6

Succession Debt and Roads

SHORT- AND LONG-TERM EFFECTS OF TIMBER HARVEST ON A LARGE-MAMMAL PREDATOR-PREY COMMUNITY IN SOUTHEAST ALASKA

David K. Person and Todd J. Brinkman

INTRODUCTION

Unlike most regions of North America, the rainforests of southeast Alaska and northern coastal British Columbia retain most of their postglacial legacy of wildlife (MacDonald and Cook 2007). Along with fish and other marine foods, those wildlife resources helped to sustain human populations for at least 9,000 years before the arrival of Europeans, despite dramatic postglacial geological and ecological changes to the landscape (Baichtal and Swanston 1996; Larsen *et al.* 2005; Carstensen 2007). Beginning in the 1950s, industrial-scale harvesting of timber occurred throughout much of the region. In coastal British Columbia, 67% of watersheds greater than 5,000 ha were developed by 1991, mostly for logging (Lertzman and MacKinnon, this volume, chapter 8). From 1954 to 2008, greater than 325,000 ha of rainforest were clear-cut logged and greater than 6,000 km of road were built in southeast Alaska (Albert and Schoen 2007a). Prior to logging, the coastal forest landscape was a product of edaphic factors, long-term abiotic forces, and short-term agents of disturbance such as wind and disease (Alaback *et al.*, this volume, chapter 4). Industrial-scale clear-cut logging does not mimic the natural agents and patterns of disturbance, and it initiates a chain of events that have complex ecological and social implications (Hanley 1993; Kramer *et al.* 2001; DellaSala *et al.* 2011;

In:

NORTH PACIFIC TEMPERATE RAINFORESTS

Ecology & Conservation

Edited by

GORDON H. ORIANS *and*

JOHN W. SCHOEN

AUDUBON ALASKA *and*

THE NATURE CONSERVANCY OF ALASKA

in association with

UNIVERSITY OF WASHINGTON PRESS

Seattle and London

Printed and bound in the United States of America

18 17 16 15 14 13 5 4 3 2 1

AUDUBON ALASKA
441 West Fifth Ave., Suite 300
Anchorage, AK 99501
ak.audubon.org

THE NATURE CONSERVANCY IN ALASKA
715 L Street, Suite 200
Anchorage, AK 99501
www.nature.org

UNIVERSITY OF WASHINGTON PRESS
PO Box 50096, Seattle, WA 98145, USA
www.washington.edu/uwpress

LIBRARY OF CONGRESS CATALOGING-IN-PUBLICATION DATA
North Pacific temperate rainforests : ecology and conservation / edited by Gordon Orians and John Schoen.
pages cm
ISBN 978-0-295-99261-7 (hardback)
1. Temperate rain forest ecology—British Colombia. 2. Temperate rain forest conservation—British Colombia. 3. Temperate rain forest ecology—Alaska. 4. Temperate rain forest conservation—Alaska. I. Orians, Gordon H., editor of compilation. II. Schoen, John W., editor of compilation.
SD146.B7N67 2013 577.34—dc23 2013007835

The paper used in this publication is acid-free and meets the minimum requirements of American National Standard for Information Sciences—Permanence of Paper for Printed Library Materials, ANSI Z39.48 1984.∞

Alaback *et al.*, this volume, chapter 4). In addition, roads built to facilitate logging provide new pathways of access, enabling the footprint of human activity to extend into previously remote inland areas. Roads alter ecosystems in ways that affect ecological processes, populations of plants and animals, and human interactions with landscapes (Forman and Alexander 1998; Trombulak and Frissell 2000; Forman *et al.* 2003; Brinkman *et al.* 2007; Brinkman *et al.* 2009). In southeast Alaska and coastal British Columbia, those changes have profound and long-term effects on many wildlife species and the ecological communities with which they are linked.

The inexorable process of forest succession following clear-cut logging in North Pacific rainforests transitions through several distinct stages with varying effects on wildlife, but it ultimately reaches a condition (corresponding to the *stem exclusion* stage) that is largely unproductive for many species (Alaback 1982; Schoen *et al.* 1988; Alaback *et al.*, this volume, chapter 4). We refer to circumstances affecting wildlife populations resulting from that chain of events as *succession debt* (Person 2001). Short-term economic and social benefits of industrial harvesting of timber will be paid for by long-term ecological consequences resulting from patterns and processes of forest succession and roads. There may be short-term benefits for some wildlife species, but succession debt implies that those benefits are ephemeral and do not reflect conditions for those species over the long term. Although succession debt will affect many species of forest-dependent wildlife within coastal British Columbia and southeast Alaska, we chose to illustrate this concept by focusing on the realized and potential effects of timber harvest and roads on a predator-prey ecological community located on Prince of Wales Island in southeast Alaska. The system is a complex network of marine and terrestrial influences and includes several predators, fish and ungulate prey, human hunters, and the land and seascapes upon which they all depend. Although our case study focuses on predator-prey dynamics within North Pacific temperate rainforests, it highlights the general difficulties of conserving large mammalian carnivores within rapidly changing landscapes and is relevant to other forest ecosystems exposed to large-scale anthropogenic disturbance. Moreover, by discussing changes at a community level, we encourage a systems approach to thinking about effects of those disturbances rather than focusing on individual species (Dörner 1996).

THE PREDATOR-PREY COMMUNITY ON PRINCE OF WALES ISLAND

Prince of Wales Island is located within the southern portion of the Alexander Archipelago in southeast Alaska (fig. 6.01). It is 6,700 km^2 and is the third largest island in the United States. The landscape is dominated by rugged mountains less than 1,200 m high, the slopes of which are covered mostly by a mosaic of coniferous forests and muskeg heaths. Most of the land is encompassed by the Tongass National Forest, however, more than 178,000 ha (8%) are owned by the state of Alaska and private landowners, which include Alaska Native corporations. Under provisions of the Alaska Native Claims Settlement Act (1971), more than 30,000 ha of additional forest land may be conveyed to Native corporations within the next decade. Approximately 130,000 ha of productive timberland (about 29% of the productive old growth) were clear-cut logged on private, state, and federal lands from 1955 to 2005 (Albert and Schoen 2007a). Most nonfederal lands were logged from 1980 through 2009. In addition, more than 4,000 km of road were built, mostly to facilitate logging. About 20% of the land area was logged and is in various stages of forest succession; 39% of the area is old-growth forest containing a volume of timber more than 45 m^3/ha, and the rest is alpine, muskeg heath, or scrub forest. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), wolves (*Canis lupus ligoni*), black bears (*Ursus americanus*), and beaver (*Castor canadensis*) are the principal components of a complex large-mammal predator-prey system. Numerous lakes and streams sustain large populations of anadromous and resident fish. Salmon (*Oncorhynchus* spp.) are important prey for both wolves and bears and serve as key agents in cycling nutrients between aquatic and terrestrial ecosystems (Willson and Halupka 1995; Hocking and Reimchen 2002; Gende *et al.* 2004; Darimont and Reimchen 2002). Hunting deer for subsistence is an important activity. For many local residents, venison constitutes their only supply of red meat (Brinkman *et al.* 2009). In addition, bear, wolves, beavers, and salmon are harvested by hunters, trappers, and fishers. Consequently, humans also play a critical role in the predator-prey community as predators on all component species and agents of habitat change.

