

Ecology of black-tailed deer in north coastal environments

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Abstract

This paper provides an overview of the ecology of black-tailed deer in different environments, with specific reference to their introduction to Haida Gwaii (Queen Charlotte Islands, British Columbia) and aspects of the ecology of Sitka black-tailed deer *Odocoileus hemionus sitkensis* that help us understand the impacts that black-tailed deer have had on Haida Gwaii; it emphasizes the flexibility of black-tailed deer in different environments. After reviewing the taxonomy of the *Odocoileus hemionus* subspecies found in British Columbia, I briefly examine the current population status and factors that influence local populations of black-tailed deer, including demographics, predation, the importance of cover and habitat, movements, and ecology. Coastal black-tailed deer are energy-limited, and their dietary and physiological flexibility are key to their success in coastal rainforests. Deer can take advantage of a large number of plant species, seasonal shifts in available species, and a variety of accessible habitats. Deer utilize high-quality food in summer to regain body mass, which is then depleted during winter, when food intake is less than energy requirements. The highest energetic costs to female deer are associated with late pregnancy and lactation, and these activities normally coincide with an abundance of new plant growth in spring. Sitka black-tailed deer impact their environment by removing large amounts of plant material during a growing season and woody material during winter. Over the long term, removal of fruiting or storage parts of plants can affect survival of the plants and, if sustained, the diversity of the forest. Overall, browsing impacts are influenced by the number and density of deer on the landscape and the ability of plants to defend themselves against and recover from browsing by deer.

1. Introduction

Sitka black-tailed deer *Odocoileus hemionus sitkensis* are an important species within the north coastal forests of British Columbia and southeast Alaska with respect to biological conservation, economic development, and human culture (Hanley 1993). Consequently, much has been written about this species, including both biological (e.g., McTaggart-Cowan 1945; Klein 1965; Wallmo and Schoen 1979; Schoen et al. 1981; Wallmo 1981a; Hanley

1984; Parker et al. 1999) and human (e.g., Nelson 1997) perspectives. Reviews of the ecology and management of Columbian black-tailed deer *Odocoileus hemionus columbianus* are even more extensive (e.g., Bunnell et al. 1978; Wallmo 1981a; Nyberg et al. 1989; Kie et al. 2002). It is impossible, therefore, to review the ecology of deer in north coastal environments in a brief and inclusive way. Instead, I focus on those aspects of Sitka black-tailed deer ecology (in relation to other black-tailed deer species) that demonstrate the flexibility of this species in a range of environments; an understanding of this flexibility should help us understand the impacts that black-tailed deer have had on Haida Gwaii since their introduction to the archipelago, a focus of this volume.

I begin with a summary of the taxonomy and distribution of the subspecies of deer found on Haida Gwaii (Queen Charlotte Islands, British Columbia) and the north coast of British Columbia and southeast Alaska. I then examine the key factors that affect their population dynamics, starting with demographics and population regulation with and without predators. Relying heavily on data collected for Sitka black-tailed deer over a continuous 2.5-year period (see Parker et al. 1993, 1996, 1999; Gillingham et al. 1997), I review nutrition and food habits and emphasize some of the interactions between these deer and their environment that should help us understand their success since being introduced to Haida Gwaii.

2. Taxonomy and range

As a species, mule deer *Odocoileus hemionus* are widespread and adaptable. The subspecies of mule deer inhabit a range of habitats, from the wet coastal forests of Alaska and British Columbia to dry desert environments and from the boreal forest of Yukon south to the interior semidesert shrub woodlands of northern Mexico (see Wallmo 1981b for a detailed review). Depending on the emphasis placed on overlap among subspecies, between 7 and 13 subspecies of mule deer have been recognized by taxonomists (e.g., McTaggart-Cowan 1956; Wallmo 1981b). More recently, Krausmann (1994) recognized 10 subspecies of *Odocoileus hemionus*, ranging from Alaska south to central Mexico.

