



BALANCING ECONOMIC DEVELOPMENT, BIOLOGICAL CONSERVATION, AND HUMAN CULTURE: THE SITKA BLACK-TAILED DEER *Odocoileus hemionus sitkensis* AS AN ECOLOGICAL INDICATOR

Thomas A. Hanley

USDA Forest Service, Pacific Northwest Research Station, PO Box 20909, Juneau, Alaska 99802-0909, USA

(Received 27 May 1992; revised version received 1 October 1992; accepted 6 November 1992)

Abstract

Economic development, biological conservation, and human culture are interrelated and ultimately interdependent. Balancing them, however, is one of the most vexing problems in natural resource management. The problem can be simplified when an ecological indicator provides a meaningful integration of the biological response of the natural ecosystem to economic development. Sitka black-tailed deer *Odocoileus hemionus sitkensis* are an important ecological indicator of resource management in the coastal, coniferous rain forests of southeastern Alaska, USA, because of four significant reasons: (1) their biology and ecology are well-known; (2) they have relatively large, seasonally migratory home ranges and so require management of landscapes rather than isolated patches of habitat; (3) their need for a productive and nutritious food supply year-around makes them largely dependent on old-growth forests and a variety of habitats, differing seasonally and in response to snow; and (4) they are an important game species in the subsistence economy of rural residents. Key ecological relations between deer and their food resources center on bioenergetics, digestible protein, and the role of forest overstory in the species composition, carbon/nutrient balance, and chemical composition of understory plants. Understanding these factors provides quantitative guidelines for timber management in an ecologically and culturally balanced framework.

Keywords: Alaska, forest management, landscapes, *Odocoileus hemionus*, old-growth forests, planning.

INTRODUCTION

Economic development touches virtually every corner of the world. It is essential for human prosperity in developed, and increasingly so in developing, countries. The goals of conserving biological resources and maintaining human culture must be undertaken with consideration for economic development, because poverty works against the long-term maintenance of both. Similarly, sustained economic development and human culture

are ultimately dependent upon biological conservation. The three endeavors are interrelated and interdependent. But balancing the three in long-term plans is one of the most difficult problems of natural resource management. All three are highly complex; interrelations are poorly understood; and common currencies are nonexistent.

In some cases, however, an ecological indicator can simplify the problem greatly if it serves as a meaningful index of the natural ecosystem and also has direct value to humans. Living organisms can be useful to indicate the effects of habitat alterations and fragmentation and the effectiveness of management plans to minimize those impacts (National Research Council, 1986). Species that are both sensitive to land management and of direct importance to people are especially useful in tying together the ecological and social effects of management.

A major conflict of economic development, biological conservation, and human culture in the coastal, coniferous rain forests of southeastern Alaska, USA, centers on the issue of commercial logging of old-growth forests (old, all-aged stands, never before logged). Old-growth forests comprise most of the commercial forest in southeastern Alaska. They also are very important as habitat for wildlife and fish (Meehan *et al.*, 1984), however, and their loss through logging is of much concern to wildlife biologists in the region (Schoen *et al.*, 1981). Political controversy focuses on trade-offs between timber management, biodiversity of old-growth forests, and the subsistence lifestyle of rural residents. The issues are complex and fraught with emotion. It is possible to quantify the economics of logging but it is most difficult to do the same for biodiversity and human cultural values.

I suggest that the Sitka black-tailed deer *Odocoileus hemionus sitkensis* is an important ecological indicator for forest management in southeastern Alaska and that it offers the prospect of quantitatively evaluating trade-offs between timber management and the biological and social values of the region's forests. The reasons can be broadly addressed in terms of four major components: (1) deer as an indicator of the forest ecosystem; (2) the biology of deer; (3) the role of natural

disturbance in biodiversity of old-growth forests; and (4) the socioeconomic climate of rural communities. My purpose here is to provide an overview of the reasons for the utility of Sitka black-tailed deer as an ecological indicator, an analysis of the limitations, and a discussion of some major implications for natural resource management. Much must be understood about indicator species in an ecological context (Natural Research Council, 1986), but their relations to the human environment also are important. The interaction of the ecological underpinnings with the socioeconomic setting is especially significant. Examples of valuable indicator species help point the way to other indicators in other ecological systems.

