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In the context of remarkable increases in many deer populations observed in temperate forests, it is critical to better understand the processes sustaining abundant populations despite dramatic declines in the vegetation they feed on. When natural predation and hunting levels are too low to control deer populations, a resource-driven negative feedback is expected. Such a feedback assumes that the remaining resources do not match the energy requirements of a current herbivore population, thereby limiting herbivore abundance. Here we take advantage of a well-documented, long-term study of abundant predator-free populations of black-tailed deer *Odocoileus hemionus sitkensis* on the Haida Gwaii archipelago (Canada) to assess the ability of a heavily browsed forest habitat to sustain abundant deer populations. For two deer populations, we: 1) compared the energy provided by various resource pools to the energy required by deer; and 2) identified what components of the environment contributed most to support them. Qualitatively, our results are robust to the many assumptions and uncertainties and identify the resources currently available that allow these abundant deer populations to meet their energy needs despite the apparent paucity in resources. Resources are provided by a flux of hardly visible plant tissue produced by perennial species highly tolerant of herbivory and able to survive via underground structures (e.g. rhizomes), and by subsidies provided by canopy trees or by plants in refuges (i.e. litterfall and seed bank). We discuss the possibility of a resource-driven feedback that may ultimately occur in the long term as a result of changes in recruitment, productivity and fertility of plants. The possible lack of resource-driven feedback in the short or medium term should be considered by managers when assessing the need for active deer population control in situations without carnivores or hunting.

The current growth of large herbivore populations in temperate forests has significant ecological and socio-economic impacts (e.g. changes in forest regeneration, crop damage, Rooney and Waller 2003, Côté et al. 2004). A better understanding of the factors limiting these populations can contribute to improving management strategies. Limits to population growth depend on a combination of both top–down (descending control of predators on their prey) and bottom–up (ascending control of available resources on their consumers) processes (Bonenfant et al. 2009, Ripple and Beschta 2012, Forrester and Wittmer 2013).

In many places of the northern hemisphere, natural predators have been reduced and/or habitats have been altered in favor of herbivore populations. Current levels of natural predation and hunting are often too low to exert significant control on large herbivore abundance (Crête and Daigle 1999). In this situation, deer populations are most likely limited by direct effects of harsh climatic conditions and/or a lack of resources via a resource-driven, density-dependent, negative feedback (Sæther 1997, Simard et al. 2008, Bonenfant et al. 2009). The speed at which such a feedback occurs depends on how quickly the total population impact translates into lower resource production. This in itself is linked to the time needed for the herbivore impact to affect the plant demographic stage that provides resources to the herbivore. Defoliation has an immediate impact on resource availability, but further resource decline may occur with habitat changes linked to slow-paced effects on plant demography (Bardgett and Wardle 2003). However, the magnitude and dynamics of these effects is not necessarily easy to quantify. Whereas palatable small-sized shrubs and forbs may be quickly overbrowsed leading to a short-term decline in this resource (Horsley et al. 2003), some herbaceous vegetation can also be strongly defoliated but their relatively inaccessible meristems ensure rapid regrowth and thus little impact on short-term plant demography (Rooney 2009). Other resources, such as tall-tree canopy litterfall subsidies, reported for black tailed deer on Vancouver Island, Canada (Rochelle 1980), for white-tailed deer *Odocoileus virginianus* on Anticosti Island, Canada (Tremblay et al. 2005) and for sika deer *Cervus nippon* in Japan (Takahashi and Kaji 2001), may also contribute to sustaining ungulate populations in heavily browsed environments with little effect on short- or medium-term reduction in resource production. The link between a strong reduction in apparent resource abundance and herbivore abundance may therefore deserve closer attention.

Here we investigated the resources that sustain unchecked deer populations where most adult females reproduce despite a severe reduction in understory vegetation available to them. We took advantage of the exceptional situation offered by some islands of the Haida Gwaii Archipelago (British Columbia, Canada), where introduced Sitka black-tailed deer *Odocoileus hemionus sitkensis* have maintained high-density populations for decades despite dramatically browsed forest understories (Stockton et al. 2005, Martin et al. 2010). Introduced over 100 years ago to the northern part of the archipelago, deer colonized most of the islands in less than 50 years. They severely reduced tree regeneration (Stroh et al. 2008) and eliminated over 90% of the understory plant cover (Stockton et al. 2005), affecting animal communities that depend on understory vegetation (insects and birds: Martin et al. 2010). Although a population crash was documented on Haida Gwaii in the 1940s following the initial population explosion, deer densities have remained high since the 1950s (Golumbia et al. 2008) and were estimated to be more than 15 deer km^{-2} (Martin and Baltzinger 2002). With such dense populations and their impacts on native ecosystems, deer are a major concern for land management on Haida Gwaii (Golumbia et al. 2008).

To assess how this heavily browsed landscape is able to sustain the local deer populations, we measured the biomass of available plant resources, converted it to available energy, and then compared available energy to a model-based estimation of energy requirements of the deer populations based on previous detailed energy studies conducted on *Odocoileus* sp. in similar habitats (e.g. in Alaska, Hanley 1984, Parker et al. 1999, Hanley et al. 2012).

Material and methods

Study area

The study took place on two islands of Laskeek Bay on the eastern coast of the Haida Gwaii Archipelago (British Columbia, Canada): East Limestone (41 ha: 52°54′28″N, 131°36′49″W) and Kunga Island (395 ha: 52°45′53″N, 131°34′16″W). The climate is cool temperate, oceanic and humid-perhumid (Pojar 2008). The weather station in Sandspit (located 40 km north of the study sites) recorded a mean annual precipitation of 1400 mm with average monthly rainfall below 200 mm between 1971 and 2000. Summers are cool and moderately wet with average daily temperature between 6 and 15°C and monthly rainfall < 100 mm. Winters are mild with average daily temperatures between 3 and 10°C between October and March and snow is rare with an annual snowfall of 62 cm and an average monthly snow depth of 1.33 cm between December and February (Environment Canada data).

The landscape is dominated by closed coniferous forests of western hemlock *Tsuga heterophylla*, western redcedar *Thuja plicata*, and Sitka spruce *Picea sitchensis* with some deciduous trees such as red alder *Alnus rubra* (Pojar et al. 1980).These study islands were colonized and heavily browsed by deer for more than 60 years (Vila et al. 2004). All groups of vascular plants (i.e. forbs, grasses, shrubs, trees and ferns) have been dramatically impacted by deer (Stockton et al. 2005) but not mosses, which are not consumed by deer and which have actually increased in cover (Chollet et al. unpubl). This herbivory has resulted in closed-canopy forests with a depleted understory, where the remaining plants are mostly < 50 cm in height (Martin et al. 2010), and with bare or moss-covered ground lacking in most plant species usually recognized as essential in the diet of black-tailed deer (McTaggart Cowan 1956, Pojar et al. 1980).

In the winter 2010–2011 hurricane-force winds (> 69 knots) occurred in our study area causing large windfall areas with no, or very little, canopy cover over 35 and 21% of the area on East Limestone and Kunga islands, respectively. As a consequence, this study considered available plant resources to deer under two habitat scenarios: in the absence and in the presence of windfall areas.