Within British Columbia, there are three subspecies of mule deer. Although there are areas where

the distributions of the subspecies overlap (see Shackleton 1999), Rocky Mountain mule deer *Odocoileus hemionus hemionus* are generally found to the east of the coastal range and throughout much of the interior of the province, where they tend to prefer open forested areas or parklands with adjacent grasslands (Shackleton 1999). Along the coast, two other subspecies use the dense coastal rainforests as well as more open habitats, such as riparian and early successional stages of forests; the dense forest canopies afford a number of advantages to both Columbian black-tailed deer and Sitka black-tailed deer. These two subspecies are difficult to distinguish in the field, especially in areas where their ranges overlap. Columbian black-tailed deer are found across Vancouver Island (Shackleton 1999), on most of the smaller islands, and on the west slopes of the Coast Mountains north towards Rivers Inlet, where they begin to intergrade with the more northern Sitka black-tailed deer. The latter are found north of Rivers Inlet to the Portland Canal, where the distribution becomes patchy (Shackleton 1999). As discussed extensively throughout this volume, Sitka black-tailed deer were introduced several times onto some of the islands of Haida Gwaii beginning in the 1870s to provide venison for the local community. They are now very abundant on most of the larger islands in this archipelago, and they have colonized all but the smallest and most isolated offshore islands (Martin and Daufresne 1999). Throughout this review, I use the common name mule deer to refer specifically to work done on *O. h. hemionus*. In those instances where I refer generically to black-tailed deer, I am referring to both Columbian (*O. h. columbianus*) and Sitka (*O. h. sitkensis*) black-tailed deer, as in Wallmo (1981a).

3. Population status

In recent years, both mule deer and black-tailed deer populations have declined in many areas of the western United States and Canada; predation has been proposed frequently as a possible explanation (see review of Ballard et al. 2001). The effects of predator-prey relationships, however, are confounded by habitat carrying capacity, weather, human use patterns, and habitat alterations (Ballard et al. 2001). Consistent with the larger pattern of decline, black-tailed deer on Vancouver Island have been declining over the last two decades (B.C. Ministry of Environment, Lands, and Parks 2001). During the severe winter of 1968–1969 on Vancouver Island in particular, as many as 100 000 deer died of starvation.

Population estimates for coastal deer populations in British Columbia are approximate. For example, Sharpe (1999) indicated that no quantitative data for Sitka black-tailed deer populations on Haida Gwaii existed, because of the difficulty in counting this species. Nonetheless, estimates from 1997 contained in Shackleton (1999) suggest that there may be in excess of 65 000 Sitka black-tailed deer in British Columbia (inclusive of Haida Gwaii and mainland populations). Martin and Baltzinger (2002), however, speculate that there might be over 113 000 deer on Haida Gwaii. Other reports suggest that although mule and black-tailed deer populations are currently declining in 31% of their historic range (predominantly on Vancouver Island; B.C. Ministry of Environment, Lands, and Parks 2001), the Sitka

black-tailed deer populations of coastal British Columbia and of Haida Gwaii are “stable” (B.C. Ministry of Environment, Lands, and Parks 2001).

4. Population demographics and regulation

As with most deer species, Sitka black-tailed deer populations can increase rapidly in number. Females usually do not breed until their second year, although first-year breeding has been observed (e.g., McCullough 1997; K.L. Parker and M.P. Gillingham, unpubl. data). After the first reproduction, females usually produce annually throughout an approximate life span of 10 years. Typically, fawns are born in early June, weighing approximately 3 kg at birth. Reproductive rates may be higher on Haida Gwaii, although reproductive data are limited. Sharpe (1999) suggested that on Haida Gwaii, onset of reproduction occurs in the first year, with females reproducing every year throughout their approximately 7- to 10-year life span. On Haida Gwaii, most litters tend to be of twins (range 1–3; Sharpe 1999).