DEER AS AN INDICATOR OF THE FOREST ECOSYSTEM

Old-growth forests of the northwestern United States and Canada have been recognized as unique and important wildlife habitats for more than a decade (Bunnell, 1976; Franklin *et al.*, 1981; Meslow *et al.*, 1981). The northern spotted owl *Strix occidentalis caurina* was an early focal species there (Forsman, 1980) and continues to be a major focus as progressive loss of old-growth forest now threatens the continued existence of the species (Bart & Forsman, 1992). Old-growth forests of southeastern Alaska also have been recognized as unique and important wildlife habitats for a similar time and reasons, but the Sitka black-tailed deer was the focal species there (Wallmo & Schoen, 1979, 1980). Ecological concern in both regions, however, was broader than owls and deer alone and extended to the whole forest ecosystem, especially the biological diversity of plant and animal communities (Franklin *et al.* 1981; Meslow *et al.* 1981; Schoen *et al.*, 1981). Other terrestrial wildlife species of interest in both regions, for example, include the marbled murrelet *Brachyramphus marmoratum*, bald eagle *Haliaeetus leucocephalus*, goshawk *Accipiter gentilis*, marten *Martes americana*, and others (Meslow *et al.*, 1981; Schoen *et al.*, 1988). The high structural diversity of old-growth forests, including dead trees and decaying logs, is believed to provide unique and important habitats for a wide range of plants and animals, resulting in diverse plant and animal communities, complex food webs, and tight nutrient cycling (Franklin *et al.*, 1981; Ruggiero *et al.*, 1991).

Spotted owls in the Pacific Northwest and black-tailed deer in Alaska are focal species because they are believed to be the wildlife species most sensitive to logging in their respective regions. As such, they are viewed as ecological indicators of not only their own populations but also of the condition of forest ecosystems as habitat for a wide variety of old-growth related plants and animals.

The concept of any one species representing the conditions of habitat for another species or anything other than its own habitat requirements, however, is fundamentally complex. Current ecological theory is that no

two species share the same ecological niche, and therefore, all species differ in their habitat requirements. On a more pragmatic level, however, the northern spotted owl and the Sitka black-tailed deer have come to be viewed as indicator species because they both require extensive areas of commercial grade, old-growth forest (Hanley *et al.*, 1989; Bart & Forsman, 1992) and, therefore, pose the greatest challenge to clearcut logging. It is presumed that the habitat requirements of other species are less restrictive than those of the spotted owl and the Sitka black-tailed deer. Such presumptions, of course, are based on very few data, and other species are likely to emerge as we learn more about the ecology of forest ecosystems in both regions. It is important, therefore, to identify precisely the factors that a species does serve to indicate.

There are several fundamental differences between owls and deer as ecological indicators. Foremost is that interest in the spotted owl is directed at the level of species viability, while that in deer is at the level of population densities relative to hunting harvest levels. The existence of deer is not threatened by logging in southeastern Alaska, but their population density and productivity and, therefore, potential harvest are sensitive to logging (Hanley *et al.*, 1989). Second, much more is known about the biology of black-tailed deer than of spotted owls. Deer can be related to their forest environment through direct cause-and-effect relations rather than the correlations and speculations required for so many lesser known species. And third, deer are of direct importance to people, especially to the economy and culture of rural residents of southeastern Alaska. Deer do not represent an ecological abstraction of indicator value to rural residents. Rather, their value is direct and immediate as a consumptive resource.