Energy balance

We compared the yearly amount of energy available to and required by the local deer populations by considering two seasons: summer (from April to September) and winter (from October to March) in consistency with the seasonal changes in deer pelage (McTaggart Cowan and Raddi 1972). For each season we estimated the resources available and required using two models: the resource and the deer models.

Resource model

Resource description. We identified three pools of resources that could contribute to sustaining deer populations: 1) understory; 2) understory fluxes; and 3) subsidies from the canopy.

1) We defined the understory resource as the biomass of vascular plants that were available to and possibly eaten by deer. These included all chlorophyllous plant tissues (green plant parts) < 1.5 m in height (the browse line height in our study area: Vila and Guibal 2001). For Sitka spruce, deer feed almost exclusively on buds and fresh shoots available in spring (Vila and Guibal 2001), therefore we only included these plant-parts in our estimates.

2) We defined understory fluxes as the biomass of vascular plants growing in the field layer each year. These fluxes included the yearly growth of green plant parts from both perennial rhizomatous plants species ‘hidden’ in the moss layer (e.g. red huckleberry *Vaccinium parvifolium* or crisp starwort *Stellaria crispa)* (Chollet 2012) and from young individuals emerging from the seed bank (e.g. red alder or Sitka spruce seedlings).

3) We defined the canopy subsidies as the biomass that falls from the canopy and becomes available to deer. These subsidies included leaves from deciduous trees, red cedar sprays, buds from adult spruce and lichens (Parker et al. 1999, Tremblay et al. 2005, Le Saout 2009).

Given the similarity in environmental conditions between East Limestone and Kunga islands (Pojar et al. 1980, Martin et al. 2010) and given similar prevalence of recent windfalls on both islands, we assumed that levels of understory fluxes and canopy subsidies were comparable on both islands. For each of these resources, we estimated average available biomass per unit area by pooling the data from both islands.

Biomass assessment. To estimate 1) the annual biomass provided by the understory resource, we collected the available biomass (as defined above) in five 1-m^2 plots, located along 40-m transects between June and July 2011. On each island, we monitored 10 transects in the intact forest areas and 12 transects in the windfall areas. To estimate 2) the biomass provided by the understory fluxes, we used 2.25-m^2 × 1.8-m high exclosures. In intact forest areas we monitored four and six such exclosures on East Limestone and Kunga islands. In windfall areas, due to logistic constraints, we monitored four exclosures on East Limestone only. Of those, one was destroyed during the winter 2011–2012. In May 2011 we removed all green biomass from a 1-m^2 field-layer in each exclosure and a year later, in May 2012, we collected the biomass that had grown over the year in these exclosures. To estimate 3) the biomass provided by the canopy subsidies, we used 1-m^2 litterfall traps set at 2 m above the ground in forest areas, with four traps on East Limestone Island and six on Kunga Island. We collected the monthly biomass fallen in each trap in June and July 2011.

We dried and weighed the biomass collected by species in each sampling unit. Masses <0.1 g were counted as zero. For each type of resource and habitat (intact forest and windfall), we estimated the average annual dry matter per m^2 for each species. For the canopy subsidies we assumed that the monthly dry matter per m^2 was constant over the period of availability of each species in order to calculate the annual dry matter per m^2.

We assumed that the biomass produced in exclosures was comparable to the situation experienced by plants exposed to regular browsing. Indeed, whereas the exclosures may overestimate the biomass produced by plant growth growing once a year (e.g. Sitka spruce buds), they may underestimate the biomass produced by plants that respond positively to browsing (e.g. grasses: Augustine and McNaughton 1998). In our study more than 97% of the dry biomass collected came from plant species tolerant to browsing through the presence of rhizomes, basal meristems and/or high shoot densities (Table 3) that facilitate regrowth after browsing events (Pojar and MacKinnon 1994). In addition, our field observations confirmed that most browsed plants regrew during the same season. Therefore, we assumed that the biomass produced in exclosures, if not underestimated, should be at least comparable to the biomass produced by plants exposed to regular browsing.

Estimation of available energy. For each habitat scenario (i.e. in the absence or presence of windfall), we estimated for each season (i.e. winter and summer) the energy available to the deer populations in two steps. First, we estimated the amount of energy provided by each resource at a 1-m^2 scale. Secondly, we assessed the energy provided by each resource and by the sum of all resources at the scale of individual islands. In the absence of windfall, forest habitat was considered to include the entire island area. When windfall areas were incorporated in the scenario, forest habitat covered 65 and 79% of East Limestone and Kunga islands, respectively, and windfall habitat covered the remaining extents.

We estimated the seasonal energy provided by each resource at a 1-m^2 scale as follows. First for each species per resource, we multiplied its annual dry matter per m^2 by the proportion of days that it was available during each season (Eq. 1). We then multiplied this value by the seasonal metabolizable energy content of the given species. We assessed the seasonal amount of energy per m^2 provided by each resource by summing the amounts of energy provided by all species present in a given resource (Eq. 1). The proportion of days when a species was available for deer was added to the model because some plant species were not available as a food resource throughout the year (e.g. deciduous trees, forbs: Pojar and MacKinnon 1994). In particular, we considered that annual understory fluxes were restricted to the summer season because most plant growth occurs in summer (Pojar and MacKinnon 1994).

For each habitat scenario (with or without windfall), we estimated the seasonal amount of energy provided by each resource at the island scale as follows: First, we multiplied the seasonal amount of energy per m^2 of each resource by the habitat area (forest or windfall) where the resource occurred. Then, we summed these values over all resources present on the island to estimate the seasonal energy value (SEV) of the island for deer (Eq. 1).

$$SEV = \left(\begin{array}{l} \left(\sum_{\text{plant sp i}}^{\text{nr}} \alpha_{\text{i.season}} \times DM_{ri} \times ME_{i.season} \right)_{r=understory} \times A_{forest} \\ + \left(\sum_{\text{plant sp i}}^{\text{nr}} \alpha_{\text{i.season}} \times DM_{ri} \times ME_{i.season} \right)_{r=understory.fluxes} \times A_{forest} \\ + \left(\sum_{\text{plant sp i}}^{\text{nr}} \alpha_{\text{i.season}} \times DM_{ri} \times ME_{i.season} \right)_{r=canopy.subsidies} \times A_{forest} \\ + \left(\sum_{\text{plant sp i}}^{\text{nr}} \alpha_{\text{i.season}} \times DM_{ri} \times ME_{i.season} \right)_{r=windfall.understory} \times A_{windfall} \\ + \left(\sum_{\text{plant sp i}}^{\text{nr}} \alpha_{\text{i.season}} \times DM_{ri} \times ME_{i.season} \right)_{r=windfall.understory.fluxes} \times A_{windfall} \end{array} \right) \quad (1)$$

where DM_{ri} is the annual dry matter per m^2 of the plant species i in the resource r (kg DM m^{-2} year^{-1}), $ME_{i.season}$, is the metabolizable energy content of the species i in a given season (kJ kg^{-1} DM), $\alpha_{i.season}$ is the proportion of days of availability of the species i during a given season (i.e. the number of days when the species i is available during the season divided by the total number of days when the species i is available over the year), and A_{forest} and $A_{windfall}$ are the habitat areas where the resource occurred under the habitat scenario considered (m^2). Under the scenario not accounting for windfalls A_{forest} is the island area and $A_{windfall}$ is zero; under the scenario accounting for windfalls A_{forest} and $A_{windfall}$ are the respective forest and windfall areas estimated for each island.

