RESILIENCE OF A DEER HUNTING SYSTEM IN SOUTHEAST ALASKA:

INTEGRATING SOCIAL, ECOLOGICAL, AND GENETIC DIMENSIONS

by

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RESILIENCE OF A DEER HUNTING SYSTEM IN SOUTHEAST ALASKA: INTEGRATING SOCIAL, ECOLOGICAL, AND GENETIC DIMENSIONS

A

DISSERTATION

Presented to the Faculty

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By

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Abstract

I examined the interactions of key components of a hunting system of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Prince of Wales Island, Alaska to address concerns of subsistence hunters and to provide a new tool to more effectively monitor deer populations. To address hunter concerns, I documented local knowledge and perceptions of changes in harvest opportunities of deer over the last 50 years as a result of landscape change (e.g., logging, roads). To improve deer monitoring, I designed an efficient method to sample and survey deer pellets, tested the feasibility of identifying individual deer from fecal DNA, and used DNA-based mark and recapture techniques to estimate population trends of deer. I determined that intensive logging from 1950 into the 1990s provided better hunter access to deer and habitat that facilitated deer hunting. However, recent declines in logging activity and successional changes in logged forests have reduced access to deer and increased undesirable habitat for deer hunting. My findings suggested that using DNA from fecal pellets is an effective method for monitoring deer in southeast Alaska. My sampling protocol optimized encounter rates with pellet groups allowing feasible and efficient estimates of deer abundance. I estimated deer abundance with precision (±20%) each year in 3 distinct watersheds, and identified a 30% decline in the deer population between 2006-2008. My data suggested that 3 consecutive severe winters caused the decline. Further, I determined that managed forest harvested >30 years ago supported fewer deer relative to young-managed forest and unmanaged forest. I provided empirical data to support both the theory that changes in plant composition because of succession of logged forest may reduce habitat carrying

capacity of deer over the long-term (i.e., decades), and that severity of winter weather may be the most significant force behind annual changes in deer population size in southeast Alaska. Adaptation at an individual and institutional level may be needed to build resilience into the hunting system as most (>90%) of logged forest in southeast Alaska transitions over the next couple decades into a successional stage that sustains fewer deer and deer hunting opportunities.

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Chapter 6. Brinkman, T. J., D. K. Person, F. S. Chapin, III, W. Smith, and K. J. Hundertmark. Estimating Abundance of Sitka Black-tailed Deer Using DNA from Fecal Pellets. (To be submitted to Journal of Wildlife Management)

Chapter 1 General Introduction

1.1 Conceptual Framework and Outline

Wildlife hunting systems typically are composed of hunters, their game species, and the environment in which those elements interact (Fig. 1.1A). Understanding how wildlife hunting systems function requires information concerning needs of hunters, their hunting patterns, life history and population characteristics of their wildlife prey, and the social and ecological components and processes that govern interactions within the system (Fig. 1.1B). To sustainably manage a hunting system, information also is needed on how system components and their interactions change over time and what intrinsic and extrinsic forces drive those changes (Fig. 1.1C). In the following chapters, I describe a hunting system involving rural hunters and Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Prince of Wales Island, Alaska (Fig. 1.2). The system was challenged by social, economic, and ecological changes stemming from industrial-scale harvesting of timber. For this system, the needs of hunters were well documented (Ellanna and Sherrod 1987, Kruse and Frazier 1988, Turek et al. 1998, Alaska Department of Fish and Game 2001, Mazza 2003) but patterns of hunting were not. The ecology of black-tailed deer and relations with habitat were well understood within the local environment (Wallmo and Schoen 1980, Schoen et al. 1988, Parker et al. 1999, Person 2001, Doerr et al. 2005, Farmer et al. 2006, White et al. 2009) but population density and structure were poorly known. There was a wealth of information concerning the potential of natural and anthropogenic disturbances to change landscapes and alter ecosystem processes (Alaback

1982, Deal and Farr 1994, Hanley 1993, Nowacki and Kramer 1998, Hanley 2005, Brinkman et al. 2007) but very little data documenting the effects of those changes on actual deer populations, and none concerning their effects on hunters. I present information on each key component obtained from previously published studies and from my own original research. I describe and model the interactions of those components, and discuss how the hunting system has changed over the last 50 years since the initiation of industrial timber harvesting. Lastly, I speculate about the future of deer, deer hunters, and deer habitat on Prince of Wales Island and discuss options that may enhance adaptation and highlight why an integrative investigation was appropriate. My goal was to supply local hunters and wildlife managers with data, tools, and a conceptual framework, that could help them prepare for changes and challenges in the future. In this way, I hoped to enhance the resilience of a subsistence hunting practice on which many people depend, both nutritionally and culturally.

In Chapters 2, 3, and appendix, I focus on the hunters and how they have perceived and responded to landscape changes. Those chapters also included information on the drivers of change. In Chapters 4 through 6, I provide the first precise estimates of population size and trends of Sitka black-tailed deer and present effective protocols for deriving those estimates. In Chapters 7 and 8, I summarize the interactions of all key components, speculate about future challenges and opportunities, and offer additional research recommendations.

1.2 Deer Hunting System on Prince of Wales Island

1.2.1 Background

The social-ecological changes taking place on Prince of Wales Island, Alaska are similar to those being experienced globally, particularly at higher latitudes. Intensive resource extraction (i.e., logging), increased human activity (i.e., population growth, tourism), and infrastructure development (i.e., road construction, expanded ferry service) have put more and more pressure on the social-ecological systems on Prince of Wales. Synergistic effects of intensive logging and increased human demand for a finite quantity of resources have made this region particularly vulnerable to change. Communities, particularly those with subsistence lifestyles, are struggling to maintain ties to the land during a time of changing economic and cultural influences. Of significant importance to Prince of Wales communities is the subsistence harvest of wild foods, which is a critical component of people's connection with the land.

Sitka black-tailed deer is the most nutritionally and culturally important big game species with respect to both subsistence and sport hunting in Southeast Alaska (Kruse and Frazier 1988, Hanley 1993, Alaska Department of Fish and Game 2001, Mazza 2003, Brinkman et al. 2007 [Ch. 2], 2009 [Ch. 3]), and healthy deer populations are important to the well-being of Southeast Alaskan communities (Turek et al. 1998). Deer are also a barometer of ecosystem health and an important indicator of effects of resource management in Southeast Alaska. Hanley (1993) suggested that Sitka deer populations could be used to quantitatively evaluate tradeoffs between timber management and the biological and social values of the region's forests. Furthermore, resilience of other wildlife species (e.g., wolf [*Canis lupus*]) in southeast Alaska is contingent on the sustained availability of healthy deer populations (Person 2001).

In recent years, subsistence hunters (Native and non-Native Alaskan) on Prince of Wales Island, Alaska (Fig. 1.2) have experienced difficulty harvesting the quantity of Sitka black-tailed deer they require to meet their needs (Unit 2 Deer Planning Subcommittee 2005). Previous subsistence research has provided valuable insight into broad topical areas relating to the deer subsistence hunting system (Kruse and Frazier 1988, Turek et al. 1998, Alaska Department of Fish and Game 2001). However, a lack of information about deer populations and the knowledge, perceptions, and behavior of subsistence hunters has hindered attempts to address this problem. Nonetheless, several hypotheses have emerged to explain problems meeting subsistence needs. For example, subsistence users may be experiencing difficulty because:

1) There is an inadequate supply of deer available for harvest.
2) Vegetation has grown up in logged areas and along roads, reducing the visibility of deer to hunters.
3) With the decline in activity of the timber industry, logging roads are being closed or are no longer maintained, which has reduced hunter access to habitat previously utilized by deer.
4) There is increased competition and interference from off-island hunters.
5) Succession has converted clearcut logging areas to second growth forest, shifting deer to habitat that has higher nutritional value but is less accessible to hunters. Subsistence users are forced to adapt to spatial changes in deer densities and

establish new hunting areas. Harvest efficiency has been reduced during this transition period.

One or a combination of those hypotheses may explain current subsistence dilemmas on Prince of Wales. However, data were not available to test any of these potential explanations. Because subsistence problems on Prince of Wales are likely a result of both ecological and social changes, an integrative approach to research that includes biological and social sciences was needed. This study aims to determine why deer hunters are experiencing difficulty meeting their subsistence demands by evaluating the linkages between deer hunting patterns, population dynamics of deer, and the rapidly changing social and ecological environment (Fig. 1.1C). To date, the lack of reliable data on deer population levels has thwarted attempts to understand the deer hunting system. The absence of this important population parameter has perpetuated uncertainty and disagreement about the cause of the difficulty experienced by hunters.

From the time deer regulations were established in Alaska, wildlife agencies have managed deer and deer hunters without reliable estimates of deer abundance. As in other thickly forested parts of the world (Ratcliffe 1987, van Vliet et al. 2008), the densely vegetated environment of southeast Alaska has hindered researchers' ability to collect basic information (e.g., population parameters) on forest-dwelling mammals. Traditional strategies using direct counts such as aerial surveys have not been effective because of closed forest canopies, and ground-sampling techniques (e.g., live capture, road-side counts) do not yield sample sizes sufficient to extrapolate to the population or landscape scale. When direct observation or counts of wildlife are not possible, researchers (including those of deer in Alaska) have often depended on fecal pellet or dung counts (Putman 1984, Koster and Hart 1988, Kirchhoff and Pitcher 1988, van Vliet et al. 2008). However, population estimates based on feces counts are often imprecise, unreliable, and not cost effective (Neff 1968, Campbell et al. 2004, Smart et al. 2004). Estimates based on fecal pellet counts are often too coarse to assess population size or trends at scales useful to wildlife managers, and estimates have been interpreted with caution or completely ignored when making policy decisions. Improving the accuracy and precision of population estimates of Sitka black-tailed deer has been identified as a top priority by both wildlife agencies mandated to monitor deer in Alaska, and by deer hunters who depend on sufficient harvest opportunities (Unit 2 Deer Planning Subcommittee 2005).

The need for reliable estimates of population size of Sitka black-tailed deer has escalated in recent years for 2 main reasons: 1) 50 years of industrial-scale logging has significantly altered landscapes in southeast Alaska, and the effects on deer are speculative, 2) landscape changes because of logging activity have begun to challenge harvest strategies of deer hunters in southeast Alaska (Brinkman et al. 2007 [Ch. 2], 2009 [Ch. 3]).

Industrial-scale timber harvest began on Prince of Wales and adjacent islands in the mid 1950s. Over the past 50 years, approximately 1,800 km^2 of forest have been harvested on US Forest Service, State, and Native-Corporation lands; 20% of total land area. This extensive timber harvest has changed important deer habitat by converting old-growth coniferous forest to young-growth seral forest (Wallmo and Schoen 1980, Hanley 1984, Schoen et al. 1988, Brinkman 2007 [Ch. 2], 2009 [Ch. 3]). Over the long term, deer researchers have speculated that changes in plant composition toward a forest with less understory vegetation (Alaback 1982) will likely reduce carrying capacity for deer and result in population decline (Wallmo and Schoen 1980, Hanley and McKendrick 1985).

To facilitate logging, at least 4,000 km of road were built on Forest Service, state, and Native-owned land on Prince of Wales Island (Southeast Alaska GIS Library 2007), constituting the highest density of roads in Southeast Alaska. These roads penetrated previously remote deer habitat, shifting hunting patterns from the use of boats to vehicles (Kruse and Frazier 1988, Turek et al. 1998, Brinkman 2007 [Ch. 2], 2009 [Ch. 3]). The impacts of these changes in hunting patterns, non-local harvest pressure, and habitat on population dynamics of deer were unknown.

In the late 1990s, logging activity declined and the annual timber harvest was reduced by approximately 90% compared to peak harvest. In response to the reduction in revenue from timber sales, approximately 50% of the current road network is designated to be closed over the next 10 years (PBS Engineering and Environmental 2005), significantly altering hunter access [Ch. 3]. The changing economy and physical landscape undoubtedly affect the way of life of Alaskan residents, particularly those leading a subsistence lifestyle. With the heavy dependence on deer populations by subsistence users, it is important to understand how hunters and deer populations are responding to these changes.

1.2.2 Study area, methodology, and objectives

My study was conducted on Prince of Wales Island (~ 55° N - 136° W), Alaska (Fig. 1.2). Rugged mountains extend to 1,160 m in elevation with habitats at <600 m dominated by temperate coniferous rainforest consisting primarily of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) (Alaback 1982). Annual precipitation varies from 130 to 400 cm, and mean monthly temperatures range from 1°C in January to 13°C in July. Most of Prince of Wales is within the Tongass National Forest that is administered by the USDA Forest Service. Prince of Wales and adjacent islands constitute game management unit 2 (GMU2) as designated by the Alaska Department of Fish and Game. Deer hunting season is open from the end of July through December. Rural residents of Alaska may harvest 5 deer annually, one of which may be antlerless.

Before the mid-1900s, Prince of Wales was occupied primarily by Tlingit and Haida Indians who lived in numerous small coastal fishing villages (Langdon 1977, Emmons 1991) and depended largely on marine resources such as wild salmon (*Oncorhynchus* spp.). Intensive logging between 1950 and 1990 led to the construction of roads, changes in forest habitat and a dramatic increase in human population, particularly of non-indigenous forest workers, who moved from the Pacific Northwest region of the continental United States. Prince of Wales currently has about 3,500 residents (40% Alaska Native) residing in 11 communities. Some communities comprise of equal proportions of both Native and non-Native residents while others are ethnically homogenous.

This study was designed to address immediate concerns regarding subsistence, but also to provide new tools to more effectively monitor deer populations as a basis for protocols for long-term investigations of human-wildlife resilience at high latitudes. My two overarching goals are to: 1) determine why hunters on Prince of Wales are experiencing difficulty harvesting the quantity of deer they require to meet their subsistence needs; 2) improve data on population size of Sitka black-tailed deer by developing a new approach that estimates abundance and density from DNA extracted from fecal pellets. Knowledge gained concerning the relations between deer populations, habitat, and hunter patterns will be extremely valuable to wildlife, hunters, and natural resource managers who are mandated to evaluate the effects of land use activities on deer herd dynamics (US Department of Agriculture 1997). Thus, we will be moving toward a balance among biological conservation, economic development, and human culture, which has been identified as "one of the most vexing problems in natural resource management" (Hanley 1993).

To determine why hunters on Prince of Wales are experiencing difficulty harvesting the quantity of deer they require to meet their subsistence needs, I drew upon the perceptions and knowledge of local hunters. Local knowledge, including traditional ecological knowledge, has provided insight into the effects of land management decisions and human-use impacts on long-term ecological composition, structure, and function (Watson et al. 2003). Further, merging local knowledge with science is argued to be an effective approach to sustainable monitoring and management of local wild resources (Kofinas 2002, Folke 2004, Berkes 2008). As discussed in Chapters 2 and 3, I used a semi-structured set of open-ended and quantifiable questions to guide face-to-face interviews with residents on Prince of Wales and two off-island communities. The interviews served to collect hunter perceptions and knowledge about three main topical areas: 1) deer hunting patterns, 2) deer population trends, and 3) deer habitat and access. Specifically, my objectives were to: 1) identify local perceptions as to why hunters are experiencing difficulty harvesting deer; 2) document local knowledge of deer population abundance and change; 3) quantify landscape change and access owing to commercial logging and road development; and 4) determine how subsistence hunters are responding (spatially and temporally) to a changing landscape (e.g., clearcut logging, forest succession, roads).

To improve data on population size of Sitka black-tailed deer, I tested a non-invasive approach that utilized DNA from fecal pellets to identify individual deer. In other situations where direct observation of wildlife is challenging or the research species is elusive and in low densities, non-invasive approaches using genetic techniques have become increasingly popular (Kohn and Wayne 1997, Bellemain et al. 2005; Ulizio et al. 2006; Pauli et al. 2008; Schwartz and Monfort 2008). Chapters 4 and 5 focused on techniques used to estimate abundance of deer, and in Chapter 6 I present estimates of deer density. Specifically, my objectives were to increase effectiveness of deer monitoring protocols at different spatial scales and evaluate the effects of logging activity by (Chapters, 4, 5, 6) 1) designing a new method to sample and survey pellet groups deposited by deer in all major deer habitats; 2) testing the feasibility of extracting DNA from fecal pellets of deer to identify individual deer; 3) applying genotypes of individual deer to mark and recapture techniques to estimate abundance, density, and population trends for deer in harvested and unharvested stands of forest.

In each chapter, I linked deer hunter and deer population information with data on landscape change. I used the geographic information systems (GIS) program ArcView 3.3, ArcMap 9.0 (ESRI, Redlands, California), and Hawth's Analysis Tools in ArcMap 9.0 (Beyer 2007) to quantify landscape changes (e.g., forest habitat, logging activity, and road composition). I analyzed changes at different temporal (i.e., past, present, future) and spatial scales (i.e., region, island, watershed, habitat patch) in relation to harvest opportunities of deer hunters, and DNA-based sampling design, deer density and abundance estimates.

In the final chapters (Ch. 7, 8), my objectives were to: 1) link all key components, 2) discuss options for sustainable management, and 3) offer future recommendations to enhance resilience of Sitka black-tailed deer hunting systems. Lastly, I strived to extrapolate my findings to a larger audience and suggest how my contributions may assist others in researching hunting systems.

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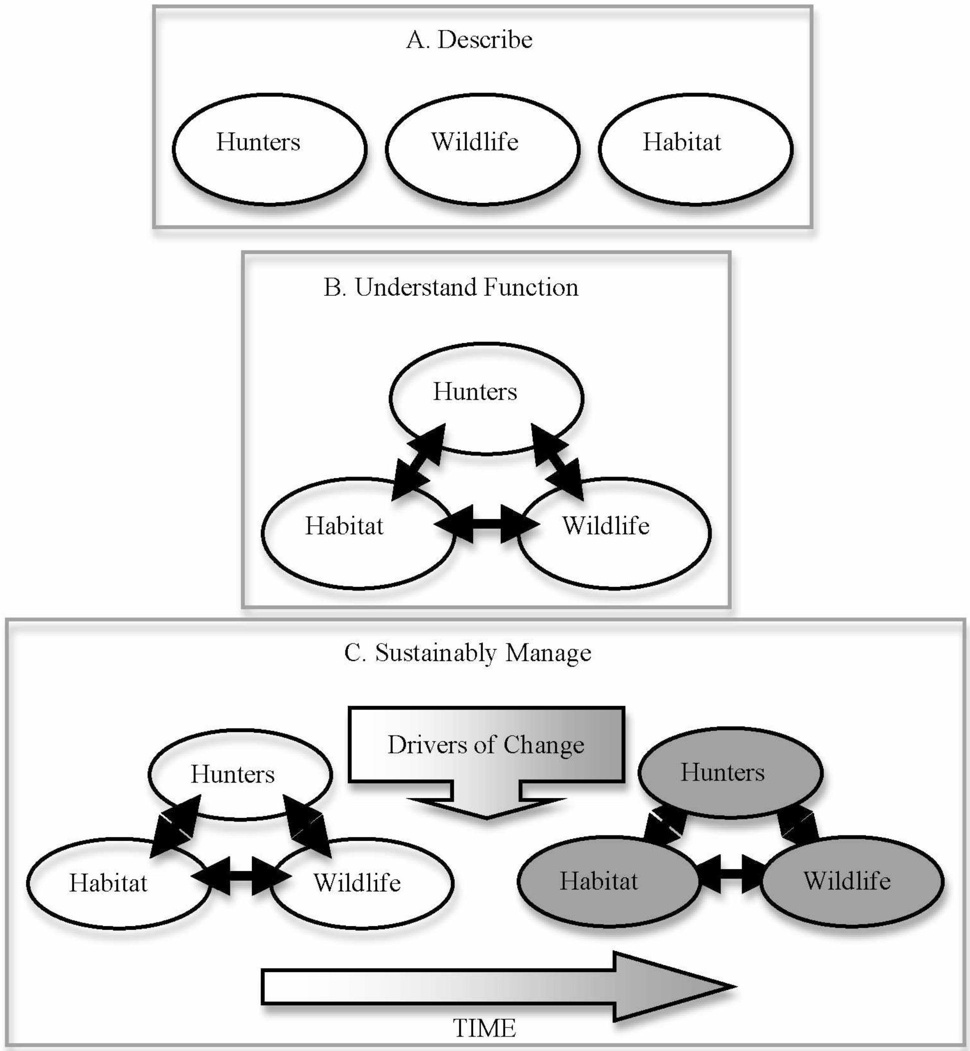

Figure 1.1. A) Description of the hunting system requires information on each key component; B) Understanding how the system functions requires information on how key components interact; C) To sustainably manage the system, information is needed on how interactions between key components change over time along with what factors are driving these changes. Ovals = key components of a wildlife hunting system. Arrows = interactions between key components.

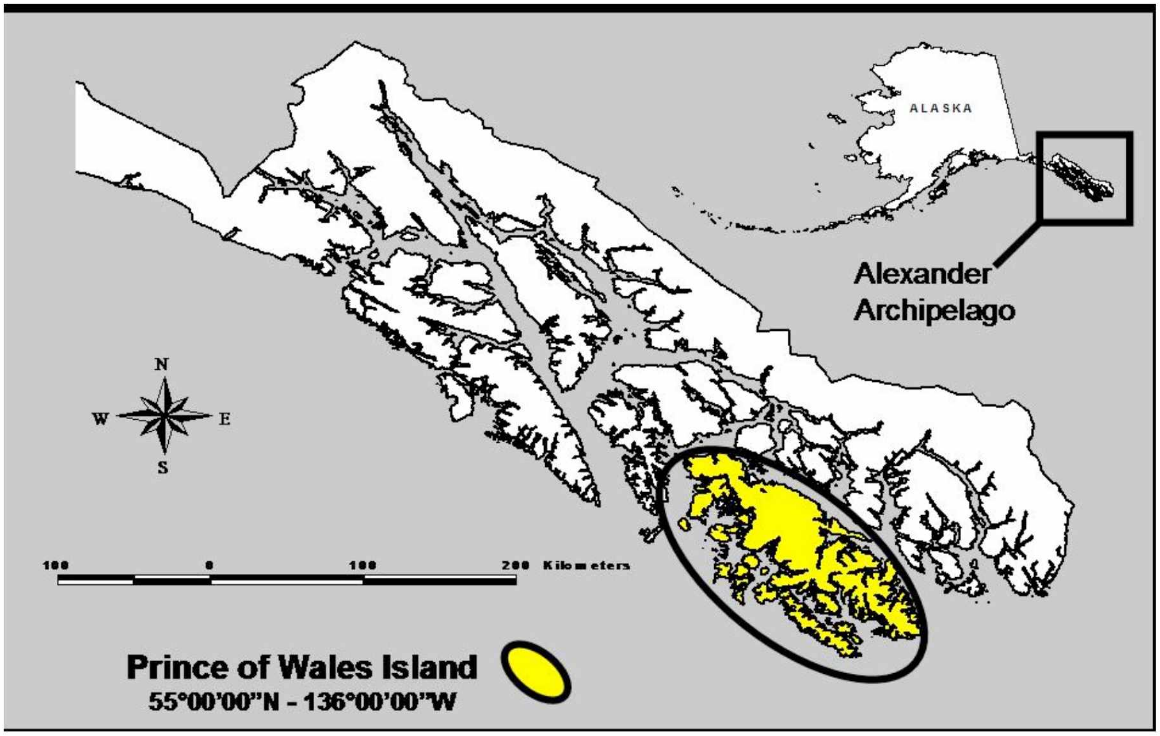

Figure 1.2. Location of Prince of Wales Island, Alaska.

Chapter 2 Influence of Hunter Adaptability on Resilience of Subsistence Hunting Systems[1]

2.1 Abstract

The capacity of hunters to shape the fundamental properties of their lifestyle at times when extrinsic factors change the availability of subsistence foods is critical to subsistence cultures. Recent changes in deer hunting on Prince of Wales Island, Alaska illustrate the social-ecological challenges to the resilience of a rural subsistence hunting system and raise the broader question of whether efficient hunting strategies necessarily enhance resilience. During the latter half of the 20th century, indigenous people of Alaska's Prince of Wales Island adapted to changing subsistence opportunities by capitalizing on increased availability of deer due to clearcut logging and the construction of roads. Consequently, deer became a more important source of protein. Four decades later, a decline in logging activity is likely to reduce deer availability due to successional changes in habitat. In the face of this social-ecological change, the resilience of the deer hunting component of subsistence traditions will depend on hunters' capacity to adapt to irreversible landscape changes by adopting different harvest strategies that may require more effort to maintain sufficient levels of subsistence harvest. For example, hunters may return to pre-road hunting methods or reduce their reliance on deer for meat and re-emphasize marine resources. These ecologically driven changes in social harvesting

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practices suggest that adaptability protecting the fundamental properties of a subsistence system from one disturbance may increase vulnerability to another. We show that increased efficiency of a subsistence system did not necessarily enhance resilience if system flexibility is reduced.

2.2 Introduction

In an environment where people have on-going access to wild plants and animals as a subsistence food source, cultural connections to the land often depend strongly on hunting and harvesting those foods (e.g., Wolfe and Walker 1987). However, rapidly changing social, ecological and economic factors often challenge people's capacity to maintain a subsistence hunting lifestyle. We describe a subsistence system in which people diversified their harvest and diet from mainly marine resources to a greater dependence on Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in response to new and more efficient (return per unit effort) hunting opportunities. In the face of more recent ecological changes, these hunters may be forced to change their harvest strategy again. We examine current and projected landscape changes—regrowth of forests following clearcut logging— and their likely effects on the availability of deer, upon which rural communities have come to depend nutritionally and culturally. Flexibility is critical to the resilience of a subsistence lifestyle and, therefore, to the resilience of cultural traditions and identity at times when extrinsic factors cause changes in the availability of subsistence foods. Further, our case study illustrates that movement of a subsistence system to a more efficient state does not necessarily enhance resilience. We describe how adoption of a more efficient hunting method increased the system's rigidity and its vulnerability to future disturbances, particularly those imposed by external forces beyond the control of local hunters. It is our hypothesis that human adaptation to higher efficiency and potentially reduced resilience often occurs rapidly, whereas the building of resilience at the cost of more effort may be slow and result in a reassessment of social-ecological values. The main components that we address are applicable to many social and ecological circumstances.

2.3 Adaptability and Resilience

The ecological anthropology of traditional hunting cultures has long focused on questions of adaptation and changing human-environment relations (Bennett 1976:243-305; Moran 1982:4). Variables such as resource diversity, social organization, and worldview have been addressed to explain the structure and function of those systems. The 'adaptive system' has been framed by some with an exclusive focus of energy flows while others have highlighted institutional dimensions. In a modern context, issues of shifting ideology and economy have been explored as factors contributing to the transformation of subsistence-based hunting systems to mixed subsistence-cash economies (Kleinfeld et al. 1983; Usher 1976). Although those issues remain important, dramatic changes in land use raise other challenges for subsistence hunting and underscores the novel and complex social-ecological dynamics underlying sustainability of subsistence hunting.

Resilience theory (Berkes et al. 2003; Gunderson and Holling 2002) provides a useful framework for understanding the persistence of subsistence hunting and harvesting systems during times of rapid change. Social-ecological resilience is the capacity of a system to persist and maintain its fundamental properties despite shocks or strong perturbations. Adaptability is the capacity of actors in a system to influence resilience (Walker et al. 2004). Together, these properties potentially contribute to the sustainability and persistence of subsistence lifestyles. Robards and Alessa (2004) argue that the natural capital on which subsistence harvesters depend waxes and wanes through time and that adaptation to those conditions is central to the system's resilience. Adaptation may therefore at times require a shift from short-term increases in efficiency to foster long-term control over the fundamental properties of the system.

In our case study, the fundamental properties of the subsistence system are communities that place a high cultural value on the harvest and consumption of wild resources (marine and terrestrial), and sufficient availability (supply and access) of these resources. Resilience could be viewed as the vulnerability of the subsistence system to losing either of these properties. Whether resilience is enhanced or reduced therefore depends on hunter response to changes in wildlife availability, as well as on subsistence hunters' perceptions of 'sufficient' supply and access. We specifically focus on how hunter responses to changes in deer availability influenced the resilience of the entire subsistence system.

2.4 Subsistence Hunting System on Prince of Wales Island

For centuries, indigenous people of Southeast Alaska depended largely on marine resources that varied seasonally (Emmons 1991:102-127). Until the mid-1900s, Prince of Wales Island, in the southern portion of the region, was inhabited primarily by Tlingit and Haida people living in small fishing villages. Tlingit and Haida Indians share many social patterns, and their cultures are largely based on the abundant availability of salmon (*Oncorhynchus* sp.). Prior to the mid-1900s, these indigenous groups harvested deer opportunistically along shorelines in conjunction with their maritime activities (Ellanna and Sherrod 1987). Deer represent the only significant terrestrial source of meat on Prince of Wales Island for subsistence hunters currently and historically.

Industrial-scale harvesting of timber began in 1954, and by 1990 about 200,000 ha of forest had been clearcut logged. Clearcut logging created favorable deer habitat, particularly during years with mild winters, and an extensive network of roads (~4800 km) that facilitated easy and efficient harvesting of deer. Roads significantly increased risk of deer death from hunting (Farmer et al. 2006) and dramatically expanded the number of areas accessible to hunters.

Shortly after industrial logging commenced, island hunters began changing their harvesting practices from hunting out of boats along beaches to driving along roads to hunt deer in open muskeg habitat and clearcuts. Road access to deer increased the stability of deer as a food resource because weather conditions (e.g., high seas) had less effect on vehicle access compared to boats, and deer were available during times of the year when marine resources were less abundant. Hunting of deer from roads required less time and effort than the early 1900s, causing most hunters to shift their subsistence focus from mainly marine resources to one that included a large proportion of deer (Ellanna and Sherrod 1987). Within one generation, accessing deer hunting areas from roads became the dominant hunting tradition, which has lasted for more than 40 years. Indeed, the minority of hunters had experience or an expectation of hunting in any other manner.

