especially at night and especially under substantially colder temperature regimes. The high elevation shrub–steppe plains of south-central Wyoming provide a possible example. There, minimum temperatures are quite cold (about −12 C°, Fig. 22, Appendix E) and windspeeds are among the highest in the United States (Marrs et al. 1982). Finally, the value of thermal cover may be greater in areas of considerably warmer temperatures than those of our study, particularly during periods of high solar radiation flux (i.e., due to winter heat stress). This would most likely occur in Arizona (Fig. 22). The relevance of these warm conditions to winter survival probably is minimal, however, because winter mortality due to acute negative energy balance likely is rare under these conditions.

Summer

We also found no evidence that the weather-sheltering effects of forest cover enhanced growth and condition of elk during either of 2 summer experiments, although our data suggest that elk lacking access to dense forest cover require more water. Growth rates, body composition, and activity profiles were unaffected by thermal cover treatments. The yearlings used in both experiments were growing rapidly on diets that likely supplied suboptimal digestible energy to support maximum growth rates. We would expect that growth of elk would be sensitive to their bioenergetic environment under these conditions.

Summer weather during both experiments provided relatively good conditions to test the thermal cover hypothesis. Temperatures in both summers were warmer than long-term averages, up to 2–3 C° warmer in several months (Table 10). Maximum temperatures were ≥25 C° during at least 30% of the days. Parker and Robbins (1984) reported that upper critical temperature (UCT) (the point at which metabolic rate increases to dissipate heat)

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of yearling elk while standing was 25–30 C° (operative temperature). Thus elk in our study, particularly those in the zero cover treatment, should have been heat stressed because operative temperatures typically range markedly higher than ambient temperatures during sunny summer days (Demarchi and Bunnell 1993). We did not compare summer temperature records among western elk summer ranges to those in our study, because most weather stations are located in valleys near towns and cities and thus are not representative of summer range conditions. The elevation of our study area (1,300 m) is probably relatively low compared to many summer ranges, particularly those in the Rocky Mountain states. We suspect that cooler temperatures than those encountered in our study predominate across the majority of elk summer ranges in the northern half of the West.

The value of thermal cover to large ungulates in summer apparently has received less scrutiny than that in winter; we are aware of no studies that have examined thermal cover effects on condition, growth, or reproduction of wild ungulates during summer. Standard operative temperature modeling of Demarchi and Bunnell (1993) and microclimatic measurements of Zahn (1985) clearly indicate that solar radiation, and to some extent longwave radiation from solar-heated substrate, markedly increase heat load of animals without access to shade. Demarchi and Bunnell (1993) estimated operative temperatures in forest openings on sunny days to be about 1.7 times higher than that in habitats providing thermal cover (50 C° in openings versus 30 C° in cover when ambient temperature is 25 C°). They speculated that such heat loads may decrease summer body-mass gains and therefore may affect overwinter survival. This contention is supported to some extent by results of livestock studies. At high ambient temperature (≥38 C°—much higher than those encountered during our study), Flamenbaum et al. (1995) showed that feed intake and milk production of dairy cattle are reduced, and Yousef and Johnson (1966) showed that food intake is reduced. Decline in food intake apparently is a common response to excessive heat in cattle, because heat generated from digested food (i.e., heat increment of feeding) is substantial and contributes to the heat load (Kelly et al. 1954).

Additionally, studies of Zahn (1985) and Demarchi and Bunnell (1995) provided evidence that elk and moose, respectively, selected for thermal cover to avoid high radiation flux. Petron (1987) reported that elk in hot desert environments often selected daytime bed sites under shrubs. In contrast, Merrill (1991) found little evidence that elk selected for forest cover to any greater extent during relatively warm, sunny conditions compared to cooler, overcast conditions in southwestern Washington.

Our results indicate that performance of elk is unaffected by thermal cover under the temperature and radiation flux conditions encountered during this study. Parker and Robbins (1984) showed that elk in summer pelage are well adapted to operative temperatures in excess of their UCT. Operative temperatures above UCT had weak and inconsistent effects on metabolic rate, and their captive elk often did not use available shade during hot ambient conditions. They reported that such tolerance likely was due to the relatively high concentration of cutaneous sweat glands; elk effectively reduced heat loading simply by sweating. Despite some evidence of selection for shade, Petron (1987) indicated that elk in hot desert environments were not particularly dependent on shade because of their ability to dissipate heat through sweating. Finally, McCorquodale and Eberhardt (1993) concluded that elk colonizing the Arid Lands Ecology Reserve, a low-elevation, hot, shrub–steppe area in south-central Washington, did so with no appreciable detriment to their fitness despite the lack of any forest cover. Because the population growth rate of this herd was among the highest of any western elk population, they concluded that thermal cover on summer range apparent-

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ly is not a requisite of quality summer habitat.