The US Forest Service's Tongass Land and Resource Management Plan (TLMP) established a series of old-growth forest reserves as part of

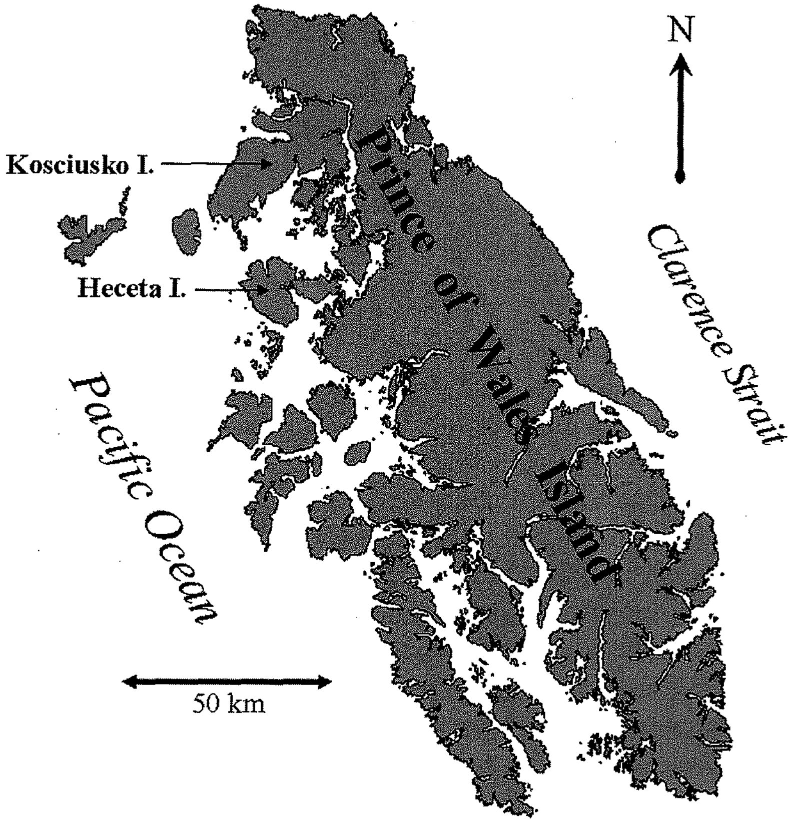

FIGURE 6.01. Prince of Wales Island in southeast Alaska. Also shown are Heceta and Kosciusko islands. Game management unit 2 designated by the Alaska Department of Fish and Game encompasses Prince of Wales and all of the smaller adjacent islands.

a comprehensive strategy for the conservation of biodiversity (USDA Forest Service 1997a, 2008a). In theory, the reserves are expected to preserve sufficient high-quality habitat to sustain ecological communities, such as the wolf-bear-deer predator-prey system on Prince of Wales Island, in the absence of suitable habitats within the intervening matrix of managed lands. In addition, TLMP-specified guidelines for managed lands are intended to reduce the risk of wildlife populations becoming extirpated or ecological functions becoming impaired (USDA Forest Service 2008a).

Prey

Suitable habitats for deer, beavers, and salmon are essential for the viability of the predator-prey ecological community on Prince of Wales Island. Humans have altered habitats and landscapes that affect each of those prey.

DEER. Prince of Wales Island supports 60,000 to 70,000 Sitka black-tailed deer, a small subspecies of mule deer adapted to northern Pacific old-growth rainforests (Person *et al.* 2009). Deer are the principal prey of wolves and an important prey for black bears (Person *et al.* 1996, Kohira and Rexstad 1997). Old-growth forest stands contain a mix of young, subdominant, and older dominant trees that create a canopy of multiple layers (see Alaback *et al.*, this volume, chapter 4). The dense forest canopy intercepts snow and rain, but numerous gaps allow sunlight to penetrate to the forest floor, enabling understory plants that provide important food for deer to flourish. Within five years after the forest canopy is removed by logging, vegetative growth responds to unrestricted sunlight by producing an abundance of forage, although much is of lower quality compared with the same species of plants grown in shade (Hanley and McKendrick 1983). Forage biomass reaches maximum abundance on productive sites 12 to 19 years after logging (table 6.1; Alaback 1982; Farmer and Kirchhoff 2007). Consequently, over the short-term (0–19 years after logging), clear-cutting enhances the quantity (but not the quality) of forage available to deer during summer and mild winters. Nonetheless, naturally regenerating conifers begin to form a dense canopy 20 to 30 years after logging that shades out understory plants (Alaback 1982). Eventually, young seral stands enter a *stem exclusion* stage in which the dense canopy of even-aged young trees almost completely eliminates forage plants, creating unproductive year-round habitat conditions that may last more than 150 years. Although during summer and mild winter conditions, deer may benefit from young clear-cuts, the long-term prognosis is permanent loss of suitable foraging habitat.

Deer populations in southeast Alaska and coastal British Columbia contain resident and migratory deer (Schoen and Kirchhoff 1985; McNay and Voller 1995). During summer, migratory deer move up in elevation as snowline recedes and eventually occupy lush alpine meadows composed of highly nutritious deciduous forbs situated above 600 m elevation. Migratory deer remain there until snowfall or senescence of deciduous plants in autumn forces them to move down to forested hillsides at lower

TABLE 6.1. Forage biomass (kg/ha) available to deer during summer in different habitats on Heceta Island in southeast Alaska (Farmer 2002; Farmer and Kirchhoff 2007). Data represent averages of oven-dried weights of evergreen and deciduous herbaceous forbs and *Vaccinium* spp. shrubs (current annual growth) sampled within 0.2-ha circular plots (n = 394).

HABITAT CLASS (N)	EVERGREEN FORBS	SE	DECIDUOUS FORBS	SE	SHRUBS	SE
Clearcuts <20 years old (73)	290.8	23.0	7.6	1.3	67.0	4.5
Clearcuts 20–39 years old (47)	168.5	47.0	8.6	2.2	71.7	10.3
Open-canopy old growth[a] (77)	165.1	16.9	19.9	2.8	38.8	3.7
Productive old growth[b] (118)	105.3	11.9	9.0	1.3	46.8	3.1
Nonforest[c] (29)	94.6	16.9	32.0	8.3	14.5	3.3
Riparian spruce old growth[d] (5)	57.1	49.7	12.1	7.7	29.2	17.8
Stem-exclusion seral forest[e] (45)	10.6	7.8	1.3	1.2	2.4	1.0

a Old-growth forest with timber volume <58.3 m^3/ha.

b Old-growth forest with timber volume ≥58.3 m^3/ha.

c Sparsely forested and nonforested lands, mostly muskeg heaths and alpine habitats.

d Closed-canopy old-growth forest with timber volume ≥290 m^3/ha situated on productive alluvial soils.

e Clear-cuts >39 years old.