Although weather can have both direct and indirect effects (e.g., on forage availability) on deer species in general (Connolly 1981), weather is likely far less important for black-tailed deer in coastal environments. This reduced effect may be greatest where natural predators are largely absent (e.g., Haida Gwaii), because snow, when present, will not influence predation success. Connolly (1981) argued that limitation of deer numbers in general results from a combination of weather, food supplies, predation (including hunting), parasites, disease, and human activities in deer habitats. Sharpe (1999) suggested that food and climate are the major factors controlling deer numbers in Haida Gwaii, but their combined effects are greatly reduced because of the absence of typical predators, such as wolves *Canis lupus* and mountain lions *Puma concolor*.

4.1 Importance of predation and competition

When predators are present, they can have significant impacts on populations of deer. Ninety percent of fecal samples from Alexander Archipelago wolves *Canis lupus ligoni* on Prince of Wales and adjacent islands, southeast Alaska, contained remains of Sitka black-tailed deer ($n = 182$; Kohira and Rexstad 1997). Deer remains occurred exclusively in 45% of the scats (Person et al. 1996). Coronation Island (southeast Alaska) has afforded the opportunity to monitor the dynamics of a Sitka black-tailed deer population first without, then with, and then again without wolves as predators (see Lewis 1992; Klein 1995): in 1960, wolves were introduced to Coronation, and the population of wolves grew quickly, along with the expected reduction in deer numbers and recovery of the vegetation; by the mid-1970s, wolves appeared to have died out on the island, and the deer population rebounded strongly by the late 1980s (see Kirchoff and Person this volume).

In a recent review, Ballard et al. (2001) concluded that although predation by coyotes *Canis latrans*, mountain lions, and/or wolves may be a significant mortality factor for mule and black-tailed deer in some areas and under

some circumstances, there are very few published studies of the effects of predation on black-tailed deer, and most of them focused on Columbian black-tailed deer on Vancouver Island. Wolves are thought to have migrated in significant numbers to Vancouver Island in the 1970s to reestablish a viable population (Jones and Mason 1983; Atkinson and Janz 1994) and have been seen as a primary cause of the decline of the local Columbian black-tailed deer populations. Wolf control on Vancouver Island resulted in demographic changes (particularly increased recruitment to the adult populations) in the black-tailed deer population (Hatter 1988; Hatter and Janz 1994).

Black bears *Ursus americanus* and grizzly bears *Ursus arctos* are also known to take Sitka black-tailed deer, but the impacts of this predation are unstudied; this may be of particular interest on Haida Gwaii, where black bears are present, their impacts as predators on deer recognized but largely undocumented. The impact of predation is influenced by severe winters and changes in wintering habits as a result of forestry (B.C. Ministry of Environment, Lands, and Parks 2001). To help identify the relative effects of predation and other factors on black-tailed deer demography, 95 adult Columbian black-tailed deer were collared from February 1982 through June 1991 (McNay and Voller 1995). Deaths were from wolves, mountain lions, legal hunting and poaching, malnutrition, and accidents; wolves and mountain lions accounted for 61% of all deaths. Mountain lions were the most important predators. Predators concentrated on adult female deer from February through July. Very few adult deer died during summer, when both predators were presumably targeting fawns (McNay and Voller 1995). McNay and Voller (1995) argued that annual survival rates of resident deer at low elevations (73%) were not high enough to sustain populations. Of the 24 female fawns ($n = 12$) and yearlings ($n = 12$) with radio collars, only 1 fawn and 9 yearlings lived to become adults (McNay and Voller 1995). The overall survival rate of adult black-tailed deer was 74%, but migratory black-tailed deer had much higher survival (90%), presumably because resident deer remained at low elevations and were most prone to predation. Beyond the direct impact of predation, McNay and Voller (1995) emphasized that an essential condition to rebuild dwindling populations of Columbian black-tailed deer on Vancouver Island will be the amount of older intact forests left at low elevations. They concluded that forest harvesting (and associated activities) and spatial isolation of winter habitats may intensify predation on resident deer and impede recruitment of migrating deer. Besides affecting survival, predation (including hunting) also influences the behaviour of herbivores (Brown et al. 1999) and the way in which they can use or not use their habitat. On Haida Gwaii, regeneration of western redcedar *Thuja plicata* was much greater and overall deer impact lower in areas where deer were more exposed to hunting (Martin and Baltzinger 2002).