We caution, however, that our summer results have unknown relevance to other ungulate species. For example, ability of deer to dissipate heat via sweating apparently is lower than that of elk (Parker and Robbins 1984). In general, ability to sweat is lower in smaller animals, sweating likely requires less energy than panting for dissipating heat, and it provides greater maximal rate of evaporative cooling than panting (Taylor 1977). Parker and Robbins (1984) demonstrated that increases in metabolic rate in response to temperatures above UCT are markedly greater in deer than that of elk, and thus the value of thermal cover to deer in summer may be greater.

MANAGEMENT IMPLICATIONS

We begin this section by re-emphasizing several key points that temper our conclusions and recommendations. First, our study did not assess effects of topographic or other landscape features that could enhance energy conservation by protecting from wind or enhancing absorption of solar radiation. Although landscape features may well qualify as "thermal cover," our findings only apply to thermal cover provided by coniferous forests, as per the formal definition of Lyon and Christensen (1993). Second, we assessed only the weather-moderating influences of forest cover (i.e., influences of windspeed, ambient temperature, and long- and shortwave radiation). We do not imply that our findings are relevant in the context of other values that forests may provide. Finally, our results may not be applicable in other regions or during winters with substantially different weather. In light of these points, our findings indicate that (1) in winter, the weather-moderating effects of thermal cover are too small, occur too infrequently, or are too variable to provide meaningful benefits, and can even have negative effects on animal performance; and (2) in summer, although shade from thermal cover provides a distinct energetic advantage that probably enhances comfort, thermal cover fails to improve performance of elk because their adaptations to heat effectively compensates for the lack of thermal cover. We conclude that our findings, combined with those of other thermal cover studies (e.g., Robinson 1960; Gilbert and Bateman 1983; Freddy 1984, 1985, 1986), offer strong evidence that influences of thermal cover on animal performance and, by extension, population dynamics is rarely of consequence.

Nevertheless, because forest cover does in fact modify weather, there certainly could be climatological conditions in which animals may derive an energetic benefit of sufficient magnitude to be biologically relevant. Although never demonstrated with empirical research using wild ungulates, such conditions might occur (1) in areas or years when windspeeds are considerably higher *and* temperatures are colder or (2) in areas or years that are considerably hotter (Oekenfels and Brooks 1994) than were encountered in the various studies of thermal cover. Therefore, categorical rejection of the concept of thermal cover probably is not appropriate. Rather, we recommend a shifting of management emphasis, such that management priorities reflect the value of thermal cover in relation to the value of various other habitat attributes. In other words, which habitat attributes that affect performance of elk populations are most important and thus should be emphasized in various models and management plans? The results of this and the other thermal cover studies indicate that thermal cover should receive low priority.

With this in mind, we stress 3 points. First, thermal cover and forage resources both address energy balance but from different perspectives: dietary energy levels and forage abundance control intake rates of energy whereas thermal cover has been perceived to reduce the rate of net energy loss. Thus, the recognition of the importance of thermal cover is an implicit recognition of the importance of adequate energy nutrition. Effects of nutrition on animal performance have been well estab-

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lished through a long history of scientific experimentation. Effects of nutrition on population demography of free-ranging ungulates have been reasonably well established as well (e.g., Clutton-Brock et al. 1982, Verme and Ullrey 1984, Coughenour and Singer 1996). However, similar effects have not been documented for thermal cover—to the contrary, the preponderance of evidence currently does not support the thermal cover hypothesis.

Yet, in the context of large-scale habitat management in the inland Northwest, the effects of nutrition generally have been ignored. In Oregon and Washington for example, none of the national forest management plans developed for the Blue Mountains Ecoregion specifically addresses forage quality for elk, even though the habitat effectiveness model for this region (e.g., Thomas et al. 1988) explicitly accounts for this variable (Edge et al. 1990). In Montana and Idaho, Christensen et al. (1993) argued that managers of elk winter ranges should focus on providing thermal cover and explicitly subordinated nutrition to a variety of other habitat factors during winter and summer.