elevations. Migratory deer tend to overwinter in forested habitat at higher elevations than resident (nonmigratory) deer, although severe winter weather may force them to move down into valley bottoms where they compete with resident deer for winter forage. Resident deer do not move to alpine habitat during summer and remain within the same home ranges throughout the year. On Prince of Wales Island, resident deer generally select young clear-cuts (<20 years post-logging) and open-canopy forest stands during summer and mild winters (Yeo and Peek 1992; Farmer 2002; Doerr *et al.* 2005; Person 2009). When snow depths exceed 10 cm, most of the herbaceous plants in open habitats are buried, making important forage unavailable to deer. Cost of locomotion increases dramatically as depth of snow approaches chest height (50 cm) (Parker *et al.* 1984), and deer (resident and migratory) select old-growth forest stands with basal areas greater than 45 m^3/ha where snow depth is less and evergreen forbs and shrubs are still available. During severe winters when snow depth exceeds brisket height, most deer select productive old-growth stands with a volume of timber greater than 175 m^3/ha at elevations below 240 m and avoid northerly exposures (Kirchhoff and Schoen 1987; Schoen and Kirchhoff 1990). Some deer may escape deep snow by moving to beaches and feeding on kelp and other seaweed. Mortality of deer from malnutrition, disease, and predation often is high during those winters (Schoen *et al.* 1988; Farmer *et al.* 2006; Person *et al.* 2009; Brinkman *et al.* 2011). Climate change may bring milder winter conditions on average, and it is tempting to speculate that winter habitat will become less important in the future (Scenarios Network for Alaska Planning 2009). Nonetheless, precipitation and probability of extreme storms may increase, and with it, risks of deep snow. Indeed, despite almost 30 consecutive years of relatively mild conditions, extreme snowfall occurred during the winter of 2006–2007 that substantially reduced deer numbers throughout southeast Alaska. Predation during and shortly after those winters can drive ungulate populations to very low levels, from which it may take years to recover. Consequently, it is not average conditions that really matter, but the probability of extreme events.

Clear-cut logging fragments forest patches, increasing edges; roads built to facilitate logging also contribute to forest fragmentation. Deer are attracted to forest edges and roadsides presumably because penetration of sunlight supports abundant forage production (Doerr *et al.* 2005). Nonetheless, deer that use edges and areas adjacent to roads frequently are at increased risk of predation by wolves, harvesting by hunters, and vehicular collisions (Person 2001; Farmer *et al.* 2006). Fragmented landscapes composed of small patches of old-growth timber may trap deer in those patches during winters in which snow hinders movement between patches (McNay 1995). Indeed, habitat suitability models for black-tailed deer in coastal British Columbia include distances between forest patches as a critical parameter (BC Ministry of Forests 1996). Mortality from predation and malnutrition may be high in logged and fragmented watersheds during snowy winters (Farmer *et al.* 2006), and deer populations may decline rapidly as a result (Brinkman *et al.* 2011).

OTHER PREY. Although deer are the principal prey of wolves, other species are important, particularly when deer abundance is low. Beaver frequently are consumed by wolves, but very little is known about their ecology in the region (Person *et al.* 1996; Kohira and Rexstad 1997). In coniferous forests of the Pacific Northwest, hardwoods such as alder (*Alnus* spp.) established along streams and on disturbed sites are important sources of food for beavers (Leidholt *et al.* 1989). In southeast Alaska, anecdotal evidence from trappers suggests beavers may benefit from alder regeneration on roadbeds and sites disturbed by logging; however, there are no data useful for evaluating population effects of logging or roads. Certainly, beavers take advantage of roadbeds adjacent to stream crossings by blocking culverts and allowing the road to dam the watercourse. Nonetheless, roads also provide trappers with convenient access to beaver habitat. Dams created by beavers may have negative effects on some anadromous fish such as sockeye (*Onchorhynchus nerka*)and chum (*O. keta*) salmon by blocking spawning migrations (McCurdy 2008) and a positive effect, particularly for coho salmon (*O. kisutch*), by creating pools (Bryant and Everest 1998).

Salmon are very important seasonal prey for wolves and bears (Person *et al.* 1996; Kohira and Rexstad 1997; Darimont and Reimchen 2002; Peacock 2004). Indeed, wolves often locate rendezvous sites near spawning streams and estuaries where they have easy access to salmon during August through October (Person and Russell 2009). In coastal British Columbia, Darimont *et al.* (2008) concluded that the availability of salmon seasonally decoupled wolves from their reliance on ungulate prey. Salmon are a critical resource for bears prior to hibernation and are likely a principle factor in sustaining high densities of black bears on Prince of Wales Island and elsewhere in the northern rainforests of Alaska and British Columbia. Fish, particularly salmon, are a vital food source for human subsistence. In addition, commercial and recreational fishing industries are the largest and most stable contributors to the island economy (Everest 2005; Crone and Mehrkens, this volume, chapter 5), but this is not necessarily the case on much of the north coast of British Columbia.

Clear-cuts and roads can change patterns of runoff and water flow and remove trees that are the sources of large woody debris in streams (Heifetz *et al.* 1986; Murphy and Koski 1989). In logged areas, streams may become channelized, banks destabilized, and pools for rearing fish lost, although unlogged forest buffers along streams and rivers can provide a source of woody debris and stabilize banks if they are wind firm (Murphy *et al.* 1986). Logged hillsides and roads increase the frequency of landslides, leading to soil erosion and sedimentation (Montgomery 1994; Swanston 1997). More immediately, roads may impair movement of fish throughout watersheds when culverts and other stream crossing structures are improperly designed or installed, or become blocked because of inadequate maintenance (Flanders and Cariello 2000; USDA Forest Service 2002). Many species of anadromous and resident fish must be able to migrate seasonally within watersheds to reach spawning and rearing habitats (Armstrong 1974; Bryant and Lukey 2004).

Abundant rainfall in the region creates high densities of streams and rivers that must be crossed when roads are built. In the Tongass National Forest, permanent roads cross anadromous fish streams more than 920 times and resident (nonanadromous) fish streams more than 1700 times (Flanders and Cariello 2000). Those numbers do not include temporary roads designed for short-term use, roads built on state and private lands, or roads crossing streams in which fish populations have not been documented. A survey of road conditions on national forest lands, including Prince of Wales Island, indicated that only 34% of culverts and bridges intersecting anadromous fish-bearing streams were adequate for adult and juvenile fish passage, and only 15% were adequate for passage of resident fish (Flanders and Cariello 2000). Surveys of forest roads on private lands on Prince of Wales Island showed similar results (Nichols and Frenette 2003). Most culverts were perched above the water level of the stream or the slope gradient was too steep to accommodate fish. Structures that did not block fish generally were recent installations, indicating that current standards may be adequate. Nonetheless, the legacy of older bridges and culverts is a persistent problem that affects the functioning of riparian ecosystems and may influence fish populations over the long term.

Predators

Wolves, bears, and humans all consume or exploit deer, beavers, and salmon on Prince of Wales Island, and therefore, they may compete for those resources during periods of scarcity. In addition, anthropogenic changes to landscapes and habitats influence the availability of prey to wolves and bears, and roads increase the risk of wolves and bears being killed by humans.

