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Thermal Cover Needs of Large Ungulates: A Review of Hypothesis Tests

John G. Cook
National Council for Air and Stream Improvement
La Grande, Oregon

Larry L. Irwin
National Council for Air and Stream Improvement
La Grande, Oregon

Larry D. Bryant
U. S. Department of Agriculture, Forest Service
Washington, DC

Robert A. Riggs
Boise Cascade Corporation
La Grande, Oregon

Jack Ward Thomas
University of Montana
Missoula

Introduction

A great deal of big game research occurred in western North America during the 1960s through the 1980s, and many advances in our knowledge occurred as a result. Timber harvest increased during this period in many localities, and this trend was often perceived to threaten ungulate populations (Hieb 1976). Thus, it is not surprising that appreciable research in this era focused on relations between forestry and elk (*Cervus elaphus*). Logging's most apparent immediate effect is modification of the forest overstory, and a concept arose that was new, at least in the West, for elk—dense forest cover moderates the effects of harsh weather sufficiently to confer survival and reproductive advantages in the winter, in particular, and during the summer. Forest stands that confer such advantages are referred to as thermal cover.

To some degree, support for the thermal cover concept arose from observations that forest cover can moderate weather. During winter, temperature can be several degrees warmer under forest canopies at night (Reifsnyder and Lull 1965, Parker and Gillingham 1990) due to long-wave radiation emitted from the forest canopy (Moen 1968, Beall 1974, Grace and Easterbee 1979). Long-wave radiation can be absorbed by animals, potentially enhancing energy balance (Grace and Easterbee 1979). Forest canopies also reduce wind speed (Grace and Easterbee 1979) and, theoretically, reduce convective heat loss. During summer, shade from forest cover reduces diurnal, ambient temperature fluctuations and provides opportunity to avoid elevated heat loads that can result from direct solar radiation (Demarchi and Bunnell 1993). A number of habitat selection studies demonstrated that ungulates use dense forest stands disproportionately to their availability at certain times (e. g., Irwin and Peek 1983, Leckenby 1984). Selective use of dense forests under several circumstances was consistent with the prediction that thermal cover was operative; thus, this was assumed to be in response to thermal protection provided by cover (Beall 1974, Armstrong et al. 1983, Leckenby 1984, Zahn 1985, Ockenfels and Brooks 1994). Such an interpretation can be supported by modeling using energy balance equations (e. g., Grace and Easterbee 1979, Parker and Gillingham 1990, Demarchi and Bunnell 1993).

Thus, over time a fairly broad base of literature was developed that supported the thermal cover hypothesis. However, arguments were made that the evidence was not sufficient to demonstrate significant biological benefits. In particular, it was unclear if observed selection for forest cover, when it occurs, was related to thermal protection from harsh weather or if it was due to some other reason (Peek et al. 1982). Evidence of support from habitat selection studies is only inferential (Riggs et al. 1993), and there is virtually no support for the thermal cover hypothesis from experimental research specifically designed to establish cause-and-effect relations. Using simulation models, Swift et al. (1980) and Hobbs (1989) concluded that thermal cover had negligible influences on ungulates during winter. Hobbs (1989) indicated that forage conditions, either during or prior to winter, exerted greater effects on winter survival of mule deer (*Odocoileus hemionus*) than did thermal cover. Although thermal cover benefits were certainly real in theory, their influences in the field may be too infrequent or inconsistent to be meaningful under many circumstances (Riggs et al. 1993).

Nevertheless, the preponderance of original research results supported the concept of thermal cover. As these results became more widely accepted, they were incorporated into a variety of habitat-evaluation models. For elk, variables that measure the abundance and, in some cases quality, of thermal cover have been widely incorporated into habitat evaluation procedures (e. g., Wisdom et al. 1986, Thomas et al. 1988a, Christensen et al. 1993). These models were used extensively to develop national forest plans (Edge et al. 1990) and often were used to make site-specific decisions regarding timber harvest or other management activities across a variety of scales.

Over the last half-century, there have been four explicit experimental tests of thermal cover's influence on well-being of big game (Robinson 1960; Gilbert and Bateman 1983; Freddy 1984, 1985, 1986; Cook et al. 1998). Herein, we briefly review these studies and discuss their management implications in the context of new problems facing the game-management community in the 21st century.