Energy contents (Appendix 1) were obtained from Seip (1979), Parker et al. (1999), Munger (2002) and Hanley et al. (2012), and seasonal estimates were assessed as follows : 1) when available, we used the seasonal digestible energy content of each plant species; 2) when seasonal data were lacking, we used the same value for both seasons; and 3) when data on a given species were lacking, we used the average seasonal content of other species from the same genus, family or guild in this order of preference, and according to their availability in the literature. We then estimated the amount of metabolizable energy as the digestible energy contents corrected by a factor of 0.80 (average value of the metabolizable energy coefficients estimated for *Odocoileus* sp for hay, deciduous and conifer browse: Robbins 1993). Appendix 1 summarizes for each species the seasonal availability and energy contents used in this model.

Deer model

Deer demographic parameters. To estimate the energy requirements of East Limestone and Kunga deer populations, we considered both sexes and three age classes: adult (> 27 months old), subadult (10–27 months old) and fawn (< 10 months old). Fawns became thus subadults after their first winter and subadults became adults before their third winter. We identified five parameters to describe the local deer populations: 1) population abundance; 2) sex ratio; 3) age ratio; 4) body mass of each sex and age class; and 5) reproductive investment of each sex and age class.

1) We estimated the abundance of East Limestone and Kunga deer populations by a capture–mark–recapture (CMR) method using camera-trap data. In July and August 2012, we used motion sensor cameras to survey six sites over 40 days on East Limestone Island and 29 sites over four sessions of four to six days on Kunga Island. For each picture we aged, sexed and identified individual deer whenever possible. We recorded 218 and 103 deer visits on East Limestone and Kunga Island, respectively. We used a recently developed spatially-explicit CMR approach (Chandler and Royle 2013) to estimate the local deer abundance. This new method has the appealing advantage that it accommodates both identified and unidentified individuals. A detailed description of the models used is available in the Supplementary material Appendix 2. We estimated that a month after the beginning of the birth season deer abundance was approximately 36 deer (95% CI: 30–44) on East Limestone Island (i.e. 88 deer km^{-2}, [95% CI: 73–107]) and 168 deer (95% CI: 42–536) on Kunga Island (i.e. 43 deer km^{-2}, [95% CI: 11–136]). The large confidence interval around the Kunga estimate resulted from a shorter survey and a lower proportion of marked deer (Supplementary material Appendix 2). Nevertheless, the confidence interval for Kunga includes possible densities for East Limestone. This is in agreement with previous research showing that both islands are exposed to comparable deer browsing pressure (Chollet 2012).

2 and 3) We estimated sex and age ratios from the camera-trap survey. We considered only pictures with either sexed or aged individuals to estimate the proportion of each sex or age class in the populations. We assumed that sex ratios were constant across age classes and seasons. We considered that adult numbers were constant over the year and that fawns became subadults at the end of the winter (Table 2).

4) We estimated the average body mass of each sex and age class for each season from deer captures during which we sexed, aged, weighed and ear-tagged individuals. Captures took place in March–April 2011 and August–October 2011 and 2012. We captured 24 individuals on East Limestone Island (10 females, 14 males) and 22 individuals on Kunga Island (11 females, 11 males). We used the data from August–October and March–April captures as equivalent to summer and winter body mass, respectively. Data from March–April captures were too limited to assess winter body mass of female and male subadults (16 to 21 month-old individuals in winter). We used the average body mass of 15-, 16-month old individuals captured in August–October instead. We considered that body mass was constant over a season.

5) We estimated the investment of females in reproduction during August–October captures via their reproductive status (i.e. lactating or non-lactating). On both islands 80% of the captured adult females were lactating and only one subadult female of the three captured was lactating. Moreover, during the camera-trap survey, adult does had either no fawn or only one fawn. A single case of possible twins has been observed on East Limestone Island over the last five years (SLS unpubl.). Thus, to simplify, we considered that only adult females invested in reproduction and that all produced a single fawn. For males, we assumed that both subadult and adult males engaged in rutting (McTaggart Cowan 1956) and hence invested energy in reproduction. Table 1 summarizes the life history and demographic parameters used to assess the energy requirements of the local deer populations.

Estimation of energy required. To assess the energy requirements of the deer populations, we used Kleiber's equation (1947 in Robbins 1993, Parker et al. 1999) to estimate metabolic requirements from basal metabolic rate (BMR (kcal day^{-1}) = 70 $W^{0.75}$, with W the body mass (kg) and 1 kcal = 4.1868 kJ), multiplied by an activity metabolic rate (AMR) factor. The basal metabolic rate represents the energy expenditure of an animal in a thermoneutral environment, in muscular and psychic repose and in a post-absorptive state (Robbins 1993) and

Table 1. Life history and demographic parameters (obtained from camera-trap data and deer captures). Estimated abundances (N), female sex ratios (P_{female}), age ratios (μ) and body masses (W: mean ± SD, number of individuals (n)) for each sex and age class (i.e. female adult, male adult, female subadult, male subadult, fawn) in summer and winter, as well as the sex and age classes investing in reproduction are presented.

	East Limestone		Kunga	
Abundance				
N	36		168	
Sex ratio				
P_{female}	0.68		0.51	
Age ratio in:	Summer	Winter	Summer	Winter
μ_{adult}	0.66	0.66	0.66	0.66
$\mu_{subadult}$	0.34	0.19	0.34	0.17
μ_{fawn}	0	0.15	0	0.17
Body mass (kg) in:	Summer	Winter	Summer	Winter
$W_{female.adult}$	34 ± 2 (n = 6)	33 ± 5 (n = 3)	32 ± 4 (n = 7)	29 ± 1 (n = 4)
$W_{male.adult}$	43 ± 12 (n = 3)	36 ± 6 (n = 3)	42 ± 10 (n = 7)	38 ± 4 (n = 3)
$W_{female.subadult}$	26 ± 6 (n = 2)	23 ± 3 (n = 2)	25 ± 5 (n = 3)	21 ± 4 (n = 2)
$W_{male.subadult}$	24 ± 3 (n = 4)	24 ± 3 (n = 3)	26 ± 2 (n = 2)	25 ± 4 (n = 2)
W_{fawn}		18 ± 3 (n = 4)		14 ± 3 (n = 3)
Reproductive investment				
Invest	Adult females, adult males, subadult males			
Do not invest	Subadult females, fawns			

hence can be considered as a metabolic constant. The activity metabolic rate integrates any kind of additional metabolic activity and hence depends on season, sex, age and reproductive state (Robbins 1993). We calculated the population energy requirements for maintenance only and for both maintenance and reproduction by adjusting the AMR factor.

Values of the AMR factor (Table 2) were obtained from Wallmo et al. (1977), Sadleir (1982) and Robbins (1993). We assumed that reproductive costs were significant for adult females when lactating (June to August) and for adult and subadult males during the early winter (rut season in October–November). We disregarded production costs for antler growth and pelage molting because they represent less than 5% of the basal metabolic rate (Robbins 1993). Fawn weaning occurs between two and four months after parturition (Robbins 1993). Thus, to simplify we considered fawns as herbivores during the winter season only, disregarding their plant requirements in late summer.