WOLVES. Wolves on Prince of Wales Island are an insular population (about 250–300 animals) probably derived from a few founders that reached the island before it was isolated from other islands and the main-

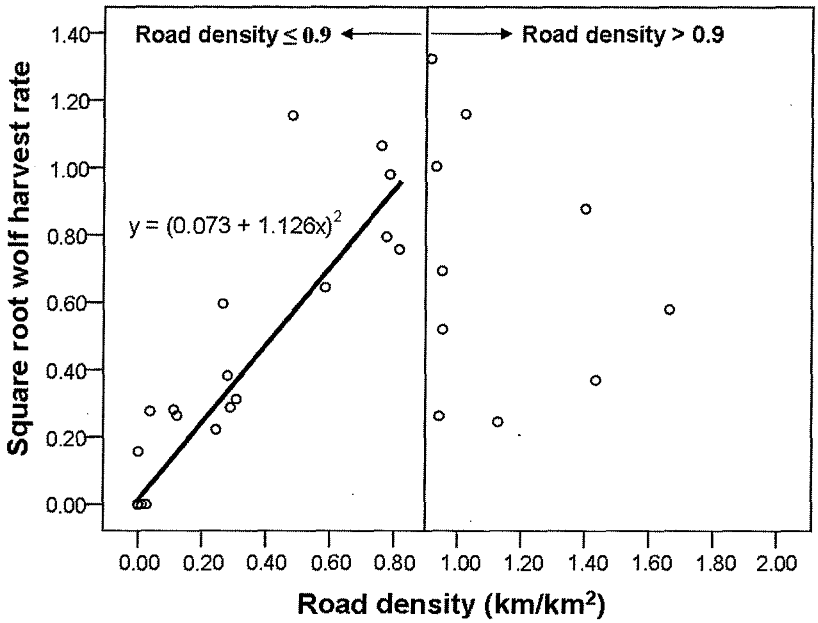

FIGURE 6.02. Relationship between road density (km/km^2) and average annual harvest rate of wolves (wolves/100 km^2) within all 32 wildlife analysis areas in game management unit 2 (Prince of Wales and adjacent islands), 1990–1999. Harvest rate is square root transformed to stabilize variance for analysis by linear regression. Data and figure are from Person and Russell (2008).

land by postglacial rise in sea level (Weckworth *et al.* 2005). Wolf populations are composed of resident pack members and nonresident wolves that are dispersing or are floating between several packs prior to or shortly after terminating dispersal (Person 2001; Person and Russell 2008). Wolves primarily prey on deer, annually consuming an estimated 18 to 32 deer per wolf (Person *et al.* 1996). In addition, salmon and beavers may constitute as much as 25% of the volume of their diet (Kohira and Rexstad 1997; Person *et al.* 1996; Szepanski *et al.* 1999).

Wolves strongly avoid young seedling and shrub-sapling stage clear-cuts but may move through older stem exclusion stands (Person 2001). Wolves avoid clear-cuts and seral forest stands when selecting den sites, however, they tend to be tolerant of logging and other human activity near dens if the disturbances are of short duration (Person and Russell 2009). Roads offer convenient pathways for wolves through logged watersheds, but they also provide access to humans, increasing risk of death of wolves from

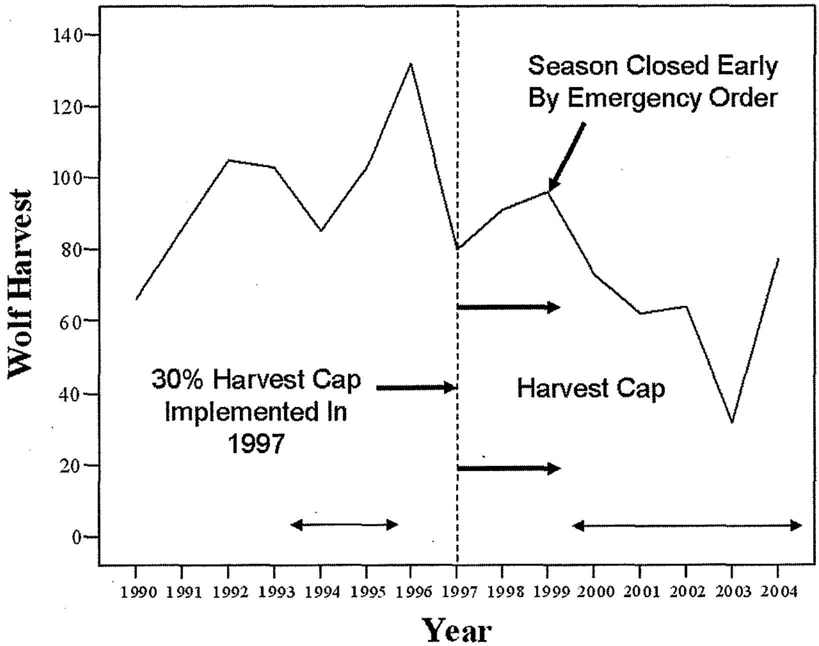

FIGURE 6.03. Wolf harvest in game management unit 2 (Prince of Wales and adjacent islands), 1990–2004. Harvest reached unsustainable limits in the mid-1990s, and the Alaska Board of Game implemented a harvest cap in 1997. The harvest quota was set at 30% of the estimated autumn wolf population in the unit. In 1999, the wolf-trapping season was closed by emergency order to prevent overharvest. Double-headed arrows indicate periods in which reliable population estimates of wolves were available. Figure and data are from Person and Russell (2008).

hunting and trapping (Person and Russell 2008). Even roads that are closed to vehicular travel provide convenient trails that facilitate harvest by humans. Person and Russell (2008) demonstrated a strong positive linear relation (r = 0.89) between road density less than or equal to 0.9 km/km^2 and harvest rates (fig. 6.02). They reported that densities greater than 0.9 km/km^2 likely resulted in unsustainable harvest. They also reported that 87% of mortality of wolves on Prince of Wales Island was from hunting and trapping. Annual survival rate of dispersing wolves (17%) was very low, with most shot or trapped before settling. Wolves are harvested legally during hunting and trapping seasons. Annually, about 50 to 95 wolves are killed and reported, but illegal take may at times equal the legal harvest (Person and Russell 2008). From 1990 through 1999, wolf harvest reached unsustainable levels, particularly within roaded watersheds, resulting in early closure of the trapping season in 1999 (fig. 6.03; Person and Russell 2008).