Competition is another possible extrinsic factor affecting black-tailed deer population dynamics. Sitka black-tailed deer, however, likely do not have significant competition from other ungulates. In areas of southeast Alaska where elk *Cervus elaphus* have been introduced (they also have been introduced on Haida Gwaii, where their diet has not been studied; see Golumbia et al. this volume), diets

of deer and elk were similar during mild, relatively snow-free winters, with both species utilizing salal *Gaultheria shallon*, red huckleberry *Vaccinium parvifolium*, and western redcedar (Kirchhoff and Larsen 1998). Elk, however, ate more grasses (Poaceae) and sedges (Cyperaceae) than deer; deer ate more forbs and low-growing evergreen plants than elk (Kirchhoff and Larsen 1998).

4.2 Importance of cover and habitat

Throughout the range of Sitka black-tailed deer, cover is important for survival: to reduce energy expenditures for thermoregulation and for locomotion during periods of high snow cover, to limit food burial by snow, and to allow for escape and hiding from human and nonhuman predators (Nyberg et al. 1989). The coastal areas of northern British Columbia and southeast Alaska are made up of rugged mountains, high-rainfall forests, and thousands of kilometres of shoreline. Although there are occasional examples of large-scale blow-down in coastal forests, wind more commonly affects individual or small groups of trees, resulting in the maintenance of multiaged, diverse stands (Brady and Hanley 1984). Consequently, unlogged coastal old-growth forests are often characterized by a high frequency of low-impact disturbances that result in an interspersed dense forest canopy with openings containing large amounts of available biomass for deer. This juxtaposition of habitats and forest edge is important to deer (Kirchhoff and Schoen 1983; Kremsater and Bunnell 1992), and their use of different seral stages and habitat types within coastal environments varies seasonally.

Throughout most of their range, the habitat of Sitka black-tailed deer has been affected by extraction of timber. Clearcuts produce large amounts of biomass in summer but offer little snow interception in winter, while the dense canopy of old-growth forests provides snow interception, as well as a litter of lichen and twigs. Several studies have demonstrated that snow can be a major factor influencing winter survival of Columbian black-tailed deer and Sitka black-tailed deer (Klein and Olson 1960; Bunnell et al. 1978; Jones and Mason 1983), both through the reduction of available forage (Harestad et al. 1982; Hanley and McKendrick 1983; Hovey and Harestad 1992) and because of the increased energetic costs of movement (Parker et al. 1984). Black-tailed deer sinking depth (Bunnell et al. 1990a,b) was greatest in clearcuts and intermediate in 20-year-old stands. It was lowest in old-growth and 80-year-old stands. The energy cost of moving through 25 cm of snow is about 2.5 times that of moving through 10 cm and increases as snowpacks become deeper (Parker et al. 1984). In southeast Alaska, when snow depth in the open was >15 cm, black-tailed deer concentrated their activities in the highest-volume old-growth stands available within their home ranges (Schoen and Kirchhoff 1990). In fact, during these severe winters, older forests were very important for the survival of deer (see Harestad 1980, 1985; Schoen et al. 1985), and persistent snow caused significant deer mortality. A severe winter with heavy, persistent snow in 1999 caused a large increase in the number of starvation-related mortalities of deer compared with the mild winter of 1997–1998 (Farmer and Person 1999).