Logging activity from 1950 to 1990 corresponded to a dramatic increase in human population on the island, particularly of non-Native immigrant loggers who arrived already accustomed to living in rural areas and hunting deer via logging roads and new clearcuts. Ferry services connected the island to other parts of Alaska in 1974 further promoting population growth and hunting by off-island residents. However, competition among hunters was likely mitigated during that period because of the simultaneous expansion and increase in density of roads, and therefore, accessibility to more deer. During this time of intensive logging, resilience of the system was enhanced by the opportunity to diversify subsistence harvest and diet. Those who previously practiced a marine subsistence lifestyle now had the opportunity to switch prey at times of the year when deer were more available than fish.

2.5 Resilience Challenged

Young clearcuts produce abundant forage for deer during snow-free months (Alaback

1982). Deer within young clearcuts are easily visible to hunters (Farmer et al. 2006). Local knowledge of island hunters indicated that clearcuts less than nine years post-logging yield abundant deer, but availability of deer begins to decline after that time. Hunters reported that it is virtually impossible to hunt in clearcuts older than 14 years. Twenty-five to 40 years after cutting, clearcuts transition into stem-exclusion second-growth forest that shades out and virtually eliminates understory vegetation needed by deer for forage (Alaback 1982; Hanley 1993; Wallmo and Schoen 1980). Because clearcut logging often occurs adjacent to logging roads, densities of deer near roads will likely decline after clearcuts transition to second-growth forest (Person 2001).

Logging activity and road maintenance declined with the collapse of the Alaskan market for timber in the 1990s (Morse 2000). Post-logging forest succession and road closures caused preferred deer habitat for hunting and access to hunting areas to decline faster than they were replaced, resulting in increased hunting pressure in fewer areas, more hunter competition, and possibly fewer deer. According to timber market projections (Morse 2000), industrial logging is unlikely to rebound to levels that would support hunting strategies relying on extensive road access and new clearcuts. Further, current land management plans do not include second-growth harvesting that would augment deer populations and will reduce hunting opportunities by closing roads that are considered unsafe, environmentally detrimental, or expensive to maintain (United States Department of Agriculture 2006). In the early 1990s, subsistence hunters of Prince of Wales Island expressed concern that they were experiencing difficulty harvesting enough deer to meet their needs (Unit 2 Deer Planning Subcommittee 2005). The recent decrease in logging may be causing ecological changes that reduce harvest efficiency within a single generation of hunters. This trend is projected to continue for many decades.

2.6 Discussion

A successful subsistence harvesting tradition requires substantial adaptive capacity to cope with seasonal and annual fluctuations in resource availability. A diversified subsistence harvest that combines multiple resources and harvest strategies fosters longterm resilience of the system. Equally important is the presence of formal and informal institutions that respond flexibly to changing ecological and social conditions. In the context of deer hunting, resilience can be assessed by determining the alternatives that are potentially available, the institutional framework that influences the feasibility of (and control over) these alternatives, and costs and benefits of adopting each alternative.

Local hunters lack control over natural (i.e., forest succession) and extrinsic (e.g., global timber market, political) forces driving landscape changes and influencing the availability of deer for harvest. The only way to temporarily maintain current success rates of hunters using vehicle-based hunting strategies is to increasingly restrict harvest opportunities of non-subsistence hunters (e.g., non-Alaskans and Alaskan hunters that reside in areas designated as urban, such as Ketchikan). This policy only delays the inevitable reduction in deer harvest all hunters using roads will experience owing to habitat changes. Harvest restrictions already implemented have created conflict among hunting groups. For instance, the current regulatory regime provides subsistence hunters of deer on Prince of Wales Island with more hunting opportunities than non-subsistence hunters. Despite the widespread perception by co-managers and agency regulators that competition with non-subsistence or non-local hunters was the most important factor, data collected through Geographic Information Systems analysis and interviews with island hunters suggested that landscape change was the primary cause of harvest difficulty, and perceptions of hunter competition was an indirect effect of these ecological changes (Brinkman 2006).

Another potential strategy is to liberalize harvest of black bears (*Ursus americanus*) and wolves (*Canis lupus ligoni*) that prey on deer, as recommended by a public and interagency deer management workgroup focusing on Prince of Wales Island (Unit 2 Deer Planning Subcommittee 2005). This solution has many ecological and wildlife management consequences (Person 2001). For example, wolves on Prince of Wales Island were petitioned in 1994 to be listed as 'threatened' under the Endangered Species Act (United States Fish and Wildlife Service 1973) in part due to concern that roads would lead to over-harvesting of wolves (Biodiversity Legal Foundation 1993). Clearly, predator reduction to enhance deer hunting may invoke extrinsic pressures beyond the control of subsistence hunters on Prince of Wales.

Although the relationship between deer population change and clearcut logging is poorly documented, deer will likely remain moderately abundant despite succession of logged stands into stem-exclusion forest. Crude estimates on deer abundance suggest a stable population over the last two decades (Alaska Department of Fish and Game 2005), which is consistent with information collected through hunter interviews. Further, alpine meadows, muskegs and productive old-growth forests important to deer will remain undisturbed by logging activity under current forest management plans (United States Forest Service 1997). Many of those lands, however, will not be directly accessible by roads, and hunters must hike or boat to reach them. The small portions of these habitats that are accessible by road will have concentrated hunting activity unless hunters are willing to expend the greater effort to hike into productive areas or hunt along shorelines using boats.

The ease and efficiency of using roads to hunt deer from clearcuts was so alluring during the logging boom that former hunting traditions were largely abandoned within one generation. We suggest that the resilience of lifestyles based on subsistence deer hunting in conditions of irreversible landscape changes will depend on the capacity of hunters to adapt their harvest strategies and revise their hunting 'traditions.' Adaptations that require more effort with less return may occur slower than the hunter adaptation to a road-hunting strategy. This may cause hunters to reassess the cultural value of deer. Alternative strategies for maintaining existing harvest efficiency through regulations that exclude competing non-subsistence hunters will only delay the necessary transition to other hunting strategies and elevate conflict between hunters.

Roads and clearcuts may represent a cultural trap analogous to ecological traps (sensu

Kokko and Sutherland 2001) in which the long-term sustainability of that strategy is questionable and cultural resilience is diminished despite short-term gains in efficiency. Ultimately, building resilience into subsistence hunting of deer by indigenous and non-indigenous people of Prince of Wales will require careful reflection on the value of deer harvesting as a way of life and a concerted effort to modify and transform local traditions, perhaps to a less desirable strategy. This new strategy may be less efficient than during the period of intensive logging, but more efficient during the post-logging era and in the long term. Because of the continued abundance of marine resources, the fundamental properties of the subsistence system could potentially be maintained with reduced opportunities to harvest deer. Nonetheless, the level of effort to which hunters have become accustomed may have reduced system flexibility, resulting in a subsistence lifestyle more vulnerable to state-altering shocks or perturbations. The implications of this case study to resilience thinking underscores the need to consider carefully the dynamics of tradition, the rate at which societies move towards greater efficiency, and the challenges associated with transforming those behavioral patterns.

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Chapter 3 Linking Hunter Knowledge with Forest Change to Understand Changing Deer Harvest Opportunities in Intensively Logged Landscapes[1]

3.1 Abstract

The effects of landscape changes caused by intensive logging on the availability of wild game are important when the harvest of wild game is a critical cultural practice, food source, and recreational activity. We assessed the influence of extensive industrial logging on the availability of wild game by drawing on local knowledge and ecological science to evaluate the relationship between forest change and opportunities to harvest Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Prince of Wales Island, Alaska. We used data collected through interviews with local deer hunters and GIS analysis of land cover to determine relationships among landscape change, hunter access, and habitat for deer hunting over the last 50 yr. We then used these relationships to predict how harvest opportunities may change in the future. Intensive logging from 1950 into the 1990s provided better access to deer and habitat that facilitated deer hunting. However, successional changes in intensively logged forests in combination with a decline in current logging activity have reduced access to deer and increased undesirable habitat for deer hunting. In this new landscape, harvest opportunities in previously logged landscapes have declined, and hunters identify second-growth forest as one of the least popular habitats for hunting. Given the current state of the logging industry in Alaska, it

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is unlikely that the logging of the remaining old-growth forests or intensive management of second-growth forests will cause hunter opportunities to rebound to historic levels. Instead, hunter opportunities may continue to decline for at least another human generation, even if the long-term impacts of logging activity and deer harvest on deer numbers are minimal. Adapting hunting strategies to focus on naturally open habitats such as alpine and muskeg that are less influenced by external market forces may require considerably more hunting effort but provide the best option for sustaining deer hunting as a local tradition over the long run. To sustain hunter opportunities, we speculate that managing deer habitat in accessible areas may be more important than managing the overall health of deer populations on a regional scale. We further suggest that the level of access to preferred hunting habitat may be just as important as deer densities in determining hunter efficiency.

3.2 Introduction

Industrial-scale harvesting of timber has altered landscapes around the world and changed the ways in which hunters interact with local forests (Robinson et al. 1999). For many of these hunters, the harvesting of wildlife is an important cultural practice, food source, and recreational activity (Rao and McGowan 2002, Wolfe 2004) that helps to strengthen the connections between people and their environment. Commercial logging usually results in: the construction of roads that alter access to hunting areas, changes in habitats that influence populations of game, and an influx of nonlocal timber workers. It is therefore important to understand the relationships between the harvesting of wildlife and the rapid social and environmental changes caused by logging. Although those relationships have been evaluated in tropical forests (Robinson and Bennett 2000), little attention has been paid to the effects of intensive logging on subsistence hunters who depend on wildlife in temperate regions. Temperate-zone studies have compared harvest data on wild game in logged and unlogged forests (Hieb 1976) and documented deer response to logging activity and changes in forage availability following clear-cutting (e.g., Wallmo and Schoen 1980, Cambell et al. 2004, Doerr et al. 2005). Other studies have explored the influence of hunters on deer in logged areas (Martin and Baltzinger 2002, Farmer et al. 2006), but not the influence of logging on deer hunters. We found no studies that specifically addressed how and why deer harvest opportunities changed over time in logged areas.

We investigated the subsistence hunting of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Prince of Wales Island, Alaska. Intensive logging has significantly altered landscapes on Prince of Wales over the last 50 yr. Because the availability of wildlife is critically important to people dependent on the resource for food and cultural identity, we drew upon the perceptions and knowledge of local hunters to identify how the increase and subsequent decline in commercial logging have affected their harvest opportunities. Local knowledge, i.e., traditional ecological knowledge, has provided insight into the effects of land management decisions and human-use impacts on long-term ecological composition, structure, and function (Watson et al. 2003). Further, a number of researchers argue that merging local knowledge with science is an effective approach to sustainable monitoring and management of local wild resources (Kofinas 2002, Folke 2004, Berkes 2008).

Our objective was to determine how opportunities to harvest wildlife changed spatially and temporally in intensively logged landscapes with changes in access to hunting areas and changes in forest age structure as the logged stands transition through the successional stages following a clearcut. We also considered options for adaptation by which institutions and individual hunters might respond to the effects of logging to sustain harvesting efficiency and cultural identity.

3.3 Study Area

Prince of Wales Island near the south end of the southeastern region of Alaska is the third largest island in the United States (Fig. 3.1). Rugged mountains extending up to 1160 m in elevation and long fjords characterize much of the topography on the island. Habitats below 600 m are dominated by temperate coniferous rain forest consisting primarily of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*; Alaback 1982). Annual precipitation varies from 130 to 400 cm, and mean monthly temperature ranges from 1°C in January to 13°C in July. Most of Prince of Wales is within the Tongass National Forest, which is administered by the U.S. Forest Service.

Before the mid-1900s, Prince of Wales was occupied primarily by Tlingit and Haida Indians, who lived in numerous small coastal fishing villages (Langdon 1977, Emmons

1991) and depended largely on marine resources such as wild salmon (*Oncorhynchus* spp.). Prior to the mid-1900s, deer were hunted along shorelines in conjunction with marine harvesting activities (Ellanna and Sherrod 1987). Intensive logging between 1950 and 1990 led to the construction of roads, changes in forest habitat, and a dramatic increase in the human population, particularly in the number of nonindigenous forest workers, who moved from the Pacific Northwest region of the continental United States. Greater access via logging roads increased the availability of deer and the dependence of local residents on deer meat. Many temporary logging camps became permanent communities during the 1960s and 1970s. In 1974, ferry service linked Prince of Wales to other parts of Alaska, Canada, and the continental United States, which further changed its community demographics. Prince of Wales currently has about 3500 residents, of whom 40% are Alaska natives, residing in 11 communities, some of which are populated with mixed native and non-native residents and others of which are more ethnically homogeneous.

Deer represents the most significant terrestrial source of meat for both indigenous and nonindigenous residents and is the most important big-game species for both subsistence and sport hunting in southeast Alaska (Kruse and Frazier 1988, Turek 1998, Alaska Department of Fish and Game 2001, Mazza 2003). Although there is limited documentation on early historical and precontact levels of deer harvesting, deer have probably always been a major source of red meat for the people of southeast Alaska (Ellana and Sherrod 1987). The number of hunters and the number of deer harvested on

Prince of Wales Island have not changed significantly over the last 25 yr (Mazza 2003). The total subsistence harvest of wild food in rural areas of southeast Alaska is estimated at 81 kg/person annually, with an estimated replacement value of U.S. $11/kg (Alaska Department of Fish and Game 2000). An average of 73% of households used deer as a subsistence resource, with deer representing approximately 20%, in terms of usable weight, of the total subsistence harvest (Alaska Department of Fish and Game 2001). Purchasing a replacement for deer meat would cost U.S. $712 for a family of four. Communities on Prince of Wales Island that have increased their per capita deer harvest generally also showed an increase in the number of people living below the federal poverty level (Mazza 2003). More difficult to quantify, but equally important, is the cultural significance of hunting, harvesting, sharing, and consuming deer. Sharing of deer meat among households is common among indigenous and nonindigenous households, and Alaska natives use deer for potlatches, ceremonies, and funeral feasts (Turek et al. 1998).

Prince of Wales and adjacent islands constitute Game Management Unit 2 (GMU2) as designated by the Alaska Department of Fish and Game. For residents of Prince of Wales, deer hunting season is open from the end of July through December, with a harvest limit of five deer annually, one of which may be antlerless. Hunters may harvest more than five deer each year by acquiring a special permit, e.g., a designated permit, that allows a hunter to harvest deer for others who are unable to hunt for themselves. Reliable estimates of the deer harvest are unavailable (Southeast Alaska Subsistence Regional

Advisory Council 2005), but the total harvest is thought to be around 6000 deer, with most being taken by island residents and the neighboring off-island communities of Ketchikan and Saxmon. Although the population of deer on Prince of Wales Island has been roughly estimated at 55,000 deer (Porter 2005), there are no population data available that are accurate and precise enough to assess population trends at the temporal and spatial scales required for comparisons with changes in forest habitat and harvest opportunities. Because the island's interior was mostly uninhabited and unhunted before commercial logging (Emmons 1991), there is no information on prelogging deer populations, although descriptive accounts suggest deer were abundant (Osgood 1901, Klein and Olson 1960).

Industrial-scale timber harvesting began on Prince of Wales and adjacent islands in the mid-1950s. From 1954 to 2005, approximately 1800 km^2 of forest were harvested on U.S. Forest Service, state, and native-corporation lands, representing 20% of the total land area. South-facing productive old-growth forest below 300 m is considered critical winter habitat for deer (Wallmo and Schoen 1980). More than 50% of that habitat has been commercially harvested for timber. To facilitate logging, the highest density of roads in southeast Alaska was constructed in areas that penetrated previously remote deer habitat. At least 4000 km of roads were built on the above-mentioned lands (Southeast Alaska GIS Library 2007). Currently, approximately 2900 km are open for passenger-vehicle travel, with 2300 km under U.S. Forest Service control. Many roads have been closed by gating, the removal of culverts and bridges, and the overgrowth of trees. In the late

1990s, poor markets for timber and environmental litigation to prevent clear-cut logging combined to severely reduce timber harvesting in the region. Indeed, 590 million board-feet (mmb) of timber were harvested annually from the Tongass National Forest in peak years during the 1970s, but by 2003, the harvest had declined to < 51 mmb (U.S. Department of Agriculture 2007).

During peak timber harvesting, most roads were suitable for motorized vehicles, which provided easy access to open habitats such as muskeg heaths and clearcuts suitable for hunting deer (Mazza 2003). Hunters no longer had to hike long distances from boats to open alpine habitat or restrict their hunting forays to beaches. They were able to exploit large areas of Prince of Wales and adjacent islands that had previously been inaccessible, and the harvest increased per unit effort. Deer hunters responded to increased road access by switching from boat-based hunting to vehicles (Ellanna and Sherrod 1987, Brinkman et al. 2007), an adaptation that helped hunters overcome restrictions characteristic of boat hunting, e.g., weather dependence, long travel distances to hunting area, and cost.

Road construction and maintenance on Prince of Wales Island depend mostly on revenues from logging (PBS Engineering and Environmental 2005), but, as a result of the recent decline in the activities of the timber industry, existing roads are being decommissioned more quickly than new ones are being built. According to the U.S. Forest Service (PBS Engineering and Environmental 2005), an additional 1500 km of roads, or approximately 50% of current road network, are designated to be temporarily or permanently closed to passenger vehicle traffic over the next 10 yr, leaving a road network of roughly 1900 km. Although some new road construction may occur to meet future logging needs, the kilometers of road built will probably be small relative to the length of the roads being closed. The market for timber from Alaska is unlikely to rebound soon and may never again reach historically high levels (Morse 2000, Brackley et al. 2006; L. K. Crone, unpublished manuscript).

Because of intensive logging, deer may shift their patterns of activity in response to forest succession, and the density of deer may decline as even-aged young-growth stands progress beyond shrub and sapling stages to stem-exclusion forests (Wallmo and Schoen 1980). Stem exclusion occurs about 25–30 yr after a stand is clear-cut and is characterized by thick unbroken forest canopies and sparse understory vegetation (Alaback 1982). Forage biomass for deer in these stands may be < 5% of that present in young (< 20 yr) clearcuts. However, data are unavailable on how deer respond to these changes in forest structure.

3.4 Methods

3.4.1 Identification of interview subjects

We used Alaska Department of Fish and Game records as well as informal community interviews conducted during the summer of 2004 to locate experienced hunters to participate in structured interviews. In some communities, we hired the environmental planner who worked for the local Alaska native village corporation to assist with the selection of interview subjects. After an initial group of key hunters was identified in each community, peer selection and chain referral methods, i.e., the snowball method, were used to locate additional interview candidates. We attempted to interview the most active hunters who concentrated their efforts in GMU2. We assumed that these hunters had an above-average understanding of hunting patterns, deer populations, and deer habitat. Because we interviewed adult Alaskan residents (native and non-native) who were considered to have an in-depth knowledge of deer and deer hunting, our data should not be interpreted as representative of all deer hunters on Prince of Wales. Instead, our sample represented the knowledge and perceptions of seasoned deer hunters who were particularly dependent on deer.

3.4.2 Interview topics

During the spring and summer of 2005, we used a semistructured set of open-ended and quantifiable questions to guide face-to-face interviews with residents on Prince of Wales and two off-island communities. The interview served to collect hunter perceptions and knowledge in three main areas: (1) deer hunting patterns, (2) deer population trends, and (3) deer habitat and access. The off-island communities of Ketchikan and Saxmon, Alaska, were included in the study because many residents of those communities commonly hunt deer on Prince of Wales and depend on the resource. Along with interview questions, we asked each participant to answer a short self-administered questionnaire. We digitally recorded interviews and also took handwritten notes. Most interviews were conducted in the respondents' work or home settings. We protected the anonymity of the respondents. All methods and questions were approved by the University of Alaska Fairbanks Institutional Review Board (#05-30) prior to the interview process.

We evaluated hunter access by asking the interviewees about mode of travel to hunting areas, e.g., foot, boat, vehicle; distance from home to hunting area; distance traveled on foot while hunting; and how road construction and road closures have affected their choice of hunting location, strategy, effort, success, and the island's deer population. We investigated hunter perceptions of habitat change in their hunting areas by asking if, how, and when they changed location, effort, and strategy in response to changing forest structure. Hunters were asked to rank major habitat types, e.g., clearcuts, old-growth forest as defined below, on Prince of Wales based on hunting preference. Hunters were also asked how harvest opportunities change as a clearcut transitions to second-growth forest. There are no empirical data with respect to the response of deer population size to forest change. Although we asked interview participants to share their perceptions of how deer abundance may have responded to habitat change, we did not include these hunter perceptions in our analysis because there was no consensus among hunters about population trends, and the variance among hunters was too large to identify relationships with habitat change.

3.4.3 Data analysis methods

We estimated mean values for normally distributed data and medians when data were asymmetrically distributed, i.e., when the ratio of skewness or kurtosis to its standard error was less than -2 or greater than +2. Data were coded and analyzed using the computer program SPSS 12.0.1 (SPSS Inc., Chicago, Illinois, USA). Chi-square tests were used to test for associations between categorical variables. We used Student's t tests to compare variables grouped within two categories and one-way analysis of variance (ANOVA) to compare scales and categorical variables grouped among > two factors. Homogeneity of variance test was used to test for the equality of group variances. The Welch statistic was used to test for differences when group variances were unequal. We used a nonparametric Mann-Whitney U test with two independent samples and the Kruskal-Wallis test with several independent samples to determine significant differences when samples were not normally distributed.

We categorized habitat for deer hunting on Prince of Wales Island into seven major land-cover types: (1) old-growth forest, (2) alpine tundra, (3) muskeg, (4) beach, (5) clear-cut forest, (6) second-growth forest, and (7) precommercially thinned forest. Old-growth forest usually consists of large old conifers undisturbed by logging, with pockets of understory vegetation such as *Vaccinium* spp., *Oplopanax horridus*, and *Lysichiton americanum* (Pojar 1994). Alpine tundra is treeless habitat usually at an altitude above 800 m that is dominated by low-growing plants adapted to snow pack and wind abrasion; this habitat is commonly occupied by migrating deer during the snow-free months (U.S.

Department of Agriculture 2007). Muskeg communities, also known as peatlands or heath, are poorly drained areas with few trees relative to old-growth forest and consist mainly of sphagnum mosses (*Sphagnum* spp.) and sedges (*Carax* spp.; U.S. Department of Agriculture 2007). Beach is tidal shoreline habitat that may contain grass and sedge meadows in flat lowlands. During times of deep snow accumulation, deer may aggregate in these areas because they are the last areas to accumulate snow. Clearcuts are forest areas harvested using an even-aged management strategy, the predominant strategy in southeast Alaska, in which all the trees are felled within a stand regardless of their value. Conifer trees regenerate naturally within clear-cut stands. One to nine yr after logging, young clearcuts generally are open and seedling trees are < 2m high, enabling hunters to easily detect deer. In those early stages of succession, forage plants are abundant and available to deer during snow-free months. Ten to 25 yr after logging, stands transition into a shrub-sapling stage in which saplings are 2–6 m tall and visibility is very limited. Between 25 and 40 yr after logging, clearcuts become second-growth forests that have high densities of young trees, thick forest canopies, and very limited understory vegetation (Alaback 1982). Those stands provide little forage for deer and are difficult to hunt because of poor visibility. Many 10- to 25-yr-old stands have been precommercially thinned, i.e., all the saplings within a specified radius of trees allowed to remain in the stand are cut prior to logging. Precommercially thinned stands are characterized by widely spaced trees (5–7 m), large gaps in the forest canopy, and thick piles of slash, i.e., downed trees, filling in the spaces between trees. Thinning stimulates rapid growth in the residual trees and can temporarily enhance understory vegetation 5–10 yr after thinning;

however, thick slash may hinder hunting in this habitat. This forest type is intended for future commercial harvest. Because most (~99%) logging activity has occurred since 1950, old second-growth forests (> 80 yr of age) are rare, and second harvests have not yet occurred on the island.

We used GIS data layers derived from U.S. Forest Service vegetation and land-management digital databases for the Tongass National Forest to delineate important habitats used by hunters and deer. We used GIS program ArcView 3.3 and ArcMap 9.0 (ESRI, Redlands, California, USA) to quantify changes in logging activity, forest habitat composition, and road access through time. Metadata for the spatial data layers used were available at the Southeast Alaska GIS Library (2007). Data concerning the years in which roads were constructed were unavailable, but, because they were built to facilitate logging, the ages of the clear-cut stands adjacent to the roads enabled us to estimate the chronology of road construction (Fig. 3.2). We determined how accessible habitats that deer hunters considered popular were to vehicles at peak open road density, current road density, and planned road density in the future by summing the lengths of the roads that were open and closed to passenger vehicle travel within each polygon representing habitat type using Hawth's Analysis Tools in ArcMap 9.0 (Beyer 2007). We determined the area (km^2) of popular habitat types for deer hunting that was accessible by foot when hunting from a vehicle by buffering the past, present, and future road networks by the median distance that hunters travel on foot when hunting, and then summing the area of each habitat type within the buffered areas. Because the median distance that hunters travel away from their vehicles may not be perpendicular to the road, we also determined area (km^2) of popular habitat types within one-third of the median distance reported from roads. We assumed that the area within one-third of the median distance was a reasonable representation of the area readily accessible from the maintained road network.

3.5 Results

We interviewed 88 deer hunters (31 native, 57 non-native) from 11 communities on Prince of Wales and two off-island communities. Five females and 83 males were interviewed, and median interview length was 42 min (range = 1 hr 27 min). The mean age of the respondents was 47 yr (SD = 13.7). The minimum age was 18 yr, and the maximum was 94 yr. The median years of experience hunting deer on Prince of Wales was 20 (range = 68). The hunters interviewed harvested a mean of 6.1 deer (SD = 5.6) per hunter during a typical hunting season, yielding roughly 109 kg of edible meat per hunter annually, with a food replacement value estimated at U.S. $1199 per hunter (Alaska Department of Fish and Game 2000). When interview participants were grouped by race as native and non-native, responses were similar ($P > 0.1$) for 22 of the 25 questions that addressed hunter access and landscape change. Further, the key findings of this paper did not change when the groups were analyzed separately for the three questions to which responses differed. Consequently, we assumed that responses from native and non-native hunters were similar, and the data from the groups were pooled for the rest of our analyses.

3.5.1 Access

Vehicles were used most (67%, SE = 5%) to access hunting areas, followed by the use of boats (23%, SE = 5%), and the rest of the hunters used a combination of boat, vehicle, ATV, and airplane (10%, SE = 3%). After reaching the hunting area, hunters often traveled away from the vehicle or boat to hunt on foot (Table 3.1). Many hunters mentioned that they often hunt roads on foot, particularly closed roads. Thus, the distance traveled on foot does not necessarily equate to the distance traveled away from maintained roads. The typical distance traveled on foot was similar (Mann-Whitney U = 244.5, P = 0.630) between hunters using vehicles and hunters using boats, but hunters using vehicles (mean = 60 km, SD = 50.2 km) traveled a greater distance (Mann-Whitney U = 493, P = 0.001) away from home than did hunters using boats (mean = 22, SD = 16.0 km).

3.5.2 Hunting habitat

Muskegs were identified as the most popular habitat type to hunt, followed by clearcuts (Table 3.2). Alpine was the third most popular habitat type for hunting and was considered the area that contains the largest and healthiest deer. Open terrain, low vegetative cover, and high visibility were the characteristics common to the habitats preferred by hunters. Older managed stands of forest, i.e., second growth, were the least popular for hunting because they impeded the hunters' ability to see deer and were thought to contain fewer deer.

3.5.3 Linking access and hunting habitat

Preferences for clearcuts (Mann-Whitney U = 266, $P < 0.001$), muskeg (Mann-Whitney U = 362.5, $P = 0.007$), and beach (Mann-Whitney U = 320.0, $P = 0.001$) were different for hunters who traveled by boat compared to those who traveled by vehicle, but preferences for all other habitats were similar among groups (Table 3.2). The distance that hunters walked from their vehicles or boats when hunting did not influence their preference for any particular habitat type except alpine. Hunters who traveled above the median distance (3.2 km, range = 9.6) from their vehicles or boats preferred to hunt alpine habitat more than those traveling below the median (Mann-Whitney U = 537.5, $P = 0.009$).

As of 2006, 44.9 km of road accessed clearcuts 0–8 yr old, and 27.9 km^2 and 31.9 $km^2$of young clear-cut habitat was within 1.0 and 3.2 km, which is the median distance that hunters travel on foot from their vehicles, of a maintained road, respectively. The length of road adjacent to muskeg habitat in 2006 was 125 km. After projected road closures occur, the length of road adjacent to muskeg habitat will decline by 75 km (46%) from a peak of 138 km. The length of road adjacent to alpine habitat in 2006 was 9 km, similar to the peak open road network. After projected road closures, 2 km of road will be adjacent to alpine habitat. When comparing areas of muskeg and alpine habitat within 3.2 and 1.0 km, which is considered immediately accessible area, from a road under different road densities, we determined that the area of muskeg habitat will decline by 17 and 32% within the 3.2- and 1.0-km buffered areas, respectively (Fig. 3.3). Area of alpine habitat will decline by 8 and 35% within the 3.2- and 1.0-km buffered areas, respectively (Fig. 3.3). We were unable to identify the relationship between habitat availability and hunters' habitat preferences; however, we speculate that habitat popularity was likely influenced more by hunting characteristics such as visibility and vegetation type than by level of access or total area. Considering that clearcuts were less popular with boat hunters and shorelines were less popular with vehicle hunters, mode of access probably influences the popularity of certain habitat types.

3.5.4 Relationships between forest change and deer harvest opportunities

3.5.4.1 Changes in road access

Most hunters reported that the presence of roads increased their hunting success and decreased their effort (Table 3.3). However, their perceptions of the effect of road closures on hunting success and effort were mixed. Hunters generally believed that roads had a negative effect on deer populations and that road closures had a positive effect. Many added that hunting is better on new roads because of increased access to previously remote deer habitat and because new roads are usually located next to young clear-cut forest, a preferred habitat type for hunting deer (Table 3.2). Nonetheless, hunters perceived a decline in hunt quality along roads over time because of increased hunting pressure and forest regrowth next to roads. Road closures have caused 47% of the hunters interviewed to change their hunting strategies. Furthermore, some hunters noted that they seek out and select areas with closed roads to avoid competition with other hunters and because they believe there are more deer in those areas.