Oregon Elk Study: Cook et al.

Of the studies attempting to directly evaluate the influence of thermal cover on animal performance, the Cook et al. (1998) study was the most intensive and extensive. Moreover, it seems the only study that directly evaluated the effects of thermal cover on big game in summer.

Study Area and Methods

This elk study consisted of a series of controlled experiments conducted from 1991 to 1995 using tractable elk. The study area was located between 4,200 to 4,400 feet (1,300–1,350 m) on a northeast-facing slope in the grand fir (*Abies grandis*) forest zone in the Blue Mountains of northeastern Oregon, land typically used by elk as summer range in the area. As such, the site afforded colder and more mesic winter conditions than typically occur on elk winter ranges in the region, and it provided weather conditions typically encountered by elk during summer.

The study area was created from a contiguous, mature, uneven-aged forest by prescriptive logging in nine 5-acre (2.3-ha) cover treatment units. By random selection, three units were clearcut, three were partially harvested to reduce overstory canopy density (providing "marginal" cover as defined by

Thomas et al. 1988a) and three were left unharvested (providing "satisfactory" cover as defined by Thomas et al. 1988a). This layout provided three replicates of four levels of cover for the experiment: (1) clear-cut habitat with no overstory cover, (2) partially cut habitat averaging 30 percent overstory canopy cover, (3) uncut habitat averaging 70 percent canopy cover and (4) units set up to provide a combination of clear-cut and dense forest habitat to the elk. In the first three treatments, elk were sequestered at the center of the units in a 0.25-acre (0.1-ha) pen. In the combination treatment units, elk were held in a pen that extended 65 feet (20 m) into the clearcut and 165 feet (50 m) into the dense forest, providing elk with the ability to choose among cover types as they desired. All understory vegetation (potential forage) was removed from the pens. The 12 pens were designed to hold 3 elk each, providing a total capacity of 36 elk in the layout.

Experiments consisted of placing elk in the pens for 4-month periods in winter (early December through mid-March) and summer (late May through late September) and of documenting differences in body mass dynamics, nutritional condition and activity. All elk received identical diets fed on a metabolic mass basis ($BM^{0.75}$); they received submaintenance rations in winter to induce loss of 5 to 10 percent of body mass, and they received good quality diets that were adequate for growth in summer. Calves were used in the winter experiment of 1991 to 1992, yearlings in summer of 1992 and yearlings in winter 1992 to 1993. A new cohort of calves were raised in 1993 and were used in the winter experiment of 1993 to 1994, the summer experiment of 1994 and the winter experiment of 1994 to 1995. Elk were randomly reassigned to new pens at the beginning of each seasonal experiment.

Elk were weighed twice weekly, body composition (percent fat, protein, water) was determined at the start and end of each experiment using dilution techniques with deuterium oxide, and activity was recorded automatically with leg-mounted activity sensors.

Findings

Microweather characteristics measured during the study demonstrated that forest canopy reduced wind speed, reduced solar radiation flux during the day, and increased net radiation flux at night. They indicated little to no effect of forest canopy on ambient temperature or relative humidity.

No positive effects of thermal cover on elk were documented during any of the four winter experiments. But, there were significant differences in body mass and body condition dynamics among cover treatments. Generally, elk in the dense forest stands lost most mass and fat; elk in clearcuts lost least mass and fat, whereas mass and fat loss of elk in the moderate cover and combination cover units were intermediate (Figure 1). Each winter of the study, elk in clearcuts lost significantly less mass and body fat than did elk in the thermal cover treatment units. No relevant differences in activity patterns were documented among treatment units during any of the winters. These patterns were consistent across all winters, despite substantial differences in winter weather conditions. They ranged from abnormally cold (monthly temperature averaging as low as minus 10 degrees Fahrenheit (-15°C) and snowy in one winter, cool with substantial rain falling in another winter and moderate to normal temperature and precipitation in the other winters). During the winter 1993 to 1994, substantial rain fell and nine elk calves either died or were removed from the study to prevent death. Of these, five were from the dense cover treatment, three were from the moderate cover treatment, and one was from the zero cover treatment.