Deer living in coastal forests, however, are usually exposed to only moderate snow depths, unlike those that can occur for interior populations of mule deer (e.g., Armleder et al. 1994). In addition, winter temperatures that frequently move above and below freezing can result in a discontinuous snow cover for much of the winter. Coastal environments also provide deer with relatively nonstressful thermal conditions in all seasons. The temperatures below which deer are thermally stressed and must begin to increase metabolic rates to maintain an acceptable body temperature vary with seasonal pelage (Parker 1988). In winter, the lower critical temperature for black-tailed deer is -6°C ; in summer, it is $+12^{\circ}\text{C}$. In some winter months in southeast Alaska, almost 40% of the weather observations showed that animals were thermally stressed (February; Parker et al. 1999), but animals were also frequently below their lower critical temperature in summer pelage in June (Parker et al. 1999). For much of the year, however, the percentage of time when animals were thermally stressed is quite low (Parker et al. 1999). Mean temperatures for Haida Gwaii are 11.4°C and 4.8°C for summer and winter, respectively (Environment Canada, based on St. James and Sandspit weather data), so deer on Haida Gwaii are also likely to be more affected by temperature when they are in summer pelage.

Old-growth and commercially exploited forests also differ greatly in their production of forage, in the protein digestibility of sun- and shade-grown leaves, and, consequently, in their relative abilities to support black-tailed deer populations (Hanley et al. 1989). On Vancouver Island, deer generally used young (6–45 years old) rather than old forests and tended to use young forests a high proportion of time (65–75% of locations) (McNay 1995). As long as suitable winter habitat is interspersed with different forest types, black-tailed deer populations survive well and, in many cases, reach higher densities than in undisturbed landscapes. In southeast Alaska, Sitka black-tailed deer select old-growth forest over even-aged, second-growth stands, particularly during winter (Wallmo and Schoen 1980; Rose 1982; Schoen and Kirchhoff 1985; Yeo and Peek 1992). These selection patterns have been explained by variation in forage abundance and availability (Wallmo and Schoen 1980), nutritional quality (Hanley et al. 1989), and snow accumulation (Kirchhoff and Schoen 1987).

During most seasons, it is likely that interspersion of habitats best explains the distribution of black-tailed deer. Research on the importance of edge to deer has produced equivocal results, but likely cannot be evaluated without consideration of local landscapes (Kirchhoff and Schoen 1983); the effects of edge appear less important when forage and cover are interspersed (Kremsater and Bunnell 1992). Sharpe (1999) suggested that large clearcuts benefit deer on Haida Gwaii only if they have a southerly aspect and therefore experience early snowmelt. Logging has likely contributed to increased deer numbers in some areas of Haida Gwaii, because openings have increased the amount of palatable forage available to black-tailed deer, while old-growth forest is often available to provide cover. The scale of forest conversion, particularly over the past 40 years, however, results in large areas of dense second growth that is not particularly good habitat for deer.

5. Patterns of movement

Although there are likely groups of both migratory and resident animals, as well as dispersal movements within populations of black-tailed deer (e.g., Bunnell and Harestad 1983; Harestad and Bunnell 1983), seasonal movements appear to be less important for Sitka black-tailed deer than for mule deer. Across a range of studies (e.g., Harestad 1980; Loft et al. 1984; Schoen and Kirchhoff 1985; McNay 1995; Boroski et al. 1999), home ranges varied from 12 to 500 ha, with migratory deer having larger home ranges than residents, in part because of their migratory behaviour. Deer living at low elevations on Vancouver Island tended to have smaller home ranges than animals at higher elevations (Harestad 1980). Nonmigratory populations of black-tailed deer in environments lacking heavy snow may be limited by forage conditions in late summer (Taber and Dasmann 1958); although vegetation is always available, the quality of the available food may be limiting.

On Admiralty Island, southeast Alaska, 75% of collared Sitka black-tailed deer ($n = 51$) made seasonal migrations from low-elevation winter ranges to high-elevation (usually subalpine or alpine) summer ranges; the remaining 25% were year-round residents at low elevations (Schoen and Kirchhoff 1985). In addition to making extensive movements between summer and winter ranges, migratory deer were located at higher elevations than resident deer during all seasons (Schoen and Kirchhoff 1985).