Responses were similar between hunters who used boats and hunters who used vehicles for all questions about roads except for how road closures affected harvesting effort (c^2 = 4.593, P = 0.032) and deer populations (c^2 = 5.128, P = 0.024). Fifty percent of the hunters using vehicles reported more harvesting effort because of closures, and only 20% of boat hunters reported more effort. However, 90% (SE = 3%) of hunters using boats believed that road closures increase deer numbers compared to hunters using vehicles (61%, SE = 5%). Hunters who changed their hunting strategies because of road closures (47%) traveled further from home (Mann-Whitney U = 620.5, P = 0.043) and walked further from their boats or vehicles when hunting (Mann-Whitney U = 669.5, P = 0.042) compared to those who did not change their hunting strategies. Hunters who perceived that deer populations had increased with an increased road network traveled further from home on average compared to those who perceived that the increased road network had decreased deer numbers or had no effect (c^2 = 10.566, P = 0.005). Further, on average, hunters who believed that deer populations increased with road closures traveled less distance from home to hunt compared to those who perceived that road closures have not affected deer numbers (c^2 = 7.339, P = 0.007).

The beliefs of hunters concerning the effects of roads on harvest opportunities and deer populations influenced their selection of hunting areas. Hunters who preferred clearcuts reported that harvest success increased ($c^2 = 10.754$, $P = 0.005$) and harvest effort decreased ($c^2 = 7.904$, $P = 0.019$) as roads increased. They also reported that effort increased when roads were closed ($c^2 = 8.075$, $P = 0.018$). Further, hunters who believed that roads increased or did not affect deer populations ($c^2 = 16.584$, $P = 0.000$) and that road closures ($c^2 = 6.265$, $P = 0.012$) had no effect on deer populations tended to prefer hunting in clearcuts. Hunters who reported a decrease in harvest success because of road closures typically had a higher preference for hunting beaches compared to other hunters ($c^2 = 6.265$, $P = 0.026$). One suggested explanation for this relationship was that more road closures may lead to more people using boats to hunt, resulting in the perception that hunter competition will increase in beach habitat. Hunters who reported that they had not changed their hunting strategy because of road closures had a higher preference for hunting in muskegs compared to hunters who had changed their strategies ($c^2 = 3.928$, $P = 0.048$).

3.5.4.2 Changes in forest structure

Hunters indicated that deer harvest opportunities in a clearcut depended on the age of the clearcut or the stage of succession. Hunters reported that hunting was best in young clearcuts (median = 2 yr, range = 5), and that hunt quality began to decline after about a decade after cutting (median = 9 yr, range = 18). Looking at harvest activity since 1950, the area of clear-cut forest at a desirable stage for hunting (0–8 yr) peaked in the 1970s and has declined rapidly since the mid-1990s (Fig. 3.4). From 1973 to 2006, the area of clearcuts < 9 yr of age declined 86%. Eighty-six percent of hunters reported that clearcuts eventually become unhuntable and that this occurred at a median age of 12 yr (range = 42) after clear-cutting. Seven percent (SE = 9%) of hunters believed that a second-growth forest could eventually be hunted again with proper management such as thinning. Many hunters (64%, SE = 5%) said that thinned habitat decreased the quality of the hunt and that they avoided those areas because of a lack of deer, low visibility, and the difficulty in walking through recently thinned habitat. During the thinning process, the canopy is opened, but the thinned trees are left on the ground wherever they fall, resulting in thick timber debris 1–2 m in height. The remaining hunters (36%, SE = 5%) reported that thinning had increased the quality of hunting in those areas, or that they believed thinning would improve the quality of their hunt in the future. Forty-nine percent (SE = 5%) of hunters believed that second-growth forest could never be hunted again regardless of management. In contrast, 44% (SE = 5%) of hunters believed that second-growth forest could be hunted again 25 to 100 yr after a clearcut (median = 40), but that the quality of the hunt in those areas would be inferior to most other habitat types.

As of 2006, the area of clearcuts ≥ 12 yr in age, i.e., in which the hunting was poor, was 25 times greater than the area of clear-cut forest aged 0–8 yr, which represented good hunting (Fig. 3.4). Hunter perceptions of changes in harvest opportunities following clearcuts were similar regardless of their mode of access, distance traveled from home to hunting area, distance traveled on foot while hunting, opinions on the effects of roads, and individual preferences for hunting areas.

3.6 Discussion

Hunting systems throughout the world face challenges from logging (Robinson and Bennett 2000). Similar to Prince of Wales Island, commercial logging in tropical forests created vast road networks that penetrated previously inaccessible habitat, leading to increased subsistence opportunities, changes in local economies and patterns of resource consumption, and increased numbers of immigrant workers dependent on local resources (Robinson et al. 1999). Vehicle-based hunting focusing on clear-cut habitat was initially fostered by intensive logging on Prince of Wales (Brinkman et al. 2007). However, the decline in logging has begun to hinder that strategy and challenge the resilience of the hunting system at institutional and individual levels. The changes that have occurred on Prince of Wales created two novel social-ecological trends that function at large spatial, i.e., landscape, and temporal, i.e., decadal, scales. The first change in dynamics was the expanded harvesting opportunities initiated by a boom in commercial logging that rapidly changed the forest structure. The second change in dynamics began as clearcuts transitioned into an undesirable habitat for hunting approximately eight years later. The impact of this ecological change on hunting opportunities was obscured until logging activity declined. With the collapse of commercial logging, the negative effects on hunting success from the successional loss of favorable deer habitat began to overshadow the positive effects of clear-cutting on deer habitat. Currently, the harvest strategies used by one to three generations of hunters are becoming less efficient, and hunting success using current practices is being constrained.

Road closures will further reduce the number of vehicle-accessible areas that are available for deer hunting. Because the main arteries of the road network on Prince of Wales Island will be maintained with the projected closures, a large portion of the preferred habitats currently available for hunting, such as alpine and muskeg, will remain within the median distance that experienced hunters travel on foot. However, because fewer preferred habitats will be directly adjacent to maintained roads, hunters may have to exert more physical effort walking to preferred hunting areas and carrying their harvest back.

The decline in the area of young clear-cut forest may have the greatest influence on deer harvesting opportunities. Because of the decline in the timber industry, young clearcuts will become uncommon within the next decade regardless of road or boat access. Most clearcuts have reached an unsuitable stage for hunting because the patches now consist of either dense stands of even-aged saplings with thick understory vegetation or dense second-growth stands with stem exclusion. Because these stands are located along roads, the ability of hunters to sight deer from roads and harvest them efficiently has decreased (Farmer et al. 2006). The amount of habitat unsuitable for hunting, e.g., second-growth and precommercially thinned forest, has increased rapidly (Fig. 3.4), and this trend will likely continue.

3.6.1 Adaptation options

3.6.1.1 Individual choice

Responses by individual hunters may be the most feasible form of adaptation to build resilience into the hunting system. This is typical of many northern indigenous people, who are proud of their ability to adapt to changing conditions. This hunter adaptation would require no changes in harvest regulations and no manipulation of forest structure and access. Hunters who focus their efforts on permanent and naturally occurring open habitat, e.g., alpine tundra, muskeg, shoreline, are the least vulnerable to logging-associated changes in vegetation and are likely to have more success sustaining their harvest opportunities in the future. On the other hand, those hunters who depend on vehicles for access, concentrate their hunting efforts in young clearcuts, and are unwilling or unable to travel on foot away from maintained roads are particularly vulnerable to forest changes. Vulnerable hunters who are unwilling or unable to adapt may have to reduce their reliance on deer for meat and expand their harvest of marine resources if they wish to sustain their subsistence lifestyle (Brinkman et al. 2007). An important alternative strategy with reduced harvesting of deer is an increased use of the marine resources that have historically provided for subsistence needs (Alaska Department of Fish and Game 2001). Although this option may be available, any reduction or abandonment of deer would result in the loss, or greatly reduced harvest, of this culturally and nutritionally desirable staple, given its role as the only major terrestrial prey item and red meat resource.

The overall numbers of deer hunters and deer harvested have not declined despite recent decreases in the extent of young clearcuts. This may indicate that challenging hunting conditions have not yet reached a threshold that triggers the abandonment of traditions. Alternatively, hunters may already exhibit resilience to changes by responding adaptively. For instance, interview data from this study indicate that many hunters have already responded to forest change in a way that shows a willingness to expend greater effort to carry on their deer hunting traditions. For instance, the 47% of hunters who reported that they altered their harvest strategies because of road closures also walked further on average when hunting compared to those who have not changed their harvesting strategies. In addition, some hunters reported a preference for closed roads because they believed deer numbers were greater in areas in which roads were closed to vehicle use. Consequently, hunting success may increase as a result of road closures as long as habitats within those areas remain huntable and support deer. The success rates of elk hunters in Idaho were reported to be several times higher in roadless areas compared to roaded and logged areas, purportedly because of a greater density of elk in roadless areas compared to logged areas and areas near roads (Thiessen 1976). Clearly, hunters will need to expend greater effort as roads are closed, but increases in the success in roadless or vehicle-restricted areas may at least partially compensate for reduced convenience and increased effort. In contrast, hunters who continue to hunt mainly along the condensed road system will likely experience greater competition from other road hunters, which may lower their success rates (Brinkman et al. 2007). Because many hunters reported that the number of deer seen along roads while driving was used an indicator of population size on Prince of Wales Island, fewer roads with less visibility from roads also may create a false perception of a declining deer population.

3.6.1.2 Forest management

From an institutional perspective, active cutting of second-growth forest and road closure strategies that minimize loss of access to preferred hunting areas may serve as adaptation options that help sustain deer-harvesting opportunities. Manipulation of forest structure and access would require relatively few changes in harvest regulations and hunter strategies. The harvest of older, i.e., 50- to 60-yr-old, second-growth forest could increase the area of young clear-cut habitat and potentially provide the revenue necessary to maintain roads that are important for the harvesting of local resources such as fuelwood, berries, and wildlife. If a market for 60-yr-old timber were identified, forest managers would have an incentive to keep roads open to foster the efficiency of revenue-generating timber sales rather than rebuild roads every 50 to 60 yr. With a market for 60-yr-old timber, an annual average up to 14 km^2, which is 5.8 times the level harvested in 2006, of second-growth forest could be made available for potential conversion back to clear-cut habitat between the years 2010 and 2030. This would create up to 112 km^2, or 2.3 times the 2006 level, of desirable 0- to 8-yr-old clear-cut habitat for deer hunting during that time period with little or no cost of additional road construction. According to our spatial analysis of harvested areas, 183 km^2 of second-growth forest harvested between 1950 and 1970, i.e., logged forest that would turn 60 between 2010 and 2030, was intersected by roads, excluding roads on private or native-owned land, that were closed or scheduled to be decommissioned. The future road system will intersect 207 km^2 of old second-growth forest logged in 1950–1970, resulting in 47% of second-growth forest becoming inaccessible by road. Given the recent and projected closure of roads accessing second growth, it appears unlikely that a potential second harvest has received or will receive serious consideration in the near future. Moreover, high fuel and labor costs may discourage the development of a large market for second growth in southeast Alaska. U.S. Forest Service decisions on road maintenance and management strategies are complex and involve more than second-growth harvest and the availability of deer, including the relative value of roads in terms of safety, access needed, and current uses (PBS Engineering and Environmental 2005). Problems associated with important resources such as fish, wildlife, vegetation, and water are typically considered during the benefit/cost assessment. Many closed roads will be placed under "storage" status, which means that they will be closed for now but could be reopened in the future.

Another forest management option to restore deer-harvesting opportunities for vehicle-based hunters who prefer clearcuts is additional harvesting of the remaining old-growth forest. This could provide a temporary solution for those who prefer hunting in young clearcuts but would further hinder the long-term sustainability of the hunting system by increasing the overall proportion of poor habitat for deer and deer hunting a decade later. Further, old-growth timber from Alaska struggles to compete with timber from other regions, and production has been stagnant or has declined in recent years (Morse 2000, Brackley et al. 2006).

3.6.1.3 Deer management

In regions with ineffective enforcement, e.g., some tropical forest regions, in which the harvesting of wild game or "bushmeat" is a source of income, the increase in the availability of game following logging may result in overexploitation and unsustainable hunting (Wilke and Carpenter 1999, Robinson and Bennett 2000, Laurance 2001, Fredericksen and Putz 2003). Limiting access can be a useful management tool to reduce the size of the harvest (Hieb 1976, Cole et al. 1997). In southeast Alaska, however, much of the range of Sitka black-tailed deer is an archipelago composed of remote areas that are relatively inaccessible to hunters, so overexploitation through human harvest is unlikely to occur at a regional scale. Nonetheless, even if deer populations remain regionally stable, hunting pressure and human disturbance can reduce game densities at smaller, e.g., watershed, scales in easily accessible areas such as habitats adjacent to roads (Hieb 1976). Farmer et al. (2006) noted that deer are at higher risk of mortality near roads and avoid open habitat such as muskeg near roads. Perry and Overly (1976) also found that roads reduced the use of adjacent habitat by deer, particularly in open vegetation types. If hunters on Prince of Wales prefer open habitat types near roads, but deer densities are not necessarily the highest in these areas, then their access and ability to see deer may be equal to or more important than the supply or deer densities as a determinant of hunter success and effort. Therefore, a management strategy focused on access and habitat manipulation may produce more harvesting opportunities than a strategy focused on maintaining population levels.

An emphasis on access points at the patch scale may also make it possible to monitor harvest efficiency, either to assess potential impacts on local deer populations or to develop strategies for efficient subsistence harvesting. The differences between boat and vehicle users in terms of their preferences and focus on specific habitat types demonstrate that hunters interact with the landscape at the patch scale in ways that depend on the distance and type of access, i.e., road or shoreline. Implementing harvest restrictions, e.g., by reducing the number of hunting permits issued or imposing stricter eligibility requirements for hunters, to reduce hunting pressure in desirable habitat for deer hunting might help those who remain eligible to sustain their harvest opportunities using currently popular hunting strategies. Also, this would reduce the need to actively manage second-growth forest. However, this policy would only delay the inevitable reduction in opportunities for all hunters owing to ecological changes (Brinkman et al. 2007). Using political tools to further restrict hunter eligibility to temporarily sustain the harvest for increasingly fewer hunters would lead to greater conflict and less compliance amongst hunter groups, especially if the deer population size could sustain a higher harvest without affecting conservation goals.

If areas easily accessed by people serve as population sinks for deer, another approach to maintaining harvesting opportunities is to manage population sources, e.g., productive recruitment habitat, relatively close to access points to counter hunting pressure. In South America, for example, Novaro et al. (2000) suggested that the dispersal of wild game from remote and productive refugia to actively hunted sites was important when evaluating the sustainability of subsistence hunting systems.

Biologists have speculated that the area's overall carrying capacity might decline if the logging of old-growth forests caused the loss of critical winter habitat (Schoen et al. 1988), although no data are currently available to test for a relationship between deer numbers and habitat change in southeast Alaska. Additional research focusing on how deer densities change with forest succession and changes in access will be critically important when evaluating and modeling the sustainability of the hunting system. This information will be needed before wildlife researchers, forest managers, and local hunters can confidently move forward together toward a more sustainable hunting system. Because hunters often focus on the patch scale, data on change in deer density by habitat patch may be the most useful when attempting to determine dynamic relationships among hunters, deer, and the land.

The potential methods of adaptation that we observed are similar to the patterns observed in many resource-based social-ecological systems. Hunters readily adapted to increased resource accessibility that reduced their hunting effort, just as society in general responds positively to regulatory and technological changes that increase their access to resources (Ostrom 1990). As deer accessibility declined, the continued harvesting of marine food and the willingness of about half of the hunters to increase their hunting efforts suggested at least two modes of individual adaptation that provided resilience in the face of declining deer accessibility. Both of these adaptations are embedded in traditional use patterns. Policy changes that initiate second-growth cutting or retain more roads adjacent to open habitat are potential institutional avenues of adaptation to sustain the deer harvest. However, to date, subsistence hunting issues have not influenced forestry policies regarding road maintenance and the harvesting of second-growth forests. Perhaps surprisingly, changes in deer management showed little potential to facilitate adaptation, because deer accessibility appeared more strongly influenced by road access and successional changes in forest structure than by variations in population dynamics. Research on deer population trends and the role of inaccessible source populations on deer densities near roads might provide further insights. These observations suggest that adaptations by individual hunters have so far contributed more to the resilience of this hunting system than have adjustments by management agencies, which would likely require more communication among agencies and stakeholders and the development of shared goals among hunters, foresters, and wildlife biologists.

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Table 3.1. Distance traveled by vehicle or boat from home to hunting area, and distance traveled away from boat or vehicle on foot when hunting according to responses from interviews with deer hunters on Prince of Wales Island, Alaska.

Hunting pattern	Minimum	Maximum	Median	SD
Typical distance traveled (kilometers) away from vehicle or boat when hunting on foot	0	10	3.2	2.2
Typical distance traveled (kilometers) away from home to hunt†	3	176	32	50.3

†Distance traveled by off-island residents who used ferry access was measured from Prince of Wales ferry terminal (Hollis, AK) to hunting area.

Table 3.2. Ranking of preferred deer hunting areas by habitat type according to interviews with deer hunters on Prince of Wales Island, Alaska.

Habitat type	Overall rank 1 = most popular 7 = least popular		
	All	Boat Hunters	Vehicle Hunters
Muskeg	1	1	2
Clearcut forest	2	5	1
Alpine	3	4	3
Old-growth forest	4	2	4
Beach/shoreline	5	3	5
Second-growth forest (stem exclusion stage)	6	6	6
Recently pre-commercially thinned forest	7	7	7

Table 3.3. Responses from interviews with deer hunters on Prince of Wales Island to questions addressing the influence of roads and road closures on hunting success, hunting effort, and deer population size.

Question	Increased	Decreased	No effect
How have road construction and the road network affected hunting success?	59%	10%	31%
How have road construction and the road network affected hunting effort?	9%	47%	44%
How have road closures affected hunting success?	33%	25%	41%
How have road closures affected hunting effort?	43%	9%	48%
How have road construction and the road network affected deer populations?	16%	49%	35%
How have road closures affected deer populations?	68%	0%	32%

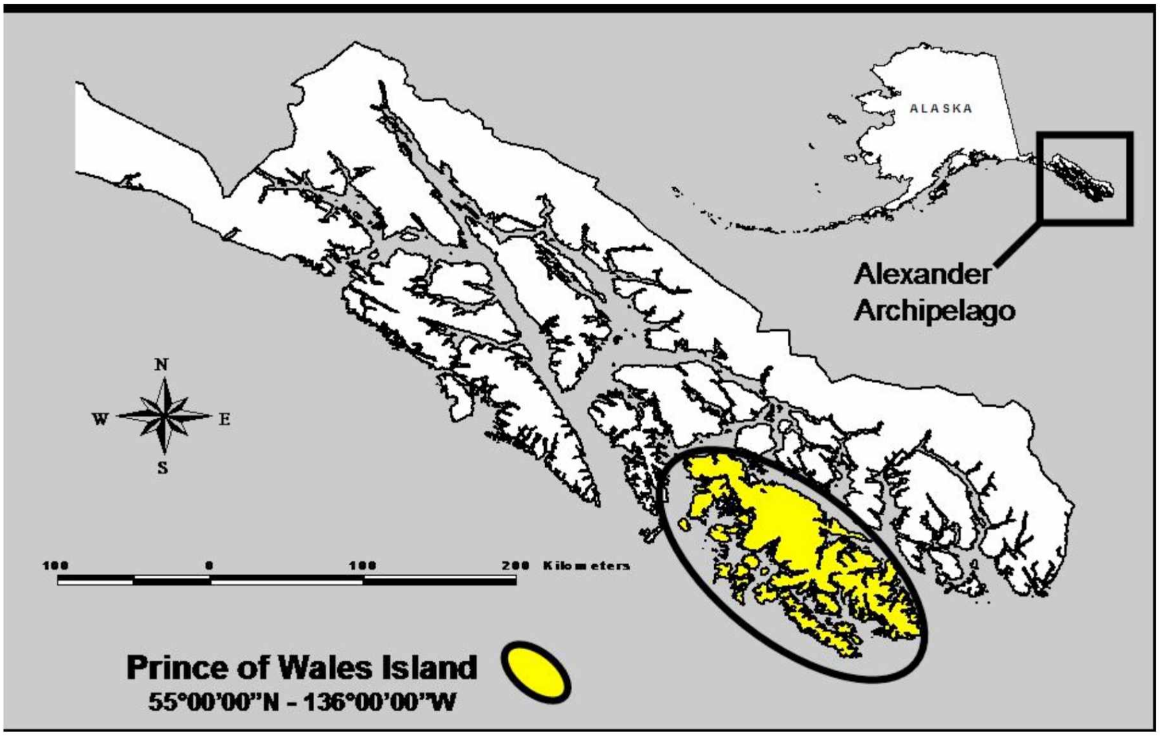

Figure 3.1 Location of the Alexander Archipelago and Prince of Wales Island in southeast Alaska.

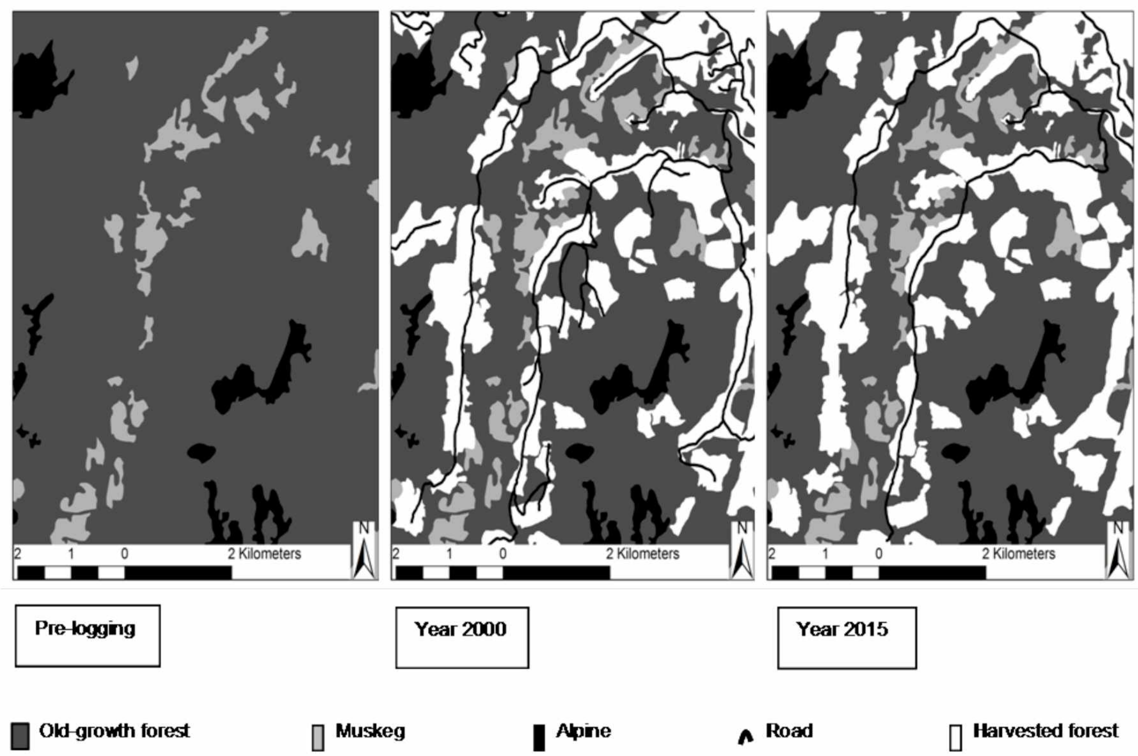

Figure 3.2. Map of common landscape change between 1950-2015 within a watershed on Prince of Wales Island, Alaska. Map "2015" was based on projected road closures and harvest activity.

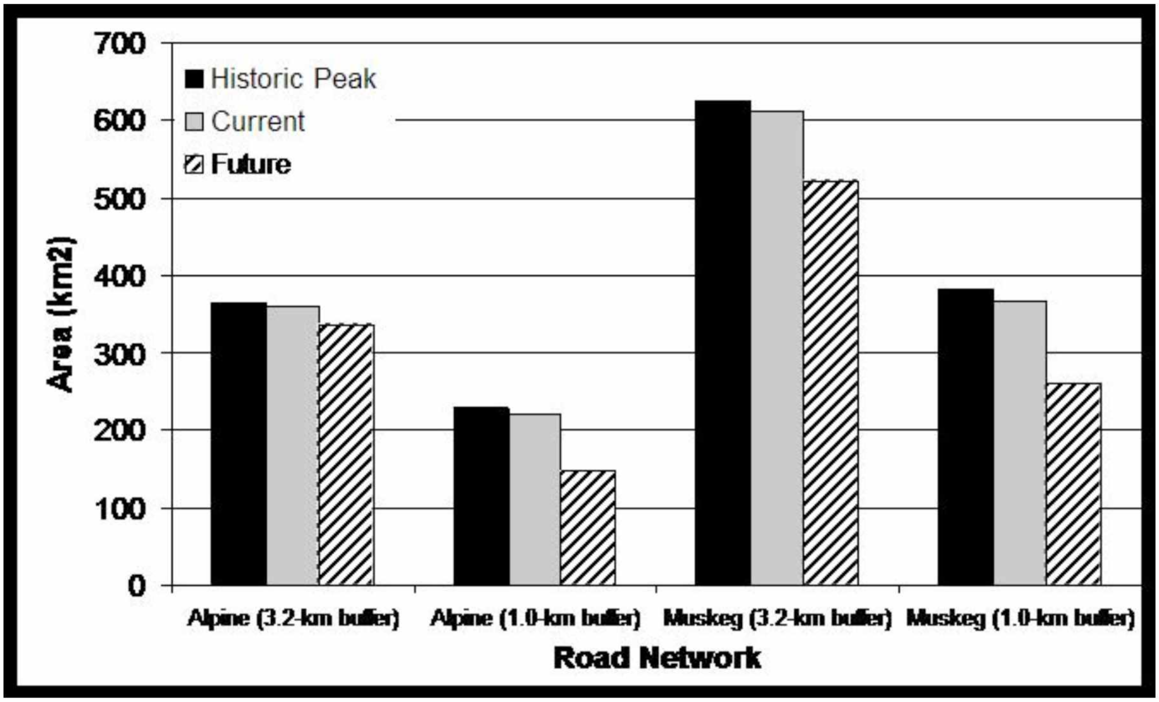

Figure 3.3. Changes in area (km^2) of popular permanent habitat types within 3.2 (median distance hunter travels on foot from boat or vehicle while hunting) and 1.0 km (area <1 km from a road is assumed readily accessible habitat for hunting) from a road at peak, current (2006), and future (2015) road densities.

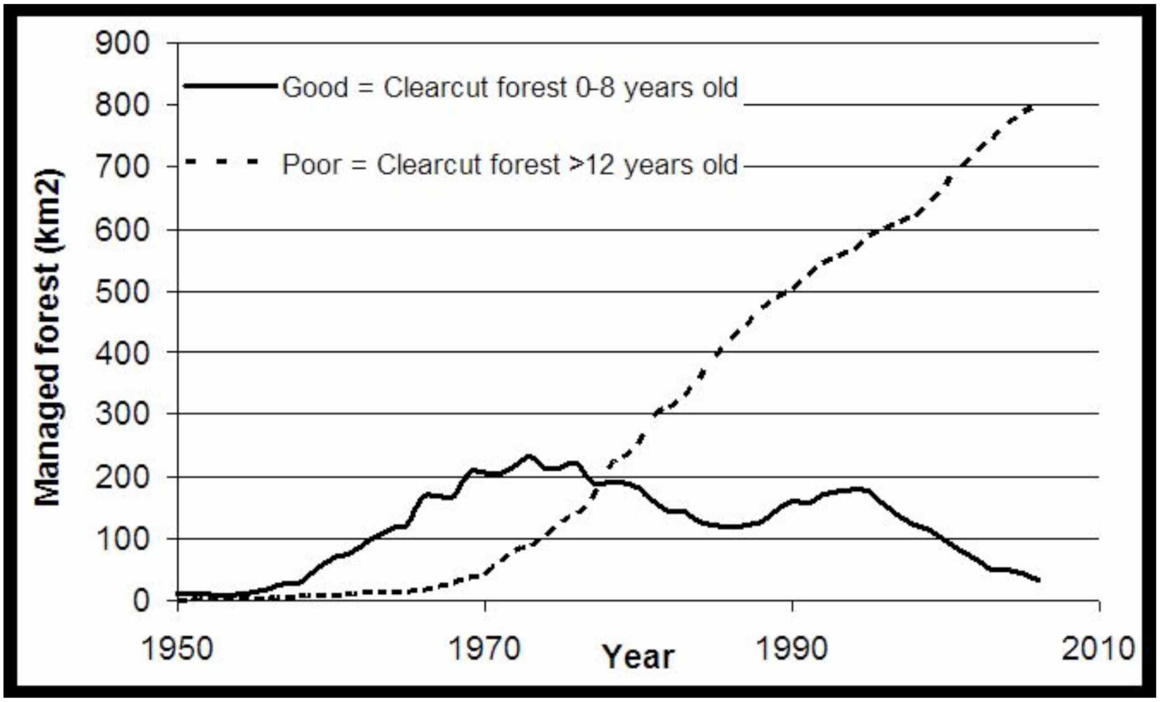

Figure 3.4. Change in areas (km^2) of managed forest considered "good" and "poor" habitat for deer hunting based on interview responses with deer hunters on Prince of Wales Island, Alaska.