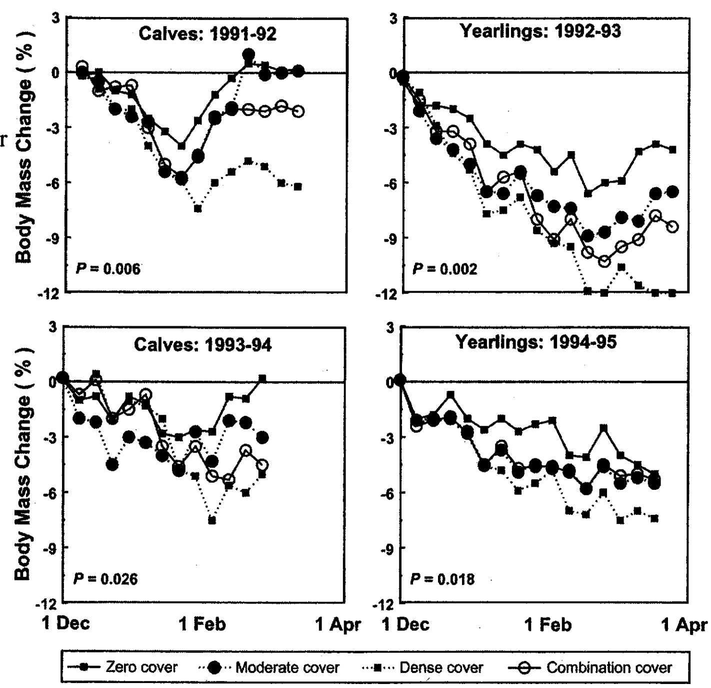

Figure 1. Body-mass dynamics of female elk calves and yearlings in four forest cover treatments during winter 1991 to 1995 in northeastern Oregon (adapted from Cook et al. 1998). P-values indicate statistical significance level of the forest cover treatments on body mass change during each winter experiment.

During the two summer experiments, no significant differences were found in body mass, fat gain or activity patterns among the four cover treatments

(Figure 2). Elk in clearcuts and moderate cover treatment units consumed more water than did elk in dense cover units, however. Both summers were warmer and drier than normal for this region of eastern Oregon.

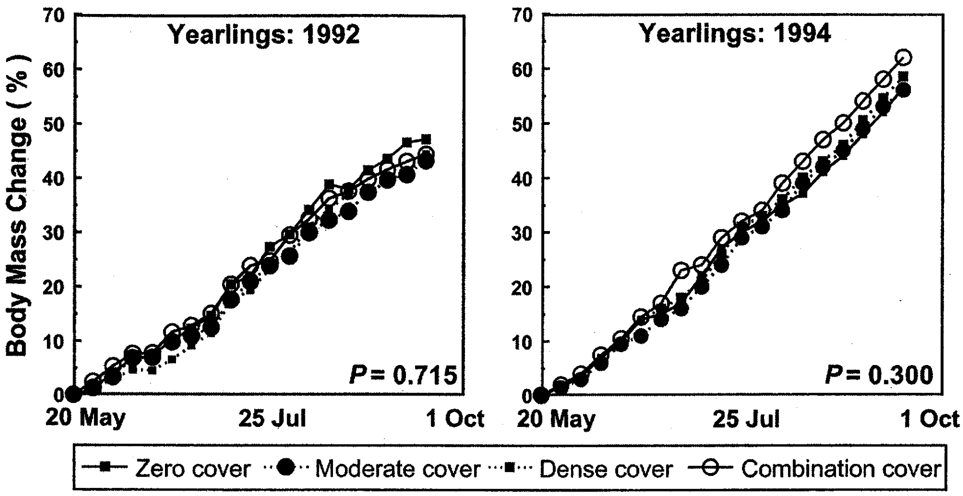

Figure 2. Body-mass dynamics of yearling elk cows in four forest cover treatments during summer 1992 and 1994 in northeastern Oregon (adapted from Cook et al. 1998). P-values indicate statistical significance level of the forest cover treatments on body mass change during each summer experiment.