McNay (1995) and others collared 17 juvenile Columbian black-tailed deer to study dispersal patterns on Vancouver Island. Only 2 of the 17 deer dispersed to new ranges, and McNay (1995) suggested that young black-tailed deer rely on their mothers' expectations of future resources for their home range. McNay (1995) documented three "types" of dispersers: "regular" migrators, which spend long periods away from their natal ranges each year; "resident" deer, which always stay close to their natal ranges; and "irregular" migrators, which move away from their natal ranges less regularly and for shorter periods. Regular migrators had natal ranges at relatively high elevations, from which they travelled an average of 5.5 km to their alternative ranges. On Vancouver Island, severe winter conditions do not occur very often at the lowest elevations, and the deer monitored there remained at their natal ranges all year. This is similar to the situation with Haida Gwaii deer (see Gaston et al. this volume).

Water is also an important component of coastal environments. Deer frequently cross water bodies to move among archipelago islands. Black-tailed deer frequently traversed large reservoirs in California, typically in groups of 2–3 animals (Boroski et al. 1999); as many as 389 black-tailed deer swam across a reservoir during daylight in a single migration. In another Californian study, black-tailed deer frequently made crossings of reservoirs up to 1.6 km (Loft et al. 1984).

6. Nutrition, food habits, and energy requirements

Extensive field assessments of black-tailed deer food habits and nutrition are rare and difficult to obtain. Parker and coworkers (1999) conducted an intensive multiyear study of Sitka black-tailed deer on Channel Island (southeast Alaska); throughout this section, I rely heavily on those results. During their study, Sitka black-tailed deer were observed eating more than 70 different plant species, 39 of which were forbs (see Parker et al. 1999 for a comprehensive list and details of seasonal use). In that study, deer ate varying amounts of all plants reported in the study area, although some were eaten only opportunistically: Alaska yellow-cedar *Chamaecyparis nootkatensis*, which washed up on the beach of the island; and European mountain ash *Sorbus aucuparia* and highbush cranberry *Viburnum edule*, which grew only on one extremely steep and relatively inaccessible slope of the study site. Other species appeared to be “tested” for palatability and eaten rarely (e.g., Sitka spruce *Picea sitchensis*) (Parker et al. 1999).

In coastal forests, deer have access to the highest forage biomass in summer, in terms of both the amount of forbs and the availability of deciduous leaves. In winter, forage biomass is reduced, but low snow accumulation under dense forest overstory leaves evergreen forbs available throughout much of the winter. As a result, diets of deer are dominated by leaves and forbs in summer and shrubs, with the addition of evergreen forbs, in winter. In southeast Alaska, deer diets indicated a general preference for herbs (excluding graminoids) over shrubs and for shrubs over conifers throughout the year (Hanley and McKendrick 1985). When herb-layer forages were buried by snow and deer consumed a shrub-dominated diet, estimated dry matter digestibility of black-tailed deer diets decreased from 58% to 38%, and digestible energy explained diet selection (Hanley and McKendrick 1985). Analyses of species composition and quality of the diet of black-tailed deer and nutritional quality of forages indicated that digestible energy and digestible protein were probably the greatest nutritional limiting factors for deer in Alaska (Hanley and McKendrick 1985).

To a large extent, weather determines what food is available in winter to Sitka black-tailed deer (see Parker 1994): wind may make arboreal lichens (*Usnea* spp. and *Alectoria* spp.) available to deer; snow cover will determine the availability of evergreen forbs, such as bunchberry *Cornus canadensis*, five-leaved bramble *Rubus pedatus*, and foamflower *Tiarella trifoliata*, or woody stems of oval-leaved blueberry *Vaccinium ovalifolium* and Alaska blueberry *V. alaskaense*; and temperature alone (through freezing the ground) can determine the availability of fern (e.g., *Dryopteris dilatata*) rhizomes (Parker et al. 1999; Gillingham et al. 2000). Finally, retreating high tides frequently expose entire beach areas that are suddenly snow free and available to foraging animals (Parker et al. 1999).