BLACK BEARS. There are few data concerning the ecology and demography of black bears in northern temperate rainforests; only harvest data are available for bears on Prince of Wales Island. Nonetheless, in southeast Alaska the densities of black bears were reported as high as 1.5 bears/km^2 within watersheds containing productive salmon streams and clear-cuts less than 25 years old (Peacock 2004). Bears are inactive in dens from November through April; dens are often located in hollow logs, dead standing trees, rock crevices, and ground nests on northern aspects (Erickson *et al.* 1982). When bears emerge in late March and early April, they forage on emergent vegetation and marine foods found along beaches. They feed on carcasses of deer that died during winter; however, they also may kill adult deer when the opportunity arises (Person 2009). The most important predation is on neonate fawns during late May and early June. For example, during a 3-year study of mortality of deer fawns on a portion of Prince of Wales Island, bears killed 60 (39%) of 154 radiocollared neonate fawns within 1 month of birth.(Alaska Department of Fish and Game 2010, 2011, 2012). During midsummer, bears consume large quantities of berries and appear to be attracted to young clear-cuts because of the abundance of blueberry shrubs (*Vaccinium* spp). Indeed, Schwarz and Franzmann (1991) reported black bear density to be higher in watersheds dominated by early successional forests compared with landscapes composed of older-seral forests. When salmon spawning begins in August, bears congregate in estuaries and along streams and rivers where low tide or shallow pools enable them to catch fish. Bears play an important role in transferring nutrients from anadromous fish to terrestrial ecosystems via their feces (Hildebrand *et al.* 1999). Spawning ebbs in late September, and thereafter bears consume deer, vegetation, and late-season berries as they make their way to winter dens.

Black bears are harvested year round except June 15 through August 31. From the years 2000 to 2009, 300 to 500 bears were harvested annually on Prince of Wales Island by mostly nonresident recreational hunters (Porter 2008). Providing logistic support to those hunters is a significant source of revenue for many local people, particularly during spring before popular summer fishing seasons open. Many hunters prefer to hunt for bears along logging roads that give them access to young clear-cuts, muskegs, and stream crossings where bears are visible. Roads and young clear-cuts may facilitate unsustainable harvesting of bears. Indeed, in 2009 the Alaska Department of Fish and Game restricted hunters from using road vehicles to access bear habitat on Prince of Wales Island in an attempt to reduce harvest to a sustainable level (Boyd Porter, pers. comm.).

HUMANS. Human occupants on Prince of Wales Island historically focused on marine food resources such as fish and shellfish. They also used boats to hunt deer and trap furbearers along beaches, particularly during winter. Thus, island interiors served as refugia for deer, wolves, bears, and furbearers. As logging proceeded in southeast Alaska and roads were built, subsistence hunters and trappers began changing their harvesting practices from using boats to using vehicles on roads to hunt inland areas (Ellanna and Sherrod 1987; Brinkman *et al.* 2009). Young clear-cuts, dominated by seedling conifers, became important habitat for hunters because deer were visible from roads. Roads increased the desirability of deer as a stable food resource because they were available during times of the year when marine resources were less abundant, and bad weather conditions had less effect on vehicle use than on boats. Hunting deer from roads required less time and effort than traditional strategies (Brinkman *et al.* 2009), causing most hunters to focus more on deer and less on marine resources (Ellanna and Sherrod 1987). Further, the timber industry attracted workers to southeast Alaska from the contiguous United States who were already accustomed to road-based hunting and trapping (Mazza 2003). Within one generation from the beginning of industrial-scale logging, hunting and trapping from roads largely replaced the traditional shoreline harvesting patterns of many local people (Brinkman *et al.* 2007). Hunters legally harvest 2,500 to 3,000 deer annually on Prince of Wales and adjacent islands; however, many more deer are killed illegally (Porter 2007). The area supports about 60,000 to 70,000 deer (Person *et al.* 2009), therefore, harvest removes 4%–8% (mostly adult and yearling males) of the deer population each year.

SUCCESSION DEBT: SHORT-TERM BENEFITS VERSUS LONG-TERM CONSEQUENCES

Predator-prey dynamics frequently are described as *top-down* (predator mediated) or *bottom-up* (habitat mediated), divisions that cannot be applied as discrete explanations of the dynamics of complex predator-prey systems, particularly those involving long-lived mammals within rapidly changing environments (Ballard *et al.* 2001; Bowyer *et al.* 2005; Jedrzejewska and Jedrzejewski 2005). Bottom-up systems generally are regulated by the productivity of habitats and intrinsic rates of growth of prey, whereas top-down systems are governed by the density of predators and rates of kill. In reality, the dynamics of predator-prey systems shift along a continuum of integrated processes that are mostly bottom-up at one extreme or mostly top-down at the other (Bowyer *et al.* 2005; Jedrzejewska and Jedrzejewski 2005), and they may change over time. In temperate rainforest ecosystems such as that on Prince of Wales Island, industrial-scale timber harvest reduces carrying capacity for deer, shifting predator-prey dynamics from a largely bottom-up driven system to one in which top-down forcing (predator limitation) exerts greater control (Person 2001). Clear-cuts younger than 30 years and open-canopy forest provide deer with abundant forage during snow-free months. Those habitats also offer deer some protection from predation by wolves. Mortality of deer in extensively logged watersheds is high during severe winters, but their numbers rebound quickly during mild years despite effects of predation and hunting, indicating that population regulation is strongly influenced by bottom-up processes. Therefore, deer thrive in watersheds dominated by early successional forest stands, provided winters are mild.

Between 1955 and 2005, about 22% of deer summer range was clear-cut logged on state, federal, and private lands on Prince of Wales Island. Of the subset of those lands below 240 m elevation and on southerly aspects (90°–270°) that constitute important winter range for deer, 38% was clear-cut by 2005. It is likely that an additional 5%–10% of deer winter range will be logged in the next 20 years, depending on the implementation of TLMP and transfers of lands to private timber corporations. Currently, the median age of a hectare of second-growth forest on federal lands is 34 years. About 75% of all second growth on federal lands is greater than 20 years old. On state and private lands the median age likely is about 5 to 10 years less. Deer are abundant and may remain so during part of the next decade (Brinkman *et al.* 2011). Nonetheless, as clear-cuts continue to age, carrying capacity for deer within logged watersheds (that have transitioned into sterile second-growth habitat) will decline, and the resilience of deer to winter weather, predation, and hunting will diminish. Net annual recruitment of deer also will decline, but in a disproportionate and nonlinear fashion (fig. 6.04). Net annual recruitment represents the portion of a deer population that can be removed additively by predation and hunting

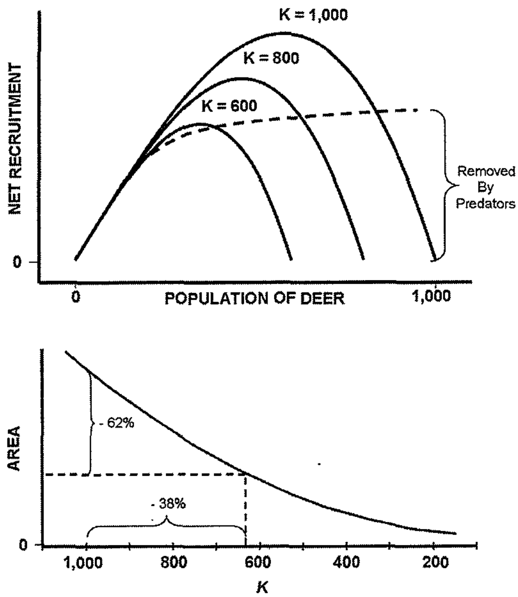

FIGURE 6.04. Relationships between net annual recruitment for deer and population density (*top graph*), and area under recruitment curve and changes in carrying capacity (K) (*bottom graph*). Area under the recruitment curves is reduced in a negative exponential fashion as K is reduced. That area represents the pool of recruits available for removal by predators and hunters without causing a decline in deer population. A 38% decline from historical levels in deer habitat capability (carrying capacity) would reduce the area under the curve by 68%. Time lags in the numerical response of predators to declining deer abundance will mean that they will remove a larger portion of net annual recruitment as K declines. That will increase competition between predators and hunters for deer and will shift the predator-prey systems more strongly toward top-down limitation.