Although inadequate technology currently may hinder routine assessments of forage quality and quantity across landscapes by land management agencies, the need for adequate nutrition should not be discounted (Cook et al. 1996). Moreover, long-recognized inverse relations between forage production and forest canopy closure (Pase 1958, Young et al. 1967, McConnell and Smith 1970) indicate that decisions that emphasize thermal cover over food production can reduce forage production and, in turn, carrying capacity (Hett et al. 1978). We contend that decisions to favor thermal cover should be based on a demonstrated need. At the very least, our data indicate the assumption that thermal cover compensates for marginal or inadequate forage conditions (e.g., *see* Christensen et al. 1993) is insupportable.

Second, our results indicate that reported selection of forest cover by elk (e.g., Irwin and Peek 1983, Leckenby 1984) is unlikely to reflect a requirement for thermal cover per se. It follows that such selection patterns most likely involve needs for security and reduced vulnerability to hunters, energy savings from reduced snow deposition and associated costs of locomotion (Pauley et al. 1993), or at times forage conditions (quality in particular; e.g., *see* Van Horne et al. 1988). Thus, we contend that managers and researchers alike should refocus from thermal cover to these other aspects of forest cover. Although it has been assumed that dense, mature forests (i.e., "satisfactory" cover sensu Thomas et al. 1988) provides energy conservation and security simultaneously (e.g., Thomas et al. 1988), the extent to which this is true likely is specific to the stresses imposed by weather, snow accumulation, and harassment. These factors vary independently. Therefore, it seems reasonable to address each independently.

Finally, we offer several recommendations regarding various habitat management plans and planning protocol. As a result of the perceived need to enhance energy balance, the concept of thermal cover has become well integrated into a variety of planning tools, including elk habitat effectiveness models (e.g., Wisdom et al. 1986, Thomas et al. 1988), management standards and guidelines for public forestlands, and national forest plans (e.g., Black et al. 1976, Edge et al. 1990, Christensen et al. 1993). Together, these guide habitat management on behalf of elk on millions of hectares of public forestlands. Foremost among these are the habitat effectiveness models, because they are a fundamental tool for developing management plans (Edge et al. 1990). Our findings suggest that a reassessment of these models is appropriate. Although we refrain from making detailed recommendations, we suggest that such a reassessment should explicitly focus on the weight given to each habitat attribute based on the linkage of each to animal performance and herd productivity. This will probably involve placing greater emphasis on forage quantity and quality. And, this probably also will require developing better techniques to assess forage

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conditions across landscapes (Cook et al. 1996).

In summary, our findings, combined with the results of other studies of thermal cover effects on animal condition, provide a preponderance of evidence indicating that thermal cover has little relevance to herd productivity and demographics. Although climatological conditions may exist under which thermal cover is relevant, those conditions have yet to be defined with empirical data. Thus, we contend that thermal cover considerations should be relegated low priority relative to other habitat attributes that can be linked to herd productivity in most circumstances.

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APPENDICES

Appendix A. Regression equations used to calibrate weather variable output from the permanent (y) and mobile (x) weather stations.

Regression equation	r^2	n	Date
Windspeed (m/sec)			
$y = 0.072 + 1.036x$	0.994	312	Dec 94
$y = -0.006 + 0.989x$	0.996	1,247	Mar 94
$y = 0.010 + 1.003x$	0.981	450	Oct 94
$y = 0.546 + 0.785x$	0.856	384	Feb 95[a]
Temperature (C°)			
$y = -0.040 + 0.979x$	0.996	312	Dec 94
$y = -0.175 + 0.992x$	0.999	1,247	Mar 94
$y = -0.033 + 0.995x$	0.999	450	Oct 94
$y = -0.410 + 0.983x$	0.999	384	Feb 95
Relative humidity (%)			
$y = 4.383 + 0.939x$	0.999	312	Dec 94
$y = 3.533 + 0.936x$	0.998	1,247	Mar 94
$y = 4.014 + 0.923x$	0.999	450	Oct 94
$y = 2.584 + 0.940x$	0.998	384	Feb 95
Solar radiation (kW/m^2)			
$y = -0.000 + 0.963x$	0.998	312	Dec 94
$y = 0.001 + 0.989x$	0.996	1,247	Mar 94
$y = -0.001 + 1.029x$	0.993	450	Oct 94
$y = 0.002 + 0.995x$	0.992	384	Feb 95
Net radiation (kW/m^2)			
$y = 0.001 + 1.016x$	0.996	312	Dec 94
$y = 0.002 + 1.030x$	0.986	1,247	Mar 94
$y = 0.003 + 1.055x$	0.996	450	Oct 94
$y = -0.004 + 1.039x$	0.958	384	Feb 95