Plant consumption also depends on temporal availability. When a range of mushroom species were available in the autumn, deer searched extensively for them; in winter, black-tailed deer searched for windblown lichens following major wind events during winter (Parker et al. 1999). In addition, the consumption of parts of some plant

species depended on plant phenology. For example, deer consumed the fiddleheads of *Dryopteris* ferns in early spring, the green fern fronds during spring and summer, and the rhizomes in winter. Similarly, *Alnus* catkins and buds were eaten in early spring, the stems during winter, and the dried leaves in autumn. Other than *Carex* and *Fucus* spp., the numerous beach plants were all seasonally dependent forbs and therefore were not eaten during winter.

Overall, forbs, ferns, and skunk cabbage *Lysichiton americanum* constituted the largest component of dry matter intake by Sitka black-tailed deer in southeast Alaska during all months except January, February, and March (Parker et al. 1999). These forage species comprised 41–46% of the diet in September, November, December, and April; and 55–58% in August and October. From May through July, the herb-layer forages made up 69–74% of the diet eaten by Sitka black-tailed deer. Animals also ate large quantities of deciduous shrub leaves throughout the summer; in September, they consumed large amounts of fallen leaves (*Malus* and *Alnus* spp.). Between January and March, when herb-layer forages were covered in snow and contributed only 8% of the diet, deer ate primarily deciduous shrub stems and some conifer foliage. Shrub and conifer consumption was highest at 65% of the diet in January, declining to 42–47% in February and March (Parker et al. 1999).

Regardless of the foraging bout lengths and the lying bout times, black-tailed deer were active about 50% of the day throughout the year (Gillingham et al. 1997). In winter, the energy requirements exceeded intake for both male and female black-tailed deer (Parker et al. 1999)—regardless of how long the deer spent foraging or how far they travelled, the costs always exceeded the gains. In summer, however, food availability is higher and food quality is greater. Consequently, during summer, males were able to exceed requirements. For female black-tailed deer nursing twins, however, energy balance was also negative in midsummer at peak lactation (Parker et al. 1999). Females met their requirements (at that time, their intake rates were 50% higher than those of the males) only during spring and fall; this indicates the key contribution of body reserves to annual survival. Body reserves accumulated during summer with abundant digestible energy were critical to winter survival. In addition, body reserves are essential for survival in winter, because energy demands cannot be met by foraging alone; therefore, body reserves are used to make up the difference in surviving animals (Parker et al. 1999). In contrast, daily protein intake remained above demand during all months of the year except February, whereas deer were unable to meet energy requirements for more than half the year (Parker et al. 1999).

Body masses are generally highest in September through October and lowest in March. Body mass for mainland Sitka black-tailed deer shows a marked seasonal pattern, with declines in body mass ranging from 14% to 31% between October and March (Parker et al. 1993); the amount of mass lost over winter depends on the peak body mass attained during fall (Parker et al. 1993). Male black-tailed deer tend to have the highest percent body fat in October to November, just prior to peak rut in November, whereas female body condition is highest in late summer (Parker et al. 1999).

7. Impacts on vegetation

Exclosure studies have repeatedly shown that black-tailed deer have diverse impacts on their food plants, especially for longer-lived plant species (e.g., Stockton et al. 2001; Warner and Cushman 2002). This is particularly true when black-tailed deer are at high densities. In southeast Alaska, Klein (1965) observed that heavy use by Sitka black-tailed deer on Coronation Island resulted in a greatly reduced biomass of the forest understory; forage species preferred by black-tailed deer were nearly eliminated. Major impacts of deer on the forests of Haida Gwaii have been extensively described (Pojar and Banner 1984; Pojar 1999) and are the subject of many of the papers in this volume. Many of the highly utilized species from the mainland (see Parker et al. 1999), including Alaska blueberry, false azalea *Menziesia ferruginea*, spiny wood fern *Dryopteris dilatata*, bunchberry, five-leaved bramble, salmonberry *Rubus spectabilis*, devil's-club *Oplopanax horridus*, false lily-of-the-valley *Maianthemum dilatatum*, and skunk cabbage, are greatly reduced in their relative abundance on Haida Gwaii compared with the coastal mainland (Pojar 1999). Browsing by Sitka black-tailed deer introduced to Haida Gwaii has radically altered the vegetation of Haida Gwaii (B.C. Ministry of Forests 1980; this volume) and virtually eliminated most of the preferred forage species of black-tailed deer (Pojar 1999). Chemical and dendroecological analyses have recently been combined to demonstrate the relationship between deer density and the release of young Sitka spruce (Vila et al. 2002). Black-tailed deer may exert moderate to strong influences on the species composition and biomass of the forest understories, but their effect on dry matter digestibility, fibre, nitrogen, and phosphorus concentrations of individual species may be negligible (Hanley 1987).