Chapter 4 Individual Identification of Sitka Black-tailed Deer Using DNA from Fecal Pellets[1]

4.1 Abstract

Our goal was to develop a genetic-based tool to overcome obstacles associated with collecting basic information (e.g., population parameters) on forest-dwelling mammals when densely-vegetated environments hinder direct observation. In this paper, we test a protocol for extracting DNA from fecal pellets from Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in southeast Alaska, and evaluate genotyping performance of previously developed microsatellite markers as well as a new suite of markers designed specifically for Sitka black-tailed deer. We screened 30 microsatellite primers, 26 markers (87%) were amplified, 20 (67%) were variable, and seven (23%) amplified consistently with low error rates and fit well into a single multiplex scheme; thus, these 7 loci were included in analysis of individual identification. DNA was extracted from 2,408 fecal-pellet samples. Of those, 1,240 (52%) were genotyped successfully at all 7 markers allowing identification of 634 genetically unique deer. Using DNA extracted from fecal pellets collected in the field was an effective technique for identifying and distinguishing among individual Sitka black-tailed deer. Our findings suggest that non-invasive investigations of ungulate population parameters may be possible using fecal

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DNA without reference data. To our knowledge, this is the first landscape-scale field study to identify unique deer using fecal DNA.

4.2 Introduction

Densely vegetated environments often hinder the collection of basic information (e.g., population parameters, behavior) on forest-dwelling mammals. In Alaska, nearly the entire southeastern panhandle of the state is a temperate, coastal rainforest containing landscape characteristics (e.g., remote areas, thick vegetation) that challenge fine-scale monitoring of wild game populations. The most important terrestrial game species in southeast Alaska is the Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) (Kruse and Frazier 1988; Turek et al. 1998; Alaska Department of Fish and Game 2001; Mazza 2003), yet wildlife agencies lack reliable estimates of deer abundance. Traditional strategies such as aerial surveys are not effective because of closed forest canopies, and ground-sampling techniques (e.g., live capture, road-side counts) do not yield sample sizes sufficient to extrapolate to population or landscape scales. Because the environment in southeast Alaska prevents sufficient sampling via direct observation of deer, we sought non-invasive methods to answer key population questions.

One of our goals was to develop a genetic-based technique to identify individual deer, which could be employed by wildlife agencies in southeast Alaska and other areas where thick forests and limited access challenge researchers. In other situations where direct observation of wildlife is challenging or the research species is elusive and in low densities, non-invasive techniques have become increasingly popular (Bellemain et al. 2005; Ulizio et al. 2006; Pauli et al. 2008; Schwartz & Monfort 2008). DNA-based sampling has advanced opportunities to collect data on rare and elusive wildlife species (Waits & Paetkau 2005). Methods utilizing DNA extracted from hair, feces, and urine have expanded rapidly, allowing scientists to gather information on an animal without disturbing the animal. In this paper, we test a protocol for extracting DNA from fecal pellets and evaluate genotyping performance of previously developed microsatellite markers as well as a new suite of markers designed specifically for Sitka black-tailed deer. Because of abundance and availability of deer fecal pellets in nearly all habitat types in southeast Alaska throughout the year, we focused on designing a genetic protocol that uses DNA extracted from fecal pellets.

Sitka black-tailed deer deposit pellet groups several times per day per individual and pellets persists up to several months (Fisch 1979; Harestad & Bunnel 1987). Pellet groups are a visible and stationary indicator of animal presence and have been widely used as an indicator of animal activity and population abundance (Kirchhoff & Pitcher 1988; Campbell et al. 2004; Forsyth et al. 2007). Pellet groups deposited by Sitka black-tailed deer are easily distinguishable from feces of other species within their geographic range. If individual deer can be genotyped using feces, the abundance and ubiquity of fecal pellets across major habitat types would allow sample sizes sufficient to make inference across geographic scales and potentially facilitate dependable monitoring techniques such as capture-mark-recapture estimates of population size.

Whereas several studies have been conducted on wild carnivores using non-invasive genetic approaches (Ernest et al. 2000; Hedmark et al. 2004; Boulanger et al. 2008; Kendall et al. 2008; Williams et al. 2009), field research on wild ungulates using DNA from feces or hair has been rare (Bonnet et al. 2002, van Vliet et al. 2008). Presumably, fecal-DNA investigations of ungulates are lacking because: 1) sufficient sample sizes of tissue are available from hunters, 2) multiple species may be present in the sampling area depositing several pellet groups each day, which complicates study designs and can overwhelm genetic laboratories, 3) or other techniques such as direct observation are more efficient. With regards to Sitka black-tailed deer, Latch et al. (2008) conducted a genetic investigation using muscle tissue and hair from harvested deer but did not use feces as a source of DNA. The potential and pitfalls of using fecal DNA from ungulates to perform genetic analyses has been explored (Maudet et al. 2004; Ball et al. 2007; Valière et al. 2007). Nonetheless, Brinkman et al. (2009) documented the reliability of fecal pellets to yield correct genotypes in black-tailed deer and demonstrated that feces are a viable source of DNA. We now seek to assess the power of fecal DNA to identify individual deer. To our knowledge, this is the first landscape-scale field study to identify unique deer using fecal DNA.

4.3 Study Area

Fecal pellets of Sitka black-tailed deer were collected on Prince of Wales Island, Alaska (Fig. 4.1). Prince of Wales Island, near the south end of the southeastern pandhandle of Alaska, is the 3rd largest island in the United States. Rugged mountains extending up to 1,160 m in elevation and long fjords characterize much of the topography on the island. Habitats below 600 m are dominated by temperate coniferous rainforest consisting primarily of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) (Alaback 1982). Within a matrix of productive old-growth forest, unproductive forests on hydric soils, alpine meadows, and open-muskeg heaths, industrial logging has created clearcuts which are present in various successional stages from 0-60 years of age. Understory vegetation was thick in most forested stands and clearcuts with the exception of seral forest >25 years post logging. Annual precipitation varies from 130 to 400 cm, and mean monthly temperature ranges from 1°C in January to 13°C in July. Most of Prince of Wales Island is within the Tongass National Forest, which is administered by the USDA Forest Service. Reliable estimates of deer density do not exist; however, deer occupy all habitat types and are considered abundant.

4.4 Methods

During Spring 2006-2008, 4-6 fecal pellets were collected from pellet groups (assemblage of pellets from a single deposition) encountered on deer trails in three watersheds on Prince of Wales Island in southeast Alaska. To avoid excessive DNA degradation from ambient conditions and to maximize DNA recovery (Murphy et. al 2007, Brinkman et al. 2009), pellets were collected from the ground within 10 days of deposition, preserved in plastic conical tubes filled with 95% ethanol so all pellets were submerged, and stored at room temperature until DNA was extracted. We were able to assume that pellets were collected ≤10 days of deposition because the sampling area was cleared of all pellet groups approximately 10 days before each sampling occasion. During collection, pellet samples were classified based on appearance as: good, average, or poor. "Good" pellet samples were those collected from what was qualitatively assessed as a freshly deposited pellet group (i.e., clumped distribution with individual pellets intact, pellets contained a smooth surface with a glossy sheen, and/or had a detectable layer of mucus on the exterior). "Average" pellet samples were collected from what appeared to be a slightly older or more weathered pellet group which still had intact individual pellets with smooth surfaces, but that lacked a tightly clumped distribution, glossy sheen, and mucus. "Poor" pellet samples were collected from spread-out groups with rough-surfaced pellets which were often showing signs of decomposition. Early experimentation after the 2006 field season revealed that all "poor" samples consistently failed to amplify and were excluded from further analysis, and were not collected during 2007 and 2008 field seasons. All samples were transported to the Wildlife Conservation Genetics laboratory at the University of Alaska Fairbanks.

We extracted genomic DNA from deer fecal pellets using the DNeasy Tissue Kit (Qiagen Inc. Valencia, CA), with slight modifications. During 2006 and 2007, we used the DNeasy Tissue Kit and a protocol described by Maudet et al. (2004) with the following modifications: we performed lysis of single fecal pellets in 25 ml scintillation vials on a rocker at room temperature for 20 min using 900 µl of lysis washing buffer. During 2008, we used the DNeasy Tissue Kit lysis buffer (ATL) instead of the lysis solution described by Maudet et al. (2004). Also during 2008, we placed two pellets each in 25ml scintillation vials on a rocker at room temperature for 1 hr using 800µl of Qiagen ATL lysis solution. We adjusted agitation during the pellet wash to thoroughly wash off intestinal mucosal cells that coated the exterior of the pellet without breaking apart the pellet.

We screened microsatellite primers for variability and suitability for use with DNA from deer pellets. Previous research indicated that primers designed for bovine, ovine, or caprine microsatellite loci successfully amplified microsatellite loci for cervids (Engel et al. 1996); however, amplification and polymorphism across species doesn’t equate to adequate amplification using DNA extracted from feces, which is often lower in quality and quantity (Waits and Paetkau 2005; Ball et al. 2007). Problems associated with fecal DNA include contamination by microorganisms or undigested food items, sensitivity to seasonal weather, high PCR-inhibitor to DNA ratios, and relatively high amplification and genotyping errors (Murphy et al. 2003; Maudet et al. 2004; Buchan et al. 2005; Brinkman et al. 2009). A marker to be used on non-invasively collected samples must meet size constraints imposed by degraded DNA templates (Sefc et al. 2003; Brinkman and Hundertmark 2009). DNA amplification of longer (>300bp) fragments is problematic because of high amplification failure and allelic dropout (Sefc et al. 2003; Buchan et al. 2005). Primers that amplified shorter fragments and fostered multiplex approaches were favored to optimize chances of genotyping success on degraded DNA, and to save time and reduce costs.

PCR was conducted in 10-µl reaction volumes using Qiagen Multiplex Master Mix® (Qiagen, Valencia, CA) according to manufacturer's instructions. Optimum thermal profile began with an initial 15-min 95°C denaturing step, followed by 45 cycles of 94°C (1 min), 61°C (1 min 30 s) and 72°C (1 min) followed by a 30-min elongation step at 60°C. Premixed samples were prepared in 96-well plates using 1 µl PCR product, 9.5 µl formamide, and 0.5 µl size standard (LIZ 500™ [Applied Biosystems, Foster City, California]). Premixed samples were heat-denatured at 94°C for 3 min and flash cooled on ice for 5 min. Plates were submitted to the Core Facility for Nucleic Acid Analysis at University of Alaska Fairbanks for microsatellite fragment analysis, and run on an ABI 3100 Genetic Analyzer (Applied Biosystems, Foster City, California).

A rigorous protocol was followed to prevent, mitigate, and report genotyping errors. Because deer were never observed or handled, tissue (e.g., muscle) or blood sample references were not available to compare with DNA extracted from fecal pellets. Therefore, our error checking protocol included the "multi-tube" approach, where DNA samples were analyzed multiple times to ensure precision (Taberlet et al. 1996; Bellemain et al. 2005). Markers were scored using GeneMapper 3.7 software® (Applied Biosystems, Foster City, California). As recommended by DeWoody et al (2006), automated and manual allele-calling of each individual sample was performed. After initial scoring, we used the computer program MICRO-CHECKER (van Oosterhout et al. 2004) to detect samples likely containing genotyping errors (scoring, stuttering, null alleles, and dropout). Error checking was performed by watershed to meet assumptions of Hardy-Weinberg Equilibrium. Markers that were monomorphic or that had high error rates and weak amplification were excluded from identity analysis. For markers used to identify unique deer, we reported errors per reaction, summarized for each locus and over all loci (Hoffman and Amos 2005). We assessed overall genotyping repeatability by re-amplifying and re-genotyping a subset (30%) of successfully-genotyped samples, and to estimate error rates and amplification failure rates.

Descriptive statistics of the genetic variability of the pellet samples were calculated using GENALEX (Paekall & Smouse 2006) including mean number of alleles per locus, probability of identity (PID), and probability of identity given siblings (PIDSIB). PID is the probability of two randomly chosen deer in the Prince of Wales Island population having identical genotypes, whereas PIDSIB is the probability of two siblings drawn from the Prince of Wales Island population having identical genotypes. In general, we want PID to be less than 0.001 and PIDSIB to be less than 0.05 (Schwartz & Monfort 2008).

4.5 Results

We screened 30 microsatellite primers, 7 of which were newly designed (Genetic Identification Services, Chatsworth, California) specifically for Sitka black-tailed deer (Table 4.1). Twenty-six markers (87%) were amplified, 20 (67%) were variable, and seven (23%) amplified consistently with low error rates and fit well into a single multiplex scheme; thus, those seven loci were included in analysis of individual identification (Tables 4.1, 4.2). PCR reactions contained altered concentrations of each primer set to achieve optimum allelic peaks and minimize amplification noise and stuttering (Table 4.2).

During 2006-2008, DNA was extracted from 2,408 fecal-pellet samples (Table 4.3). At least 1 marker amplified PCR products from all samples, and 1,240 (52%) were genotyped successfully at all 7 markers. Genotyping success during 2008 (87%) was roughly double that of 2006 (41%) and 2007 (50%). Pooling all years, success rates of pellet samples classified as “good” (66%) was double that of pellets samples classified as “average” (33%) during collection (Table 4.3). The highest amplification efficiency was 91%, observed in “good” pellets in 2008 after we altered our extraction method. We found no evidence of scoring error due to stuttering and no evidence for large-allele dropout. When all years were grouped, evidence for null alleles was present at locus T7 in one watershed and T159S in one watershed due to an excess of homozygotes.

However, this problem was assumed to be minor because we found no evidence of null alleles at these loci in the other watersheds or when years were analyzed separately.

A total of 634 genetically unique deer were identified, revealing that 832 samples were from deer that we genotyped on ≥2 separate occasions and 402 samples were from deer genotyped once. Probability of identity for the population was 0.0003, and the probability of two siblings drawn from the Prince of Wales Island population having identical genotypes was 0.021 (Table 4.4). Of 382 samples re-amplified for error checking, 10% contained ≥1 error with a mean of 0.2 (SE = 0.040) errors per reaction. Summarized by individual loci, error rates per reaction did not exceed 5% (Table 4.4). Nine reactions (2.3%) failed to amplify at ≥1 locus, and amplification failure rate by individual locus did not exceed 1%, varying between 0.2% and 0.8% (n = 7).

4.6 Discussion

Using DNA extracted from fecal pellets collected in the field was an effective technique for identifying and distinguishing among individual Sitka black-tailed deer. Our findings suggest that field investigations of ungulate population parameters may be possible using fecal DNA without reference data. While only 23% of the microsatellites screened were determined to be adequate for inclusion in analysis of individual identification, these markers worked well in a single multiplex reaction and our error rates (10%) rival other non-invasive studies (Hedmark et al. 2004 [12%]; Pilot et al. 2007 [16%]). Despite low levels of polymorphism, we were able to achieve an acceptable probability of identity (Schwartz & Monfort 2008). Adding a locus for gender determination of Sitka black-tailed deer (Brinkman and Hundertmark 2009) would increase the discriminatory power of our suite of loci by up to 2×, depending on the sex ratio.

Other polymorphic primers we screened that were not included in analysis of individual identification may be used with higher-quality DNA (i.e., extracted from blood or tissue), or if single multiplex approach is abandoned. We did not test feasibility under different circumstances because that would require us to abandon our underlying objective of creating an effective field protocol (compromise between data quality and cost of obtaining it [Kendall et al. 2008]) that utilizes ungulate feces.

By the final year of our study, genotyping success (87%) was comparable to other non-invasive wildlife investigations (Hedmark et al. 2004 [65%]; Belant et al. 2007 [75%]; Kendall et al. 2008 [74%]) and likely was influenced by extraction protocol and condition of fecal pellet at time of collection. The dramatic increase in success rate in 2008 likely was attributable to: 1) a longer pellet wash with a different lysis solution and a second pellet, 2) shortened time between DNA extraction and PCR, 3) a more experienced field crew that may have been able to identify and select less degraded pellets with more mucosal cells. Clearly, differences in genotyping success between pellet groups classified as “good” (66%) and “average” (33%) illustrates that DNA quality can be assessed in the field.

Successful individual identification of Sitka black-tailed deer using DNA from fecal pellets provides wildlife managers with a new tool to monitor populations. Specifically, this technique may enable mark-recapture studies that can estimate key population parameters such as abundance and survival (White & Burnham 1999). This opportunity is particularly valuable because reliable estimates of population size for Sitka black-tailed deer have never been available. In addition, DNA-based identification from fecal pellets potentially will allow researchers to advance understanding of social structure, paternity, kinship, sex ratios, gene flow and phylogeography (Kohn & Wayne 1997), all of which are poorly understood for Sitka black-tailed deer.

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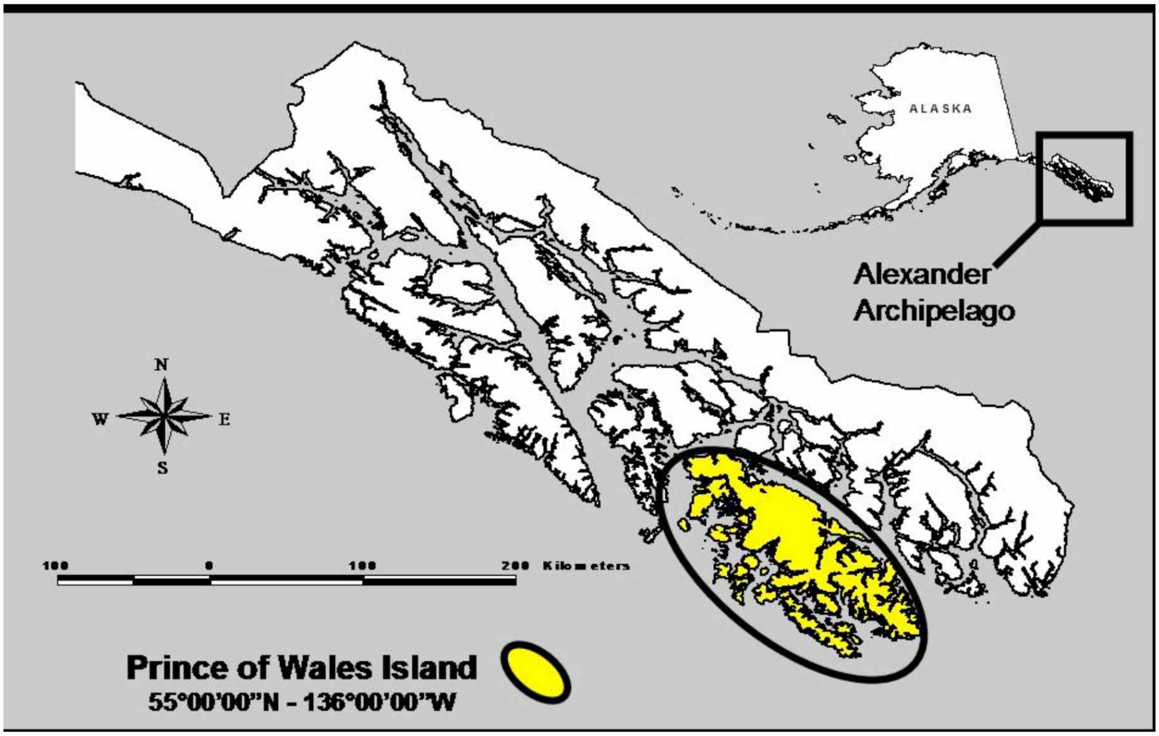

Figure 4.1. Location of Prince of Wales Island, Alaska.

Table 4.1. Description and performance of 30 microsatellite loci screened for use to identify individual Sitka black-tailed deer.

Locus	GenBank accession no.	Used for Individual Identification	*N*	Amplify?	Variable in SBTD?	Size (bp)	Number of Alleles
C89[a]	AF102247	Y	2408	Y	Y	161-169	2
SBTD06[j]	FJ986212	Y	2408	Y	Y	176-188	3
SBTD04[j]	FJ986215	Y	2408	Y	Y	238-302	8
SBTD05[j]	FJ986216	Y	2408	Y	Y	110-130	3
SBTD07[j]	FJ986214	Y	2408	Y	Y	177-197	5
T159S[a]	AF102245	Y	2408	Y	Y	195-211	4
T7[a]	AF102240	Y	2408	Y	Y	219-227	2
C106[a]	AF102243	N	2032	Y	Y	289-297	3
T27[a]	AF102244	N	2032	Y	Y	275-287	4
RT7[b]	U90740	N	784	Y	Y	209-217	2
BL42[d]	EU009439	N	784	Y	Y	244-250	2
BM1225[d]	G18419	N	784	Y	Y	230-232	2
C217[a]	AF102242	N	784	Y	Y	192-204	2
C273[a]	AF102246	N	784	Y	Y	144-172	2
RT24[b]	U90746	N	784	Y	Y	218-234	3
SBTD02[j]	FJ986211	N	784	Y	Y	142-150	2
SBTD01[j]	FJ986210	N	784	Y	Y	121-157	2
SR-CRSP-1[e]	L22192.1	N	784	Y	Y	141-143	2
T32[a]	AF102241	N	784	Y	Y	275-283	3
Texan4[f]	L24781	N	784	Y	Y	134-136	2
BM 4107[d]	G18519	N	10	Y	N	161	NA
IDVGA55[g]	X85071	N	10	Y	N	181	NA
INRA121[h]	X71545	N	10	Y	N	205	NA
RT5[b]	U90738	N	10	Y	N	160	NA
SBTD03[j]	FJ986213	N	96	Y	N	243	NA
VH 110 (OarVH110)[i]	NW_001494486	N	10	Y	N	270	NA
BM 203[d]	G18500	N	10	N	N	NA	NA
BM 757[d]	G18473	N	10	N	N	NA	NA
TGLA53[c]	DS490633.1	N	10	N	N	NA	NA

[a]Levine et al. 2000, [b]Wilson et al. 1997, [c]Bonnet et al. 2002, [d]Bishop et al. 1994, [e]Arvelo et al. 1994, [f]Holder et al. 1994, [g]Mezzelani et al. 1995, [h]Vaiman et al. 1995, [i]Hanrahan et al. 1993, [j]This study

Table 4.2. Muliplex master mix for 7 microsatellite primers used to genotype individual Sitka black-tailed deer.

Primer (2 μM)[a]	Dye color	Forward (μl)	Reverse (μl)
B122	6-FAM™ (blue)	10	10
C89	NED™ (yellow)	5	5
SDD104	6-FAM™ (blue)	15	15
SDD116	NED™ (yellow)	10	10
SDD130	VIC® (green)	10	10
T159S	PET® (red)	15	15
T7	NED™ (yellow)	15	15
T27L[b]	PET® (red)	20	20
Total Primer		80	80
TE Buffer		340	
Total Mix		500	

[a]Initial primer concentration

[b]Withdrawn from individual-identification analysis because of high error rates.

Table 4.3. Descriptive statistics of genotyping success using DNA extracted from fecal pellets deposited by Sitka black-tailed deer. “Average” and “Good” represent physical appearance of fecal pellets as classified by field researchers at time of collection.

	Samples tested			Samples genotyped			Success rate		
Year	Average	Good	All	Average	Good	All	Average	Good	All
2006	492	616	1,108	124	327	451	0.25	0.53	0.41
2007	465	459	924	160	302	462	0.34	0.66	0.50
2008	77	299	376	55	272	327	0.71	0.91	0.87
Total	1034	1374	2,408	339	901	1,240	0.33	0.66	0.51

Table 4.4. Descriptive statistics of the 7 variable microsatellites used for individual identification. PID is the probability of identity assuming random individuals, and PID_{SIB} is the probability of identity assuming siblings, Ho is observed heterozygosity, He is expected heterozygosity, and F_{IS} is a fixation index (Fis). Mean error rate per reaction includes false alleles and dropouts.

Locus	Sample size	PI	PI_{SIB}	Mean error rate (SE) per reaction (n = 382)
C89	634	0.672	0.822	0.010 (0.005)
SDB122	634	0.376	0.596	0.026 (0.010)
SDD104	634	0.156	0.459	0.042 (0.012)
SDD116	634	0.369	0.591	0.021 (0.007)
SDD130	634	0.305	0.555	0.045 (0.012)
T159S	634	0.192	0.471	0.050 (0.012)
T7	634	0.384	0.605	0.008 (0.005)

Chapter 5 A Practical Approach for Sampling Along Animal Trails[1]

5.1 Abstract

We propose a technique for counting or sampling animal sign that allows the researcher to follow pathways created by animals. We demonstrate our method by applying it to fecal pellet count surveys for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in southeast Alaska. In theory, sampling efficiency will be higher along animal trails compared to straight-line transects as long as trail density does not exceed 0.5 m^2 of animal trail/m^2 of study area, and animals deposit ≥50% of their sign on trails. In our field evaluation, sampling efficiency using animal-trail transects was 48% higher than using straight-line transects. Our technique may be particularly useful when using mark-recapture techniques and when unsurpassable landscape features (e.g., thick vegetation, debris, steep topography) prevent the establishment of straight-line transects.

5.2 Introduction

Researchers frequently use straight-line transects and grids when attempting to estimate animal abundance using tracks, feces, or mark-recapture methods. Nonetheless, terrestrial animals seldom travel through landscapes in straight-line paths (Nelson et al. 2004; Wiens 2001), so why do biologists collect data on animal activities using those approaches? In theory, randomly selected straight-line transects or systematically arranged grids reduce sampling bias by incorporating a sampling design that is independent of the distribution of the objects being sampled (Burnham et al. 1980, Krebs

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1998, Garton et al. 2005). They also facilitate representative and repeatable sampling. However, if indirect measures such as animal sign are the sampling units, those approaches may suffer from low rates at which sign is encountered and reduced power to detect changes, particularly when animal density is low. Sampling from animal trails rather than straight-line transects can dramatically increase rates at which sign is encountered because all sampling is done at locations where the majority of sign is deposited. Maximizing rates of encounter may enhance sampling efficiency, which often is an important consideration because of limited budgets and geographic scope of sampling. Mark-recapture methods may benefit from increased encounter rates particularly those involving DNA-based estimators. Straight-line transects can also suffer from serious logistical disadvantages. For instance, a random straight-line path may be difficult or impossible to survey in thick forest or landscapes with rugged terrain. Under those circumstances animal trails may be far easier to travel on foot than straight-line transects (Karanth and Sunquist 1992, Walsh and White 1999, Hiby and Krishna 2001). Further, vegetation on trails often is beaten down or eliminated by animal use making it easier to detect animal sign.

Sampling animal paths traditionally has been discouraged because: 1) defining and recognizing paths may be difficult or subjective making it difficult to repeat over time, 2) trail selection and sampling may not be random, and 3) animal use of trails may depend on individual animal preferences, population density, habitat selection, and season, confounding homogenous capture-recapture probabilities. We propose and test an adaptive sampling design for collecting data along animal trails that addresses objections 1–2, and we suggest a sampling strategy that addresses objection 3. We conducted field trials that involved surveys of fecal pellet groups from Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) located on Prince of Wales Island in Southeast Alaska. We simultaneously employed our path sampling protocol and straight-line transect sampling and compared rates of encounter between the two methods.

5.3 Study Area

Our field trials were located on Prince of Wales Island (~ 55° 00' 00"N - 136° 00' 00" W) in the southern portion of the southeast panhandle of Alaska (Fig. 5.1). Rugged mountains extend to 1,160 m in elevation with habitats <600 m dominated by temperate coniferous rainforest consisting primarily of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and yellow cedar (*Chamaecyparis nootkatensis*) (Alaback 1982). Annual precipitation varies from 130 to 400 cm and mean monthly temperatures range from 1° C in January to 13° C in July. Study sites were located in 4 watersheds within the north-central portion of the island to field test our sampling protocol: 1) Maybeso Creek, 2) Upper Staney Creek, 3) Upper Steelhead Creek, and 4) Snakey Lakes. Each study site contained a matrix of productive old-growth forest, unproductive forests on hydric soils, clearcuts at various successional stages, and open muskeg heaths. Estimates of deer density are lacking; however, deer were considered relatively abundant (~10 deer/km^2) at all study sites. Deer activity was mostly concentrated in younger-aged clearcuts and productive old-growth forests. Understory vegetation was thick in most forested stands and clearcuts with the exception of seral forest >25 years post logging.

5.4 Methods

We selected random starting points and assigned a bearing that would allow us to remain within the habitat patch of interest. Similar to a straight-line transect, we traveled in the direction of a predefined bearing (e.g., 45°) from the starting point until an evident animal trail was encountered. We followed the trail in the direction that most closely aligned with the predefined bearing until another trail was encountered. If another trail intersected the trail being surveyed, we used a compass to determine which trail better corresponded to the direction of the predefined bearing (45°) and continued surveying along that trail. If the trail ended or an animal trail could no longer be identified, we followed a straight-line path in the initial bearing direction (45°) until another animal trail was encountered and repeated the process. We did not follow an animal trail that traveled in a direction more than ±90° of the predefined bearing. This prevents the sampler from looping around to previously surveyed trails. Those 4 rules are the key components of our new design.

Key assumptions associated with our protocol were that animals deposited the majority of their sign on trails, and the area of animal trails within landscapes was <50% of the total land area. If those assumptions are met, encounters with animal sign on trails should be greater than encounters off deer trails. To examine these assumption, sampling efficiency (sampling units encountered per unit area surveyed) between straight-line transects and animal trail transects can be calculated using a simple equation that incorporates proportion of area covered by trails (PAT) and pellet density rates on trails (PDT):

We input hypothetical values into the equation to calculate differences in sampling efficiency between sampling along animal trails and using straight-line transects for various combinations of PDT and PAT. We let PDT equal 0.25, 0.50, and 0.75, and then varied PAT from 0.0-1.0 in increments of 0.10. We then let PAT equal 0.25, 0.50, 0.75 and then varied PDT from 0.0-1.0 in increments of 0.10.

During spring 2007, we field-tested our key assumptions by randomly establishing 6-8 100-m^2 square plots in each study site (27 total) in old-growth forest to estimate proportion of area covered by trails (PAT) and pellet density rates on trails (PDT). We estimated PAT by measuring length (m) of trail within each plot and assigning 0.5-m buffer to each side of the center of the animal trail, which represented the pellet detection area. We estimated PDT (pellet density on trails) by counting the number of pellet groups on the trails within the plot and dividing by the total number of pellet groups within the plot. We then used those estimates to calculate sampling efficiency using our equation.