[a] Changes in regression coefficients and the lower r^2 were due to occasional malfunctioning of the anemometer on the mobile station.

Appendix B. Prediction equations for windspeed in each zero cover, moderate cover, and dense cover treatment unit during summer and winter. The equations provide windspeed estimates (y) at elk holding pens based on windspeed estimates (x) collected at the permanent weather station (*see* Fig. 1).

Treatment	Unit[a]	Regression equation	r^2	n
Zero cover	L	$y = 0.278 + 0.688x$	0.755	3,849
Zero cover	M	$y = 0.240 + 0.793x$	0.831	1,736
Zero cover	T	$y = 0.394 + 0.847x$	0.725	2,427
Moderate cover	L	$y = 0.356 + 0.534x$	0.587	2,760
Moderate cover	M	$y = 0.306 + 0.413x$	0.721	1,729
Moderate cover	T	$y = 0.428 + 0.433x$	0.615	3,584
Dense cover	L	$y = 0.272 + 0.362x$	0.702	2,671
Dense cover	M	$y = 0.540 + 0.226x$	0.344	1,903
Dense cover	T	$y = 0.431 + 0.129x$	0.349	2,771

[a] Unit refers to the individual replicate within treatments, and T, M, and L simply are arbitrary designations.

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Appendix C. Coefficients of multiple determination (r^2) and sample sizes (n) for equations used to predict temperature, relative humidity, solar radiation, and net radiation in each zero cover, moderate cover, and dense cover treatment unit during winter. The statistical parameters are for equations used to predict weather variables at each elk holding pen based on weather data collected at the permanent weather station (*see* Fig. 1).

		Temperature		Relative humidity		Solar radiation		Net radiation	
Conditions[a]	Unit[b]	r^2	n	r^2	n	r^2	n	r^2	n
Zero cover	L								
Day; AWC		0.992	759	0.980	759	0.990	234	0.927	248
Night; AWC		0.992	1,007	0.976	1,007			0.972	152
Zero cover	M								
Day; AWC						0.997	328	0.971	353
Day; 25NP		0.959	334	0.913	334				
Day; 100P		0.999	73	0.974	73				
Day; 75NP		0.987	170	0.978	170				
Night; AWC								0.940	248
Night; 25NP		0.915	448	0.806	448				
Night; 100P		0.999	215	0.985	215				
Night; 75NP		0.989	197	0.976	197				
Zero cover	T								
Day; AWC						0.987	504	0.974	527
Day; 25NP		0.988	108	0.766	108				
Day; 100P		0.997	194	0.993	194				
Day; 75NP		0.980	535	0.919	535				
Night; AWC				0.801	1,090			0.910	232
Night; 25NP		0.989	113						
Night; 100P		0.983	285						
Night; 75NP		0.951	692						
Moderate cover	L								
Day; AWC		0.993	1,515	0.976	1,515	0.469	714	0.463	714
Night; AWC		0.994	1,518	0.974	1,518			0.931	288
Moderate cover	M								
Day; AWC						0.496	595	0.559	595
Day; 25NP		0.983	453	0.937	453				
Day; 100P		0.996	274	0.979	274				
Day; 75NP		0.979	545	0.935	545				
Night; AWC								0.980	198
Night; 25NP		0.975	353	0.936	353				
Night; 100P		0.989	513	0.968	513				
Night; 75NP		0.978	554	0.766	554				
Moderate cover	T								
Day; AWC						0.607	605	0.646	607
Day; 25NP		0.959	453	0.921	453				
Day; 100P		0.984	428	0.959	428				
Day; 75NP		0.964	415	0.926	415				
Night; AWC								0.917	430
Night; 25NP		0.963	299	0.686	299				
Night; 100P		0.934	724	0.673	724				
Night; 75NP		0.940	392	0.770	392				
Dense cover	L								
Day; AWC						0.435	569	0.468	498
Day; 25NP		0.957	350	0.775	350				
Day; 100P		0.986	636	0.898	636				
Day; 75NP		0.966	870	0.795	870				
Night; AWC								0.870	127
Night; 25NP		0.987	327	0.940	327				
Night; 100P		0.971	1,336	0.674	1,336				
Night; 75NP		0.986	1,118	0.853	1,118				

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Appendix C. Continued.