without causing a decline in population. Wolves and bears will remove an increasing proportion of that recruitment until deer populations decline in heavily logged watersheds dominated by stem exclusion seral forest (Person 2001). Future harvesting of seral forest may return those stands to states that are productive for deer but will still leave them vulnerable to severe winter weather with deep snow packs. Moreover, harvesting second growth depends on future demand for Alaska timber, which may be weak owing to the high costs of production, transportation, and competition from producers located where wood is cheaper to grow, harvest, and transport (Crone 2005; Crone and Mehrkens, this volume, chapter 5).

Wolf packs will respond to a decline in deer density in logged watersheds by focusing on areas where deer abundance is higher (unlogged watersheds) or by expanding home ranges into neighboring pack territories, causing strife between packs. Wolves may also focus on alternative prey, but it is unlikely that salmon, which are only seasonally available, and beavers will sustain them indefinitely if deer abundance becomes very low (Person *et al.* 1996; Person 2001). Nonetheless, predation on salmon may temporarily decouple synchrony between deer and wolf population trends by subsidizing summer survival of wolves, particularly pups (Person 2001; Darimont *et al.* 2008). Thus, the time delay between a decline in deer population and similar trend in wolves would be lengthened, causing a stronger and more rapid shift toward top-down forcing.

Black bears are not obligate predators of deer; thus in the short term, a decline in deer will not precipitate a simultaneous decline in bears, a circumstance that likely will exacerbate the effects of bear predation on deer. Eventually, the predator-prey system will shift strongly toward top-down forcing, resulting in a more rapid decline in deer population than would be predicted from simply loss of carrying capacity, as well as periods in which deer populations within logged watersheds are suppressed well below carrying capacity by predation (fig. 6.05; Person 2001).

Migratory deer tend to be at lower risk of predation and benefit from abundant forage in alpine areas during snow-free months (McNay and Voller 1995). They will be less affected by loss of carrying capacity within logged stands, which tend to be concentrated at low elevations. However, during severe winters when they are pushed down into the valley bottoms, migratory deer will be exposed to the same habitat conditions and risks of predation endured by resident deer. Populations of migratory deer should rebound more quickly than resident deer during mild years because they have access to high-quality range in summer and have lower risk of predation. Consequently, the ratio of migratory deer to resident deer within logged watersheds adjacent to alpine terrain should increase over time.

As deer numbers decline and predator-prey dynamics shift more strongly toward predator limitation, subsistence and recreational hunters increasingly will be alarmed at what they perceive as competition by wolves and bears for deer. Strong proprietary attitudes concerning deer exist within many communities on the island and many resident hunters resent sharing "their deer" with off-island hunters. Protective attitudes will precede actual changes in deer population because clear-cuts greater than

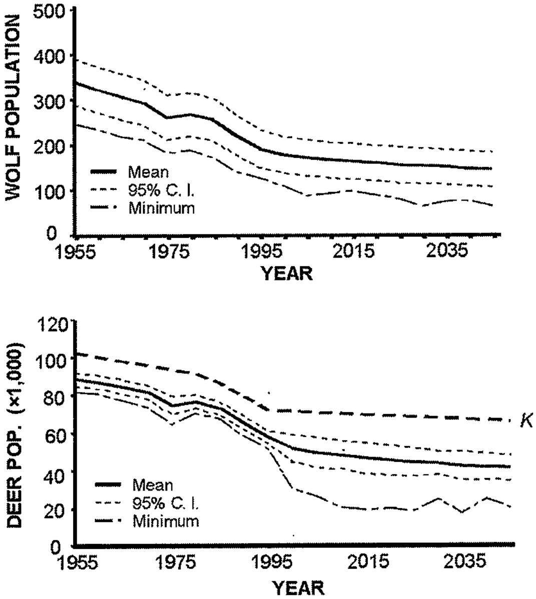

FIGURE 6.05. Results averaged for 2,000 Monte Carlo simulations of a predator-prey model described by Person (2001) that represents past and future conditions on Prince of Wales and Kosciusko islands in southeast Alaska. Simulations account for timber harvest and road construction on federal, state, and private lands; harvest of wolves and deer; and periodic severe winters in which all recruitment to the deer population is lost. Changes in carrying capacity (K) represent loss of deer habitat capability predicted in the Tongass Land Management Plan. Results indicate that wolf and deer populations will decline substantially by 2045. Decline in the deer population will be disproportionately greater than the proportional loss of K. Simulations do not account for bear predation on deer.

10 years old usually are unsuitable for hunting (as a result of increasing cover) despite supporting abundant deer (Brinkman 2007; Brinkman *et al.* 2009). Therefore, unless new cuts are created at the rate existing ones become too old to hunt, there will be a net loss of land preferred for hunting, even along roads that remain open to vehicle use. As a result, as clearcuts age, hunters will perceive fewer deer in popular hunting areas; feelings of competition with wolves, bears, and other hunters will increase demands for liberal harvests of predators and restrictions on hunting by off-island hunters. Indeed, a perception of competition led to federal regulations implemented in 2003 that restricted hunting opportunities for most off-island hunters (Brinkman *et al.* 2007). Legal and illegal take of

deer, wolves, and bears likely will increase particularly in watersheds accessible by roads or from boats (Person *et al.* 1996; Person 2001), and they may be overharvested despite regulations designed to sustainably manage their populations (Person and Russell 2008). In time, subsistence harvesters may return to a diet that focuses more on seafood. However, salmon spawning and survival of young may be impaired if the long-term effects of logging and roads on stream habitat are not properly addressed. In that event, fewer fish would be available to sustain populations of black bears, provide alternative prey for wolves, and satisfy subsistence needs. Eventually, populations of deer, bears, and wolves in logged landscapes dominated by stem-exclusion forest may only be a fraction of what they were historically (Person 2001).

Succession debt refers to the fact that a healthy predator-prey ecological community during the early stages of forest succession after logging is not a reliable indicator of future conditions. As the capacities of logged landscapes to support deer diminish, nonlinear predator-prey dynamics will dramatically alter those conditions such that populations of wolves, black bears, and deer likely will decline substantially. Moreover, social factors will complicate the situation and could result in further depletion of some species, particularly if harvest (both legal and illegal) is facilitated by roads that leave few inaccessible refugia. In particular, the viability of the wolf population on Prince of Wales and adjacent islands could be at risk (Person 2001).