We compared sampling efficiency of transects that follow a straight line with our technique within the field. Twenty-six transects (13 animal trail, 13 straight-line) were located in productive old-growth forest, which is critical habitat type for deer survival during winters with high snow accumulation (Wallmo and Schoen 1980). Only old-growth forest was selected because traditional straight-line transects have occurred only in this habitat type because it is thought to be a good indicator of overwinter deposition (Kirchhoff 1990). During early May 2007, these transects were surveyed within the same week. Both straight-line and animal-trail transects had the same starting points and followed the same compass bearings. Transects were designed to survey the same area and conducted during the same time period. Observers were trained to recognize a deer trail as a path that contained the following: 1) deer sign (pellets, hair, tracks, or rubs), 2) ground worn or disturbed in a linear direction without obstacles that could serve as barrier (e.g., large boulder, excessive debris) to movement of a deer. We understand that several different species use the same trail; therefore, we define a deer trail as an animal trail used by a deer. A surveyor's string line (Forestry Suppliers, Inc., Jackson, MS) was used to measure length sampled using the animal-trail method. We used florescent ribbon to mark animal trail surveyed. We tied ribbon to tree branches approximately every 5 m of trail and near all deer-trail intersections to help indicate which trail was surveyed. Following Kirchhoff and Pitcher (1988), a 20-m cord was used to measure length sampled using straight-line transects. Using a cord allowed researchers to follow a straighter line through thick forest and prevented tangling. Sampling area was 0.5 m on each side of the center of the animal trail, and 0.5 m on each side of the cord for the straight-line transects. Number of pellet groups encountered was recorded approximately every 20 m of transect and summed at the end of the transect. Although distance sampled using each sampling method was not significantly different, we standardized by calculating density. Pellet density for each transect was calculated by dividing the total number of pellet groups encountered by the total area surveyed. Because transects we surveyed had prescribed widths, they could be defined as strip rather than line transects (Seber 1982).

To test the ability of researchers to sample the same area using the deer-trail method in subsequent surveys, we re-sampled 3 deer-trail transects in 3 different study sites (9 transects total) 2 weeks later and again approximately 1 year later to test repeatability (i.e., field investigators ability to re-sample the exact same area previously sampled). We quantified repeatability by calculating the length (m) of a previously established deer-trail transect that was correctly re-sampled during a subsequent survey. Field investigators conducting subsequent surveys sampled deer-trail transects that they had not sampled previously. Field investigators responsible for establishing and marking the original deer-trail transect monitored field investigators during subsequent surveys and recorded length (m) of transect correctly re-sampled.

Student's *t* and chi-squared tests were used to compare differences ($\alpha = 0.05$) in encounter rates with pellet groups between sampling methods and among study sites using the computer program SPSS 12.0.1 (SPSS Inc., Chicago, Illinois).

5.5 Results

Results from our equation indicated that sampling along animal trails would be more efficient than straight-line transects if the proportion of area covered by trails (PAT) <0.5 m^2 and the pellet density on trails (PDT) >0.5 (Fig. 5.2). Predicted sampling efficiency was greater using animal trails when PAT was >0.5 if PDT also was >0.75 (Fig. 5.2).

Mean PAT within plots was 0.31 m animal trail/m^2 area surveyed ($n = 27$, SE = 0.01). We counted a mean of 7.1 ($n = 27$, SE = 1.2) pellet groups within each plot. Our mean PDT was 67.7% ($n = 27$, SE = 0.04). Trail density ($\chi^2_3 = 3.664$, $P = 0.300$), and pellet deposition on trails ($\chi^2_3 = 5.330$, $P = 0.149$) were similar among old-growth forest patches across study sites.

Based on our equation, we predicted that 119% more pellet groups would be encountered sampling along animal trails compared to sampling using straight-line transects. Based on our observed PDT and PAT, a 1 km transect (sample area 1000 m^2) following a straight-line would encounter 71 pellet groups and a transect similar in length following an animal trail would encounter 157 pellet groups.

Combining all transects, encounter rates using animal-trail transects was 48% greater ($t_{24} = -2.104$, $P = 0.046$) than using straight-line transects (Table 5.1). Sampling efficiencies were similar among study areas for straight-line transects ($\chi^2_3 = 5.093$, $P = 0.165$) and animal-trail transects ($\chi^2_3 = 6.110$, $P = 0.106$). Typically, animal-trail transects with the same starting point and approximately the same ending point as straight-line transects surveyed about 15% more area.

When marked deer-trail transects were re-sampled 2 weeks later by a new field investigator, repeatability (length of transect correctly re-sampled / total length of transect) was 99.4% ($n = 9$, SE = 0.00). When transects were re-sampled 1 year later, mean repeatability was 96.7% ($n = 9$, SE = 0.01).

5.6 Discussion

Sampling along animal trails has rarely received consideration. Hiby and Krishna (2001) proposed a method that simply follows the path of least resistance and uses distance sampling (Buckland et al. 1993) to estimate animal density. To our knowledge, this was the only study that utilized animal trails. Animal-trail sampling has largely been ignored because of our previously stated objections.

Sampling animal paths traditionally has been discouraged because defining and recognizing paths may be difficult or subjective, thus hindering repeatability. Using our method, we overcame this problem by establishing a specific definition of a deer path and requiring all observers to follow these criteria. Rules defining a trail should be made on a species-by-species or case-by-case basis. Because of the importance of evident trails, our method may only be applicable to larger animals. If questions arose concerning trail recognition and transect establishment, repeatability could be tested using double-blind trials of the same animal-trail transect.

After deer trails were selected for sampling, proper marking of trails (particularly where trails intersect, split, or end) during sampling allowed high repeatability (≥97%) in subsequent surveys of the same deer-trail transect. Sampling repeatability after 1 year was slightly lower (~2%) than after 2 weeks mainly because of disturbance to forest structure by harsh weather in between sampling events. A natural wind event (common in southeast Alaska [Nowacki and Kramer 1998]) uprooted and toppled patches of trees in 2 study sites covering previously established transects and trail markers. Using the 4 key rules of our sampling approach, we adaptively adjusted our transect through the fallen trees and thick debris (just as a deer may adjust its path).

A second objection is that animal-trail selection and sampling may not be random. Buckland et al. (1993) noted that the serious problem associated with following paths or trails was the lack of a random design. Our method is no less random than a straight-line transect. Similar to a straight-line transect, we have a random starting point with systematic sampling. Using a compass to select trails to be surveyed rather than the sampler is the fundamental aspect of our technique that minimizes subjectivity of trail selection.

Lack of a random design may result in difficulties when trying to extrapolate the density estimate on the trail system to the whole study area because of inconsistent selection or avoidance of the trail by the focal species (Burnham et al. 1980). This problem relates to another objection, which is that animal use of trails may depend on individual animal preferences, population density, habitat selection, and season confounding homogenous capture-recapture probabilities. If the trail network and pellet deposition on trails is uniformly distributed within a habitat type (as evident in our field experiment), then estimates may be extrapolated across the patch. Designing transects to sample each habitat type in proportion to the amount of each habitat type within the study area can overcome problems associated with adequate representation of available habitat. An important factor to consider is that in some habitats, the use or avoidance of trail systems may be inconsistent and pellet deposition may not be uniformly distributed. In this case, either a correction factor must be developed by determining the relation between encounter rates, trail density, and absolute animal numbers within each habitat type, or encounter rates should simply not be compared between habitat types. Rather, encounter rates would produce an estimate of relative density. When patch sizes are large (equal or greater than the animals home range) or habitat selection by the focal species is known a priori, problems with representative sampling in regards to habitat should be minor.

In general, if most of the area is not animal trail, and animals deposit the majority of their pellet groups on their trail system, then sampling along animal trails would focus field effort on areas within the landscape with the highest likelihood of containing pellet groups. Following animal trails resulted in 48% higher encounter rates compared to sampling along straight-line transects. However, sampling efficiency was not as high as we predicted using our equation (119%). We believe that this difference was because straight-line transects are seldom perfectly straight, especially within our field environment, and unintentionally may follow animal trails more than assumed. Sampling was conducted in a thick forest where large old-growth trees greater than 2 meters in diameter are common. Observers were often unable to see 50 m in a straight-line and it was nearly impossible to walk a straight line for that distance. Southeast Alaska is also prone to frequent disturbance to forest structure from wind events (Nowacki and Kramer 1998) resulting in many deadfall trees that are impossible to travel over or under in a straight-line path. Further, the rugged terrain contains loose and steep slopes that are not safe to climb in a straight-line path. Therefore, field crewmembers must slightly alter their path (just as a deer might) to traverse over or around obstacles. While a crewmember is walking around a large tree or crawling through an opening between branches of a deadfall, the likelihood that a straight-line transect follows an animal trail increases and the assumption the straight-line path is random and avoids any human bias in selection is violated. As straight-line paths increasingly cross animal trails, the difference between encounter rates would be expected to lower.

Another explanation for a lower sampling efficiency of animal trails in the field compared to efficiency predicted was because our equation assumed the sampler is surveying animal trail 100% of the time. In the field, trails ended or looped around occasionally which resulted in samplers surveying off of animal trails and following a straight-line path when rules specify.

As hinted above, following animal trails had logistical and safety advantages. Two field researchers were needed to insure that an exact bearing was followed during the straight-line transects, whereas only 1 field researcher was needed to sample a transect following animal trails. Because animal trails in a forest are worn and open relative to the rest of the matrix, detection error may be lowered due to increased visibility of the forest floor. Kirchoff (1990) estimated a detection error of approximately 15% when counting pellet-groups of Sitka black-tailed deer in southeast Alaska using straight-line transects. Kirchhoff (1990) presumed that the amount of light and degree of visibility controlled by vegetation structure mainly influenced error rates in addition to crew experience, ambition, and concentration. Hiby and Krishna (2001) noted that animal trails are often the path of least resistance. This physical quality may result in elevated crew concentration by alleviating frustration experienced by crew members when attempting to maintain a straight-line transect which penetrates dense understory or requires the scaling of obstacles that push the limits of safety.

Animal trails that we surveyed along a predefined bearing usually stayed within 50 m of straight-line path over a 500 m transect. This was likely due to the high density of trails encountered, which allowed selection of trails within ±10 degrees of the predefined compass bearing. Further, ending points of animal-trail transects were often within 50 m of ending points of straight-line transects regardless of transect length. Animal trails selected using compass bearings seemed to "self-correct" and samplers would often cross the straight-line transect several times during sampling. Because the animal-trail method resulted in a fairly straight path relative to habitat patch size and home range of deer, using this method should allow field investigators to sample areas within a pre-determined boundary at a useful spatial scale. In areas with high densities of animal trails, researchers should be able to keep a relatively straight heading and sample habitat patches representatively. This may allow issues related to spatial patterns to be addressed ad hoc for incorporation into sampling design.

5.7 Management Implications

Because of increased encounter rates with pellet groups, using our method may increase efficiency of management plans designed to monitor population trends. For instance, sampling along animal trails may be particularly appropriate when modeling relationships between fecal density indices and deer density (Forsyth et al. 2007) or when using mark and recapture methods to estimate abundance. Mark and recapture methods (Seber 1982, Pollock et al. 1990) have rapidly become a valuable and cost effective technique for wildlife biologists, particularly estimates using DNA extracted from animal sign (Morin and Woodruff 1996, Kohn and Wayne 1997, Murphy et al. 2000, McKelvey and

Schwartz 2004). These non-intrusive methods are particularly attractive because they can be more efficient and less biased than live-trapping and can be applied over a large geographic area (Boersen et al. 2003). Ultimately sample size (capture and recapture rates and probabilities) may determine the success of these methods. Therefore, high-grade sampling toward areas with high animal activity using animal trails is beneficial, and may be particularly valuable if a level of randomness can be incorporated to test hypotheses on spatial patterns.

To determine which method (animal trail, straight-line) results in following animal density trends with greater accuracy and precision, relationships between encounter rates with sign and actual animal numbers would need to be tested. We recommend that future studies testing the potential of sampling along animal trails as a wildlife research technique address this issue.

5.8 Acknowledgments

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Table 5.1. Encounter rates with pellet groups of Sitka black-tailed deer using straight-line and animal-trail transects in old-growth forest on Prince of Wales Island, Alaska.

Study Site	Transect type	Number	Area sampled (m^2)	Pellet groups counted	Pellet group density (pellet groups/m^2 of transect)
Maybeso	Straight line	3	1,520	191	0.119 (SE=0.286)
Maybeso	Animal trail	3	1,548	341	0.216 (SE=0.060)
Snakey	Straight line	3	5,800	447	0.078 (SE=0.007)
Snakey	Animal trail	3	6,950	806	0.118 (SE=0.017)
Staney	Straight line	4	2,180	185	0.070 (SE=0.022)
Staney	Animal trail	4	2,624	275	0.097 (SE=0.017)
Steelhead	Straight line	3	1,180	162	0.137 (SE=0.007)
Steelhead	Animal trail	3	1,184	204	0.171 (SE=0.024)
All	Straight line	13	10,680	975	0.099 (SE=0.012)
All	Animal trail	13	12,306	1,626	0.146 (SE=0.019)

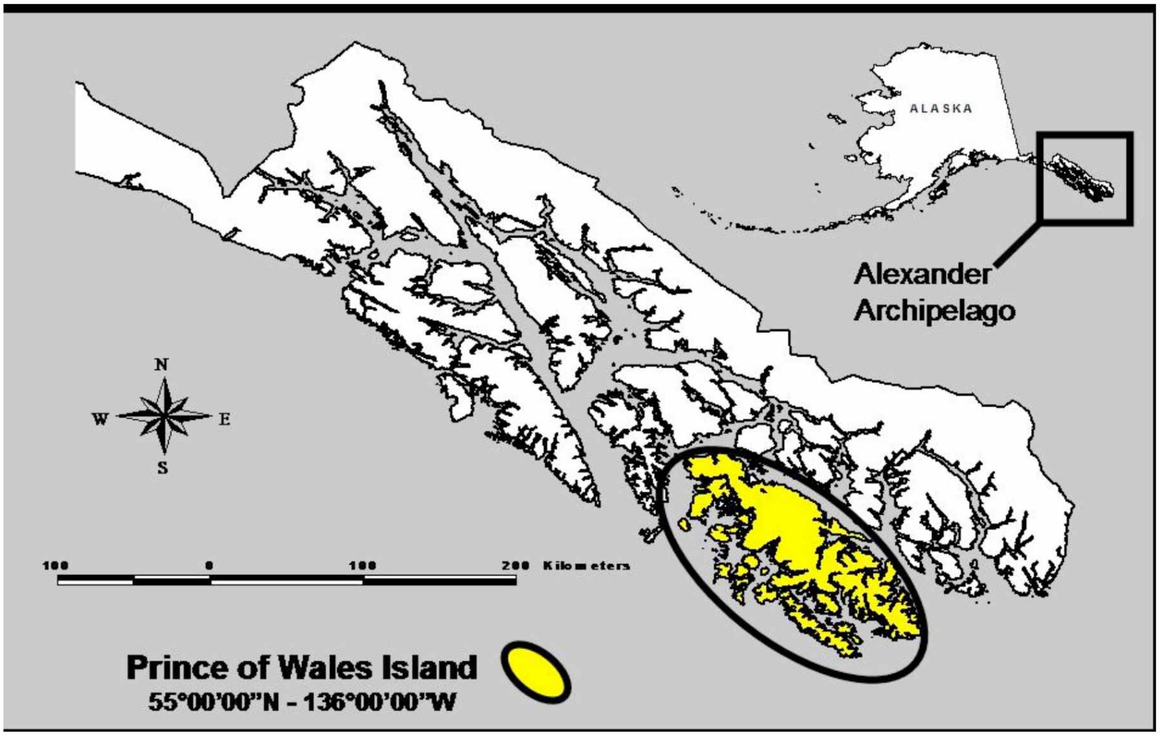

Figure 5.1. Our study was conducted on Prince of Wales Island, located in the southern panhandle of southeast Alaska.

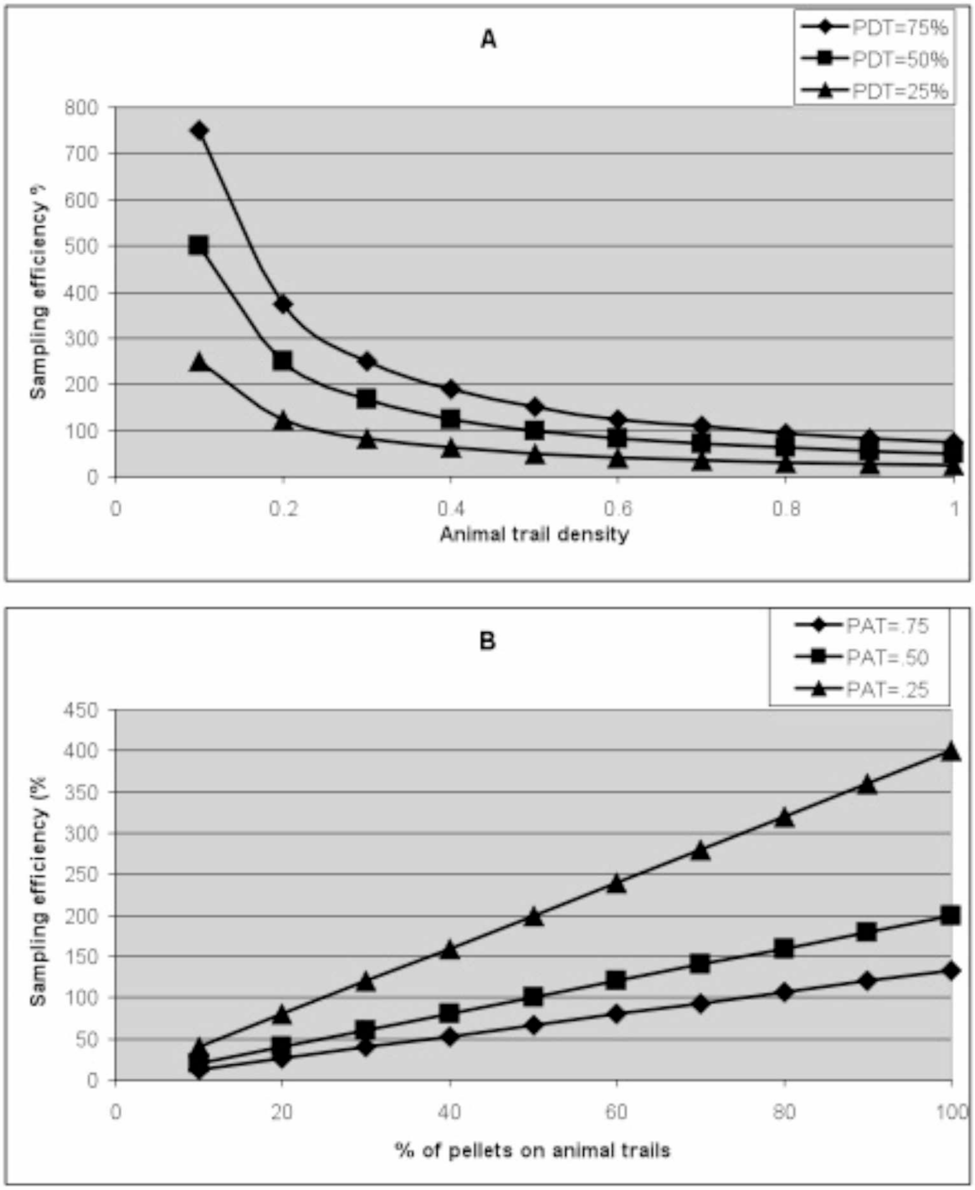

Figure 5.2. Predicted sampling efficiency using animal trails compared to using straight-line transects with: A) varying pellet deposition rates on trails (PDT), and B) varying proportion of area covered by animal trail (PAT). If sampling efficiency equals 200%, then twice as many pellet groups were encountered using animal trails than using straight-line transects.

Chapter 6 Estimating Abundance of Sitka Black-tailed Deer Using DNA from Fecal Pellets[1]

6.1 Abstract

In Southeast Alaska, wildlife managers monitor populations of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), the most important big-game species in the region, without reliable data on population size and change. Because the densely forested environment of Southeast Alaska prevents the use of direct observation methods, our objective was to develop a mark and recapture technique that used DNA from fecal pellets to estimate abundance of deer. With those estimates, we advanced understanding of how populations of Sitka black-tailed deer respond to factors (i.e., winter weather, logging) theorized to influence population change. We estimated abundance of deer with precision (±20%) in three unique watersheds, and identified a 30% decline in abundance during our 3-year study, which we attributed to 3 consecutive severe winters. We determined that deer densities in managed forest logged >30 year ago (7 deer/km^2) supported significantly fewer deer compared to both managed forest logged <30 years ago (12 deer/km^2) and unmanaged forest (12 deer/km^2). We provide the first estimates of abundance (based on individually identified deer) for Sitka black-tailed deer, and the first estimates of abundance of an ungulate species using DNA from fecal pellets. With the availability of our tool, wildlife managers in Alaska and in other densely-forested

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environments have a new opportunity to monitor deer more effectively at different spatial and temporal scales and can better anticipate changes in deer numbers owing to slow (succession of managed forest) and fast (winter weather) moving variables.

6.2 Introduction

From Africa to Alaska, densely forested environments have hindered the ability of wildlife managers and researchers to estimate and monitor populations of forest-dwelling ungulates (Ratcliffe 1987, van Vliet et al. 2008). Direct counts from aerial surveys are not feasible because many animals are hidden under forest canopies that cannot be penetrated even with infrared sensors and other advanced remote sensing technologies. Ground surveys such as road-side or spotlight counts also are often unreliable because animals are difficult to detect in forested habitat, and thus surveys often are limited to easily accessible roads or trails. Live-capture and photographic mark recapture methods usually are very expensive and limited in spatial scope. Those techniques rarely yield sample sizes sufficient to extrapolate to population and landscape-level scales. Consequently, population indices derived from fecal pellet counts have become widely used to monitor ungulate populations in forested landscapes (Putman 1984, Koster and Hart 1988, Kirchhoff and Pitcher 1988, van Vliet et al. 2008) and are sometimes employed to monitor trends at large regional scales (Kirchhoff and Pitcher 1988, Patterson and Power 2002). However, fecal counts are confounded by seasonal and weather-related variability that influence persistence of pellets in the environment, defecation rates, and detectability of pellets in different habitats. Moreover, in many circumstances, procedures to convert pellet counts to numbers of deer are based on few empirical data and rarely evaluated over time. As a result, population estimates based on pellet counts usually are imprecise and often unreliable (Neff 1968, Campbell et al. 2004, Smart et al. 2004).

During the last two decades, genetic techniques for extracting DNA from hair or feces were developed with applications for estimating abundance of animals in forested landscapes (Bellemain et al. 2005; Waits and Paetkau 2005, Ulizio et al. 2006; Pauli et al. 2008; Schwartz and Monfort 2008). Non-invasive genetic methods commonly are used to monitor forest carnivores (Boulanger et al. 2004, Ernest et al. 2000, Hedmark et al. 2004, Kendall et al. 2008, Williams et al. 2009); however, similar efforts to apply genetic methods to ungulates are rare (Belant et al. 2007, Van Vliet et al. 2008). The potential and pitfalls of using DNA from feces or hair of ungulates to genotype individuals, a necessary prerequisite of mark-recapture techniques, are described by several authors (Ball et al. 2007, Maudet et al. 2004, Valière et al. 2007). Van Vliet et al. (2008) successfully distinguished between ungulate species based on fecal DNA and Belant et al. (2007) identified individual white-tailed deer (*O. virginianus*) using DNA from hair. Nonetheless, no one has successfully estimated abundance of ungulates using fecal DNA. The abundance of fecal pellets and relative ease of sample collection are attractive properties of using pellets for DNA, particularly at landscape scales. Problems associated with fecal DNA include contamination by microorganisms or digested food items, sensitivity to seasonal weather, high PCR-inhibitor to DNA ratios, and relatively high amplification and genotyping errors (Maudet et al. 2004, Buchan et al. 2005, Murphy et al. 2007, Brinkman et al. 2009a). Wet weather conditions (typical of Southeast Alaska), also contribute to high rates of error in DNA sequenced from pellets because the genetic material is degraded by water, washed off the pellets, or pellets fully dissolve (Brinkman et al. 2009a). In addition, the sheer number of pellets deposited by ungulates (Fisch 1979, Harestad and Bunnel 1987) can swamp the processing capacity of genetic laboratories requiring carefully designed sampling criteria to reduce the number of pellets collected without introducing sampling bias.

Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) are the most widely distributed and abundant ungulates in the temperate rainforests of southeastern Alaska. Deer are the principal prey of wolves (*Canis lupus ligoni*), important prey of black bears (*Ursus americanus*) and brown bears (*Ursus arctos*), and primary sources of red meat for subsistence hunters (Kruse and Frazier 1988, Hanley 1993, Person et al. 1996, Alaska Department of Fish and Game 2001, Mazza 2003, Brinkman et al. 2007). Landscapes in Southeast Alaska are mountainous with elevations <400 m generally covered by a matrix of dense coniferous forest interspersed with open peatlands (muskeg heaths). Rock and ice interspersed with lush alpine meadows of herbaceous plants dominate landscapes above 400 m. The thick forested hillsides and lowlands complicate efforts to monitor deer populations, leaving state and federal wildlife agencies with the challenges of managing deer harvests and assessing effects on deer of land management activities, such as logging, without reliable estimates of population or local abundance. Similar to other thickly forested areas, wildlife managers use counts of fecal pellet groups to estimate population trends of deer (Kirchhoff and Pitcher 1988). However, those estimates are often too coarse to assess population size or trends at scales useful to wildlife managers, and suffer from other confounding factors that we described previously. Improving the precision and reliability of abundance estimates is an important priority for wildlife agencies responsible for managing Sitka black-tailed deer and for subsistence hunters who depend on deer as a source of food (Unit 2 Deer Planning Subcommittee 2005).

Several circumstances underscore a need for reliable estimates of deer population size in Southeast Alaska. Fifty years of industrial-scale logging significantly altered landscapes by converting old-growth forest stands into clearcuts and young-growth forests. In regions where snowfall typically exceeds 50 cm, forest stands at low elevation on southerly aspects are important winter habitat for deer. Clearcutting logging completely removes the forest canopy and its capacity to intercept snow, which during winters with snow limits availability of understory plants for forage and increases costs of locomotion. Moreover, conifer regeneration in clearcuts eventually grows into a stem-exclusion stage in which the dense, even-aged trees form a continuous canopy that prevents light from reaching the forest floor. Stem-exclusion forests usually occur 25-30 years after logging, and understory vegetation typically is very sparse (Alaback 1982). Indeed, these stands may retain <5% and <15% of the forage biomass that exists in clearcuts <20 years old and in old-growth forest stands, respectively. Those changes reputedly will cause a long-term decline in deer populations and make them more vulnerable to winter weather conditions (Wallmo and Schoen 1980, Schoen et al. 1988). In addition, following the initiation of logging and road building, hunters became accustomed to hunting deer in clearcuts near roads (Brinkman et al. 2007, 2009b). However, a collapse in markets for timber dramatically reduced new logging and, as old clearcuts develop into young-growth forest, they are no longer suitable for deer hunting. Roads that were once open to vehicle use are being closed, concentrating hunter activity in fewer areas where roads remain open and young clearcuts still exist. Consequently, wildlife managers are concerned that deer may be harvested unsustainably in many of those road-accessible watersheds. There are few reliable quantitative data concerning changes in deer abundance following timber harvest. Furthermore, without adequate methods to monitor populations it is difficult to evaluate the impact on deer of changes in patterns of hunting. Although studies were conducted to better understand the response of hunters to forest changes caused by logging (Brinkman et al. 2009b), hunter concerns about those changes cannot be effectively addressed without information on deer population trends (Unit 2 Deer Planning Subcommittee 2005).

Our objectives for this study were two-fold. First, we wanted to develop a method for estimating black-tailed deer populations using DNA extracted from fecal pellets that was reliable, flexible to local environmental conditions, and useful at varying temporal and spatial scales. This objective required both testing of several DNA protocols suitable for extracting and amplifying DNA from fecal pellets, and identification of a suite of polymorphic loci useful for identifying individual Sitka black-tailed deer. We had to develop a pellet sampling design and protocol that maximized sampling efficiency and simultaneously minimized the degrading effects of wet weather on the epithelial-cell DNA adhering to pellets. We also had to adapt accepted methods of mark-recapture analyses to our sampling design and genetic data. Our second objective was to use our estimates of population abundance to compare deer populations among 3 distinct watersheds that were composed of different proportions of old-growth forest, clearcut, and stem-exclusion forest habitats. During our 3-year study, we experienced 2 winters in which snow depth greatly exceeded 50 cm and snow cover persisted well into April and even May. Those winters afforded us an opportunity to examine the effects of winter weather on deer abundance among watersheds that differed in composition of logged and unlogged habitat. Contributions of our study include: 1) the first population estimate for an ungulate using DNA extracted from fecal pellets. 2) the first precise estimates of population abundance and density of Sitka black-tailed deer, and 3) the first direct evaluation of the effects of timber harvest on relative habitat distribution and density of deer.