Colorado Mule Deer Study: Freddy

The thermal cover research reported by Freddy (1984, 1985, 1986) evaluated the effects of thermal cover on mule deer during winter from 1982 to 1985, with the majority of data collected in winters of 1983 to 1984 and 1984 to 1985. It was unique in that thermal cover was provided by human-made structures designed to reduce the effects of heat loss on deer. Deer had free choice among different cover structures that mitigated wind-chill heat loss, radiant heat loss at night and conductive heat loss to snow-packed frozen soil while bedded. They had full access to solar radiation during the day.

Study Area and Methods

The study was conducted at the Colorado Division of Wildlife Junction Butte Research Center near Kremmling, an area located in the sagebrush (*Artemisia* spp.) vegetative zone in a high mountain basin (7,300 feet [2,226 m]) of northcentral Colorado. Twelve individual deer pens were constructed on the site with six equipped with artificial cover and the other six providing no cover. All vegetation was removed within and adjacent to pens, and snow was packed to prevent deer from using snow as a source of cover. Pens were 33 by 33 feet (10 x 10 m), were constructed of large mesh woven wire that was 7 feet (2.2 m) high and were contained within a 5-acre (2.2-ha) fenced pasture that excluded neighboring wild deer.

Deer of various age classes (fawns to adults) were paired by body mass and randomly assigned to either the cover or no-cover treatments in experiments lasting from mid-December through mid-March. In 1983 to 1984, deer were fed pelleted rations ad libitum. Response variables included changes in weight measured at 2.5-week intervals, amount of food consumed at 3-day intervals, and activity determined during 6 behavioral trials during the winter. During the winter of 1984 to 1985, deer were fed a lower quality pellet offered in amounts equaling 60 percent of maintenance, adjusted to declining body mass every 2.5 weeks, such that the deer would be nutritionally stressed over the winter. During this second winter, cover was enhanced by incorporating a three-sided roofed wooden hut that was 4 feet (1.2 m) tall and improved wind-breaks. And, more extensive darkened soil was added to enhance solar absorption and warming.

Findings

The winter of 1983 to 1984 was unusually severe with periods of high winds and very cold ambient temperature to about minus 30 degrees Fahrenheit (-35°C) (minimum temperature averaged below minus 5 degrees Fahrenheit (-20°C) during much of the winter). Mortality in wild deer in the surrounding area represented 50 to 55 percent of the population (D. Freddy, personal communication 2004). Deer with cover lost on average 5.0 percent of their body mass over the entire winter (from December 9 through March 17), whereas deer without cover lost 4.3 percent of their mass. There were no consistent patterns of mass loss within 2.5-week intervals of the winter period (Figure 3A). Amount of food consumed and activity budgets did not differ between deer with and without cover across the entire winter period or within any 2.5-week interval.

Weather during the winter of 1984 to 1985 was milder; although, high winds and cold temperatures (less than minus 5 degrees Fahrenheit [-20°C]) again were common. The restricted feeding regime imposed this year of the study resulted in all deer consuming virtually identical amounts of food per pound of