In addition we also integrated thermoregulation costs with maintenance costs. Indeed, the thermal environment can be an important factor in deer energy requirements (Parker 1988). For example, on Channel Island (Alaska, US, 6° north of the study area), Parker et al. (1999) reported that black-tailed deer experienced a winter peak of thermal stress in February and a summer peak in June. In February, thermal stress occurred during ca 40% of weather observations and resulted in an additional metabolic cost for deer estimated to be 7% above the cost of standing (Parker et al. 1999, p. 26). We estimated this cost to be equivalent to 15% of deer winter basal metabolic rate (BMR) (Parker et al. 1999: see definition of standing

Table 2. Metabolic parameters used in the deer model. For each sex and age-class (i.e. female adult, male adult, female subadult, male subadult, fawn), for each season (i.e. summer and winter), and for each reproductive stage (i.e. maintenance and reproduction), the estimates of the seasonal proportion of day spent in a given stage (β), the estimates of the proportion of day within the stage considered during which thermoregulation costs is considered (ω) and the activity metabolic rate factor (AMR) of the stage considered are presented.

Sex	Age	Season	Stage	β	ω	AMR
Female	adult	summer	maintenance	0.33[2]	1	2[1]
Female	adult	summer	reproduction	0.67[2]	0.25	3.5[2]
Female	adult	winter	maintenance	1	1	2[1]
Female	subadult	summer	maintenance	1	0.5	2[1]
Female	subadult	winter	maintenance	1	1	2[1]
Male	adult	summer	maintenance	1	0.5	2[1]
Male	adult	winter	reproduction	0.33[1]	1	2.5[1]
Male	adult	winter	maintenance	0.67[1]	1	2[1]
Male	subadult	summer	maintenance	1	0.5	2[1]
Male	subadult	winter	reproduction	0.33[1]	1	2.5[1]
Male	subadult	winter	maintenance	0.67[1]	1	2[1]
Both	fawn	winter	maintenance	1	1	2[1]

[1] Wallmo et al. 1977.

[2] Sadleir 1982. The activity metabolic rate factor of black tailed females with a single fawn was estimated to be 3.89 during the two first month of lactation, and to be 2.9 during the last two months of lactation. Thus, on average we estimate it to be 3.5 during the four month post parturition.

metabolic rate, p. 13). In June, thermal stress occurred during ca 50% of the observation and increased energy cost of standing by $<6\%$ (i.e. $<13\%$ of deer summer BMR, Parker et al. 1999, p. 13 and 29). Air temperature, rain and wind are the main factor affecting deer thermal balance (Parker 1988). During their study period, Parker et al. (1999, p. 10) recorded mean minimum air temperatures in winter and summer > -3°C and > 6°C, respectively, with important rainfall > 290 mm in November and > 100 mm during the summer. Snow is also common on Channel Island with snow depth exceeding 80 cm in some areas. In comparison, our study area presents overall milder climatic characteristics with average minimum daily temperature > 0°C in winter and > 6°C in summer (except in April when the average minimum and maximum daily temperature were ca 3°C and 10°C), average monthly rainfall < 200 mm in winter and < 100 mm in summer, and snow depth < 3 cm (Sandspit weather station: Environment Canada data). Deer at our study sites are thus likely to experience lower thermal stress than deer on Channel Island, even in April when the effect of lower temperatures may be buffered by a gradual spring pelage molt (April to late June in black-tailed deer on Vancouver Island, Canada, 2° south of the study area; McTaggart Cowan and Raddi 1972). To be conservative we considered that deer would experience thermal stress from October to June with an additional daily cost equal to 15% of deer BMR. As the average snow depth recorded at the Sandspit weather station always fell below the 30-cm and 55-cm thresholds beyond which additional locomotion costs should be added to black-tailed deer energy requirements (Parker et al. 1984), we did not consider extra locomotion costs in our model.

For each season we estimated the energy requirements of deer populations by summing over sex and age classes the energy requirement of each class multiplied by the sex and age ratios of the class and by the deer population abundance.

Based on the above description we calculated the seasonal maintenance energy requirements (MER) of the deer population of each island according to Eq. 2.

$$MER = N \times nd_{season} \left[\sum_{sex} \rho_{sex} \left[\sum_{age} \mu_{age.season} \left(\left(AMR_{a..x.s} + 0.15 \times \omega_{season} \right) \times BMR_{a.x.s} \right) \right] \right] \quad (2)$$

where N is the local deer abundance, nd_{season} is the number of days of the season considered (i.e. 183 days in summer and 182.25 days in winter), ρ_{sex} is the sex ratio of the sex considered, $\mu_{age.season}$ is the age ratio of the age considered during a given season, ω_{season} is the within-season proportion of days during which a thermoregulation cost of 0.15 BMR is integrated to deer maintenance costs (i.e. 0.5 in summer (thermoregulation costs from April to June) and 1 in winter (thermoregulation costs from October to March)), $AMR_{a.x.s}$ is the activity metabolic rate factor for maintenance of the class of age a and sex x considered during the season s, and $BMR_{a.x.s}$ is the basal metabolic rate of the class of age a and sex x during the season s, considered to be equivalent to $70.W_{a.x.s}^{0.75}$ with $W_{a.x.s}$ being the average deer body mass of the class of age a and sex x during the season s.

Similarly, the seasonal energy requirements of the local deer population including reproductive costs (RER) were computed for each island by adding reproduction-related parameters to Eq. 2 (Eq. 3).

$$RER = N \times nd_{season} \left[\sum_{sex} \rho_{sex} \left[\sum_{age} \mu_{age.season} \left[\sum_{stage} \beta_{stage} \times \left(AMR_{stage.a.x.s} + 0.15 \times \omega_{stage.a.x.s} \right) \times BMR_{a.x.s} \right] \right] \right] \quad (3)$$

where β_{stage} *is* the proportion of days of the season s during which the class of sex x and age a is in a given reproductive stage, $AMR_{stage.a.x.s}$ is the activity metabolic rate factor of the stage for the class of age a and sex x during the season s and $\omega_{stage.a.x.s}$ is the proportion of days of the reproductive stage during which a thermal cost is integrated to maintenance costs for the class of age a and sex x during the season s).

Analysis

For each island, we compared the estimates of the energy available from the vegetation with the energy required by the deer population by assessing the proportion of deer maintenance energy requirements met by each resource for each season and for each habitat scenario (i.e. in the absence or presence of windfall). To compare the energy requirements including reproductive costs with the energy resources available, we assessed the proportion of energy required by the deer model including reproductive costs (Eq. 3) as a function of the energy required as estimated by the model including maintenance costs only (Eq. 2) and compared it with the proportions calculated for the energy resources. Reproduction costs increased deer energy requirements on East Limestone and Kunga islands, respectively, by 22 and 16% in summer and 2 and 4% in winter.

To account for variability in the three main parameters measured in the field (i.e. available dry biomass, deer population density and body mass), we conducted 5000 simulations for both models (i.e. resource and deer models) where these parameters were randomly generated from normal distributions calibrated on their means and their standard deviations. To be conservative, for body mass, we used for each island a single standard deviation value per age class, estimated to be the higher values assessed for the given age class on both sexes during both seasons (Supplementary material Appendix 3). We compared the average and the 95% confidence interval of the energy available to and required by East Limestone and Kunga deer populations for each habitat scenario (i.e. in the absence or presence of windfall). The results from the simulation models were consistent with those obtained from the model run with the average field values. Here we present the results assessed with the average values measured in the field only and the simulation analysis is detailed as supplementary information (Supplementary material Appendix 3).