The critical requirement that black-tailed deer must meet to be an indicator of biological diversity is that their habitat requirements must be dependent on specific conditions associated with important limiting factors to a wide range of other species. Those conditions for Sitka black-tailed deer are primarily related to their food supplies (Hanley *et al.*, 1989), the landscape dispersion of a variety of forest stands providing a relatively high quantity and diversity of high-quality forage year-around. Food requirements are largely incompatible with even-aged stand management (clear-cutting) in Alaska. Old-growth forest is especially important for the deer, and it also is the most structurally and biologically diverse seral stage for plant and animal communities (Schoen *et al.*, 1981, 1988; Alaback 1982, 1984). An understanding of the biology of deer and the role of disturbance in the structure and composition of forests in the region clarifies the importance of old-growth forests for Sitka black-tailed deer, the factors that are important to deer, and the value of deer as an ecological indicator. An understanding of the rural socioeconomic climate of southeastern Alaska clarifies the value of deer as an integrator of social and economic concerns in relation to development of the timber economy.

BIOLOGY OF SITKA BLACK-TAILED DEER

The biology of deer is well-known in comparison to that of other wild species. Deer of the genus *Odocoileus* have been studied extensively. Much is known about their behavior, population biology, nutritional and habitat requirements, and response to management by humans (Moen, 1973; Wallmo, 1981; Halls, 1984). There is a scientific basis for estimating carrying capacity of habitats (Hobbs & Swift, 1985) and projecting population size and demographics (Hobbs, 1989) in response to habitat change. Deer provide a more sound basis for management than do other, less well-known species that come to attention because of sudden population declines (e.g. the northern spotted owl in the Pacific Northwest—Salwasser, 1986).

Sitka black-tailed deer inhabit the Pacific coastal forests of northern British Columbia and southeastern Alaska. They require a high-quality food resource, especially a variety of evergreen forbs, which is available in old-growth forests (Wallmo & Schoen, 1980). Evergreen forbs (e.g. *Cornus canadensis*, *Rubus pedatus*) are highly digestible and a very important energy source for deer in winter (Hanley & McKendrick, 1985). The combined effects of food availability, quality, and snow interception by forest canopies make old-growth forests a critical habitat for Sitka black-tailed deer and make deer sensitive to the effects of logging (Wallmo & Schoen, 1980, Hanley *et al.*, 1989).

Black-tailed deer have relatively large, seasonally migratory home ranges, with summer and winter ranges often separated by tens of kilometers (Schoen & Kirchoff, 1985). Therefore, management must be planned at the level of the entire landscape rather than isolated patches of habitat. On the other hand, seasonal home ranges are small enough (usually on the order of 100–200 ha—Schoen & Kirchoff, 1985) that habitat requirements must be met within relative close proximity (food and cover, for example). Furthermore, because individual deer maintain a high fidelity to their home range once it is established, management must be planned over time as well as landscapes to ensure a sustained existence of suitable habitat.

Habitat-based projections of carrying capacity (Hobbs & Swift, 1985; Hanley & Rogers, 1989) yield quantitative predictions over time for alternative management plans. Monitoring is an important consideration for any ecological indicator; and deer population densities usually are sufficiently high that they can be monitored.

THE ROLE OF DISTURBANCE IN OLD-GROWTH FORESTS

The climate of southeastern Alaska is maritime: mild and wet year-around. As a result, fire is rare in the all-aged, Sitka spruce *Picea sitchensis*–western hemlock *Tsuga heterophylla*, old-growth forests (Harris & Farr, 1974). The natural disturbance regime is one of high-frequency, low-magnitude events: death or windthrow of scattered, individual trees or small groups of trees.

The old-growth forest environment is one of a continuously shifting pattern of canopy gaps with variable intervals of space and time between gaps (Deal *et al.* 1991). Understory species respond to gaps but differ greatly in their rates of establishment and growth (Tappeiner & Alaback, 1989; Alaback & Tappeiner, 1991). The differential time-lags of understory species, coupled with the constantly shifting light environment of the forest floor, enable no one species or group of species to achieve widespread dominance over the others. Environmental heterogeneity within the old-growth forest is great, and understory plant communities are diverse, productive, and rich in the evergreen forbs important to black-tailed deer. Old-growth forests also are structurally highly diverse, with all ages and sizes of trees and decaying logs (Deal *et al.*, 1991).