Conditions[a]	Unit[b]	Temperature		Relative humidity		Solar radiation		Net radiation	
		r^2	n	r^2	n	r^2	n	r^2	n
Dense cover	M								
Day; AWC						0.578	474	0.481	526
Day; 25NP		0.961	415	0.874	415				
Day; 100P		0.987	134	0.986	134				
Day; 75NP		0.946	336	0.920	336				
Night; AWC								0.908	322
Night; 25NP		0.987	430	0.939	430				
Night; 100P		0.993	275	0.955	275				
Night; 75NP		0.945	536	0.957	536				
Dense cover	T								
Day; AWC						0.538	326	0.390	314
Day; 25NP		0.919	189	0.837	189				
Day; 100P		0.954	330	0.779	330				
Day; 75NP		0.934	385	0.676	385				
Night; AWC								0.834	156
Night; 25NP		0.958	150	0.829	150				
Night; 100P		0.970	535	0.868	535				
Night; 75NP		0.956	430	0.778	430				

[a] Codes for weather conditions are AWC = all weather conditions; 25NP = 0–50% cloud cover, no precipitation; 100P = virtually 100% cloud cover with at least occasional precipitation; and 75NP = 50–100% cloud cover with virtually no precipitation.
[b] Unit refers to the individual replicate within treatments, and T, M, and L simply are arbitrary designations.

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Appendix D. Coefficients of multiple determination (r^2) and sample size (n) for equations used to predict temperature, relative humidity, solar radiation, and net radiation in each zero cover, moderate cover, and dense cover treatment unit during summer. The statistical parameters are for equations used to predict weather variables at each elk holding pen based on weather data collected at the permanent weather station (*see* Fig. 1).

		Temperature		Relative humidity		Solar radiation		Net radiation	
Conditions[a]	Unit[b]	r^2	n	r^2	n	r^2	n	r^2	n
Zero cover	L								
Day; AWC		0.997	2,016	0.995	2,016	0.986	1,396	0.962	1,396
Night; AWC		0.995	1,249	0.998	1,249			0.973	726
Zero cover	M								
Day; AWC		0.994	600	0.988	600	0.986	517	0.982	517
Night; AWC		0.980	376	0.981	376			0.922	253
Zero cover	T								
Day; AWC		0.971	1,004	0.970	1,004	0.963	900	0.953	900
Night; AWC		0.876	748	0.946	748			0.735	641
Moderate cover	L								
Day; AWC		0.979	529	0.976	529	0.416	490	0.380	490
Night; AWC		0.982	270	0.981	270			0.966	225
Moderate	M								
Day; AWC		0.982	651	0.979	651	0.392	597	0.358	597
Night; AWC		0.964	400	0.969	400			0.934	323
Moderate cover	T								
Day; AWC				0.966	1,000	0.426	667	0.390	667
Day; 25NP		0.976	668						
Day; 100P		0.994	74						
Day; 75NP		0.970	258						
Night; AWC		0.926	676	0.937	676			0.791	325
Dense cover	L								
Day; AWC		0.981	1,307	0.953	1,307	0.213	643	0.265	643
Night; AWC		0.994	705					0.318	293
Night; 25NP				0.957	175				
Night; 100P				0.908	224				
Night; 75NP				0.954	306				
Dense cover	M								
Day; AWC		0.985	892	0.967	892	0.214	552	0.221	552
Night; AWC		0.984	522					0.864	226
Night; 25NP				0.974	286			0.342	330
Night; 100P				0.979	65				
Night; 75NP				0.717	171				
Dense cover	T								
Day; AWC						0.224	600	0.136	600
Day; 25NP		0.972	545	0.742	545				
Day; 100P		0.997	55	0.996	55				
Day; 75NP		0.973	134	0.983	134				
Night; AWC								0.342	330
Night; 25NP		0.966	456	0.921	456				
Night; 100P		0.971	185	0.954	185				
Night; 75NP		0.942	58	0.982	58				

[a] Codes for weather conditions are AWC = all weather conditions; 25NP = 0–50% cloud cover, no precipitation; 100P = virtually 100% cloud cover with at least occasional precipitation; and 75NP = 50–100% cloud cover with virtually no precipitation.