Results

Energy available versus energy required

In the absence of windfall (Fig. 1), we estimated the energy available in summer to exceed the energy required by deer populations on both islands. On East Limestone Island, the energy available to the local deer population covered 178% of their energy requirements when we did not include reproductive costs and 146% when we included these costs (Fig. 1A). On Kunga Island we estimated these values to be 375 and 323%, respectively (Fig. 1C). In winter the energy available met ca. 25 and 50% of the energy required by East Limestone and Kunga deer populations, respectively (Fig. 1B, D).

Under the habitat scenario that included windfall areas (Fig. 2), we estimated the energy available to the deer population on East Limestone Island in summer to cover 138% of the deer energy requirements when we did not include reproductive costs and 113% when we included these costs (Fig. 2A). On Kunga Island we estimated these values to be 325 and 280%, respectively (Fig. 2C). In winter we estimated the energy available to deer to meet ca 30 and 60% of their energy requirements on East Limestone and Kunga islands, respectively (Fig. 2B, D).

What component of the vegetation contributes to maintaining the deer populations?

In the absence of windfall (Fig. 1), the understory biomass met respectively ca 5 and 11% of the energy requirements of East Limestone and Kunga deer populations whatever the season. In summer, understory fluxes and canopy subsidies each met ca 70% of the energy requirements including reproductive costs of the East Limestone deer population and more than 150% of the energy requirements including reproductive costs of the Kunga deer population. In winter the canopy subsidies met ca 20 and 40% of the energy requirements of the deer populations on East Limestone and Kunga islands, respectively.

Under the habitat scenario that included windfall (Fig. 2), the contribution of understory fluxes and canopy subsidies to the summer energy requirements of the East Limestone population, including reproduction costs, decreased from 70 to 54% and from 71 to 46%, respectively. These values varied from 155 to 134% and from 157 to 123% for the Kunga population, respectively. In winter the contribution of the canopy subsidies to the energy requirements of East Limestone and Kunga populations, including reproductive costs, decreased to 7 and 9%, respectively. However, the presence of windfall areas increased the proportion of the deer energy requirements met by the understory of ca 10–15% on both islands for both seasons.

For both habitats (i.e. forest and windfall areas, respectively) the energy provided by the understory fluxes came primarily from perennial rhizomatous grasses (81% and 66%, respectively), forbs (19% and 2%, respectively) and shrubs ($<1\%$ and 30%, respectively) (Table 3). In forest areas, red alder provided 90% of the energy provided by the canopy subsidies in summer and 54% in early winter; red cedar and lichen provided the remaining energy available in late winter (i.e. 42 and 4%).

Discussion

Despite the dramatic reduction in understory vegetation resulting from decades of unrestricted browsing (Stockton et al. 2005, Martin et al. 2010, Chollet et al. 2013) our results suggest that food resources in summer are adequate, accounting for the successful reproduction observed in most adult females. Energy needs are met principally through understory fluxes and canopy subsidies, two food sources that are relatively cryptic to the casual observer. Kunga Island, especially, was estimated to provide three times more energy than required to maintain the local population, although some uncertainty is created by the large confidence limits on our population estimate.

However, our results also indicate that black-tailed deer on our study sites suffered an overall energy deficit during the winter period. The ability of deer to persist in situations where food is abundant in summer but insufficient in winter has been well documented (Moen 1976, Wallmo et al. 1977, Parker et al. 1996, 1999). Over-winter survival is achieved by the use of body reserves built up during summer, as shown by Parker et al. (1999) in Sitka black-tailed deer and by Mautz (1978) and Huot (1982) in white-tailed deer. This is consistent with the 9% average body mass gain observed in eight adult deer we captured in March–April and recaptured in August–October of the same year.

Despite assumptions and uncertainties in estimating the amounts of energy available and energy required by the deer populations, our results are qualitatively robust and the overall pattern observed stands up to variations of many model parameters. Numerical results particularly depend on the three main parameters we estimated in the field (i.e. specific dry biomass, deer body mass and deer density). To better assess this variability we simulated 5000 sets of these parameters within the ranges observed. In spite of the high levels of variability in deer body mass (SD = 6–12 kg) or in deer density (SD = 10–31 deer km^{-2}) considered, we obtained similar results (i.e. a positive summer balance) for 84% and 97% of simulations for East Limestone and Kunga deer energy balance, respectively, supporting the overall pattern described (Supplementary material Appendix 3). Further studies, especially multi-year surveys of resource availability and deer demography would 1) improve the accuracy and