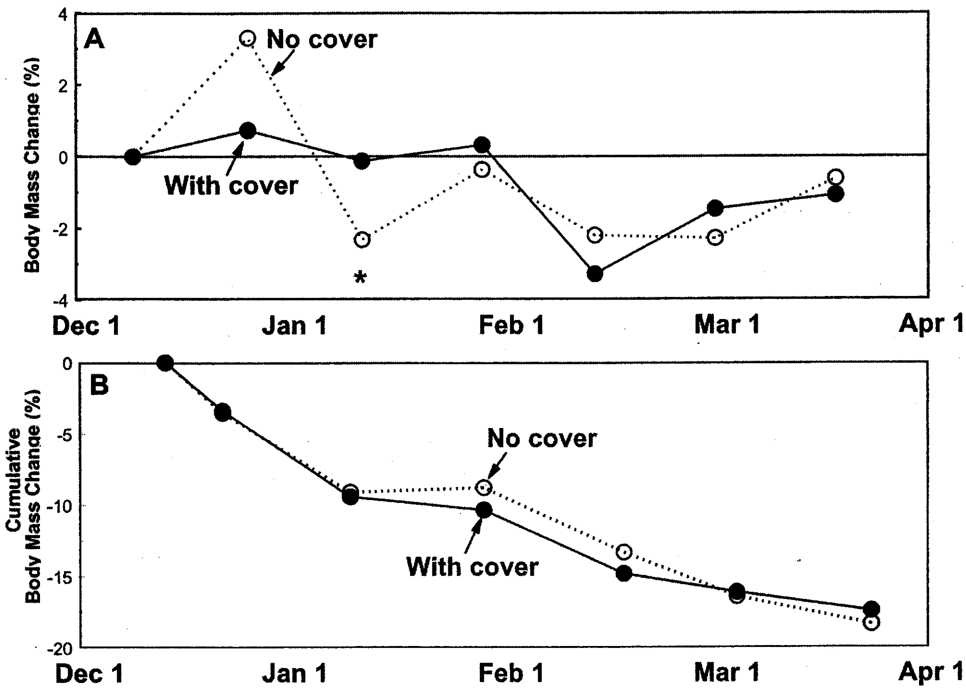

Figure 3. Body-mass dynamics of mixed-age mule deer with and without access to thermal cover during winter 1983 to 1984 (A) and 1984 to 1985 (B) in northcentral Colorado (adapted from Freddy 1984, 1985). In A, data values indicate percent change in body mass during each 2.5-week period of the winter; the asterisk denotes statistically different body-mass change during the 2.5-week period of late December to early January. In B, data values indicate cumulative body-mass change over the entire winter (no significant differences due to cover availability detected).

body mass. Between December 13 and March 23, no significant differences in body mass loss were detected between treatment groups (Figure 3B). At least during the first half of winter, deer without cover spent 5 to 10 percent more of each day attempting to forage than did deer with cover (attempts at foraging were on aspen logs present in the pens only in 1984 to 1985).

Overall, findings of the study indicated that thermal cover failed to significantly improve the ability of mule deer to survive in winter. It was noted that cover in the form of roofed huts with three covered sides along with additional wind breaks provided high-quality thermal protection, at least as good as cover provided by natural forest conditions. Thus, these experiments likely provided a "100-percent test" (Freddy 1985:17) of thermal cover's influence on deer in winter.

Maine White-tailed Deer Study: Gilbert and Bateman

Study Area and Methods

The Gilbert and Bateman study of 1983 was conducted at the D. B. Demeritt Forest at Orono, Maine. The area received 76 inches (193 cm) of snowfall each winter and mean January temperature averaged 18.5 degrees Fahrenheit (-7.5°C). Eleven pens, each 0.25 acres (0.10 ha), were constructed to provide three to four replicates of three overstory conditions: (1) natural tree cover averaging 72 percent canopy cover, (2) absolute clear-cut averaging 6 percent cover and (3) clear-cut with vertical wall windbreaks, averaging 8 percent cover. Each pen contained a feeder in which pellets were provided ad libitum. Brush and tree limbs within reach of deer were removed; snow cover eliminated access to herbaceous vegetation. Eleven mixed-gender white-tailed deer (*Odocoileus virginianus*) fawns were used, with one deer per pen. This study was conducted over a single winter from December 1970 through March 1971.

Response variables included behavior, food intake, changes in body mass and changes in fat levels. Behavior was estimated by direct observation. Food intake was measured at weekly intervals. Body mass was measured at the start and at the end of the experiment. At the end of the experiment, the deer were euthanized and kidney fat and femur fat indices were calculated.

Findings

Ambient temperatures were not clearly defined but ranged as low as minus 30 degrees Fahrenheit (-34°C) in this study. Deer in the natural forest and absolute clear-cut pens consumed equal amounts of food; whereas, deer in the clear-cut pens with windbreaks tended to consume less food. Similarly, body mass loss was virtually identical for deer in the natural forest pens (6.1 percent) and deer in the absolute clear-cut pens (6.2 percent); whereas, deer in the clear-cuts with windbreaks lost 9.6 percent of their starting mass. Femur and kidney fat indices tended to be higher for deer in the natural forest pens than for deer in either of the clear-cut treatments. However, apparent differences in food intake, fat indices and body mass changes failed to vary significantly among deer in any of the three cover treatments. Activity patterns were affected by changes in weather, but no differences were detected as a function of cover treatments.