Plants have evolved a number of methods of deterring herbivory, including physical defences, such as spines (e.g., devil's-club), and complex secondary compounds, such as terpenes (Connolly et al. 1980) and tannins (Robbins et al. 1987a,b; McArthur et al. 1993). Many of the forages that Sitka black-tailed deer consume have evolved such defences, although some of these defences may be reduced on Haida Gwaii (see Vourc'h et al. 2002). The amount and type of defensive compounds that plants develop in an attempt to deter herbivory depend on the conditions in which the plants are growing. For example, leaves of Alaska blueberry and bunchberry growing in three open clearcuts contained lower concentrations of nitrogen and higher concentrations of nonstructural carbohydrates and soluble phenolics (and greater astringency) than in two forests, but did not differ in *in vitro* dry matter digestibility (Hanley et al. 1987; Van Horne et al. 1988).

Black-tailed deer, however, have coevolved with these defences. Proteins in the saliva of deer bind to plant tannins to minimize absorption of tannins in the digestive tract and thus counteract the effects on digestibility (Robbins et al. 1987b; McArthur et al. 1993). In spring and summer, skunk cabbage can make up almost all of the diet of deer within some foraging bouts (Parker et al. 1999; Gillingham et al. 2001), despite the relatively high concentrations of cyanide. Black-tailed deer appear completely unaffected by

these compounds and readily select skunk cabbage because of the high intake rate that they can achieve when eating large leaves. Another example of the adaptability of black-tailed deer is their extensive use of devil's-club despite the spines that cover the stems, petioles, and underside of the leaves. Deer consume these leaves from the top and are seemingly undeterred by this physical defence.

8. Conclusions

Across their range in British Columbia and Alaska, Sitka black-tailed deer populations are affected by weather, predation, habitat alterations, and energy limitation. The effects of these factors are interdependent. The effects of predation, for example, appear to be confounded by habitat alterations.

Black-tailed deer have a tremendous potential for rapid increases in number due to their early age of first reproduction, annual breeding, and capacity for twinning. This can be seen both in population recoveries after severe winters and in areas where they have recovered after predators have died out (e.g., Coronation Island). They are able to survive and reproduce in a system in which they can be in an energy deficit for much of the year. Their high reproductive rates combined with the absence of significant predation have resulted in the dramatic increase in Sitka black-tailed deer populations on Haida Gwaii over the last century and resultant effects on the native vegetation of Haida Gwaii described elsewhere in this volume. The likely presence of resident, migratory, and dispersing individuals within populations needs to be considered in terms of their ability to recolonize areas.

Black-tailed deer appear to be able to deal with a range of plant defences, and they can have a marked effect not only on the amount of plant biomass, but also on plant community structure. They can exploit a variety of habitats and consume a wide range of seasonally available forage species. Their life history is well timed to take advantage of the spring flush of foods that are high in energy and protein. Black-tailed deer appear to make the most of a relatively short period of time when they can consume more energy than they expend. This is demonstrated in their marked fluctuations in body mass and their ability to put on reserves to get through winter when forage availability is reduced, even in severely browsed systems. The challenges posed by Sitka black-tailed deer are in part due to the flexibility of black-tailed deer as a species.

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