A similar process involving black-tailed deer, wolves, black bears, and cougars (*Felis concolor*) developed on Vancouver Island in British Columbia (Hatter 1982; Atkinson and Janz 1994; BC Ministry of Forests 1996). Beginning in the 1960s, extensive logging eliminated important winter range for deer, compromising their resilience to predation, hunting, and winter weather (BC Ministry of Forests 1996). Deer numbers declined, hunting opportunities for deer were restricted, and predator control was implemented as an emergency measure to restore deer (Hatter 1982; Atkinson and Janz 1994). Despite reducing predators, deer population density remains much lower than historical levels, and wildlife managers chronically are concerned about the effects of predators on deer. In a further twist, because of low deer population and isolation of habitat, wolves were suspected of being significant predators of Vancouver Island marmots, an endangered species (Bryant and Page 2005).

DISCUSSION AND MANAGEMENT IMPLICATIONS

Globally, the conservation of large-mammal predator-prey systems disturbed by extensive environmental changes and subject to competing human interests is a daunting challenge, because the objective must be to sustain the entire ecological community rather than focusing on individual species. In many places, including southeast Alaska, planning for and implementing actions to conserve ecological communities is more difficult because multiple management agencies are responsible for different components and often have priorities and mandates that are contradictory. Treating individual discrete components of a complex system without regard to interactions between those components is a recipe for failure (Dörner 1996). For example, on Prince of Wales Island, simply closing roads or changing harvest regulations to protect wolves will not guarantee the population remains viable if landscapes can no longer sustain abundant and resilient deer populations (Person 2001). Indeed, it is likely that as the predator-prey system shifts more strongly towards top-down limitation, wolves will need to be harvested to some extent to prevent depletion of deer (fig. 6.06). The challenge will be how to manage that harvest to boost deer population without risking the viability of wolves. It is not enough to maintain deer abundance sufficient for wolves because subsistence hunters rely on those deer as well, and they will kill wolves legally or illegally to protect that resource. The situation is compounded by the extensive road network that greatly facilitates human access and eliminates many refugia for wolves. An additional complication is that the wolf population is genetically distinct and isolated. If wolves are extirpated or reduced to a small population, rescue or recolonization by dispersing wolves from the mainland is unlikely. Deer populations must also be resilient to bear predation, which can have a substantial effect on annual recruitment. Underlying everything are the social and economic pressures to continue logging and sustain a timber industry. As more old-growth forest is logged and additional roads constructed, fewer options remain to conserve intact ecological systems, yet human interests and needs cannot be dismissed easily.

The Tongass Land Management Plan incorporates a conservation strategy that attempts to protect the integrity and functioning of ecological systems on national forest lands in southeast Alaska while allowing

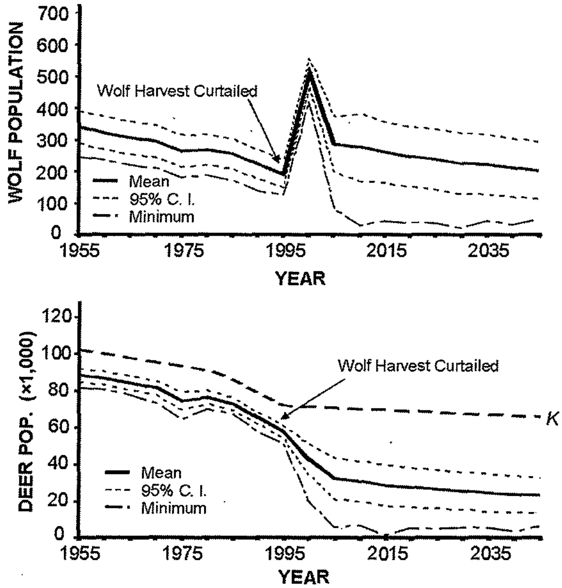

FIGURE 6.06. Results averaged for 2,000 Monte Carlo simulations of a predator-prey model described by Person (2001) that represents past and future conditions on Prince of Wales and Kosciusko islands in southeast Alaska. Simulations account for timber harvest and road construction on federal, state, and private lands; harvest of wolves and deer; and periodic severe winters in which all recruitment to the deer population is lost. Wolf harvest is hypothetically curtailed in 1996, representing changes in regulations if wolves had been listed as threatened under the Endangered Species Act by the US Fish and Wildlife Service (see Person *et al.* 1996). Changes in carrying capacity (K) represent loss of deer habitat capability predicted in the Tongass Land Management Plan. Results indicate that if wolf harvest were curtailed, the wolf population would still decline in the long term as deer are reduced to very low levels. Deer hunters would be alarmed at competition by wolves for deer and likely would demand harvests of wolves or kill them illegally. Simulations do not account for bear predation on deer.

industrial-scale harvesting of timber. The plan specifies guidelines for densities of roads to reduce risk of mortality of wolves from hunting and trapping. It also sets minimum limits for habitat capability (carrying capacity) for deer; it is presumed that these limits will sustain deer abundance capable of supporting viable wolf populations and meeting the needs of subsistence hunters. Thus, it attempts to address wolves and deer at a community level while also trying to satisfy human desires. The heart of the plan is the establishment of a system of forest reserves and other lands on which logging is deferred; these lands encompass a portion of the productive old-growth forest left on national forest lands (see Lertzmann and MacKinnon, this volume, chapter 8, for a discussion of reserves and a case study in coastal British Columbia). Unlike other areas in the Pacific Northwest, southeast Alaska still has many intact and ecologically functioning watersheds distributed throughout the region. Some of those watersheds are part of the old-growth forest reserve system established by the Tongass Land Management Plan (USDA Forest Service 1997a, 2008a). They are critical to ensuring the long-term sustainability of populations of fish and wildlife (Bryant and Everest 1998; USDA Forest Service 1997a; Albert and Schoen 2007a). Protected and roadless lands at a watershed or larger scale can safeguard important salmon streams from headwaters to their outlets. They maintain the natural composition and connectivity of landscapes, minimize forest fragmentation from roads and other human activities, and limit accessibility of wildlife to human exploitation.