6.3 Study Area

We conducted our research on Prince of Wales Island (~ 55° 00' 00"N - 136° 00' 00" W), the 3rd largest island in the United States, which was located near the south end of the southeastern panhandle of Alaska (Fig. 6.1). Most of the island is within the Tongass National Forest that is administered by the USDA Forest Service. The topography included rugged mountains extending to 1,160 m in elevation with habitats at <600 m dominated by temperate coniferous rainforest consisting primarily of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) (Alaback 1982). Annual precipitation varied from 130 to 400 cm, and mean monthly temperatures ranged from 1°C in January to 13°C in July. Between winters 1948-2008, mean annual snowfall at sea level was 115 cm (SE = 9.5) at the weather station for southern Southeast Alaska (Annette Island Weather Station: Alaska Climate Research Center 2009)

Industrial-scale timber harvest began on Prince of Wales and adjacent islands in the mid 1950s. During the past 55 years, approximately 1,800 km^2 of forest were harvested on US Forest Service, state, and private lands, which represents 20% of the total land area. Greater than 50% of productive old-growth forest on southerly aspects below 300m, considered to be critical winter habitat for deer (Wallmo and Schoen 1980), was clearcut logged. To facilitate logging, the highest density of roads in Southeast Alaska was constructed on Prince of Wales Island, which penetrated previously remote deer habitat and provided better hunter access (Brinkman et al. 2009b). At least 4,000 km of road were built on Forest Service, state, and private lands (Southeast Alaska GIS Library 2007). In the late 1990s, poor markets for timber and litigation concerning the implementation of the Tongass National Forest Land Management Plan (TLMP) severely reduced timber harvesting in southeast Alaska. During peak years (1970s), 590 million board-feet (mmb) of timber were harvested annually across southeast Alaska from the national forest, but by 2003, annual harvest had declined to <51 mmb (USDA 2007). This trend was similar on Prince of Wales Island. Timber harvest on state and private lands also declined substantially after 2003. Currently on Prince of Wales, about 2,900 km of roads are open for passenger-vehicle travel with 2,300 km under US Forest Service control. According to the Forest Service (PBS Engineering and Environmental 2005), an additional 1,500 km of roads (approximately 50% of current road network) are designated to be temporarily or permanently closed to passenger vehicle traffic over the next 10 years. Although some new road construction may occur to meet future logging needs, the figure will likely be small relative to length of roads being closed. The market for timber from Alaska is unlikely to rebound soon and may never again reach historically high levels (Morse 2000, Brackley et al. 2006).

We established study sites in the Maybeso Creek (Maybeso), upper Staney Creek (Staney), and upper Steelhead Creek (Steelhead) watersheds located within the north-central portion of Prince of Wales Island. Each study site encompassed a mosaic of productive old-growth forest, unproductive forests on hydric soils, clearcuts at various successional stages including stem-exclusion forest, and open muskeg heaths. In Maybeso, all managed stands were logged >40 years ago and were stem-exclusion forest. In Staney and Steelhead, managed forest stands were <30 years old. All study areas were within the Tongass National Forest and accessible by roads maintained for passenger-vehicle use during snow-free months. Evidence of deer was abundant in all study areas suggesting population densities were moderately high. Other mammals that occurred within the study areas included wolves, black bears, marten (*Mustela americana*), beaver (*Castor canadensis*), and several species of rodents. Winter snowfall was above the 60-year mean (115 cm) for southern southeast Alaska in all sites during our study period (2006-2008). A nearby weather station located at sea level reported snowfall of 128 cm, 187 cm, and 161 cm for 2006, 2007, and 2008, respectively (Annette Island weather station; Alaska Climate Research Center 2009). Within each study site, habitat started below 100m in elevation and extended above 500m. Snowfall, snow depth, and persistence increased with elevation.

6.4 Methods

We collected fecal pellets from our study areas at the beginning of snow melt (about 15 March) during 2006, 2007, and 2008. We continued each year to collect samples until leaf out occurred (about 15 May). Each watershed was bounded by rugged mountains with snow depths forcing deer to remain below ~300 meters during most of the period we sampled.

To maximize encounter rates with deer fecal pellets, we sampled along transects that followed deer paths rather than straight-line transects. Our path sampling strategy was described in detail by Brinkman et al. (2009c). Briefly, we positioned path transects to ensure they traversed a proportionally representative sample of habitat types in our study sites. Furthermore, transects traversed a variety of other landscape features (e.g., different slopes, elevations, aspects, and distances from roads). To optimize opportunities to collect pellets from different individual deer across our study sites, we separated transects by at least the radius of winter home ranges of deer as estimated from radiocollared deer on Prince of Wales Island (Alaska Department of Fish and Game, unpublished data). Similar to a straight-line transect or sampling grids, we had a pre-determined starting point and survey direction with systematic sampling. We traveled in the direction of a predefined bearing (e.g. 45°) from the starting point until a deer trail was encountered. If another trail intersected the trail being surveyed, we used a compass to determine which trail more closely paralleled the direction of the predefined bearing (45°) and continued surveying along that trail. We intensively marked trail transects with florescent flagging to ensure the same deer trails could be surveyed during the next sampling occasion.

Using a pre-determined compass bearing to select trails to be surveyed was the fundamental aspect of our technique that minimizes subjectivity of trail selection. Because deer trails are ubiquitous across our study sites (e.g., all different habitat types), extrapolation of estimates may be possible (Brinkman et al. 2009c). Deer path transects have several advantages over traditional straight-line transects including: higher encounter rates with pellet groups, applicability in all habitat types, better pellet-detection rates, easier travel through thickly-vegetated habitats, and greater repeatability. Fundamentally, the deer-trail transect is an adaptive-sampling technique that focuses sampling along trails where activity of deer is greater compared to randomly located straight-line transects. We demonstrated that this sampling approach was more efficient than straight-line transects and showed no sampling bias, relative to straight-line transects (Brinkman et al. 2009c).

We categorized habitats within our study areas as old-growth forest, alpine tundra, muskeg, clearcut, stem-exclusion forest, and pre-commercially thinned forest. Old-growth forest consisted of uneven-aged stands of large and old conifers undisturbed by logging. The forest canopy was dense but with many openings and patches of thick understory vegetation (e.g., *Vaccinium spp., Oplopanax horridus, Lysichiton americanum*) (Pojar 1994) were widely distributed. Alpine tundra was treeless habitat usually above 800 m that was dominated by low-growing plants adapted to snow pack and wind abrasion; this habitat was occupied by migrating deer during the snow-free months (Schoen and Kirchhoff 1990). We did not sample pellets within alpine tundra because deer do not occupy that habitat during spring. Muskeg (peatlands or heath) communities were poorly drained and sparsely forested areas dominated by ground cover of sphagnum mosses (*Sphagnum* spp.) and sedges (*Carax* spp.) (United States Department of Agriculture 2007). Clearcuts were habitats in which all overstory trees were removed by timber harvest. Conifer regeneration occurred within 5 years of logging and clearcuts <10 years old typically contained sapling stage conifers and thick growth of shrubs and herbaceous plants. After 10 years, the conifer regeneration was usually >2 m high (pole stage) and surrounded by thick understory vegetation. Clearcuts transitioned into stem-exclusion forests at about 25-30 years after harvest. Stem-exclusion forests were thick, even-aged stands of trees with depauperate understory vegetation (Alaback 1982). Pre-commercially thinned forest consisted of sapling and pole-stage clearcuts that were thinned ~10-20 years after being logged (Deal and Farr 1994). Thinned stands had sparse canopies that tended to delay their transition into stem-exclusion forest by 10-15 years. However, they also contained abundant slash from the thinning process, which may hindered movements of deer through the habitat (Farmer et al. 2006).

We resampled path transects multiple times during each annual sampling period. During the first sampling occasion of the year for each transect, we only collected pellets from groups that appeared to be recently deposited (shiny with a mucus sheen) to avoid sampling pellets from which we were unlikely to extract useful DNA. After collecting pellets, we removed all pellet groups from the sampling area during each sampling occasion. We resampled each path transect after an interval of about 10 days. Therefore, we assumed all pellet groups encountered during the next sampling occasion were deposited within that 10-day period. We determined by experimentation that the interval provided time for deposition of new pellets but was sufficiently short to ensure that most pellets would yield useable DNA (Brinkman et al. 2009a). We collected 4-6 pellets from each pellet group deposited within 1 meter from the center of the deer-trail transect; thus, we were sampling a prescribed width of 2 m (e.g., strip transect [Seber 1982]). Using a handheld Global Positioning System, we recorded time and location of each pellet group from which we sampled. Pellets were collected with sterile latex gloves, preserved in plastic conical tubes filled with 90% ethanol and stored at room temperature until DNA extraction.

We extracted genomic DNA from deer fecal pellets and performed a multiplex PCR using 7 microsatellite loci to genotype individual deer (Brinkman et al. 2009c). We followed a rigorous protocol to prevent, mitigate, and report genotyping errors. Because deer were never observed or handled, muscle, blood or other tissue sample references were not available to compare with DNA extracted from fecal pellets. Therefore, our error-checking protocol included the "multi-tube" approach, in which DNA samples were analyzed multiple times to ensure accuracy (Taberlet et al. 1996, Bellemain et al. 2005). Microsatellite marker alleles were scored using GeneMapper 3.7 software® (Applied Biosystems, Foster City, California); however, we also visually inspected each sample rather than using the automated process (as recommended by DeWoody et al. 2006). After initial scoring, we used the computer program Micro-Checker (van Oosterhout et al. 2004) to detect samples containing genotyping errors (scoring, stuttering, null alleles, and dropout). We tested assumptions of Hardy-Weinberg equilibrium in each watershed. Our estimated probability of identity (PID) calculated using GenAlex (Peakall and Smouse 2006) was 0.0003 (Brinkman et al 2009c). In general, PID should be <0.001 (Schwartz and Monfort 2008). Summarized by individual marker, error rates did not exceed 5%. Brinkman et al. (2009c) detailed the genotyping performance of these data.

To estimate population size, we used Huggins-Pledger closed mixture models (Huggins 1991, Pledger 2000) in Program MARK (White and Burnham 1999; White 2008). We assumed that populations were closed within our study site during our sampling period (15 March-15 May) because deer were not migrating, dispersing, fawning, or being legally harvested by hunters. Sitka black-tailed deer also show high site fidelity while occupying seasonal ranges (Alaska Department of Fish and Game, unpublished data). Some deer may have been killed by predators (i.e., wolves, illegal hunting) and factors related to winter weather; however, we assumed that these variables were not significant within our annual sampling periods, and did not warrant using open-population models for estimating abundance. We evaluated our assumptions of closure using Program CloseTest (Stanley and Burnham 1999), which tests the null hypothesis of a closed population model with time variation against the open-population Jolly-Seber as a specific alternative (Stanley an Burnham 1999). We tested (using α = 0.05) all sites and years independently (n = 8) and did not identify a violation of closure; however, we did not have sufficient data to test the Steelhead study site during the 2007 sampling period.

We developed encounter histories tabulated for all sampling occasions during a year for each deer in each study area. We estimated total population size as outcomes derived from the Huggins model for each year within each study site. To obtain an estimate of abundance in managed and unmanaged forest within in each study site during each year, we entered year and presence in managed or unmanaged forest within each study site as group covariates; which created 18 groups (2 habitat types × 3 years × 3 study sites). Managed forest included clearcuts, stem-exclusion forests, thinned stands and roads. Unmanaged forest combined old-growth forests, muskegs, and alpine habitat into 1 category. Although we combined unmanaged forest, canopy cover and biomass of deer forage varies among unique habitat types within managed and unmanaged forest (Hanley and McKendrick 1983, Parker et al. 1999). Also, risk of mortality among individual deer varies among unique habitat types within managed and unmanaged forest (Farmer et al. 2006). However, sampling design and sample size did not allow analysis of unique habitat types within each general category of forest. Because snow forced deer below 300 m during our field season, we did not survey alpine tundra for pellets. However, alpine habitat provides abundant high-quality forage during summer and early autumn. Consequently, alpine tundra may have an important influence on the density of deer in a watershed.

We constructed biologically plausible models a priori, which included time variation (*t*), linear-trend time variation (T), varying capture probability during 1st capture occasion (time 1), and a habitat covariate which represented capture histories for deer located in managed or unmanaged forest. We included time variation to incorporate differences in capture probabilities between sampling occasions within years. We included linear-trend time variation to incorporate a potential increase in capture probability with each subsequent capture occasion within sampling period. Because we sampled during late winter and early spring, a time period in which forage intake of deer may increase with green up of vegetation, we hypothesized that pellet deposition by deer would increase, elevating capture opportunities. We incorporated differences in capture probability during 1st capture occasion because we predicted that over-winter deposition and persistence of pellet groups on sampling transects may inflate captures during our first sampling occasion. Because previous investigators have speculated that managed forest (particularly older stands of managed forest) may support fewer deer, we anticipated lower encounter rates with fecal pellets in managed forest versus unmanaged; that is, capture probabilities varied by habitat type. Also, a habitat covariate allowed us to model differences in capture probabilities during each sampling occasion in young-managed (logged ≤30 year ago) and old-managed forest (logged >30 years ago) separately because each study site mainly contained only one age class. For example, adding the habitat covariate to rows within the design matrix of Program MARK that correspond to Maybeso capture probabilities allowed us to incorporate differences between old-managed and unmanaged forest. Similarly, adding the individual covariate to rows corresponding to Staney or Steelhead study sites allowed us to incorporate differences in young-managed and unmanaged forest. We assumed that behavioral response of deer to our sampling strategy was minimal because we were using a non-invasive approach that resulted in no direct disturbance to deer and minimal indirect disturbance to deer from our presence on path transects every 10 days.

We used Akaike's Information Criterion (AIC) and AIC weights to evaluate relative support for each candidate models. We considered the model with the lowest AIC score as the model that best balanced bias and precision (Burnham and Anderson 2002). We used changes in AIC values to compare models. Within program MARK, we averaged population estimates (with unconditional standard errors) based on their support by the data as estimated by AIC weights to further account for model selection uncertainty (Burnham and Anderson 2002).

Abundance estimates suffer from an unknown bias due to boundary effects that vary with transect layout and home range size (Efford et al. 2004). Locations of our sampling transects did not allow for density to be calculated using maximum likelihood or inverse prediction methods (program DENSITY [Efford et al. 2004; http://www.otago.ac.nz/density]). Our sampling transects were placed irregularly within study sites with regards to spacing and density. We did this to allow representative sampling of all habitat types. However, varying distances between transects did not create opportunities for recaptures along a continuum of distances in all directions. Nonetheless, we were able to incorporate our spatially-explicit capture and recapture location data using maximum mean distance between successive captures of an individual because nearly all transects were longer than this value. We quantified our "effective" sampling area (A_{hat}; Efford et al. 2004) by estimating the full maximum recapture distance (MMRD) of genotyped individuals, and then assigning a strip boundary around each transect using each value. Parmenter et al. (2003) found MMRD to be the most accurate method to delineate the area over which abundance was estimated for several species of small mammals.

Using MMRD is one of several conventional approaches for establishing A_{hat} (Otis et al. 1978, Efford et al. 2004). We estimated density (D_{hat}) by dividing our abundance estimate (N_{hat}) by effective sampling area (A_{hat}) (i.e., $D_{hat} = N_{hat}/A_{hat}$). We calculated availability of managed and unmanaged forest by calculating area of each habitat type in A_{hat} around transects in each habitat type. We used the delta method to calculate variance of our density estimates (Wilson and Anderson 1985).

We used geographic information system (GIS) program ArcView 3.3, ArcMap 9.0 (ESRI, Redlands, California), and Hawth's Analysis Tools in ArcMap 9.0 (Beyer 2007) to quantify forest habitat composition) in relation to transect, individual deer location as assigned from fecal DNA, and deer density and abundance estimates. GIS geodatabases and shapefiles of landcover types and logging activity used in analyses were initially created by the US Department of Agriculture Forest Service. Metadata for spatial data layers used were available at the Southeast Alaska GIS Library (2007). Descriptive statistics not included in output files of programs MARK and DENSITY were calculated using computer program SPSS (SPSS Inc., Chicago, Illinois). To determine the effects of forest habitat (managed vs. unmanaged) and year on abundance and density estimates, we conducted a series of Student's t-tests (observed significance level adjusted using the Bonferroni test), and non-parametric Mann-Whitney U and Chi-Square tests.

6.5 Results

We established 31 transects with a mean length of 663 m (range = 310-1,955m), and sampled each transect a mean of 5.0 (SE = 0.12) times (i.e., capture occasions) per year and collected 4-6 pellets from each pellet group we encountered (Table 6.1). We collected 2,254 fecal-pellet samples for DNA analysis, successfully genotyped 1,200 (53%) samples, and identified 760 unique deer (Table 6.2). We recaptured many deer during succeeding years; however, these deer were assigned unique IDs because estimates were calculated on an annual basis. Our genotyping success during 2008 (87%) was roughly double that of 2006 (41%) and 2007 (50%).

Our data supported four models as indicated by AIC_c weight (Table 6.3). All supported models allowed capture probabilities to vary by time with each sampling occasion and three models incorporated differences in capture probability between managed and unmanaged forest. We determined that 2 models that shared equal weight as the best fit model; 1) the model allowing for time variation, and 2) the model that allowed for time variation and differences in capture probability among old-managed forest, young-managed forest, and unmanaged forest. Combining years, study sites, and forest types, we determined that mean capture probability of deer over all sampling occasions was 0.13 (SE = 0.017) (Fig. 6.3). Capture probabilities among individual sampling occasions were different ($\chi^2 = 34.317$, $P = <0.001$); however, the variation through time did not follow a linear trend (Fig. 6.3). In our models incorporating a habitat covariate, we determined that young-managed forest covariate increased the probability of deer capture relative to other habitat types, and old-managed forest covariate decreased the probability of deer capture relative to other habitat types (Fig. 6.3). However, the influence of young-managed and old-managed forest covariates did not result in statistically different capture probabilities across sampling occasions (Mann-Whitney U = 15.0, $P = 0.74$). Our data did not fit models incorporating differences in capture probability during the first sampling occasion or models incorporating a linear-trend in capture probability over time. Both those models received $<1.0\times10^{-5}$ AIC_c weight.

Analyzing forest habitat separately within sites, we identified abundance estimates in each study site declined in unmanaged forest by 63% in Maybeso, 22% in Staney, and 13% in Steelhead from 2006 to 2008 (Table 6.4). In managed forest, we estimated that abundance in Maybeso (old-managed forest) increased by 26%; however, Staney (young-managed forest) and Steelhead (young-managed forest) declined by 29% and 10%, respectively. Within sites and independent of forest habitat, we determined that abundance estimates declined by 48% in Maybeso, 24% in Staney, and 12% in Steelhead. Combining all sites, years, and forest types, we estimated that deer abundance declined 30% from 426 (SE = 16.8) in 2006 to 297 (SE = 13.6) in 2008 (Table 6.4).

Combining all study sites across years, we determined that maximum mean recapture distances (MMRD) (mean = 443m, SE = 61.0) were similar ($\chi^2 = 5.186$, $P = 0.746$). Also, our estimates of MMRD were similar among study sites ($\chi^2 = 1.644$, $P = 0.440$) and among years ($\chi^2 = 1.959$, $P = 0.388$). Using our estimate of MMRD to assign a strip boundary around transects, we calculated an effective sampling area (i.e., spatial extent of the trappable population) of 8.8 km^2, 16.8 km^2, and 9.7 km^2 in Maybeso, Staney, and Steelhead, respectively. Combining all sites, years, forest types, our mean estimate of deer density declined 32% ($\chi^2 = 5.422$, $P = 0.066$) from 12.5 (SE=2.51) deer/km^2 in 2006 to 8.5 (SE = 0.32) deer/km^2 in 2008 (Fig. 6.3). Combining years and habitat types, our mean estimates of deer density were not different ($\chi^2 = 0.327$, $P = 0.849$) among sites.

Our effective trap area for deer in managed forest in Maybeso, Staney, and Steelhead was 4.7 km^2, 5.9 km^2, and 1.6 km^2, respectively. Our effective trap area in unmanaged forest in Maybeso, Staney, and Steelhead was 4.1 km^2, 10.9 km^2, and 8.1 km^2, respectively. Combining sites and years, but analyzing forest habitat separately, our mean estimates of deer density were similar (Mann-Whitney U = 38.00, $P = 0.825$) in managed forest (10.4 deer/km^2, SE = 0.95) and in unmanaged forest (12.6 deer/km^2, SE = 2.60) (Fig. 6.3). Combining all sites, our estimates of deer densities were not statistically different among years in managed ($\chi^2 = 1.156$, $P = 0.561$) and unmanaged forest ($\chi^2 = 1.689$, $P = 0.430$), although deer densities declined by approximately 8 deer/km^2 (44%) from 2006 to 2008 in unmanaged forest. Combining years, our estimates of deer densities were statistically similar among sites in managed forest ($\chi^2 = 5.067$, $P = 0.079$) and unmanaged forest ($\chi^2 = 5.422$, $P = 0.066$). However, within the Maybeso study site during 2006, our estimates of deer densities in unmanaged forest were more than double estimates of deer densities in unmanaged forest in Staney and Steelead (Fig. 6.3). Furthermore, our estimates of deer densities in managed forest within the Maybeso study site during 2006 were less than half deer densities in managed forest within the other study sites (Fig. 6.3), which was likely because of the age of managed forest (>30 years old) in Maybeso.

Combining years, we determined that old-managed forest (Maybeso) supported lower deer densities than young-managed forest (Staney and Steelhead) (Mann-Whitney U = 1.000, $P = 0.039$) (Fig. 6.3). In contrast, our mean estimates of deer densities in unmanaged forest (20.5 deer/km^2, SE = 5.8) in study sites with old-managed forest (Maybeso) were more than double deer densities in unmanaged forest (8.7 deer/km^2, SE = 0.427) in watersheds with young-managed forest (Mann-Whitney U = 0.0, $P = 0.02$)

6.6 Discussion

This study makes significant contributions to deer ecology and management in at least three different ways. First, we provide the first population estimate for an ungulate using DNA extracted from fecal pellets. Our findings suggest that non-invasive sampling is an effective method for monitoring deer in environments where direct observation is impractical. The deer-trail sampling protocol enabled us to encounter large numbers of pellet groups, which made mark and recapture estimates of deer abundance feasible and efficient. Moreover, we would not have been able to survey young clearcut habitat or pre-commercially thinned young growth without this technique because dense regeneration and slash piles prevented us from following straight-line transects (Brinkman et al. 2009c). By the final year of our study, genotyping success (87%) became comparable to other non-invasive wildlife investigations (Hedmark et al. 2004 [65%], Belant et al. 2007 [75%], Kendall et al. 2008 [74%]) and likely was influenced by optimization of extraction protocol, sampling fewer fecal pellets that appeared degraded during first sampling occasion, and strictly adhering to 10-day intervals between sampling occasions (Brinkman et al. 2009c).

Secondly, we provided the first rigorous estimates of abundance and density with precision for Sitka black-tailed deer. Mark and recapture techniques consistently estimated abundance with ±20% precision. Our density estimates represent deer that are confined to winter ranges during late winter and early spring, which typically comprises about 60-70% of the total habitat available to deer during snow-free months. This is particularly true for deer that migrate to alpine habitat during summer. Consequently, our density estimates likely would be reduced about 30-40% if computed for all deer habitat available during summer within our study areas.

Although our estimates of abundance had good precision (±20%), corresponding density estimates were based on a strip boundary (MMRD) that has not been tested against true densities of deer; thus warrants further investigation. Nonetheless, estimates were within range of previous estimates derived from other indices, and those using traditional knowledge of local hunters. For future studies, careful attention should be given to the layout of sampling transects. A sampling design that allows recaptures across a continuum of distances in multiple directions would better fit likelihood-based estimators of density (Program Density; Efford et al. 2004) calculated using spatially-explicit capture and recapture data.

Our erratic capture probabilities among sampling occasions (Fig. 6.2) explain why the best models all incorporated parameters for time variation. The area of forest floor encompassed by a single transect represents a small proportion of the total habitat used by deer while on winter range; thus, it is reasonable to expect that deer activity on our sampling area varied considerably during subsequent sampling occasions. Habitat covariates such as old-managed forest and young-managed forest influenced AIC weight of the best fit models; but the level of influence was minor relative to the differences in capture probabilities over time (i.e., sampling occasions). Models allowing capture probabilities to vary during the first sampling occasion received no AIC weight, which suggests the persistence of pellets deposited over winter prior to sampling likely did not result in differences in capture probabilities between the first sampling occasion and subsequent capture occasions (Fig 6.2). Rather, we speculate pellets that persisted through much of the winter and were collected during the first sampling occasion failed to yield sufficient DNA to be included in our analyses. The lack of fit of our models that incorporated a linear-trend in time indicated that capture probability did not increase with each subsequent sampling occasion. Therefore, either pellet deposition rates by deer did not increase sufficiently with green up of vegetation during our sampling period, or the effects of an increase in deposition rates were minor relative to variation in capture probabilities over time because of other aspects of deer activity during our sampling period.

We discourage direct comparisons of our estimates of population density with other studies located in Southeast Alaska because all previous estimates were based on very limited data from pellet surveys and were usually derived from data collected in subset of habitats with certain landscape features. Nonetheless, Sitka black-tailed deer densities have been estimated for deer on winter range in unmanaged forest (29-57 deer/km^2 [Smith and Davies 1975 *in* Herbet 1979], 10-23 deer/km^2 [Herbert 1979], 12 deer/km^2 [Wallmo and Schoen 1980], 34 deer/km^2 [Kirchhoff 1994], 19 deer/km^2 [McNay and Doyle 1987]) and mixed unmanaged and young-managed forest (7-8 deer/km^2 [US Department of Agriculture 1997]) in various locations within the coastal forests of British Columbia and Alaska using alternative methods (e.g., pellet group indices, habitat capability model estimates). Our estimates of deer densities (8.5–17.0 deer/km^2) using DNA-based mark and recapture techniques fall within the lower range of previous estimates. Further, if we tentatively extrapolate our mean estimate across sites and years (11 deer/km^2) to an island-wide scale (≈6,200 km^2 available winter/spring habitat), population estimates on Prince of Wales Island would be 68,200 (±13,640) deer. This biologically plausible estimate lies between the population goal on the island (75,000 deer [Porter 2005]) and previous estimates based on pellet counts and hunter harvest (55,000 [Porter 2005]). Similarities between our deer densities (derived from minimum known number of individuals and recapture probabilities) and previous densities and population sizes (derived from other indices) provide some reassurance that past management and policy were based on reasonable estimates.

Thirdly, we compared estimates of deer density in managed and unmanaged forest and determined that age of managed forest significantly influences abundance and density. Whereas our estimates of deer densities in young-managed forest was equal to or exceeded estimates in unmanaged forest when compared within the same watershed within the same year, old-managed forest (Maybeso) consistently supported the lowest densities of deer. Those high densities in young-managed forest and low densities on old-managed forest likely reflect the steep decline in forage biomass as a young clearcut transitions into second-growth forest, whereas old-managed forest (>30 years) often contains sparse understory forage important to deer (Alaback 1982, Hanley 1993). The findings of previous studies indicated that Sitka black-tailed deer reduced their use of young-managed forest during winter (Doerr et al. 2005, Wallmo and Schoen 1980). Our density estimates suggest that deer use is equal to or slightly higher in young-managed forest during the winter compared to unmanaged and old-managed forest, which corroborates Yeo and Peek's (1992) findings for female deer on northern Prince of Wales. However, direct comparisons with previous studies are not recommended because investigators were comparing young-managed forest with several different types of unmanaged habitat (e.g., beach, high volume old growth) with certain landscape features (e.g., aspects, slope, elevation). Although we grouped all unmanaged habitat, there are opportunities to use our method to estimate abundance at finer scales with finer resolution, including individual landscape features. Because forage biomass for deer varies between habitat types (Alaback 1982, Hanley and McKendrick 1983, Parker et al. 1999) and risk of mortality of deer varies among habitat types (Farmer et al. 2006), we suggest future investigations that evaluate abundance and density estimates in different habitat categories of unmanaged habitat. To evaluate those differences, such information would have to be incorporated into the initial sampling design, and sampling intensity would have to be adjusted.

An unexpected and somewhat surprising finding (because of habitat composition) was that the Maybeso watershed initially had the highest density of deer among the 3 watersheds we sampled. Maybeso is dominated by old-managed forest, which was identified as one of the least popular habitats for deer hunting (Brinkman et al. 2009b). Consequently, deer hunting pressure may have been low in the Maybeso because of less road access (Farmer et al. 2006). However, after 2 consecutive harsh winters (2006 and 2007), deer abundance declined most in Maybeso and by the end of our study it had the lowest density. Deer populations in Maybeso likely were above the carrying capacity of a typical winter because of a combination of consecutive mild winters and a relatively high percentage of high-quality alpine habitat available to migratory deer, as compared to the other two watersheds. Typically, pellet-group counts are very high in watersheds adjacent to large areas of alpine habitat as compared to counts in watersheds without adjacent alpine meadows (Alaska Department of Fish and Game, unpublished). The abundance of highly nutritious forage typical of alpine habitat offers migratory deer a superior summer diet and the terrain reduces risk of predation (McNay and Voller 1995). Consequently, deer abundance may be high in alpine habitat during summer and autumn. Those deer typically winter in forests at higher elevation than resident deer (Schoen and Kirchhoff 1990). However, in severe winters deer are pushed down to lower elevations by snow and overlap habitats used by resident deer. If migratory deer during our study were forced to lower elevations because of accumulating snow, then deer likely were concentrated in areas surrounding our path transects. This also would explain why the deer population in Maybeso declined more than in other watersheds. The addition of migratory deer on traditional winter range of resident deer probably resulted in competition for forage that greatly exceeded winter carrying capacity. Whereas deer densities in old-managed forest within Maybeso remained low (albeit, relatively stable), deer abundance in unmanaged forests within the watershed experienced the steepest decline during our study.

Mean estimates of deer densities declined by approximately 30% over the 3-year study, and we speculate this was caused by consecutive mild winters followed by consecutive harsh winters during our study period. During 2006-2008, winter snowfall in the region was 37% greater than the long-term average; furthermore, 3 consecutive harsh winters have not occurred consecutively since the 1970s (Annette Island Weather Station, Alaska). Before 2006, winter snow depths were below average for several years. The extended period of mild winters likely allowed deer populations to reach or exceed the carrying capacity of forage typically available during severe winters, which likely exacerbated the negative impact of consecutive harsh winters on mortality. Sitka black-tailed deer are at the northern extent of the range of the genus *Odocoileus*, and are strongly influenced by snow depth and persistence (Klein 1965, Wallmo 1981, White et al. 2009). In southeast Alaska, snow influences deer by elevating energy expenditure through higher costs of locomotion and reduces energy intake by burying forage (Parker et al. 1999). White et al. (2009) determined that, for Sitka black-tailed deer, browse biomass became buried and unavailable to deer at snow depths substantially lower than pre-winter twig heights.

6.7 Management Implications

With the availability of our tool, wildlife managers in Alaska and in other densely-forested environments have a new opportunity to estimate population size and monitor population change at fine (and broader) spatial and temporal scales. The empirical data we provided creates an opportunity for sound science to direct management decisions and can potentially ease contention among stakeholders (e.g., sport/subsistence hunters, wildlife/forest agencies).