Forest overstory controls the light environment of understory plants, which in turn determines their carbon/nutrient balance (Rose, 1990). Increasing light results in increasing accumulation of carbon and increased growth rate; but as growth rates approach their maximum, carbon allocation shifts to production of carbon-rich storage compounds (starches, sugars) and secondary compounds, especially tannins (Rose, 1990). Open-grown plants are more productive but also usually more tannin-rich than shade-grown plants of the same species (Van Horne *et al.*, 1988; Rose, 1990). Tannins reduce protein digestibility for deer (Robbins *et al.*, 1987), which is of significant importance for lactation and, therefore, reproduction (Hanley & Rogers 1989).

Forest overstory also is important in its effect on winter snowpack. Snow is a major factor affecting the bioenergetics of black-tailed deer (Parker *et al.*, 1984; Wickstrom *et al.*, 1984; Hanley & McKendrick, 1985), principally through its effect on food resources (burial of evergreen forbs) and secondly through elevating energy costs of locomotion. Snow accumulates faster and persists longer in forest openings than under the canopy; and snowpack varies with topography and forest canopy coverage (Hanley & Rose, 1987; Kirchoff & Schoen, 1987). Old-growth forest habitats vary temporally in their relative quality for deer, open-canopied stands producing more forage but also accumulating more snow than closed-canopied stands. Their relative carrying capacities shift both seasonally and in response to snow.

A mix of habitats with different stand characteristics, therefore, is important for black-tailed deer and is an important factor in the value of deer as an ecological indicator. Landscape diversity of patches of old-growth forest with differing stand characteristics is consequential as well as is the species or chemical diversity of food resources within those patches. Both types of diversity contribute to the carrying capacity of habitat for deer (Hanley & Rogers, 1989) and are important components of biodiversity of landscapes.

In contrast to the processes within the old-growth forest, clearcut logging imposes a low-frequency, high-magnitude disturbance regime. It results in a very

different pattern of secondary succession from that of gap-phase succession: a brief, 20- to 30-year period of high understory productivity before conifer domination of the site, followed by a long, 100- to 150-year period of conifer canopy closure and very low understory productivity (Alaback, 1982). Understory production is great during the initial period, but it is quickly dominated by one or a few species of shrubs (*Vaccinium* spp. or *Rubus spectabilis*) (Alaback, 1982) with high concentrations of tannins (Van Horne *et al.*, 1988). The young clearcuts can provide a great quantity of forage during snow-free periods and can contribute significantly to maintenance requirements of deer (less so for lactation requirements), but they are of little value when snow-covered. More importantly, however, the closed-canopy forests provide only a sparse, though nutritious, understory and have low carrying capacity year-around. Silvicultural thinnings are of little value for understory in the Sitka spruce-western hemlock forests, because the understorey is quickly dominated by shrubs or a second layer of western hemlock soon after thinning and closed-out by the overstory again shortly thereafter (Alaback, 1984; Hanley *et al.*, 1989).

Both clearcut logging and silvicultural thinnings impose a disturbance regime that lacks the high temporal and spatial heterogeneity necessary for a diverse understory. Snow-free clearcuts can sustain deer populations for a decade or two but eventually close to second-growth forest. No combination of even-aged stands can provide habitat of similar quality to old-growth stands; in fact, even-aged stands are much inferior. They have low carrying capacity for deer because of their sparse understory (Hanley *et al.*, 1989) and very low structural and plant species diversity compared to old-growth stands (Alaback, 1984).

RURAL SOCIOECONOMIC SETTING

Commercial fishing, timber, and tourism are the principal industries of southeastern Alaska. Commercial fishing is the oldest and largest of the three and is of major significance throughout the region. Importance of timber and tourism varies greatly between communities. Although timber, for example, is critical to logging communities, it is insignificant to small fishing communities. Southeastern Alaska is mostly an archipelago, so transportation is primarily by water or air. Rural communities are widely separated and largely independent of one another.