Despite finding no effect of forest cover on deer, including on food consumption, the authors held to a conservative conclusion that, "if fawns have access to an adequate food supply, they can withstand severe winter weather even in the absence of shelter" (Gilbert and Bateman 1983:399). But, the authors also indicated that, "increasing attention should be given to the quality of food available on winter range," (Gilbert and Bateman 1983:399) and they referenced the importance of physical condition of fawns in late autumn.

Maine White-tailed Deer Study: Robinson

Study Area and Methods

The Robinson study (1960) was conducted at Orono, Maine, during the winters of 1957 to 1958 and 1958 to 1959. Forests in three 1.5-acre (0.6-ha) pens were modified to produce sparse, moderate and dense coniferous cover. The sparse cover pen consisted of trees no larger than 5 inches (12.7 cm) diameter at breast height (d.b.h.) and supported canopy cover of 34 percent. The moderate pen contained an all-ages mixture of hardwood and conifers with a coniferous canopy cover of about 55 percent. The dense cover pen was described as an early-mature stand of several species of conifers with canopy cover of 73 percent. Natural browse within access of the deer was removed from the pens. Temperature during the study ranged as low as minus 22 degrees Fahrenheit (-30°C) up to about 34 degrees Fahrenheit (1°C), and snow accumulations seldom exceeded 2 feet (0.6 m).

During the first winter experiment, one male and one female fawn were placed in each pen; three males and two females were placed in each pen during the second winter experiment. Deer were fed a pelleted ration, the quantity of which was restricted to induce a submaintenance level of nutrition. At the start and at the end of the experiments, body mass, girth and hind foot length were estimated, and blood samples were collected. A condition factor was calculated based on body mass and hind foot length. A visual body condition score also was used to evaluate status of the deer. At the end of the experiment, deer were euthanized, and femurs were used to estimate femur fat levels. Meteorological measurements, including nocturnal minimum temperatures, humidity and wind speed, were collected during the study.

Findings

Minimum temperature at night was lower and wind speed was greater in the sparse cover unit than in either of the other two treatment units.

Nevertheless, decline in condition based on the condition factor was virtually identical among the three treatment areas in both winters of the study, and no differences in condition based on their body condition score were detected. Femur fat levels indicated no differences among treatments at the end of the first winter. Femur fat tended to be lower in deer in the sparse cover unit than in the moderate and dense cover units after the second winter experiment, but this was attributed to generally poorer condition of deer in the sparse unit at the start of this experiment.

Conclusions were conservative in that the failure to find significant benefits of dense forest cover was attributed to flaws in the study. In particular, the sparse cover pen contained a small patch of relatively dense forest cover. The author indicated this patch provided sufficiently moderate microclimatological conditions to preclude differences in animal response among the three treatment units.

Discussion

Observations that dense forests can moderate harsh weather in summer and winter intuitively support the thermal cover hypothesis and provide the bioenergetic basis of models that illustrate a significant benefit of thermal cover (e. g., Grace and Easterbee 1979, Demarchi and Bunnell 1993). But, what has never been clear was whether or not the magnitude of the thermal cover effect, relative to the anatomical and physiological adaptations of large mammals, was sufficient to induce a biologically relevant improvement in energy balance over sufficient time to improve survival and reproduction (Freddy 1984, Riggs et al. 1993). The preponderance of experimental evidence indicates that the weather-moderating effects of thermal cover are probably insufficient to be of much biological value, at least under the conditions reflected in the experimental studies. Furthermore, findings that thermal cover could actually be detrimental (Cook et al. 1998) indicate that energetic benefits of greater solar radiation levels in the clearcuts can far outweigh whatever benefits may arise from thermal cover. Solar radiation effectively warms the animal (Parker and Robbins 1984, Parker and Gillingham 1990), thereby reducing the amount of food or endogenous energy required for thermal stasis. In the Colorado deer study, failure to show a positive effect of solar radiation would be expected because solar radiation was equally available in all pens. Reasons are unclear for failure to show a positive effect of solar radiation in the two Maine deer studies, but overcast skies typical of the northeastern United States would reduce the frequency of direct solar input.