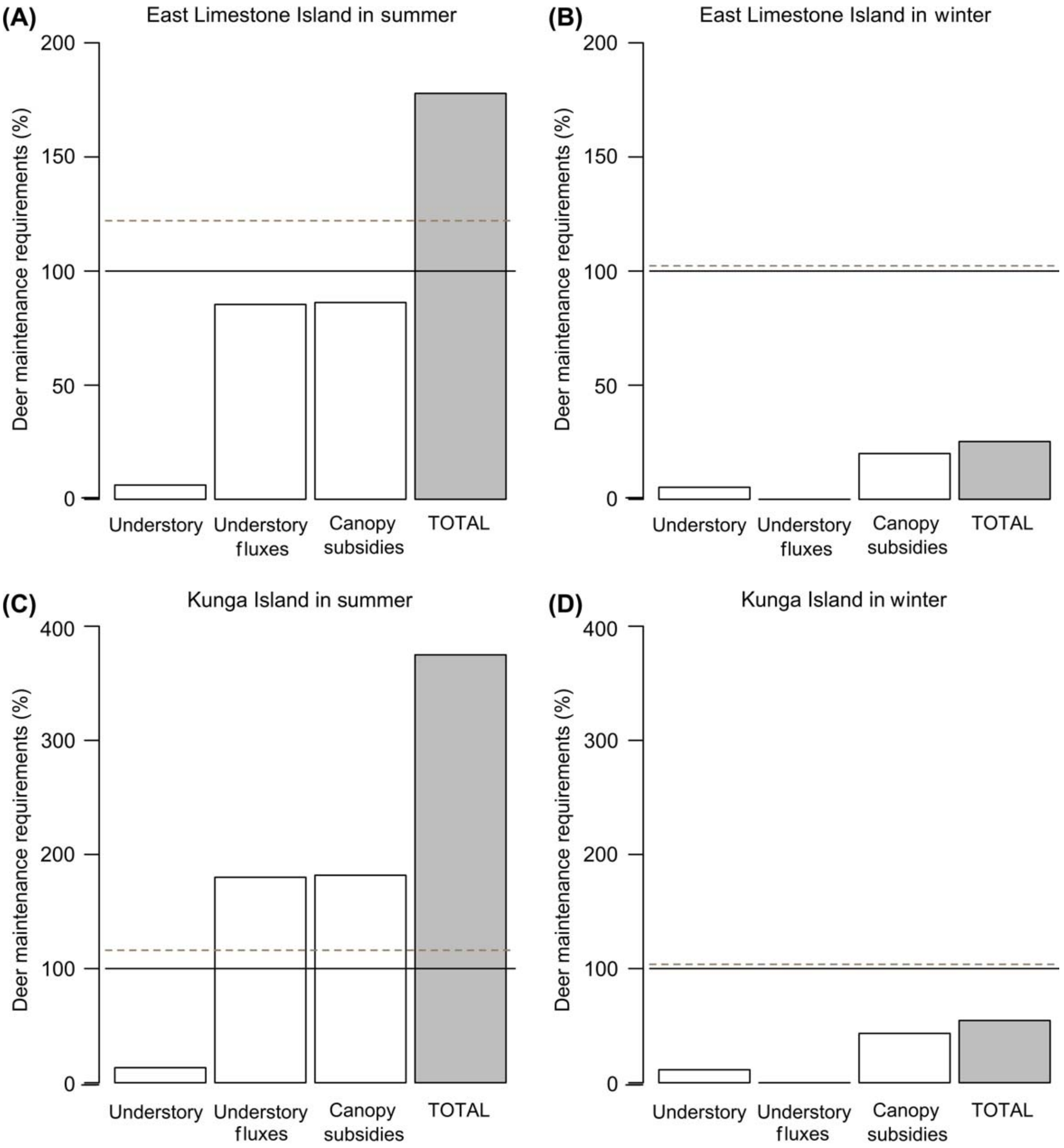

Figure 1. Estimated energy balances on East Limestone (A, B) and Kunga islands (C, D) under the scenario not accounting for windfall areas. Open bars give the percentage of the deer maintenance energy requirements (i.e. energy needed to maintain the studied deer populations without accounting for reproductive costs) that are covered by the energy available from each type of resource (i.e. understory, understory fluxes and canopy subsidies). The grey bars give the sum of the white bar values (i.e. the total percentage of the maintenance energy requirements of the deer population covered by all resources available). The solid lines refer to the level of energy needed to maintain the deer populations without accounting for reproductive costs (100%). The dashed lines refer to the energy requirements of the deer populations when accounting for reproductive costs (i.e. on East Limestone Island 122% in summer (April–September) and 102% in winter (October–March), and on Kunga Island 116% in summer and 104% in winter).

scope of our quantitative results and 2) document interannual variation in deer energy balance and in the relative contribution of each pool of resources to the maintenance of these populations. Nevertheless, despite current uncertainties, the present work can be considered as a qualitative modeling exercise highlighting the remarkable potential of a heavily browsed environment to support dense deer populations via understory fluxes and canopy subsidies.

For simplicity, we did not consider spatial heterogeneity in food access and distribution, nor the ability and preferences of deer to find, handle, ingest and digest each type of resource. Such behavioral and physiological constraints may be critical in the response of plants to herbivory (Power 1992) and in the efficiency with which deer can use the resources available (Robbins 1993). This might affect the spatio-temporal dynamics in resource use by deer, but likely not the overall pattern observed.

Resources not included in our study may also participate in maintaining the local deer populations. Similar to Scottish red deer *Cervus elaphus* on the Isle of Rum that use seaweed as a food supply (Conradt 2000), our direct

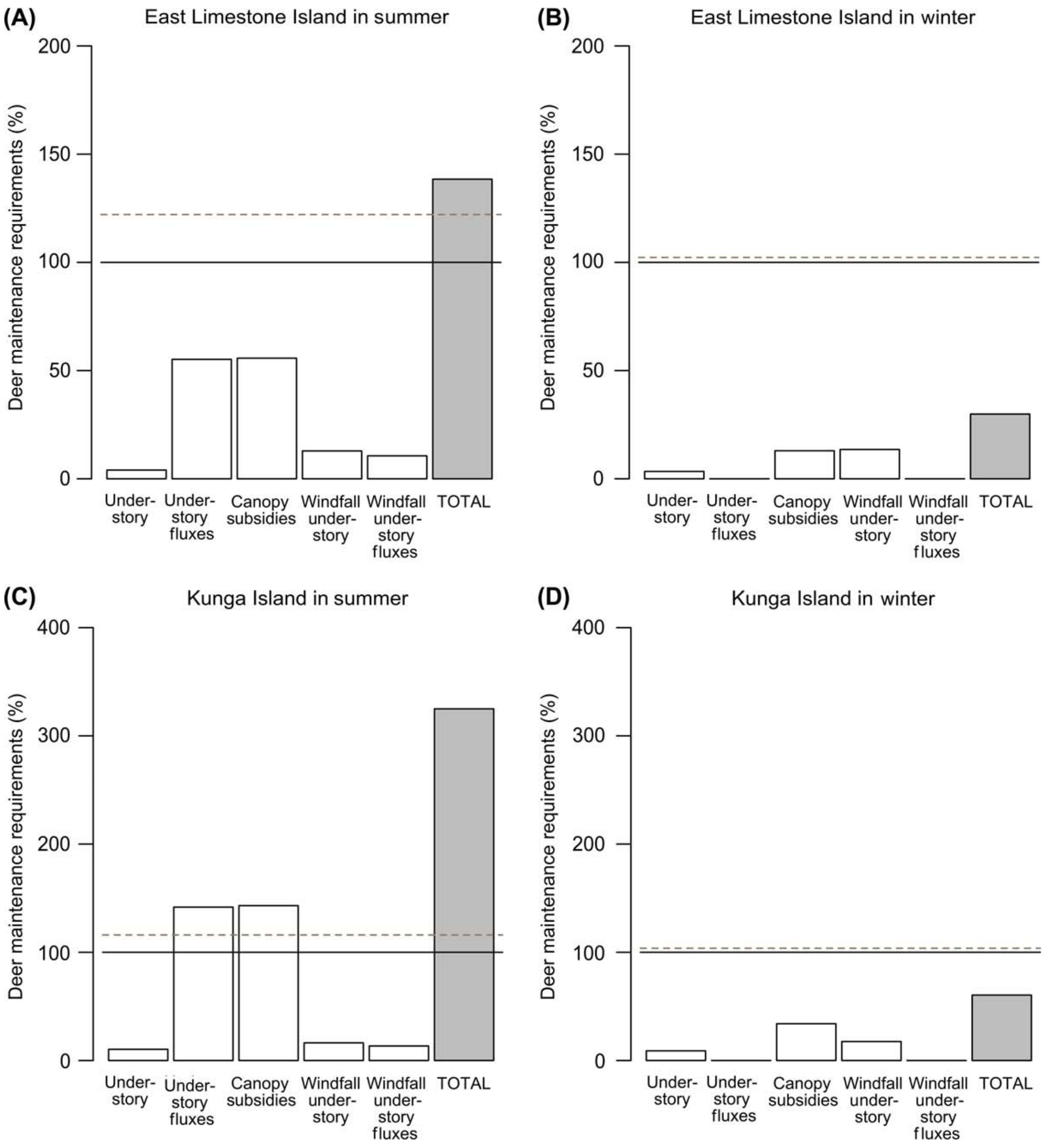

Figure 2. Estimated energy balances on East Limestone (A, B) and Kunga islands (C, D) under the scenario accounting for windfall areas. Open bars give the percentage of the deer maintenance energy requirements (i.e. energy needed to maintain the studied deer populations without accounting for reproductive costs) that are covered by the energy available from each type of resource (i.e. understory, understory fluxes and canopy subsidies in forest areas and understory and understory fluxes in windfall areas). The grey bars give the sum of the white bar values (i.e. the total percentage of the maintenance energy requirements of the deer population covered by all resources available). The solid lines refer to the level of energy needed to maintain the deer populations without accounting for reproductive costs (100%). The dashed lines refer to the energy requirements of the deer populations when accounting for reproductive costs (i.e. on East Limestone Island 122% in summer (April–September) and 102% in winter (October–March), and on Kunga Island 116% in summer and 104% in winter).

observations and fecal micro-histological analyses (E. Poilvé pers. comm.) support the use of brown and red algaes in the winter and summer diet of East Limestone and Kunga deer. Given that brown seaweeds such as *Alaria* sp. have an energy value of about 10 kJ g^{-1} dry matter (Applegate and Gray 1995) similar to that of ferns (Appendix 1), seaweed may be a non-negligible energy resource for deer, especially in winter.