On Prince of Wales Island, about 62% of the habitat capability (surrogate for carrying capacity of winter range) for deer remains after 50 years of industrial-scale logging (Albert and Schoen 2007a). About 58% of that capability is located on lands currently deferred from logging. A key assumption in the TLMP is that deferred lands are sufficient to conserve viable populations of all wildlife species currently inhabiting the island with little additional contribution from managed lands. That untested expectation requires evaluation, using monitoring programs and research focusing on its implicit assumptions (see Smith and Zollner 2005; Smith and Person 2007; Smith *et al.* 2011). For example, with respect to wolves, no single reserve or aggregate patch of deferred lands is sufficiently large to encompass an entire wolf pack home range. Therefore, very few wolf packs will be immune from logging, road access, hunting, and trapping; managed lands should be considered an integral part of the conservation strategy. Indeed, conservation strategies that focus primarily on systems of habitat reserves and roadless patches frequently fail to meet their objectives because they ignore the importance and function of the intervening matrix of unprotected lands (Noon and Blakesly 2006; Franklin and Lindenmayer 2009). That is particularly true for the conservation of large vagile mammals such as wolves and bears. Moreover, selection of reserve lands must be based on thorough ecological evaluation (Murphy and Noon 1992; Lertzmann and MacKinnon, this volume, chapter 8), rather than simply selecting lands that have not yet been developed or that are not economically valuable. Indeed, a conservation area design proposed for Prince of Wales Island included the protection of intact watersheds with the highest biological values (including winter deer habitat) and restoration for high-value watersheds that had previously been logged and roaded (Schoen and Albert 2007). In the conservation strategy in the TLMP, old-growth forest reserves comprise existing congressionally protected lands and a selection from some of the largest remaining roadless patches of unmanaged forest within the Tongass National Forest (USDA Forest Service 1997a). In extensively logged areas such as Prince of Wales Island, timber harvest targeted the most productive forested watersheds first; therefore, less productive forest often predominates in the unlogged and unroaded watersheds aggregated into forest reserves (Albert and Schoen 2007a). Any strategy to conserve large-mammal predator-prey communities must be able to accommodate their nonlinear dynamics; therefore, they should have large margins for error. In the case of Prince of Wales Island, that includes maintaining as much functionality within the matrix of managed lands as possible, while also maintaining current reserves and adding new high-quality landscapes within reserves. The objective should be to maximize the amount of suitable summer and winter range available to deer, providing habitat capability well in excess of the minimums established by the TLMP so that resilience of deer to predation, hunting, and winter snow conditions is maintained.

The matrix of managed lands surrounding reserves contains the most productive forest lands in southeast Alaska and likely will play a critical role, along with reserve lands, in sustaining wildlife and meeting human subsistence needs. Timber harvest on managed lands on Prince of Wales Island will need to shift away from old growth to seral forest. Indeed, we suggest that all old-growth forest left on federal lands on Prince of Wales and immediately adjacent islands be protected permanently to assure future conservation options and provide a hedge against the transfers of many parcels of productive forested lands to private ownership under provisions in the Alaska Native Claims Settlement Act of 1971. Conveyed lands almost certainly will be logged with little consideration for ecological values and wildlife. If harvest of old growth on federal lands is inevitable, then logging should be done in ways that approximate natural disturbances spatially and temporally (see Alaback *et al.*, this volume, chapter 4 and Beese, this volume, chapter 9). Because highly productive old-growth forest is underrepresented within reserves, it is important that the structure and heterogeneous character of old-growth forest be restored in as many logged watersheds as possible. For example, within stem exclusion seral forest, habitat for deer may be enhanced by thinning and small patch cuts that create gaps in the forest canopy sufficient to reestablish understory plants preferred as forage (Hanley *et al.* 2005; Alaback *et al.*, this volume, chapter 4). Silvicultural treatments to enhance deer habitat (as well as other species) need to be widespread; however, concentrating much of the effort in areas accessible to subsistence hunters by road may help sustain hunters' needs while reducing their motivation to kill wolves and bears illegally. It would also be helpful if timber harvest of seral forest targeted hunter-accessible areas whenever possible.

Most logging roads built in southeast Alaska, and particularly those within the Tongass National Forest, were conceived as long-term capital improvements. Their status as permanent additions to the landscape mandates a commitment by land managers to maintain them and monitor their ecological effects over many years. Weather, climate, topography, and remoteness of the region make maintaining and monitoring roads very expensive and difficult. In addition, managing road access on national forest lands is a difficult process because local residents usually demand use of forest roads, which were paid for by public funds, often making road closures for conservation purposes contentious. Budgets used to maintain, monitor, and close roads, particularly on national forest lands, usually are linked to timber harvesting activities. Timber harvesting, which may entail the construction of new roads, is necessary to pay for the maintenance, monitoring, and decommissioning of old ones. Fluctuations in the amount of timber put up for sale have a direct influence on funds available for roads. Consequently, funding for long-term maintenance and monitoring may not be stable or adequate for the task. That problem is particularly acute on Prince of Wales Island because it has the highest density of logging roads in southeast Alaska.

New roads construction should be avoided or kept to a minimum by careful planning to reduce fragmentation of remaining productive forest stands and wetlands. Where roads are necessary, construction should employ best management practices with respect to methods of construction and placement of drainage and stream-crossing structures. Existing roads that penetrate old-growth reserves should be decommissioned by removing culverts, pipes, and bridges to restore the natural flow of water and limit human access. Culverts and bridges that are inadequate for fish passage should be replaced. Long-term monitoring of the condition of roads within a diverse array of landscapes and research examining the hydrological and ecological effects of roads should be supported. This is particularly critical given the unknown impacts of climate change on the hydrology of this rainforest ecoregion. Alternative sources of funding independent of timber harvesting likely will be needed to sustain those long-term monitoring and research programs.

Rates of harvest and population trends of wolves, bears, deer, and furbearers should be closely monitored to prevent unsustainable harvesting and enable informed decisions concerning seasons and bag limits. Harvest reporting is mandatory for wolves, bears, and deer; however law enforcement efforts to insure compliance need to be stepped up. We urge fish and wildlife managers to take an ecological perspective when setting harvest objectives, to avoid overemphasizing human desires and neglecting the requirements of other species and their interactions within the system. Long-term programs for adequately monitoring deer, wolf, and bear populations (and other forest-dependent species) need to be implemented. They should take advantage of new developments in estimating populations using noninvasive techniques (Peacock 2004; Brinkman *et al.* 2011) whenever possible and cost effective. Finally, the responsible management agencies need to agree on a common set of goals to conserve the predator-prey community, and results from monitoring and research should be used to set population, harvest, and ecological thresholds that trigger appropriate management actions in a timely fashion.

We focused on a subset of wildlife species inhabiting North Pacific rainforests and ignored other forest-dependent species. For example, brown bears (*U. arctos*), northern flying squirrels (*Glaucomys sabrinus*), marten (*Martes caurina*), goshawks (*Accipiter gentilis*), and spruce grouse (*Falcipennis canadensis*) also are affected by timber harvesting and roads in southeast Alaska and coastal British Columbia (Schoen 1990; Iverson *et al.* 1996; Small *et al.* 2003; Smith *et al.* 2005). Nonetheless, our case study illustrates the overarching importance, regardless of species involved or geographic location, of addressing conservation at the level of ecological communities rather than individual species. We demonstrate that forest management practices or developments in North Pacific temperate rainforests that deviate from natural patterns of disturbance likely will have long-term and possibly intractable consequences for wildlife, humans, and ecosystems. We also emphasize the need to consider social factors, hunting and trapping in our case, when designing and implementing plans to conserve biodiversity. Indeed, ignorance or denial of those factors could easily derail an otherwise scientifically sound conservation strategy.

ACKNOWLEDGMENTS

The authors thank the senior leadership of the Alaska Department of Fish and Game, particularly Dale Rabe, Doug Larsen, and Rod Flynn for their support of the conference that spawned this chapter. We also thank the sponsors and organizers of that conference. Finally, we appreciate the thorough comments provided by anonymous reviewers of our manuscript.