About 25 500 people living in 30 communities in southeastern Alaska constituted the 'rural' population in 1988 (Kruse & Muth, 1990). That was about 40% of the total population, the other 60% residing in two urban centers—Juneau and Ketchikan. Fish, game, and wild plant resources play a major role in both the economy and culture of rural Alaska. The subsistence lifestyle of rural Alaskan residents is much more than simply an economic factor. Subsistence refers to a traditional and current reliance on fish, game, and wild plant resources in the food budget. It is a way of life

and an important component of the social fabric. It is even protected by Federal law (Alaska National Interest Lands Conservation Act of 1981).

The cultural significance of the subsistence lifestyle is great throughout the rural communities, where subsistence resources are shared among family and friends, and their harvest is an important social and recreational activity. Resource sharing is an important factor binding together kinship groups, friendships, and social networks (Kruse & Muth, 1990).

Subsistence use of wild resources is a major sector of the rural economy, with 85% of all households participating in harvest, which provides at least 25% of all meat and fish consumed (Kruse & Muth, 1990). The importance of subsistence in the economy is inversely related to community size, with some communities relying on subsistence for as much as 80% of their meat (Kruse & Muth, 1990).

Sitka black-tailed deer are the single most valuable subsistence resource in southeastern Alaska and constituted 21% of the total weight of subsistence resources harvested by rural residents in 1987, an amount of meat equal to the combined use of all five species of salmon *Oncorhynchus* spp. (Kruse & Muth, 1990). Thirty-seven percent of all households participated directly in deer hunting, and 23% of the deer meat was reported shared with other families. Not surprisingly, old-growth forests with natural open areas (such as muskeg, beach, meadows, or alpine) were the major hunting areas. Clearcuts were used less often than unlogged areas, and closed-canopy, even-aged stands were the least-used habitat by hunters (Kruse & Muth, 1990).

Black-tailed deer, therefore, are a significant component of the economy, lifestyle, and culture of rural residents of southeastern Alaska, especially in small communities where employment opportunities are few or seasonal. The economy of some communities is benefited by employment in the logging industry, but all communities are affected by the availability of deer. Jobs and higher incomes reduce the need for deer meat but do not substitute for the social and recreational importance of deer. Rural residents are very aware of the status of local deer populations and concerned about their survival and productivity.

LIMITATIONS

The role of Sitka black-tailed deer in rural lifestyles is too complex to reduce the problem of trade-offs between the timber and subsistence economies to a common currency. Logging, too, is a lifestyle that is part of the cultural environment, and subsistence is an important part of life in logging communities. Furthermore, the broader aspects of culture cannot be reduced to economic metrics. Deer serve only as an indicator of part of the cultural environment—the part that is diminished by the environmental effects of logging. They help to integrate the biological and social costs of logging, but they can serve only as an index, not a direct measure.

Although Sitka black-tailed deer are a valuable ecological indicator for most of the upland forests, they are a poor indicator for other habitats and unique habitat requirements for other species. Riparian forests, wetlands, and marine environments, for example, are very important habitats for many plants and animals yet are relatively unimportant for deer. Unique habitat requirements for other species, such as large nest trees for bald eagles *Haliaeetus leucocephalus* or hollow logs and root systems for rodents and mustelids, have little relevance to deer. Similarly, recreation and subsistence requirements of rural residents are much broader than those provided by deer alone or even the characteristics of the upland forest that are most favorable for deer.

Sitka black-tailed deer, therefore, serve as an indicator of only certain conditions—disturbance regime, carbon/nutrient balance of understory plants, landscape and species diversity of plant communities, canopy interception of snowfall. Those are the conditions responsible for a productive, nutritious, and available food resource. Deer habitat requirements are best met in old-growth forest but do not depend on the myriad of other features deemed important in old-growth forests—habitat for other plants and animals, ecosystem function (nutrient cycling, water quality), or aesthetic values for humans. The use of Sitka black-tailed deer as an ecological indicator cannot substitute for the greater knowledge that is ultimately necessary for sound forest management. An index of biodiversity is necessarily only a partial measure of the whole.