Interestingly the results obtained for the scenario including windfall highlighted the importance of canopy subsidies and understory fluxes as food supplies. Despite the loss of more than 20% of forest area and its associated canopy subsidies, on both islands the remaining forested area and its canopy subsidies accounted for more than 40% of the energy available to deer during both winter and summer and covered more than half of the summer

Table 3. Specific contributions to the dry biomass and to the seasonal available energy of the two main resources: understory fluxes and canopy subsidies.

Species	Percentage of dry biomass (%)	Reproduction and/ or production structures	Guild	Percentage of energy available in summer within a resource (%)	Percentage of energy available in winter within a resource (%)
Understory fluxes					
Forest areas					
Carex sp.	42.04	rhizome	grass	44.08	no flux
Calamagrostis nutkaensis	31.89	rhizome	grass	29.59	no flux
Stellaria crispa	14.43	rhizome	forb	14.74	no flux
Luzula parviflora	7.18	rhizome	grass	7.04	no flux
Galium sp.	2.15	rhizome	forb	2.19	no flux
Cardamine oligosperma	1.75	rhizome	forb	1.78	no flux
Athyrium filix-femina	0.18	rhizome - propagule	fern	0.19	no flux
Vaccinium parvifolium	0.17	rhizome	shrub	0.18	no flux
Listera sp.	0.15	rhizome	forb	0.17	no flux
Tsuga heterophylla	0.06	seed	tree	0.03	no flux
Moneses uniflora	0.00	rhizome	forb	0.00	no flux
Picea sitchensis	0.00	seed	tree	0.00	no flux
Windfall areas					
Luzula parviflora	44.48	rhizome	grass	42.72	no flux
Vaccinium parvifolium	29.15	rhizome	shrub	30.48	no flux
Bromus sp.	21.56	rhizome	grass	23.10	no flux
Tsuga heterophylla	1.47	seed	tree	0.73	no flux
Maianthemum dilatatum	1.33	rhizome - seed	forb	1.53	no flux
Picea sitchensis	1.17	seed	tree	0.59	no flux
Moneses uniflora	0.62	rhizome	forb	0.65	no flux
Calamagrostis nutkaensis	0.22	rhizome	grass	0.20	no flux
Canopy subsidies					
Forest areas					
Alnus rubra	77.40	canopy tree	tree	90.06	53.57
Thuja plicata	21.16	canopy tree	tree	9.00	42.35
Lichen sp.	1.44	canopy tree	lichen	0.94	4.08
Picea sitchensis (bud)	0.00	canopy tree	tree	0.00	0.00

maintenance energy requirements of the local deer populations, supporting the studies by Rochelle (1980), Takahashi and Kaji (2001) and Tremblay et al. (2005) that highlighted the potential of canopy windfalls as a food supply for deer. In addition, windfall areas by themselves covered about 20% of the energy requirement of the reproductive deer population on both islands, via understory fluxes (ca 9–12%) and via an extra food supply in the understory layer (ca 11–14%) provided by the temporary access to the crown foliage of the fallen trees.

Because the consumption of canopy subsidies (leaves and twigs of red alder and redcedar, especially) does not directly affect the growth, survival or reproduction of the resource-producer plants (i.e. tall canopy trees), there is no feedback effect of the deer on canopy subsidies, except possibly indirectly through changes in soil quality (e.g. soil structure, texture, and composition: Bardgett and Wardle 2003). This was reported in Isle Royal National Park where moose browsing decreased soil fertility (Pastor et al. 1993). Understory fluxes resulted mostly from perennial rhizomatous plant species tolerant of herbivory and to a lesser extent from tree seedlings germinating from the seed bank (Table 3). By definition, herbivory has a low impact on the survivorship of tolerant plant species (Augustine and McNaughton 1998) and hence a low impact on the availability of the resource. Similarly the persistence of the seed bank depends on the productivity and fertility of plants that grow above browsing height or in refuges inaccessible to deer (Chollet et al. 2013). The seed bank subsidies may be affected by herbivory via changes in future recruitment and/or in biomass productivity and fertility rates (Louda et al. 1990, Abbas et al. 2012), but such changes would happen only in the long term. Thus, currently both canopy subsidies and understory fluxes are only weakly linked to resource consumption. Consequently they help to mitigate the effects of high herbivory on deer population density.

Our approach, though simplified, provides qualitative support for the existence of processes that may delay resource-driven feedback on herbivore populations. Such a delay may be particularly critical to consider when herbivores occur in predator-free environments where costs associated with vigilance or habitat shifts are reduced and/or in mild environments where climate-controlled population dynamics are unlikely. Within the current framework of worldwide increases in temperate forest herbivore populations, managers should be aware of the existence of potential delays in the control of herbivores via resource-driven feedback processes and hence may have to consider other processes including top–down control to achieve their management goals of limiting herbivore populations before dramatic changes in vegetation occur. Indeed, whereas a strategy for herbivore management may be the 'laisser-faire' that claims that a natural area left alone will reach a notional "wilderness equilibrium" (Gordon and Prins 2008), here we highlighted that such equilibrium may be far different from the current forest state, as herbivore abundance may continue to be high right up to the point where the canopy begins to disappear.

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Supplementary material (available online as Appendix wb-13-048 at <www.wildlifebiology.org/readers/appendix>). Appendix 2–3.

Appendix 1

Parameters used in the resource model: For each plant species inventoried as a resource we recorded for each season (i.e. summer and winter) its seasonal availability (number of days available in the season), its digestible energy content (kJ g^{-1} dry matter), the species and season considered in the published data used and the publication.