[b] Unit refers to the individual replicate within treatments, and T, M, and L simply are arbitrary designations.

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Appendix E. Weather stations, locations, and associated elk herds used to develop temperature and precipitation descriptions of elk winter ranges in Oregon, Washington, Idaho, Montana, Wyoming, Colorado, Utah, and Arizona. Coupling of weather stations with winter range complexes was based on survey results provided by game biologists in each state. However, survey results were not received from Montana; selection of weather stations was based on our collective knowledge of Montana wintering areas.

Weather station[a]	Region	Closest town	Herd name[b]
Oregon			
1 Unity[c]	East-central	Baker City	n.g.
1 Ironside 2 W	East-central	Baker City	n.g.
2 Enterprise 2 SE	Northeast	Enterprise	n.g.
2 Wallowa	Northeast	Enterprise	n.g.
3 Brothers	Central	Bend	n.g.
3 Paulina	Central	Bend	n.g.
4 Baker FAA Airport	Northeast	Baker City	n.g.
5 Silver Lake Ranger Station	South-central	Bend	n.g.
6 Lakeview 2 NNW	South-central	Lakeview	n.g.
7 Prineville 4 NW	Central	Bend	n.g.
8 Cove	Northeast	La Grande	n.g.
8 Minam[d]	Northeast	La Grande	n.g.
8 Union Exp. Station	Northeast	La Grande	n.g.
9 Dayville 8 NW	Central	Bend	n.g.
9 Mitchell 2 NW	Central	Bend	n.g.
10 Walla Walla 1 ESE	Northeast	Pendleton	n.g.
10 Pendleton Branch ES	Northeast	Pendleton	n.g.
10 Pilot Rock 1 SE	Northeast	Pendleton	n.g.
Washington			
1 Ellensburg[e]	Central	Ellensburg	Yakima
2 Wenatchee Exp. Station	Central	Wenatchee	Colockum
3 Dayton 1 WSW	Southeast	Walla Walla	Blue Mountains
Idaho			
1 Hamer 4 NW	Southeast	Rexburg	Sand Creek
2 Soda Springs	Southeast	Pocatello	Soda Face
3 Idaho Falls 16 SE	Southeast	idaho Falls	Tex Creek
4 Elk City Ranger Station	North-central	Grangeville	South Fork Clearwater
5 Salmon 1 N	East-central	Salmon	Salmon River Area
6 Middle Fork Lodge	Central	Challis	Middle Fork Salmon River
7 Headquarters	North-central	Elk River	North Fork Clearwater
8 Garden Valley Ranger Station	West-central	Boise	Garden Valley
9 Mullan	North	Kellogg	Silver Valley
9 Wallace Woodland Park	North	Kellogg	Silver Valley
10 Brownlee Dam	West-central	McCall	Brownlee
Montana			
1 Sula 3 ENE	Southwest	Hamilton	n.g.
2 Townsend	Central	Helena	n.g.
3 East Glacier	Northwest	Cut Bank	n.g.
3 Saint Mary	Northwest	Cut Bank	n.g.
4 Hungry Horse Dam	Northwest	Kalispell	n.g.
4 Polebridge	Northwest	Kalispell	n.g.
4 West Glacier	Northwest	Kalispell	n.g.
5 Ennis	Southwest	Bozeman	n.g.
5 Gallatin Gateway 10 SSW[f]	Southwest	Bozeman	n.g.
5 Gardiner	Southwest	Bozeman	n.g.
6 Augusta	West-central	Great Falls	n.g.
7 Bigfork 13 S	West	Kalispell	n.g.
7 Seeley Lake Ranger Station	West	Missoula	n.g.
8 Saint Regis	West	Thompson Falls	n.g.
8 Superior	West	Missoula	n.g.
Wyoming			
1 Big Piney	Southwest	Big Piney	Piney Front
2 Darwin Ranch	Northwest	Jackson	Jackson Area
2 Jackson	Northwest	Jackson	Jackson Area
3 Kemmerer 2 N	Southwest	Kemmerer	West Green River
3 La Barge	Southwest	Kemmerer	West Green River

(Continued on following page.)