Although forests can moderate harsh winter weather, substantially in the case of wind, Cook et al. (1998) showed that the magnitude of the modification may be negligible, depending on short- and long-term weather patterns. For example, Cook et al. (1998) reported that elevated winds normally occurred during the day when temperature was moderate; thus, the potentially deleterious effect of wind was reduced (see Blaxter et al. 1963, Chappel and Hudson 1978). However, wind was typically calm at night when cooler temperatures prevailed. Additionally, the contribution to energy balance of long-wave radiation from forest canopies is only relevant at night under clear skies because clouds also radiate long-wave radiation (Reifsnyder and Lull 1965). Clear skies at night are a relatively infrequent occurrence in maritime ecosystems of the Northwest (Cook et al. 1998). Similarly, because long-wave radiation accounts for temperature differences between forested and nonforested areas, it is only on clear nights when ambient temperature differences occur between forested and nonforested stands (Reifsnyder and Lull 1965). Even on clear nights, however, gentle breezes and cold airflows across unlevel terrain mix air masses and reduce temperature differences (Cook et al. 1998)

The study by Cook et al. (1998) was the only study to directly test the effect of thermal cover in summer. In both summer experiments, the yearling elk were fed diets that were suboptimal, that is, adequate to support growth but below growth rates which these animals are capable. Thus, this diet should have induced moderate energetic stress and would be expected to heighten sensitivity of these elk to their energetic environment. In both summers, maximum ambient temperatures were greater than or equal to 77 degrees Fahrenheit (25°C) during at least 30 percent of the days. Parker and Robbins (1984) reported that upper critical temperature (the point at which metabolic rate increases to dissipate heat) of yearling elk while standing was 77 to 86 degrees Fahrenheit (25–30°C) (operative temperature, which integrates effects of wind, solar radiation and long-wave radiation). Thus, elk in this study, particularly those in the no-cover treatments, should have been heat-stressed because operative temperature ranges markedly higher than ambient temperature during sunny days (Demarchi and Bunnell 1993).

Studies with livestock indicate severe heat stress can affect performance, particularly of high producing breeds (e. g., milk cows) (National

Research Council 1984, Young 1988). This occurs because high ambient temperature reduces feed intake (Young 1988) and may induce panting and elevate respiration, thus increasing maintenance requirements (National Research Council 1984). Heat-stress effects are greatest when temperature and humidity are both high and when nocturnal cooling is minimal, such as in the southeastern United States (National Research Council 1984, Young 1988). Despite observations that large ungulates often use shade in summer (Zahn 1985, Demarchi and Bunnell 1993, but see Merrill 1991), results of the Oregon experiments show that regimes of ambient temperature, humidity and solar radiation occurring on western montane summer ranges in forest zones fail to exert sufficient heat stress to affect performance of elk.

Parker and Robbins (1984) showed that elk in summer pelage are well-adapted to high operative temperature, even that in excess of their upper critical temperature, mostly due to a relatively great concentration of cutaneous sweat glands. Merrill (1991) calculated that heat loss of elk standing in openings during hot summer days was sufficient to compensate for solar radiation flux and high ambient temperature in the Cascades of western Washington. McCorquodale and Eberhardt (1993) concluded that elk colonizing the Arid Lands Ecology Reserve, a low-elevation, hot, shrub-steppe area in Washington, did so with no appreciable detriment to their fitness (e. g., population growth rate was among highest ever reported for elk) despite the lack of any forest cover.

The reductionist approach used in the four studies directly testing the thermal cover hypothesis certainly is open to some criticism because these studies cannot possibly account for all of the complex interactions among habitat, weather, animal behavior and animal performance inherent to free-ranging settings. Nevertheless, the value of such manipulative studies is that they can indeed tease out possible cause-and-effect relations and test their veracity. In contrast, most empirical support for the thermal cover hypothesis arose from observations of habitat selection. Linking animal survival and reproduction to availability of thermal cover, based on observations of animal choice for dense forests, was first questioned over two decades ago (Peek et al. 1982). Since then, recognition has increased that habitat selection studies as typically conducted must infer explanations for observed selection patterns because they generally are ineffective for identifying cause-and-effect mechanisms, particularly mechanisms that link habitat characteristics to animal performance and carrying capacity (Hobbs and Hanley 1990, Parker et al. 1999, Morrison 2001). Thus, the practice of attributing effect (in this case, observed habitat use) to cause (in this case, enhancing energy balance) amounts to hypothesis generation, not hypothesis testing.