Population density and productivity are the most important measures of deer response to habitat; but both, especially productivity, are difficult to measure in the forests of southeastern Alaska. Furthermore, deer populations may be out of synchrony with the carrying capacity of their habitat. High mortality during winters of heavy snow accumulation will occur in even the best habitats, and predation by wolves may delay population recovery. Such problems are common with any species considered an ecological indicator. They emphasize the importance of knowledge of the biology and ecology of the species and the problems inherent in relying on population data alone. The Alaska Department of Fish and Game currently monitors black-tailed deer populations with the fecal pellet-group technique (Neff, 1968). It provides an imprecise index of density, but is suitable as an index of trend (Kirchhoff, 1990). Equally necessary, however, are habitat-based analyses of potential carrying capacity of limiting factors. Habitat-base analyses (e.g. Hanley & McKendrick, 1985; Hobbs & Swift, 1985; Hanley & Rogers, 1989) are independent of realized population densities, provide a quantitative evaluation of habitat quality, and can be used to prepare a quantitative forecast of the results of anticipated changes in habitat resulting from logging, silvicultural treatments, or succession. Population trend data and habitat-based analyses provide most understanding when used together in combination.

IMPLICATIONS

Sitka black-tailed deer provide an objective basis for balancing timber management and conservation of natural resources. Carrying capacity models based on food resources and deer nutritional requirements (Hobbs & Swift, 1985; Hanley & Rogers, 1989) yield quantitative measures of habitat that can be projected over time. Long-term planning is critically needed, because the carrying capacity of deer populations at the landscape level is dependent on the spatial and temporal mix of stand ages. Retention of old-growth stands within the managed forest is a key element of conservation planning in southeastern Alaska (Samson *et al.*, 1989) and also of deer habitat management (Hanley *et al.*, 1989). Monitoring population response over time is an integral requirement of long-term management and must be part of the planning process.

The economic and cultural importance of deer to rural residents fosters political and public support for conservation plans involving deer, especially at the local level. People relate better to deer than to other ecological attributes of old-growth forests (e.g. biodiversity), especially when it concerns their economy, social interactions, and recreation as well as aesthetics. Trade-offs between economic development, biological conservation, and human culture can be seen more clearly when the indicator is something of direct importance to the people affected.

Timber management and biological conservation are not incompatible endeavors in southeastern Alaska. Both are beneficial to the local residents. The problem is one of balancing them. It is not only a question of how much timber to cut, but also a question of how, when, and where to cut it. The Sitka black-tailed deer, as an ecological indicator, may constrain timber management significantly. Even if species viability or regional population levels are not an issue, local population levels can be affected very significantly by intensive timber harvest. Management that includes the objective of harvestable populations of deer within access to rural residents requires balanced use of the landscape. Black-tailed deer, in that sense, help to optimize the solution of balancing timber harvest with biological conservation. Furthermore, an understanding of cause-and-effect relations between deer and their habitat provides a basis for developing new management systems or techniques that make timber management and biological conservation more compatible.

Desired levels of timber harvest and deer habitat capability are societal decisions that are beyond the ecological relations. The latter however, provide the link that quantifies the trade-offs between the two. Habitat models that project population response over time, coupled with a monitoring system, provide the capability for analysis of cumulative effects.

Indicator species that tie together both the ecological and the socioeconomic environments have high utility for management. They are especially valuable for bio-

logical conservation because they include the human element and the need for economic development, thus making them acceptable and of interest to a broad segment of the human population. An understanding of their cause-and-effect relations with habitat is of fundamental importance to analysis and planning.