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Appendix E. Continued.

Weather station[a]	Region	Closest town	Herd name[b]
3 Sage 4 NNW	Southwest	Kemmerer	West Green River
4 Shell	North-central	Greybull	n.g.
5 Ten Sleep 4 NE	North-central	Worland	n.g.
5 Ten Sleep 16 SSE	North-central	Worland	n.g.
6 Baggs	South-central	Rawlins	n.g.
6 Encampment 11E	South-central	Saratoga	n.g.
6 Rawlins Airport	South-central	Rawlins	n.g.
7 Sheridan WSO Airport	North-central	Sheridan	n.g.
8 Centennial 1 N	South-central	Laramie	n.g.
8 Elk Mountain	South-central	Laramie	n.g.
8 Encampment 11E	South-central	Saratoga	n.g.
9 Dubois	Northwest	Dubois	Dubois
Colorado[g]			
1 Gunnison 1 N	Southwest	Gunnison	Gunnison–Sapinero
2 Steamboat Springs	Northwest	Steamboat Springs	Bear Ears
3 Spicer[h]	North-central	Estes Park	North Fork
4 Craig 4 SW[i]	Northwest	Craig	White River
5 Del Norte	South-central	Monte Vista	San Luis Valley
6 Collbran	Northwest	Clifton	Grand Mesa
7 Cortez	Southwest	Cortez	San Juan Basin
Utah[j]			
1 Woodruff	North-central	Logan	n.g.
2 Scofield Dam	Central	Price	n.g.
2 Hiawatha	Central	Price	n.g.
3 Coalville	North-central	Park City	n.g.
3 Wanship Dam	North-central	Park City	n.g.
4 Kamas 3 NW	North-central	Park City	n.g.
5 Bear Lake State Park	North-central	Logan	n.g.
6 Logan Radio KVNU	North-central	Logan	n.g.
6 Richmond	North-central	Logan	n.g.
7 Ferron	Central	Ephraim	n.g.
7 Salina 24 E	Central	Richfield	n.g.
8 Salina	Central	Richfield	n.g.
8 Richfield Radio KSVC	Central	Richfield	n.g.
8 Fremont Indian State Park	Central	Richfield	n.g.
9 Manti	Central	Ephraim	n.g.
10 Kanosh	Central	Richfield	n.g.
10 Fillmore	Central	Richfield	n.g.
Arizona[k]			
1 Snowflake 15 W	Central	Snowflake	Apache East
2 Pleasant Valley Ranger Station	Central	Payson	Tonto
3 Winslow WSO Airport	Central	Winslow	Apache West
4 Williams	Central	Williams	Kaibab
5 Chino Valley	Central	Chino Valley	Prescott
6 Whiteriver 1 SW	East-central	Show Low	Reservation
7 Beaver Creek Ranger Station	Central	Flagstaff	Coconino South

[a] National Oceanic and Atmospheric Administration weather stations. The number associated with each station is the left to right sequence number for weather data presented in Figure 22. Within states, data from stations with the same sequence number were averaged together to estimate weather for the wintering complex.

[b] Herd name supplied by regional big-game biologists (n.g. = herd name not given).

[c] Temperature data lacking.

[d] Virtually no data were presented during 1980–94; station was omitted from calculations.

[e] Used data from the Ellensburg station, although the Naches 10 NW station was identified most suitable, because no data from the Naches station were available.

[f] Data available from 1980 to 1984.

[g] Although the Trecio 4 NW station was identified most appropriate for the Spanish Peaks herd in south-central Colorado, data were not available. This herd was omitted from calculations.

[h] Used data from the Spicer station, although the Rano station was identified most suitable, because no data from the Rano station were available.

[i] Used data from the Craig 4 SW station, although the Hamilton station was identified most suitable, because no data from the Hamilton station were available.

[j] The Fairview and Helper Carbon stations in central Utah and the Oakley 3 NE station in north-central Utah were identified as appropriate stations, but data were not available.

[k] The Walnut Canyon National Monument station was identified as appropriate for the Coconino North herd in central Arizona, but data were not available so this herd was omitted from calculations.

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