With most (~90%) of the logged forest in southeast Alaska transitioning to a late successional stage within the next two decades, manipulation of stand structure and plant composition in developing second-growth likely will be necessary to sustain high densities of deer and hunter opportunities. Experimental methods, such as inclusion of red alder (*Alnus rubra*) to create alternative pathways of succession with higher levels of deer forage (Hanley 2005), deserve serious consideration.

We have established a foundation of an important population parameter that will foster further analysis of trends in deer populations on Prince of Wales Island. We suggest additional research in other areas within Southeast Alaska with varying levels of landscape disturbance, climatic conditions, and predator occupancy to confirm the feasibility of incorporating our methods into a region-wide monitoring program.

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Table 6.1. Number of transects established, area of forest sampled, and mean number of sampling occasions per year in 3 study sites on Prince of Wales Island, Alaska.

Study Site	Transects	Area sampled (m^2)	Mean sampling occasions (SE)
Maybeso	6	13,372	6.2 (0.27)
Staney	16	17,796	5.0 (0.11)
Steelhead	9	9,970	4.1 (0.22)

Table 6.2. Number of deer fecal pellets collected in each study site during each year that were tested for DNA and successfully genotyped at a level allowing identification of individual deer.

Site	Year	Tested	Genotyped	Success rate	Unique ID
Maybeso	2006	349	159	0.46	104
Maybeso	2007	281	141	0.50	82
Maybeso	2008	101	83	0.82	54
Staney	2006	496	196	0.40	127
Staney	2007	379	194	0.51	111
Staney	2008	170	153	0.90	97
Steelhead	2006	175	96	0.55	61
Steelhead	2007	228	106	0.46	71
Steelhead	2008	75	72	0.96	53
All	2006	1020	451	0.44	292
All	2007	888	441	0.50	264
All	2008	346	308	0.89	204

Table 6.3. Model selection results from program MARK analysis of Sitka black-tailed deer populations on Prince of Wales, Alaska.

Model no.	Model[a]	AIC_c	ΔAIC_c	AIC_c Weight	Estimated Parameters	Deviance
1	$\pi(.)p(t)$	4041.4	0	0.469	8	4025.5
2	$\pi(.)p(t + u + y + o)$	4042.2	0.7	0.321	10	4022.2
3	$\pi(.)p(t + o)$	4043.9	2.4	0.138	10	4023.9
4	$\pi.p(t + m + u)$	4045.2	3.8	0.071	10	4025.2
5	$\pi(.)p(t1)$	4083.3	41.8	0.000	2	4079.3
6	$\pi(.)p(t1 + u + m)$	4087.2	45.8	0.000	4	4079.2
7	$\pi(.)p(u + y + o)$	4125.3	83.8	0.000	4	4117.3
8	$\pi(.)$	4127.4	86.0	0.000	1	4125.4
9	$\pi(.)p(T)$	4128.8	87.3	0.000	2	4124.8
10	$\pi(.)p(u + m)$	4131.4	89.9	0.000	3	4125.4
11	$\pi(.)p(T + u + m)$	4132.7	91.2	0.000	4	4124.7

[a]Model parameter definitions: $\pi(.)$ = mixtures were held constant, p = capture probability, t = time variation in capture probability, u = capture probability in unmanaged forest, y = capture probability in young-managed forest, o = capture probability in old-managed forest, m = capture probability in managed forest, t1 = capture probability variation during first sampling occasion, T = linear trend in time variation in capture probability.

Table 6.4. Derived estimates of abundance for Sitka black-tailed deer captured in each study site in managed, unmanaged, and all habitats using weighted averages of program MARK models with unconditional standard errors (Buckland et al. 1997).

Site	Maybeso			Staney			Steelhead		
Year	2006 (SE)	2007 (SE)	2008 (SE)	2006 (SE)	2007 (SE)	2008 (SE)	2006 (SE)	2007 (SE)	2008 (SE)
Unmanaged forest	127 (9.3)	75 (6.6)	47 (5.0)	107 (8.3)	95 (7.7)	84 (7.1)	69 (6.3)	79 (6.9)	60 (5.8)
Managed forest	26 (4.9)	47 (7.4)	33 (5.7)	77 (7.3)	65 (6.5)	55 (5.8)	20 (3.1)	24 (3.5)	18 (3.0)
Habitats grouped	153 (10.5)	122 (9.9)	80 (7.6)	184 (11.1)	160 (10.1)	139 (9.2)	89 (7.0)	103 (7.7)	78 (6.5)

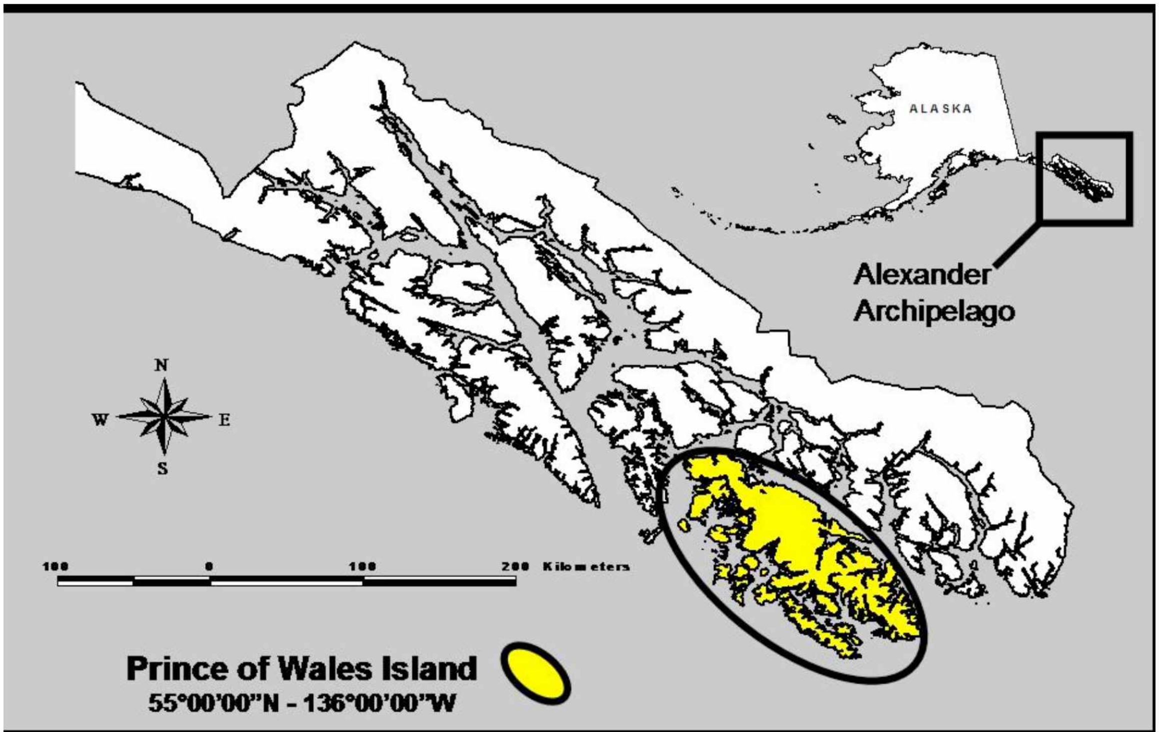

Figure 6.1. Location of Prince of Wales Island, Alaska.

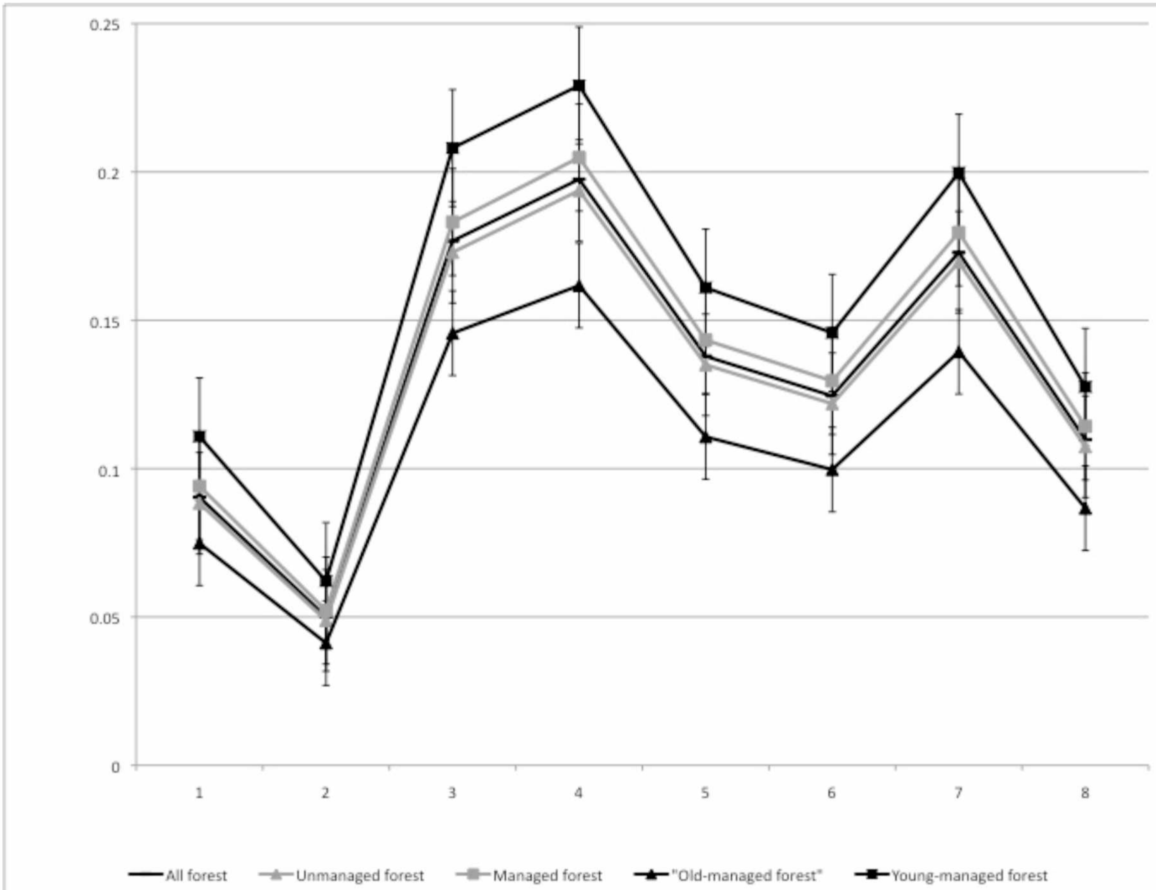

Figure 6.2. Estimates (error bars = standard error) of capture probabilities of Sitka black-tailed deer on Prince of Wales Island, Alaska, during consecutive sampling occasions incorporating the influence of habitat covariates. Data from study sites (Maybeso, Staney, Steelhead) and annual sampling periods (2006, 2007, 2008) were combined. Y axis = capture probability, X axis = sampling occasions.

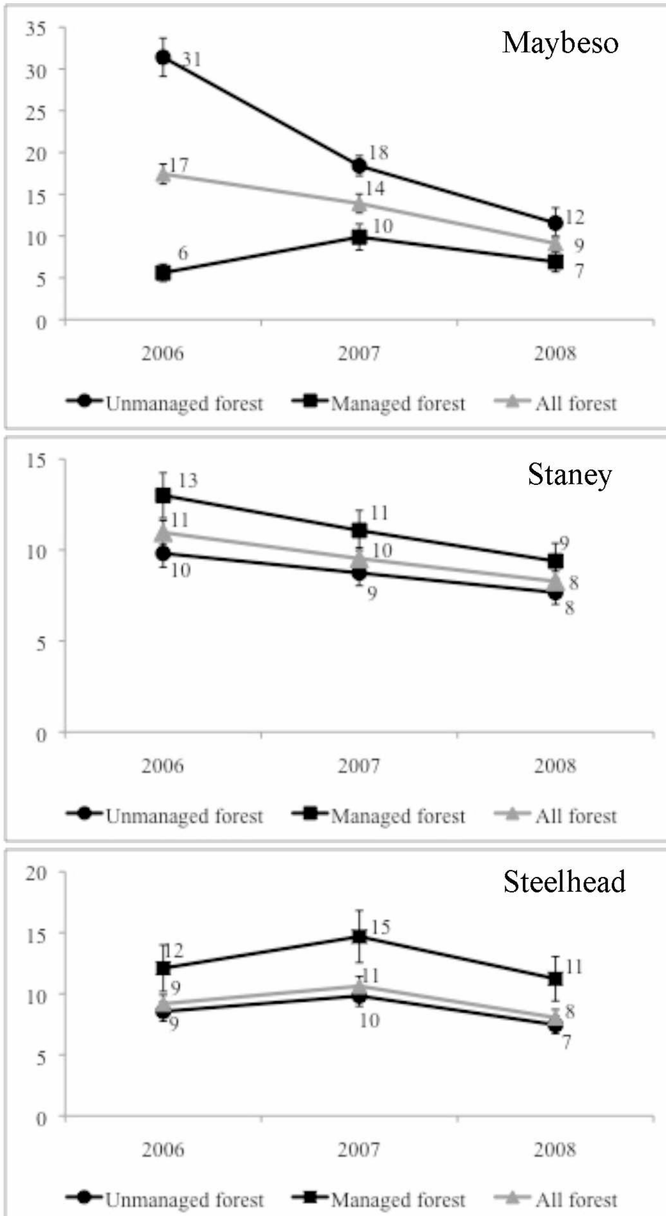

Figure 6.3. Changes in density (deer/km^2 ± SE) of Sitka black-tailed deer during 2006, 2007, and 2008 in managed forest, unmanaged forest, and all forest habitats in 3 study sites (Maybeso, Staney, Steelhead) on Prince of Wales Island, Alaska. Managed forest in Maybeso was >30 years old. Managed forest in Staney and Steelhead was <30 years old. X axis = number of deer/km^2, Y axis = year.

Chapter 7 Summary

In the previous chapters, I provided an example of an integrative approach to describe a wildlife hunting system. I provided information on each key component of a Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) hunting system on Prince of Wales Island, Alaska. I explained the interactions of these components and discussed how these interactions have changed over time. I determined how deer and deer hunters have altered their behaviors because of rapid landscape change driven mainly by intensive logging, and suggested that this wildlife hunting system was moving toward one that may require more hunter effort to harvest deer. I found that the transition of a clearcut to second-growth forest creates fewer harvest opportunities for hunters for 2 reasons: 1) changes in vegetation reduces ability of hunters to see and stalk deer, and 2) late-successional managed forests supported fewer deer overall. Whereas deer densities in young-managed forest were equal to or exceeded densities in unmanaged forest, old-managed forest (>30 years old) support the lowest densities of deer.

I provide empirical data to support both the theory that changes in plant composition because of succession of logged forest may reduce long-term (i.e., decades) carrying capacity (Wallmo and Schoen 1980, Hanley 1984, Schoen et al. 1988) and that severity of winter weather may be the most significant force behind short term (i.e., annual) changes in deer population size in southeast Alaska (Klein 1965, Wallmo 1981, Parker et al. 1999, White et al. 2009). Because annual weather was shown to drive deer densities, the negative effects of landscape change on hunter opportunities were less evident during consecutive mild winters, but the challenges deer hunters face were exacerbated during consecutive harsh winters.

My findings suggest that non-invasive sampling using DNA from deer fecal pellets was an effective method for monitoring deer in a wet and densely-vegetated environment where direct observation is challenging. Mark and recapture techniques successfully estimated abundance with precision (±20%) useful at fine spatial scales (i.e., patch, watershed). With further research in other areas of southeast Alaska with varying weather and landscape characteristics, non-invasive methods show real promise for region-wide use as a protocol for monitoring, and estimating abundance and trends of deer (see Ch. 8).

7.1 Hypothesis Testing

Our findings suggest that several hypotheses (hypotheses 2-5, Ch. 1) formulated to explain difficulties experienced by deer hunters have validity. Expanded harvest opportunities were initiated by a boom in commercial logging that increased road access and rapidly changed the forest structure to a desirable successional stage for deer hunting. As clearcuts along roads transitioned into older managed forest (>12 years old), vegetation reduced the visibility of deer and hunter efficiency in harvesting them. The impact of this ecological change on hunting opportunities was obscured while an abundance of new clearcuts was being created annually. With the decline in logging activity, the negative effects on hunting success from the successional loss of favorable deer habitat began to overshadow the positive effects of clearcutting on deer hunter opportunities. Currently, popular harvest strategies (e.g., vehicle-based hunters focusing on muskeg and clearcuts adjacent to roads) used by one-to-three generations of hunters are becoming less efficient, and hunting success using current practices is being constrained. With roads being closed and the overall clearcut availability declining, hunters are being condensed into a smaller area relative to past decades. Reduced area for hunting results in higher hunter density; thus, more opportunities for contact between hunters creating the perception of increased interference and competition.

Hypothesis 1, (Ch. 1) stating that hunter difficulties were caused by an inadequate supply of deer available for harvest, was partially valid because forest changes have began to decrease the access to supply (i.e., availability), but was invalid because deer supply was probably adequate. Most interviewed hunters responded that deer populations have either remained stable (44%) or increased (30%) in recent years (2000-2005). The deer population size on Prince of Wales Island when hunters began reporting difficulty (mid 1990s) was likely as abundant as it has ever been. From 1976 to 1998, the average snowfall was 69 cm (40% less than the 60yr [1948-2008] average [115 cm]), and the first 5 years of the 1990s were particularly mild (average snowfall = 41 cm; Annete Island, Alaska weather station; http://climate.gi.alaska.edu/Climate/Location/TimeSeries/Data/annSn). Those mild winters in combination with abundant forage created by clearcut logging likely resulted in consistently high deer densities.

The circumstances used to evaluate hypothesis 1 suggests that access is more important than supply, and supply should not be confused with availability (supply + access). During the mid 1990s, the influence that older stands of managed forest (>12 years old) were having on harvest opportunities became evident. Although there was probably an abundant supply of deer in regrowth forest adjacent to roads, thick vegetation reduced deer hunter's ability to spot, stalk, and harvest those animals; thus, reducing availability. For example, data in the Staney study site suggested that recently pre-commercially thinned stands of forest contain equal or higher deer densities relative to unmanaged forest, but that habitat type was the least popular habitat for deer hunting and was often avoided. With the proportion of older managed forest (>12 yrs) increasing along roads, and with most hunters (66%) mainly using the number of deer seen along roads and while hunting to estimate deer population (Appendix), it is understandable that hunters began perceiving a decline in deer numbers even though the densities were probably high and stable.

Within a resilience framework, ecologically driven changes in social harvesting practices suggest that adaptability that maintains the fundamental properties of a hunting system from one disturbance (logging boom) may increase vulnerability to another (logging bust). Our research shows that transition in hunting strategies to increased efficiency did not necessarily enhance resilience of the hunting system because flexibility of future options was reduced. With reduced deer numbers because of natural succession of logged forest and reduced access (road closure) and sightability, the deer hunting system may become more vulnerable.

7.2 Future Scenario for Hunters and Deer

The decline in the area of young clearcut forest and loss of access because of road closures may have the greatest immediate influence on deer harvest opportunities. Due to the decline in the timber industry, young clearcuts will become uncommon within the next decade regardless of road or boat access. Most clearcuts have reached an unsuitable stage for hunting in which the patch either consists of a dense stand of even-aged saplings with thick understory vegetation or dense second-growth stand with stem exclusion. Because these stands are located along roads, hunters' visibility and efficiency in harvesting deer from roads have decreased. Area of unsuitable habitat for hunting (i.e., second-growth and pre-commercially thinned forest) has increased rapidly, and this trend will likely continue. Most (>90%) of logged forest in southeast Alaska will be old (>30 years) second-growth within the next couple decades. Because many hunters reported that the number of deer seen along roads while driving was used an indicator of population size on Prince of Wales Island (Appendix), fewer roads with less visibility from roads also may exacerbate perceptions of a declining deer population and lead to inflated hunter concern with regards to harvest opportunities.

Consecutive harsh winters in the early 1970s and healthy deer populations thereafter shows that deer have the reproductive capacity to recover well within a human generation. However, the time-scale required for deer to rebound from recent harsh winters to historic highs with the effects of forest succession following clearcut logging is unknown. The hypothesis that an inadequate supply (not just availability) of deer is causing hunter difficulties likely will gain support as more forest transitions into older second-growth stands. In the Maybeso study site, all managed forest was >30 years old and this habitat type contained the lowest densities of deer. Given that peak logging occurred during the 1970s, large swaths of forest are reaching this successional stage annually, and overall carrying capacity and population size may continue to decline. A combination of reduced deer numbers and an increase in undesirable habitat for deer hunting may further challenge hunters that depend on deer, both for nutritionally and culturally. Forest managers need to think carefully about how logged forest is managed as it transitions into old-managed forest, which we determined to support fewer deer. Further, managers and hunters should expect the problem to seem less evident during years preceded by mild winters, but escalated during years preceded by harsh winters.

7.3 Adaptation Options

Responses by individual hunters may be the most feasible form of adaptation to increase the resilience of the hunting system. This is typical of many northern indigenous people, who are proud of their ability to adapt to changing conditions. A major advantage of hunter adaptation is less reliance on changes in deer harvest regulations and in manipulation of forest structure and access to sustain hunting practices. Therefore, hunters would be less dependent on factors they can't control directly. Hunters who focus their effort on permanent and naturally occurring open habitat (e.g., alpine tundra, muskeg, shoreline) are least vulnerable to logging-associated changes in vegetation and are likely to have more success sustaining their harvest opportunities in the future. On the other hand, those hunters who depend on vehicles for access, concentrate their hunting effort in young clearcuts, and are unwilling or unable to travel on foot away from maintained roads are particularly vulnerable to forest changes.

From an institutional perspective, active management of second-growth forest and road closure strategies that minimize loss of access to preferred hunting areas may serve as adaptation options that help sustain deer numbers and harvest opportunities. Manipulation of forest structure and access would require relatively few changes in hunting regulations and strategies. Harvest of older second-growth forest (50 to 60 to years old) could increase the area of young clearcut habitat and potentially provide the revenue necessary to maintain access to desirable hunting habitat and sustain higher deer densities. If clearcut logging of second-growth stands isn't feasible, commercial thinned stands of older (>50 years), even-aged conifer has been shown to contain 10 times more understory biomass than unthinned stands (Zaborske et al. 2002, Hanley 2005). If a commercial market is not identified, manipulation of plant composition in second-growth stands may be possible using experimental methods where inclusion of red alder (*Alnus rubra*) leads to an alternative pathway of secondary succession with higher levels of deer forage (Hanley 2005) relative to traditional pathways (Alaback 1982).

Another forest management option to restore deer harvest opportunities for vehicle-based hunters preferring clearcuts is additional harvest of remaining old-growth forest. This could provide a temporary solution for those who prefer hunting in young clearcuts, but would further hinder the long-term sustainability of the hunting system by increasing the overall proportion of poor habitat for deer and deer hunting a decade later. In addition, the reduced proportion of old-growth habitat would eliminate habitat that is favorable for deer. Further, the market for old-growth timber from Alaska struggles to compete with markets of other regions, and production has been stagnant or has declined in recent years (Morse 2000, Brackley et al. 2006).

Hunter opportunities can only be maintained through careful consideration of both access and supply. Focusing on one of these factors without the other will not build resilience into the hunting system. Second-growth management to improve deer habitat will be particularly important in areas easily accessed by hunters. My findings highlight the idea that deer availability (supply + access) should be the central aim of game managers rather than just reaching a priori deer population goals (supply).

7.4 Integrative Approach

A lack of information on either social or ecological factors is a common explanation why problems can't be adequately addressed. I argue that a failure to integrate this information further hinders resolution. Information I collected on hunter patterns suggested that forest change was influencing harvest opportunities of deer. However, I would have been unable to suggest the level of influence this factor was having without including information on population dynamics of deer on similar spatial and temporal scales. My situation would have been the same if population parameters of deer were addressed, while hunter patterns and habitat change were not. Integrating social-ecological data was an effective approach to understanding how this wildlife hunting system has responded and changed over the last 50 years. Further, an integrative approach clearly identified the major challenges and provided insight into how resilience may be enhanced in the future. Ultimately, building resilience into a wildlife hunting system will require careful reflection on the value of harvesting wildlife as a way of life in combination with managers' ability to maintain availability of deer and habitat for hunting deer above a threshold that corresponds to abandonment of traditions. This is a moving target that involves continued adaptation and compromise by all stakeholders.

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Chapter 8 Future Recommendations

8.1 Overview

Nearly all the protocols I used were either developed specifically for my study or developed previously and used for the first time on Sitka black-tailed deer. Because many of the techniques were experimental and unproven, I used an adaptive approach and incorporated what I learned during data collection to optimize methods. However, to avoid compromising opportunities to make comparisons among data collected at different times, some aspects of my study design remained constant, even though improvements were possible. The first objective of my final chapter is to articulate how my methods could be improved in future studies.

Within my dissertation, I detailed important contributions derived from a rigorous analysis of data. Nevertheless, additional contributions are possible. My second objective is to suggest other research questions that can be evaluated with my data.

Because extracting DNA from fecal pellets deposited by deer proved to be an effective approach to estimate abundance and density, I anticipate that this tool may be incorporated into the deer-monitoring program in southeast Alaska. My final objective is to discuss the feasibility of expanding this tool region-wide and speculate about the additional information that such an expansion would provide.

8.2 Study Design

For future studies, careful attention should be given to layout of sampling transects. Although estimates of abundance had good precision (±20%), density estimates based on a strip boundary (MMRD) that has not been tested against true densities of deer warrants further investigation. For future studies, careful attention should be given to layout of sampling transect. A sampling design that allows recaptures across a continuum of distances in multiple directions would better fit likelihood-based estimators of density (Program Density; Efford et al. 2004) calculated using spatially-explicit capture and recapture data. For example, establishing transects that intersect perpendicularly would allow recaptures in multiple directions rather than only along a linear transect. Using a sampling array that is more representative of a systematic grid also may foster recaptures across a continuum of distances.

Varying the intensity of sampling may provide insight into what level of effort is needed to achieve a desired level of precision. For instance, to make a DNA-based protocol as efficient as possible, we would need to know how many transects need to be positioned in a certain area of landscape to allow inference at different temporal and spatial scales useful to wildlife and forest managers. Studies with varying levels of sampling also would provide insight into how many sampling occasions are needed to analyze data with mark and recapture estimators.

During my study, we focused our research on 3 study sites located on the southern tip of southeast Alaska that are very different from other areas within the range of Sitka black-tailed deer with regard to climate, landscape change, hunting pressure, and predators. My study sites were all heavily logging and easily accessible by hunters via roads. Although my research establishes a baseline of data for additional investigations on Prince of Wales Island, future research in more remote and pristine areas may help to identify differences between disturbed and undisturbed landscapes. With regards to the range of Sitka black-tailed deer, Prince of Wales Island has a relatively mild climate. For instance, in central Southeast Alaska, mean annual snowfall (250 cm [Juneau, Alaska, weather station) is more than double that received in the southern reaches of Southeast Alaska (115 cm). With winter weather being considered the major driver of population trends of Sitka black-tailed deer on an annual basis, deer hunting systems in more northern latitudes may respond and function differently than those I studied because of their greater snowfall. Prince of Wales Island contains a high density of both wolves and black bears, both known to be significant predators of Sitka black-tailed deer. However, in the northern half of the range of Sitka black-tailed deer, those predators are absent, and relative high densities of brown bears are present. This also may change the dynamics of the key components of the hunting system.

8.3 Additional Deliverables

8.3.1 Genetic analyses

The use of genetics to provide information about the ecology of wildlife continues to expand. DNA-based identification from fecal pellets potentially has allowed researchers to advance understanding of social structure, paternity, kinship, sex ratios, gene flow and phylogeography (Kohn and Wayne 1997), all of which are poorly understood for Sitka black-tailed deer. Brinkman and Hundertmark (2009) successfully determined gender of Sitka black-tailed deer using DNA extracted from fecal pellets. With these techniques, my pellet samples can be used to identify sex ratios in each of the watersheds surveyed.

Sex ratio may have a significant effect on deer productivity and the level of sustainable annual harvest (McCullough 2001, White et al. 2001, Clutton-Brock et al. 2002), especially under hunting regulations allowing few females to be harvested relative to males. Indeed, during household interviews on Prince of Wales Island (Turek et al. 1998), respondents reported seeing sufficient numbers of deer, but not many males.

A previous study had found population structure among Sitka black-tailed deer between islands in the Alexander Archipelago, and indications of population structure across the Kodiak Archipelago (Latch et al. 2008). Using DNA extracted from my pellet samples, research is currently underway to use genetic markers to investigate the possibility of population structure of Sitka black-tailed deer on an intra-island scale. Additionally, information is being sought to characterize the level of genetic diversity in deer on Prince of Wales Island.

8.3.2 Relationships between pellet group counts and deer density

Successful application of a DNA-based technique for estimating deer population size and change also may increase the value of 3 decades of pellet-group count surveys in Southeast Alaska. Research is currently underway to identify the relationship between my estimates of deer densities and pellet-group counts. During all my field seasons, all pellet groups encountered (even those not sampled) were counted, assigned a unique ID, and assigned a geographic location (i.e., UTMs). In addition to using our deer-trail technique to do this (Ch. 5), we also conducted 3-4 straight-line transects in each watershed during all years using traditional protocols.

8.4 Other Needs

As mentioned in Chapter 1, the key components of a deer hunting system are the hunter, the deer, and the landscape or habitat in which they interact. While important information has been gathered on the hunter component, and how the interaction between hunter and the other components changed over time (Ch. 2, 3), addressing hunter difficulty is still largely a qualitative process. Accurate harvest information is lacking and disagreement exists on the definition of "hunter needs" and "hunter effort". For instance, during hunter interviews (Appendix), many hunters reported that an active day of hunting was devoting an entire day to a hunt; whereas, some hunters consider opportunistic hunting (harvesting a deer when the opportunity presents itself but never devoting part of the day to just hunting) to be actively hunting. The remainder considered an active day of hunting to be when a hunter devoted part of the day to the hunt. Without reliable information on hunter harvest and a consistent quantitative measurement of subsistent need and catch per unit effort, the task of addressing hunter difficulty will be challenging and contentious. A baseline needs to be identified from which to make comparisons.