ACKNOWLEDGEMENTS

I thank M. D. Kirchhoff, I. M. Korhonen, R. K. Nelson, C. M. Schonewald-Cox, and two anonymous referees for their reviews of earlier drafts of the manuscript.

REFERENCES

- Alaback, P. B. (1982). Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology*, **63**, 1932-48.
- Alaback, P. B. (1984). Plant succession following logging in the Sitka spruce-western hemlock forests of southeast Alaska: Implications for management. *USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report*, No. PNW-173.
- Alaback, P. B. & Tappeiner, J. C. II (1991). Response of western hemlock *Tsuga heterophylla* and early blueberry *Vaccinium ovalifolium* seedlings to forest windthrow. *Can. J. For. Res.*, **21**, 534-9.
- Bart, J. & Forsman, E. D. (1992). Dependence of northern spotted owls *Strix occidentalis caurina* on old-growth forests in the western USA. *Biol. Conserv.*, **62**, 95-100.
- Bunnell, F. L. (1976). Forestry-wildlife: Whither the future. *For. Chron.*, **52**, 147-49.
- Deal, R. L., Oliver, C. D. & Bormann, B. T. (1991). Reconstruction of mixed hemlock-spruce stands in coastal southeast Alaska. *Can. J. For. Res.*, **21**, 643-54.
- Franklin, J. F. *et al.* (1981). Ecological characteristics of old-growth Douglas-fir forests. *USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report*, No. PNW-118.
- Forsman, E. D. (1980). Habitat utilization by spotted owls in the west-central Cascades of Oregon. PhD thesis. Oregon State University, Corvallis, Oregon.
- Halls, L. K. (ed). (1984). *White-tailed Deer: Ecology and Management*. Stackpole Books. Harrisburg, Pennsylvania.
- Hanley, T. A. & McKendrick, J. D. (1985). Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, southeastern Alaska. *J. Wildl. Manage.*, **49**, 103-14.
- Hanley, T. A., Robbins, C. T. & Spalinger, D. E. (1989). Forest habitats and the nutritional ecology of Sitka black-tailed deer: A research synthesis with implications for forest management. *USDA Forest Service, Pacific Northwest Research Station Portland, Oregon, General Technical Report*, No. PNW-GTR-230.
- Hanley, T. A. & Rogers, J. J. (1989). Estimating carrying capacity with simultaneous nutritional constraints. *USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, Research Note*, No. PNW-RN-485.
- Hanley, T. A. & Rose, C. L. (1987). Influence of overstory on snow depth and density in hemlock-spruce stands: Implications for management of deer habitat in southeastern Alaska. *USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, Research Note*, No. PNW-RN-459.
- Harris, A. S. & Farr, W. A. (1974). The forest ecosystem of southeast Alaska, 7. Forest ecology and timber management. *USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report*, No. PNW-25.
- Hobbs, N. T. (1989). Linking energy balance to survival in mule deer: Development and test of a simulation model. *Wildl. Monogr.*, **101**, 1-39.
- Hobbs, N. T. & Swift, D. M. (1985). Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *J. Wildl. Manage.*, **49**, 814-22.
- Kirchhoff, M. D. (1990). Evaluations of methods for assessing deer population trends in southeast Alaska. Federal Aid in Wildlife Restoration Research Final Report. Study number IIB-2.9. Alaska Department of Fish and Game. Juneau, Alaska.
- Kirchhoff, M. D. & Schoen, J. W. (1987). Forest cover and snow: Implications for deer habitat in southeast Alaska. *J. Wildl. Manage.*, **51**, 28-33.
- Kruse, J. A. & Muth, R. M. (1990). Subsistence use of renewable resources by rural residents of southeast Alaska. Final report under the US Forest Service/University of Alaska Cooperative Agreement PNW-88-553. Institute of Social and Economic Research, University of Alaska, Anchorage, Alaska.