Management Implications

The experimental studies outlined above evaluated the weather-moderating influences of forest cover (i. e., influences on wind speed, ambient temperature, and long- and short-wave radiation fluxes). They did not evaluate other potentially beneficial aspects of forest cover, which under some circumstances could include enhanced security, reduced snow depth and a better foraging environment. Thus, results of these experimental studies cannot be used to categorically reject all potential benefits of forest cover to elk. Together, however, they indicate the thermal cover benefit attributed to dense forest cover is probably not operative across a considerable range of climate, including climates in boreal ecosystems of the northeastern United States, maritime ecosystems of the inland Pacific Northwest, and in cold, dry ecosystems of the central Rocky Mountains. We see little justification in these ecological settings for retaining thermal cover as a primary component of habitat evaluation models for elk.

Wildlife management's focus on thermal cover has had an important influence on the profession's thinking in that it implicitly directed attention to the importance of energy balance to reproductive success and survival. Regardless of the thermal cover hypothesis' lack of veracity, the central theme it addressed remains credible. Among habitat attributes that can be managed, these remain fundamental to energy balance: forage quality and forage quantity, due to their effect on energy intake, and structural attributes of habitat that mediate energy expenditures associated with travel and harassment (e. g., snow intercept, security cover).

Reducing human disturbance via minimizing unrestricted road traffic, reducing attendant harassment and providing security cover have hardly been controversial among biologists. Along with providing thermal cover, these goals formed the primary emphasis and focus of current management paradigms embodied in habitat planning models and procedures used on behalf of elk (Christensen et al. 1993). Meanwhile, attention to nutrition was low and, in some cases, was deemphasized (Edge et al. 1990, Cook et al. 1998). This occurred despite a growing body of science demonstrating nutrition's importance to animal performance (e. g., National Research Council 1984, Verme and Ullrey 1984, Cook 2002).

Continued attention to cover management may be warranted in many circumstances where security is low or where snow accumulations limit animal performance. However, it may be time to shift our attention toward relationships between herd productivity and nutrition-based attributes of habitat. The inverse relation between overstory canopy density and forage abundance (McConnell and Smith 1970, Klinka et al. 1996) indicates an important tradeoff between providing dense forest cover and providing forage resources that affect carrying capacity (e. g., Hett et al. 1978). Although research has certainly demonstrated the importance of energy balance to animal performance, the last 30 years of research has paid little attention to developing coarse-scale, management-level habitat models and planning procedures that address nutritional issues, and it has paid little attention to the effects of specific silvicultural systems that may influence the nutritional value of large landscapes to large herbivores. Defining overstory-understory relationships and their relation to animal nutritional status, particularly in the context of specific silvicultural systems, remains a substantial hurdle to modeling elk-production relations in western forest landscapes.

The biopolitical setting has changed considerably over the last two decades, creating new challenges to elk managers and researchers. First, gone are the days of comparatively high timber harvests on federal land and, with them, the concerns that emerged 30 years ago (Hieb 1976). The declines in timber harvest, in turn, may increase concern about reductions in the benefits from timber harvest, namely increased forage abundance. Where forestry practices have intensified on private land, more articulate understanding of how intensive forestry practices influence elk forage values would certainly be useful.

Second, in many areas, particularly in the northwestern United States, elk herds are declining (Irwin et al. 1994, Gratson and Zager 1999, Ferry et al. 2001), like mule deer herds across much of the West (Carpenter 1998). Thus, to a greater degree than in the past, if habitat models are to be relevant, they must integrate those aspects of habitat that significantly influence productivity and demographics of elk herds. Most extant elk-habitat models, "predict only effectiveness of the habitat to facilitate elk use. They are neither designed nor expected to predict elk numbers or productivity" (Thomas et al. 1988b:6). Yet, numbers and productivity are indeed the variables ultimately of interest to elk managers and the public. Thus, it seems to us that we should refocus our attention on these variables and their relationship to forestry to a greater extent in the 21st century than we have in the past.

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