Lastly, because natural succession of logged forest was determined to significantly influence both hunters and deer, I suggest continued monitoring of hunter opportunities and deer population trends as managed forest continues to age. With the importance of deer availability (supply + access) for hunters, relative to just deer supply, future road-closure strategies should take into consideration importance of adjacent habitat for deer hunting now and as the forest ages. Adaptation will need to occur at both an individual and institutional level to sustain the hunting system in a manner that can support those that depend on it. All stakeholders (e.g., sport hunters, subsistence hunters, wildlife managers) share the common goal to sustain opportunities to harvest deer in southeast Alaska. All stakeholders will need to make sacrifices and work together as allies rather than opponents to build resilience into the hunting system of Sitka black-tailed deer.

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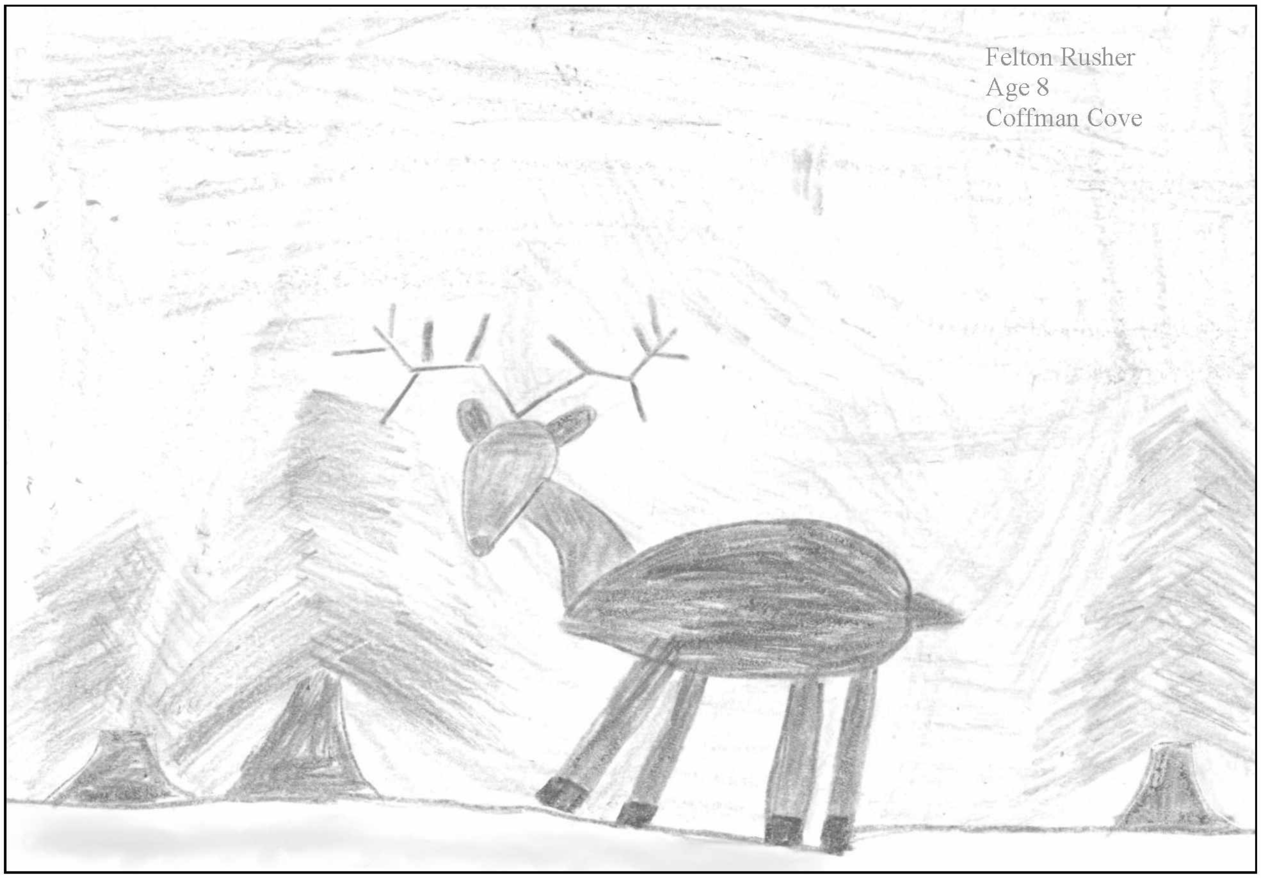
Appendix

The Prince of Wales Island Deer Hunter Project: Preliminary Summary of Hunter Responses to Interview Questions[1]



[1] Prepared in the format as published. Published as: Brinkman, T. J. 2006. The Prince of Wales Island Deer Hunter Project: Preliminary Summary of Hunter Responses to Interview Questions. Community Report, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska.

Executive Summary

In recent years, subsistence hunters on Prince of Wales Island (POW) have expressed concern that they are experiencing difficulty harvesting enough deer to meet their needs. The objectives of the *Prince of Wales Island Deer Hunter Project* were to better understand the extent of this problem and determine why hunters are experiencing difficulty. During spring and summer 2005, I conducted 88 face-to-face interviews with Alaska residents with in-depth knowledge of deer hunting on POW. Through these interviews, I collected hunter perceptions on 3 main topical areas: i) deer hunting patterns, ii) deer population trends, and iii) deer habitat and hunting access. In this report, I present a basic summary of hunter responses to interview questions. I will provide more detailed explanations of key factors that may be causing subsistence hunters to experience difficulty in future papers.

According to interviews, forty-nine percent of hunters perceived that time and effort needed to harvest a deer have remained the same over the last 5 years; whereas, 36% perceived more time and effort, and 14% perceived that less time and effort were needed to harvest a deer. Those who felt more time and effort were needed attributed this change to more hunting competition and pressure, followed by less desirable deer population characteristics (low supply, age structure with low percentage of mature animals, and sex structure with low percentage of bucks). Those who perceived less time and effort were needed attributed this change to milder winters and better access to deer, followed by an abundant supply of deer available for harvest.

Hunters reported harvesting a median of 4 deer each year, which was equal to the number of deer required to meet the typical hunter's own household needs. However, this was less than the number required to meet both the average hunter's own household needs and other households he or she provided deer for. Seventy-three percent of hunters reported that they shared deer meat, and 51% of those provided deer for 3 or more other households.

Muskegs were identified as the most popular habitat type to hunt followed by clearcut forest. The quality of hunting in clearcuts depended on the age of the clearcut. Hunters reported that the best hunting in clearcuts began on average 2 years after an area has been logged, and hunt quality began to decline on average when a clearcut reached 9 years of age.

Vehicles were used the most to access hunting areas. Most hunters reported that roads increased their hunting success and decreased hunting effort. In contrast, hunters generally reported that road closures had no effect on their hunting success and effort. Hunting was reported to be better on new roads because of increased access to previously remote hunting areas and new roads are usually located next to new clearcut forest. However, hunters often perceived a decline in hunt quality along roads over time due to increased hunting pressure and increased forest growth next to roads. Many hunters reported that they seek out and select areas with closed roads to avoid hunter competition and because there were more deer.

Over the last 5 years, 44% of hunters perceived that the deer population on POW has remained stable. Hunters who perceived an increase (30%) in deer population size mainly attributed this change to mild winters. Hunters who perceived a decline (26%) mainly attributed this to over harvest.

On average, hunters predicted that the deer population on POW will slightly decline over the next 25 years. That decline was mainly attributed to hunting pressure and harvest followed by habitat change (i.e., clearcuts converting to second-growth forest) and weather.

Introduction

In recent years, subsistence hunters on Prince of Wales Island (POW) have expressed concern that they are experiencing difficulty harvesting enough deer to meet their needs. The objectives of the *Prince of Wales Island Deer Hunter Project* were to better understand the extent of this problem and determine why some hunters are experiencing difficulty.

During spring and summer 2005, I conducted face-to-face interviews with residents of POW, Ketchikan, and Saxman to collect hunter perceptions on 3 main topical areas: i) deer hunting patterns, ii) deer population trends, and iii) deer habitat and hunting access. I used informal interviews conducted in communities during summer 2004, Alaska Department of Fish and Game records on deer hunters, and notes and reports from the Unit 2 Deer Planning Subcommittee of the Southeast Regional Advisory Council to identify key informants in each community. Key informants along with representatives from Tribal Associations suggested and helped me locate interview candidates. I interviewed adult Alaska residents who have in-depth knowledge of deer hunting seasons, methods, and areas; traditional and contemporary patterns of deer hunting; and changes in hunting practices over time.

In this report, I present a basic summary of hunter responses to interview questions. For interview questions that resulted in a quantifiable response by hunters, I mainly provide averages, but also provide medians when the average is not a good overall representation of the responses provided by hunters.

General Information from Interviews

I interviewed 88 deer hunters from 11 communities on POW and 2 off-island communities (Table 1). A total of 5 females and 83 males were interviewed, and median interview length was 42 minutes (Table 2).

Table 1. Number of hunters interviewed in each community

Coffman Cove	7
Craig	9
Hollis	6
Hydaburg	11
Kassan	3
Ketchikan & Saxman	20
Klawock	7
Naukati	7
Point Baker	2
Port Protection	4
Thorne Bay	6
Whale Pass	6

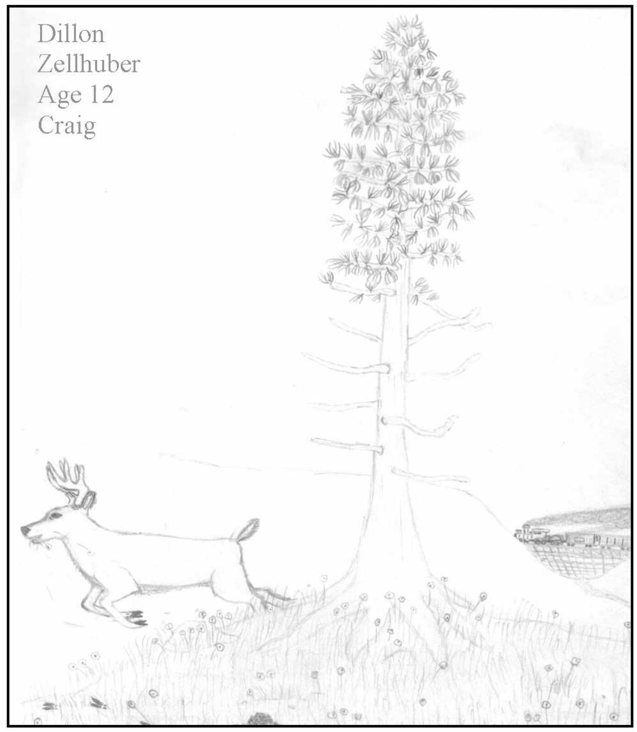
Table 2. General information about interviewed hunters

	Minimum	Maximum	Average
Age	18	94	47
Members in household	1	8	3
Years hunting deer on POW	3	71	22

Hunting Patterns

Hunting effort

Hunters actively hunted deer a median of 17.5 days each year (Table 3), but the definition of an active day of hunting varied among individuals. Many hunters (64%) reported that an active day of hunting was devoting an entire day to a hunt; whereas, some hunters (9%) consider opportunistic hunting (harvesting a deer when the opportunity presents itself but never devoting part of the day to just hunting) to be actively hunting. The remainder considered an active day of hunting to be when a hunter devoted part of the day to the hunt.



Timing of hunt

The beginning of the season (i.e., July & Aug.) and rut (deer breeding season) were the most popular times to hunt deer, and hunting pressure was lowest during September and early October. Hunters were most active during the morning hours (57%), but many reported that they hunt all day (31%). According to interviews, hunting pressure was the lowest during the middle of the day.

Mode of hunting

Vehicles were used most (67%) to access hunting areas, followed by use of boats (23%). Some hunters used a combination of boat, vehicle, and ATV (7%). After reaching the hunting area, hunters often traveled away from vehicle or boat to hunt on foot (Table 3). Although not specifically asked during interviews, many hunters mentioned that they often hunt roads on foot, particularly closed roads.

Table 3. Hunting patterns reported by hunters during interviews

Hunting pattern	Minimum	Maximum	Average	Median
Typical number of days hunting deer on POW each year	3	100	22.5	17.5
Average distance traveled (miles) away from vehicle or boat when hunting on foot	0	6	1.7	1.5
Average distance traveled (miles) away from home to hunt[1]	2	110	34.2	20.0

[1]Distance traveled by off-island residents who used ferry access was measured from Hollis terminal to hunting area.

Hunter competition

According to POW residents, slightly more than half (54%) perceived that off-island hunters have affected their hunting experience and their households' deer hunting success, but less than half reported that off-island hunters competed with them for deer (43%), interfered with their hunt (19%), or forced them to change where (41%) or how (38%) they hunt. According to off-island residents, 45% said they have competed with other hunters while on POW, none reported that their hunt had been interfered with, 30% have changed how they hunt because of competition, and 70% have changed where they hunt because of other hunters. Eighty percent of off-island residents reported they hunt the northern half of POW, and few reported that they hunt the outer islands or the southern portion of POW.

Harvest Patterns

Harvest numbers and needs

Typically, hunter households harvested a median of 4 deer each year, which was equal to the number of deer required to meet their own household needs, but less than the number required to meet both their needs and other households for which they provide deer (Table 4). Most hunters (73%) reported that they share deer meat, and 51% of those sharing provided deer to 3 or more other households. Sixty-four percent of hunters reported that their household needs did not change from year to year. For those hunters whose household needs changed (36%), change (increase and decrease) was attributed to a shift in the age and number of members in the household (50%) followed by needs of others (21%) and amount of other types of harvest (21%) such as fish, moose, or caribou. On average, deer were reported to be the main source of red meat in hunter households according to both POW and off-island residents (Table 4).

Dependence on deer as a meat resource was not predicted to change over the next 20 years according to 43% of hunters interviewed. Those who predicted an increase (26%) in dependence on deer mainly attributed this change to a future decline in the desire for beef followed by decline in the economy and a rise in the human population on POW in the future. Those hunters that predicted a decline (31%) in dependence on deer mainly attributed this to a shift in human values where more humans will perceive deer as a non-consumptive resource rather than a harvestable resource. Other reasons given for a predicted decline in dependence include: an increased difficulty to harvest a deer, a younger generation of people that hunt less, and groceries becoming more accessible.

Harvest effort

According to interviews, 49% of hunters perceived that time and effort needed to harvest a deer have remained the same over the last 5 years; whereas, 36% perceived more time and effort and 14% perceived that less time and effort were needed to harvest a deer. Those who felt more time and effort were needed attributed this change to more hunting competition and pressure, followed by less desirable deer population characteristics (low supply, age structure with low percentage of mature animals, and sex structure with low percentage of bucks). Those who perceived less time and effort were needed attributed this change to milder winters and better access to deer, followed by an abundant supply of deer available for harvest.

Table 4. Harvest patterns reported by hunters during interviews

Harvest pattern	Minimum	Maximum	Average	Median
Number of deer harvested during a typical year	1	30	6.1	4.0
Number of deer required to meet the hunter's household needs for a year	1	20	5.4	4.0
Number of deer required to meet needs of both hunter's household and others households that hunter provides deer for	1	25	7.6	6.0
Portion of red meat (fish not included) that hunter's household consumes that comes from deer	5%	100%	64.4%	68.5%

Deer Population Trends

Deer population abundance & supply

Forty-four percent of hunters perceived that the deer population on POW has remained stable over the last 5 years in the areas where they hunt. Hunters who perceived an increase (30%) in deer population size mainly attributed it to mild winters (Table 5). Hunters who perceived a decline (26%; Table 6) mainly attributed this to over harvest. Hunters (66%) reported that they mainly used the number of deer they see along roads and while hunting to estimate deer population. Other popular indicators used by hunters to estimate deer numbers were sign (38%; pellets, rubs, tracks) followed by deer harvest efficiency (5%). Less than 3% of hunters reported that they use biological data, word-of-mouth, or other indicators to form an opinion on deer population size on POW.

Table 5. Ranking of potential causes of an increase in deer population size over the last 5 years

Cause of increase in deer population	Overall rank: 1 = main cause, 4 = least cause
Mild winters	1
Less predation	2
Less hunting pressure	3 (tie)
Better habitat	3 (tie)
Other	4

Forty-three percent of hunters perceived that there were enough deer on POW to meet human demand; however, 30% reported that there was a surplus and 28% of hunters reported a shortage of deer. Hunters mainly used their harvest efficiency and number of deer observed to determine whether there was a shortage, surplus, or enough to meet demand.

Table 6. Ranking of potential causes of a decline in deer population size over the last 5 years

Cause of decline in deer population	Overall rank 1 = main cause, 7 = least cause
Over harvest	1
Legal doe harvest	2
Illegal harvest	3
Wolf predation	3
Habitat loss	4
Bear predation	5
Harsh winters	6
Other	7

Physical condition of the deer population

Nearly all hunters (90%) reported that the deer they harvested or observed on POW over the past 5 years were in good physical condition. Eight hunters (9%) reported that deer were in average condition, and 1 (1%) hunter stated that deer were in poor physical condition. Fat content and appearance were the primary indicators used by hunters to determine condition of a deer. Many hunters (38%) reported that there seemed to be more or healthier deer in certain areas, particularly in alpine habitats but also in clearcut forest and remote areas. Some hunters reported that less healthy deer were located in second-growth forest habitat.

Research to improve management of the deer population

Although deer management and hunting regulations were not the focus of interviews in this study, hunters were asked for their thoughts concerning deer research needs. Hunters reported that research on estimation of illegal deer harvest followed by research on the effects of wolf predation would be the most valuable types of research to improve deer management on POW (Table 7). Research on population estimation of deer was reported as the top research priority by many hunters; however, an equal number of hunters

reported that population estimation of deer was the least needed type of research. Because of the overall lack of consensus on the value of this type of research, population estimation received a middle ranking.

Table 7. Ranking of types of research needed to improve management of the deer population on POW

Type of Research	Overall rank 1 = most needed 7 = least needed
Estimate illegal harvest	1
Effects of wolf predation	2
Fawn survival & recruitment	3
Effects of bear predation	4
Population estimation	5
Deer habitat decline	6
Deer reproduction	7
Other	8

Habitat and Hunting Access

Hunting areas

Muskegs were identified as the most popular habitat type to hunt followed by clearcuts (Table 8). Areas that were recently pre-commercially thinned were the least popular. Many hunters (64%) said thinned habitat decreased the quality of the hunt and that they avoided those areas. The remaining hunters (36%) reported that thinning had increased the quality of hunting in those areas, or they perceived that thinning will improve the quality of their hunt in the future.

Table 8. Ranking of preferred hunting areas by habitat type

Habitat type	Overall rank 1 = most popular 8 = least popular
Muskeg	1
Clearcut forest	2
Alpine	3
Old-growth forest	4
Beach/shoreline	5
Second-growth forest (stem exclusion stage)	6
Recently pre-commercially thinned forest	7
Other	8

Habitat change

The reported quality of hunting in clearcut forest depended on the age of the clearcut. Hunters reported that the best hunting in clearcuts began on average 2 years (ranged from 0 to 5 years) after an area has been logged, and hunt quality began to decline on average when a clearcut reached 9 years of age (ranged from 2 to 20 years). Eighty-six percent of hunters reported that cleacuts eventually can no longer be hunted and this occurred on average at year 14 (ranged from 3 to 45 years) and a median of 12 years. After a clearcut forest converts to second-growth forest, 49% of hunters don't feel it can be hunted again;

whereas, 7% feel it can be hunted again with proper management such as thinning. Forty-four percent of hunters believed that a second-growth forest can be hunted again after reaching an average age of 50 years (ranged from 25 to 100 years) and a median age of 40 years, but the quality of the hunt in those areas is still inferior to most other habitat types.

Road construction and closure

Hunters had mixed opinions on the effects of roads on deer hunting and the deer population, and some responses were contradictory. For instance, most hunters reported that road construction and the extensive road network on POW had increased their hunting success and decreased effort. However, most hunters also reported that road closures had no effect on their hunting success and effort (Table 9). Contradictions like these are complicated and will be further explored and explained in future papers.

Hunters generally perceived that road construction and the extensive road network have had a negative effect on deer populations and that road closures have had a positive effect. Many added that hunting is better on new roads because of increased access to previously remote deer habitat, and new roads are usually located next to young clearcut forest (Table 8). Nonetheless, hunters perceived a decline in hunt quality along roads over time due to increased hunting pressure and increased forest growth next to roads. Road closures have made 47% of the hunters interviewed change their hunting strategy. Further, many hunters reported that they seek out and select areas with closed roads to avoid competition with other hunters, and because they believe there are more deer in those areas.

Table 9. Responses by hunters to questions addressing roads and road closures

Question	Increased	Decreased	No effect
How have road construction and the road network affected hunting success?	59%	10%	31%
How have road construction and the road network affected hunting effort?	9%	47%	44%
How have road closures affected hunting success?	33%	25%	41%
How have road closures affected hunting effort?	43%	9%	48%
How have road construction and the road network affected deer populations?	16%	49%	35%
How have road closures affected deer populations?	68%	0%	32%

Historic Estimates and Future Predictions of the Deer Population

Over the next 25 years, hunters predicted that the largest effect on the deer population on POW will be hunting pressure and harvest, followed by habitat change (i.e., clearcuts converting to second-growth forest) and weather (Table 10).

Table 10. Categorized factors predicted to have the largest effect on deer populations over the next 25 years

Factor[1]	% of hunters
Hunting pressure and harvest	36.4
Habitat decline	23.9
Weather	23.9
Predation	15.9
Deer management/regulations	14.8
Human development and population growth	12.5
Forest management (particularly second-growth)	10.2
Decline in logging activity	9.1
Illegal harvest	5.7
Shift in human attitude (deer looked at as a non-consumptive resource instead of sport or subsistence resource)	2.3

[1]Hunters often stated more than 1 factor

In contrast to responses by hunters on the question about deer research needs (Table 7), illegal harvest was not a common response by hunters when asked about large effects on the deer population over the next 25 years. This may be because hunters perceive illegal harvest as a problem that can be fixed with proper management in the near future. Further investigation on this issue is needed.

Hunters were given a graph and asked to draw a line that illustrated their historic estimate and future prediction of deer abundance on POW (Fig. 1). Estimates and predictions of deer abundance from 1975 to 2045 varied considerably among hunters, and the average of the estimates fluctuated around 40,000 deer with a slight increase in deer numbers during the 1980s followed by a slight but steady decline into the future. Hunters estimating an increase over the last 30 years mainly attributed this to mild winters and intensive logging activity creating better habitat for deer. Hunters estimating a decrease over the last 30 years mainly attributed this change to hunting pressure. Hunters predicting an increase in deer numbers in the future attributed this to less hunting pressure, improved management, and continued mild winters. Hunters predicting a pressure, improved management, and continued mild winters. Hunters predicting a decrease in deer numbers in the future attributed this to over harvest and a decline in deer habitat because of a less logging activity and clearcuts converting to second-growth forest. Many hunters reported a best-case and worst-case scenario for deer abundance in the future. Often, the worse-case scenarios reported by hunters were the result of poor deer and forest management, particularly management of second-growth forest.

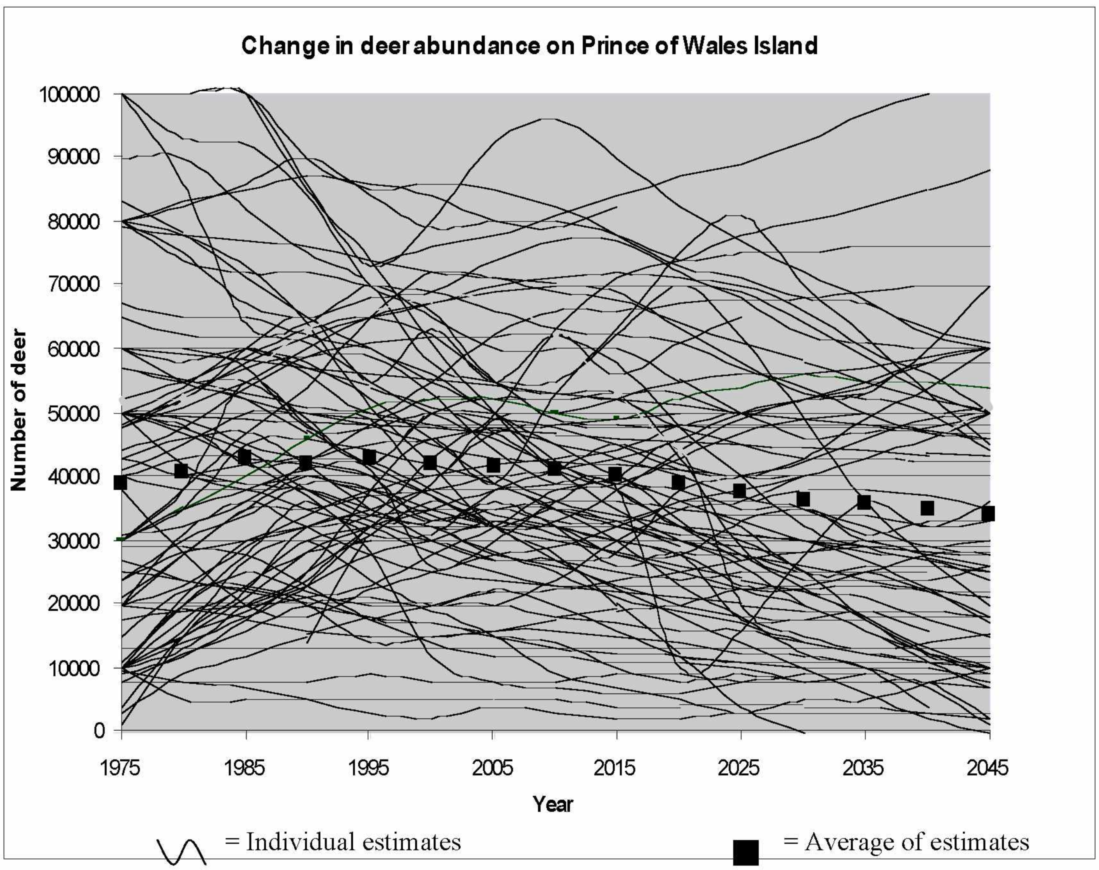


Figure 1. Hunters' historic estimates and future predictions of deer abundance on POW

Additional Comments by Hunters

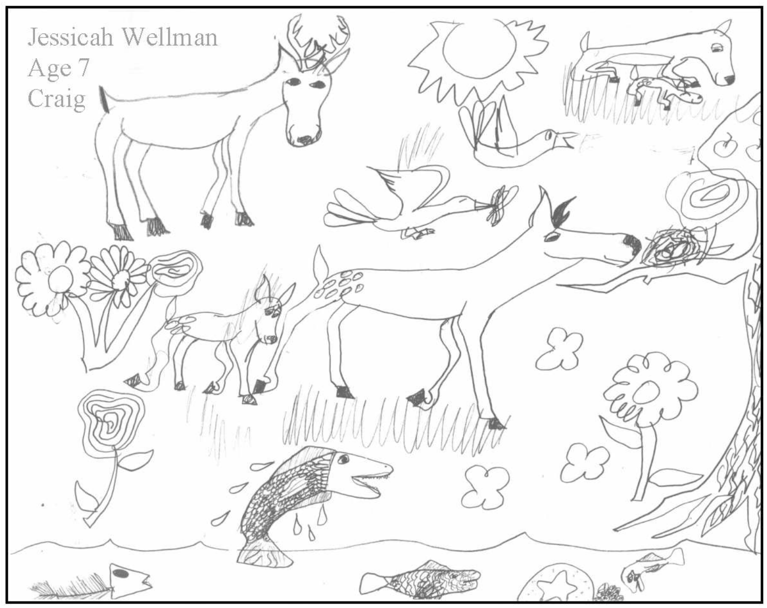
the negative effects of the doe season and illegal harvest. Some felt that length and timing of the deer hunting season should be changed and regulations with antler size restrictions (e.g., "forked horn" or better) should be initiated. Regarding forest management, hunters expressed concerned about the indirect effects (e.g., less access due to road closures) that a future decline in logging activity will have on hunting. In addition, management of second-growth forest was mentioned by many hunters as a critical step to sustaining high-quality deer hunting on POW.

Acknowledgments

I sincerely thank all the hunters who participated in this study for kindly sharing their time, knowledge, and hunting experiences. Many hunters and their families, who will remain anonymous, went well beyond normal hospitality to assist me with my research and make me feel welcome. Craig Community Association, Hydaburg Cooperative Association, Klawock Cooperative Association, and the Organized Village of Kassan assisted with interview participation and scheduling. Alaska Department of Fish and Game Division of Wildlife and USDA Forest Service provided logistical support. Thank you T. Chapin, A. Christianson, G. Killinger, G. Kofinas, S. McCurdy, D. Person, K. Peterson, B. Porter, L. Trimmer, W. Smith, B. Wright, and A. Wyatt. Funding for this study was provided by Alaska Trappers Association; National Science Foundation's IGERT and LTER Programs; University of Alaska Fairbanks' (UAF) Biology and Wildlife Department, Institute of Arctic Biology, and Resilience and Adaptation Program. Winning drawings from the *Prince of Wales Island Wildlife Art Competition*

were used to illustrate this report. The theme of the art competition was "Prince of Wales Island deer hunting". I thank all the schools and teachers on POW who participated in the competition, and especially the talented students who submitted their drawings. Professor Joan Hornig and students from her UAF Art Seminar helped select winning drawings.

Additional Information



Detailed information collected during interviews was not included in this summary report. A comprehensive analysis of hunter interview information is currently in progress and results will be presented in future papers. I welcome feedback on the results and encourage help from communities in interpreting findings. If you would like to request copies of future papers, have questions about this report, or have general questions about *The Prince of Wales Island Deer Hunter Project*, please don't hesitate to contact me.