- Meehan, W. R., Merrell, T. R. Jr & Hanley, T. A. (eds). (1984). *Fish and Wildlife Relationships in Old-Growth Forests: Proceedings of a Symposium (Juneau, Alaska, 12-15 April 1982)*. American Institute of Fishery Research Biologists, Morehead City, North Carolina.
- Meslow, E. C., Maser, C. & Verner, J. (1981). Old-growth forests as wildlife habitat. *Trans. N. Amer. Wildl. & Nat. Resour. Conf.*, **46**, 329-35.
- Moen, A. N. (1973). *Wildlife Ecology: An Analytical Approach*. W. H. Freeman, San Francisco, California.
- National Research Council (1986). *Ecological Knowledge and Environmental Problem-solving: Concepts and Case Studies*. National Academy Press, Washington, DC.
- Neff, D. J. (1986). The pellet-group count technique for big game trend, census, and distribution: A review. *J. Wildl. Manage.*, **32**, 597-614.
- Parker, K. L., Robbins, C. T. & Hanley, T. A. (1984). Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manage.*, **48**, 474-88.
- Robbins, C. T., Hanley, T. A., Hagerman, A. E., Hjeljord, O., Baker, D. L., Schwartz, C. C. & Mautz, W. W. (1987). Role of tannins in defending plants against ruminants: Reduction in protein availability. *Ecology*, **68**, 98-107.
- Rose, C. L. (1990). Application of the carbon/nutrient balance concept to predicting the nutritional quality of blueberry foliage to deer in southeastern Alaska. PhD thesis, Oregon State University, Corvallis, Oregon.
- Ruggiero, L. F., Aubry, K. B., Cary, A. B. & Huff, M. H. (1991). Wildlife and vegetation of unmanaged Douglas-fir forests. *USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report*, No. PNW-GTR-285.
- Salwasser, H. (1986). Conserving a regional spotted owl population. In *Ecological Knowledge and Environmental Problem-solving: Concepts and Case Studies*, National Research Council. National Academy Press, Washington, DC, pp. 227-47.
- Samson, F. B. *et al.* (1989). Conservation of rain forests in southeast Alaska: Report of a working group. *Trans. N. Amer. Wildl. & Nat. Resour. Conf.*, **54**, 121-33.
- Schoen, J. W. & Kirchhoff, M. D. (1985). Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. *J. Wildl. Manage.*, **49**, 96-103.
- Schoen, J. W., Wallmo, O. C. & Kirchhoff, M. D. (1981). Wildlife-forest relationships: Is a reevaluation of old growth necessary? *Trans. N. Amer. Wildl. & Nat. Resour. Conf.*, **46**, 531-44.
- Schoen, J. W., Kirchhoff, M. D. & Hughes, J. H. (1988). Wildlife and old-growth forests in southeastern Alaska. *Nat. Areas J.*, **8**, 138-45.
- Tappeiner, J. C. II & Alaback, P. B. (1989). Early establishment and vegetative growth of understory species in the

- western hemlock–Sitka spruce forests of southeast Alaska. *Can. J. Bot.*, **67**, 318–26.
- Van Horne, B., Hanley, T. A., Cates, R. G., McKendrick, J. D. & Horner, J. D. (1988). Influence of seral stage and season on leaf chemistry of southeastern Alaska deer forage. *Can. J. For. Res.*, **18**, 90–9.
- Wallmo, O. C. (ed.) (1981). *Mule and Black-tailed Deer of North America*. University of Nebraska Press, Lincoln, Nebraska.
- Wallmo, O. C. & Schoen, J. W. (ed.) (1979). *Sitka Black-tailed Deer: Proceedings of a Conference in Juneau, Alaska*. USDA Forest Service, Alaska Region, Juneau, Alaska.
- Wallmo, O. C. & Schoen, J. W. (1980). Response of deer to secondary forest succession in southeast Alaska. *For. Sci.*, **26**, 448–62.
- Wickstrom, M. L., Robbins, C. T., Hanley, T. A., Spalinger, D. E. & Parish, S. M. (1984). Food intake and foraging energetics of elk and mule deer. *J. Wildl. Manage.*, **48**, 1285–1301.