Guild	Family	Species latin name	Summer availability (nb days)	Winter availability (nb days)	Digestible energy (kJ/gDM)-summer	Digestible energy (kJ/gDM)-winter	Species with published energetic values when not the same	Period of published summer data	Period of published winter data	Source of summer data	Source of winter data
Tree	Betulaceae	*Alnus rubra*	183	31	13.6899	10.1739	same (leaves, buds, catkins)	summer	oct 77	Hanley et al. 2012	Seip 1979
Forb	Ranunculaceae	*Aquilegia formosa*	122	31	11.9498	11.9498	same	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Fern	Woodsiaceae	*Athyrium filix-femina*	183	182.25	12.0357	12.0357	same (leaves, fiddleheads)	apr-jun-aug-sept 89-apr-may-aug 90	apr-jun-aug-sept 89-apr-may-aug 90	Parker et al. 1999	Parker et al. 1999
Fern	Blechnaceae	*Blechnum spicant*	183	182.25	9.4240	11.6233	same	apr-aug-sep 89-jun-aug 90	oct 88-dec 89-mar 90	Parker et al. 1999	Parker et al. 1999
Grass	Poaceae	*Bromus* sp.	183	182.25	12.8082	12.8082	Poacea *(Elymus arenarius, Deschampsia caespitosa , Hordeum brachyantherum)*	apr-sept 89-mar-aug 90	apr-sept 89-mar-aug 90	Parker et al. 1999	Parker et al. 1999
Grass	Poaceae	*Calamagrostis nutkaensis*	183	182.25	10.8548	10.8548	Graminoids	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Orchidaceae	*Calypso bulbosa*	122	31	13.5530	13.5530	*Listera* sp	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Campanulaceae	*Campanula rotundifolia*	122	31	11.9498	11.9498	other forbs	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Brassicaceae	*Cardamine oligosperma*	122	31	11.9498	11.9498	other forbs	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Grass	Cyperaceae	*Carex sitchensis*	183	182.25	12.2675	11.6800	*Carex* sp.	apr-jun 89-may-jun 90	dec 88-mar 90	Parker et al. 1999	Parker et al. 1999
Forb	Asteraceae	*Cirsium* sp.	183	182.25	13.0863	13.0863	Asteracea *(Prenanthes alata, Achillea millefolium)*	may-aug-sept 89-may-jun-aug 90	may-aug-sept 89-may-jun-aug 90	Parker et al. 1999	Parker et al. 1999
Forb	Apiaceae	*Conioselinum pacificum*	153	31	13.1300	13.1300	same	jun-sept 89-jun 90	jun-sept 89-jun 90	Parker et al. 1999	Parker et al. 1999
Fern	Dryopteridaceae	*Dryopteris expansa*	183	182.25	10.5224	7.7851	same	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Fern	Pteridophyte	Fern sp.	183	182.25	10.7461	10.5907	Fern *(Athyrium filix-femina* (leaves, fiddleheads), *Blechnum spicant, Dryopteris dilatata* (leaves, rhizomes, fiddleheads), *Polypodium vulgare, Polystechum Braunii)*	summer-apr-jun-aug-sep 89-apr-may-jun-aug 90	winter-mar-apr-jun-aug-sep-dec-oct 89-apr-may-aug-mar-dec 90	Parker et al. 1999, Hanley et al. 2012	Parker et al. 1999, Hanley et al. 2012
Grass	Poaceae	*Festucarubra*	183	182.25	12.6953	13.2600	Poacea *(Elymus arenarius, Deschampsia caespitosa, Hordeum brachyantherum)*	apr-sep 89-aug 90	mar 90	Parker et al. 1999	Parker et al. 1999
Forb	Rubiaceae	*Galium aparine*	122	31	11.9498	11.9498	*Galium* sp	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Rubiaceae	*Galium triflorum*	122	31	11.9498	11.9498	*Galium* sp	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Shrub	Ericaceae	*Gaultheria shallon*	183	182.25	5.7419	5.7419	same (leaves, twigs)	summer	winter	Hanley et al. 2012	Hanley et al. 2012

(Continued)

Appendix 1 *(Continued)*

Guild	Family	Species latin name	Summer availability (nb days)	Winter availability (nb days)	Digestible energy (kJ/gDM)-summer	Digestible energy (kJ/gDM)-winter	Species with published energetic values when not the same	Period of published summer data	Period of published winter data	Source of summer data	Source of winter data
Lichen	Lichen	Lichen sp.	183	182.25	13.3966	12.4000	Lichen *(Alectoria* sp, *Usnea* sp, *Lobaria* sp, *Conocephalum conicum)*	summer	oct-dec 88-mar-sept-dec 89-mar 90	Hanley et al. 2012	Parker et al. 1999
Forb	Orchidaceae	*Listera caurina*	122	31	13.5530	13.5530	*Listera* sp	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Orchidaceae	*Listera cordata*	122	31	13.5530	13.5530	same	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Orchidaceae	*Listera* sp.	122	31	13.5530	13.5530	*Listera* sp	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Shrub	Caprifoliaceae	*Lonicera involucrata*	183	182.25	18.5301	11.8696	*Lonicera japonica* (leaves & twig)	apr-may-jun-jul-aug-sept	dec	Munger 2002	Munger 2002
Grass	Juncaceae	*Luzula parviflora*	183	182.25	11.4805	11.4805	same	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Ruscaceae	*Maianthemum dilataturn*	122	31	13.7840	13.7840	same	may- aug-sept 89- may-aug 90	may-aug-sept 89-may-aug 90	Parker et al. 1999	Parker et al. 1999
Tree	Rosaceae	*Malus fusca*	183	31	14.0060	14.0060	same	may- aug-sept 89- jun- aug 90	may-aug-sept 89-jun-Aug 90	Parker et al. 1999	Parker et al. 1999
Shrub	Ericaceae	*Menziesia ferruginea*	183	182.25	10.6940	6.4200	same (leaves & stem)	jun-aug-sep 89-may-aug 90	oct 88	Parker et al. 1999	Parker et al. 1999
Forb	Ericaceae	*Moneses uniflora*	122	31	12.3995	12.0280	same	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Tree	Pinaceae	*Picea sitchensis*	183	182.25	5.9667	5.2237	same	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Tree	Coniferous	*Picea sitchensis, Tsuga net*	183	182.25	5.9667	5.2237	same	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Fern	Polypodiaceae	*Polypodium glycyrrhiza*	183	151.25	11.4800	12.8833	*Polypodium vulgare*	sept-89-aug 90	mar-dec 89-90	Parker et al. 1999	Parker et al. 1999
Fern	Polytrichaceae	*Polystichum munitum*	183	151.25	10.2683	8.6259	*Polystechum brauni*	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Forb	Asteraceae	*Prenanthes alata*	122	31	13.3100	13.3100	*same*	may-aug-sept 89-may-aug 90	may-aug-sept 89-may-aug 90	Parker et al. 1999	Parker et al. 1999
Shrub	Grossulariaceae	*Ribes lacustre*	183	182.25	8.6943	5.3215	*Ribes* sp (leaves & twig)	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Shrub	Rosaceae	*Rubus spectabilis*	183	31	13.1650	9.5961	same	may 89-jun 90	oct 77	Parker et al. 1999	Seip 1979
Shrub	Ericaceae	*Sambucus racemosa* ssp. p	183	31	9.8674	9.8674	same (leaves, twigs)	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Forb	Caryophyllaceae	*Stellaria crispa*	122	31	11.9498	11.9498	same	summer	summer	Hanley et al. 2012	Hanley et al. 2012
Tree	Cupressaceae	*Thuja plicata*	183	182.25	8.5867	8.5867	same	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Tree	Pinaceae	*Tsuga heterophylla*	183	182.25	5.9667	5.2237	same	summer	winter	Hanley et al. 2012	Hanley et al. 2012
Shrub	Ericaceae	*Vaccinium parvifolium*	183	182.25	12.5000	10.1740	same (leaves, twigs)	mar-may-sept 89-apr-may-aug 90	oct 88-mar-dec 89-mar 90	Parker et al. 1999	Parker et al. 1999