HABITAT USE BY BLACK-TAILED DEER IN RELATION TO RATE OF FORAGE INTAKE

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ABSTRACT: Availability of digestible energy is potentially the most important limiting factor for black-tailed deer (Odocoileus hemionus sitkensis) from a nutritional perspective, but patch use by other ruminants has been better correlated with intake rates of digestible protein and digestible dry matter. We hypothesized that black-tailed deer would concentrate their use in habitats in which intake rates of digestible energy or protein were highest. Using direct observations of 9 tractable deer over a continuous 2-year period, we examined animal-specific rates of: (1) dry matter intake; (2) protein intake; and (3) metabolizable energy intake in 4 habitats. Those habitats were Vaccinium, devil’s club (Oplopanax), skunk cabbage (Lysichiton), and beach. For each animal, we compared the observed time spent active in each habitat to predictions of time allocation based on the measured rates of intake. Intake rates in summer differed significantly for all animals among habitats. In the first summer, animals used habitats on the basis of habitat availability and not relative to intake rates obtained in each habitat; the second summer deer used habitats in proportion to digestible dry matter and intake rates of metabolizable energy. In winter, when intake rates varied significantly among habitats, deer used habitats in proportion to their availability. Habitat use cannot be predicted by intake rates in winter. When we compared actual habitat use by black-tailed deer with use predicted by observed pellet defecation, we concluded that pellet groups did not accurately predict habitat use by black-tailed deer in spring, summer, or on an annual basis in the fine-grained habitats of our study area.


Keywords: Alaska, black-tailed deer, forage intake, habitat selection, habitat use, Odocoileus hemionus sitkensis, pellet-group counts

Sitka black-tailed deer (Odocoileus hemionus sitkensis) inhabit the coastal coniferous forests of Southeast Alaska, USA, north of British Columbia, Canada, where they live in a highly seasonal environment. A detailed study of energy and protein balance in Sitka black-tailed deer indicated that availability and nutritional quality of forage dominate all other environmental factors in determining physical condition, growth, and reproduction of black-tailed deer in Southeast Alaska (Parker et al. 1999). Those deer spent ~92% of their active time foraging, independent of sex or season (Gillingham et al. 1997). That allocation of time to forage intake was slightly higher than average for ruminants in general (70-90%; Bunnell and Gillingham 1985).

The process of forage selection is hierarchical. Selection of habitats in which herbivores forage will determine quantity and quality of available food (Langvatn and Hanley 1993); a premise that is central to the theory of habitat choice (MacArthur and Pianka 1966, Kamil and Roitblat 1985, Stephens and Krebs 1986). We therefore expect that choice of feeding patches would be a major focus for the foraging ungulate.
Despite this high dependence of deer on their forage, predicting foraging efficiency is difficult (sensu Parker et al. 1999) based on natural vegetation, and more generally in terms of habitat selection (Langvatn and Hanley 1993). Much of the recent focus of wildlife managers, however, has been on habitat selection for management of populations and for predicting effects of habitat disturbance on ungulates (e.g., habitat suitability models; Boroski et al. 1996). Habitat suitability models, however, are frequently unreliable (Rolloff and Kenoahan 1999).

To examine whether animals selectively use those habitats in which they have the greatest rates of forage intake we must identify the correct currency for quantifying intake. For example, using 5 tame red deer (Cervus elaphus) in an enclosure planted with 4 treatments of timothy grass differing in stage of growth, Langvatn and Hanley (1993) demonstrated that 90% of the observed variation in patch use could be explained by deer selecting patches on the basis of intake rates of digestible protein.

In Southeast Alaska, male black-tailed deer lost as much as 30% of their body mass over winter, whereas females lost ~20% (Parker et al. 1993a). Those fluctuations in body mass indicate that energy may be limiting and that animals should use foraging strategies that maximize their energy intake. Both male and female black-tailed deer (with no young) met or exceeded their energy requirements only in summer; females with twins experienced high demands for energy even in summer (Parker et al. 1999). By contrast, male and female black-tailed deer (with and without young) were able to meet their protein requirements throughout the year (Parker et al. 1999).

Assuming that the foraging animal experiences differences in intake rate among habitats, we expect habitat use to be sensitive to differences in intake rates of energy.

In this paper, we examine the relation between habitat use and rates of forage intake by black-tailed deer. We used direct behavioral observations to test 3 working hypotheses related to nutrition and 1 null hypothesis. Given significant differences in intake rate among habitats, and that 92% of time active by those animals was spent foraging (Parker et al. 1999), we hypothesized that black-tailed deer would allocate active time among habitats in direct proportion to their intake rates of: (1) digestible dry matter (g/min); (2) digestible protein (g/min); or (3) metabolizable energy (kJ/kg/min). All 3 metrics (digestible dry matter, digestible protein, and metabolizable energy) tend to be intercorrelated, but one may be a more variable and sensitive correlate with habitat use than others (as reported for protein by Langvatn and Hanley 1993). Our null hypothesis was that black-tailed deer, when active, would allocate their time among habitats in direct proportion to availability of habitats.

Managers often assess habitat use by much more indirect indices than field observations such as fecal-pellet counts. Pellet-group surveys are an established method for studying ungulate density in North America (Harestad and Bunnell 1987) and often are extensively used, despite disagreement about the utility of counting pellet groups (Collins and Urness 1981, Leopold et al. 1984). Data sets comparing in situ rates of defecation with actual habitat use are few, although a few studies have examined defecation rates (Rogers 1987, Sawyer et al. 1990) and persistence of pellet groups (Wallmo et al. 1962, Harestad and Bunnell 1987). Therefore, we also combine our direct observations of deer behavior with habitat use and rates of deposition of pellet groups to test whether observed pellet defecation accurately predicted habitat use.
STUDY AREA

We conducted our study on Channel Island, located ~20 km southeast of Wrangell, Alaska, USA (56°22′N, 132°10′W). The study island was ~65 ha and provided a natural environment similar in size to the home ranges of free-ranging deer in Southeast Alaska (Schoen and Kirchhoff 1985). The island rose from sea level to an elevation of ~125 m. Habitats were typical of old- and second-growth forests; the island had been subjected to selective logging in the early 1900s and there were no clearcuts on the island. The study area consisted of 4 distinct habitat types: (1) approximately 48% of the island was covered with habitats dominated by *Vaccinium* (*V. alaskaense, V. parvifolium*) (Pawuk and Kissinger 1989), large blueberry-bearing shrubs that are important winter browse for black-tailed deer; (2) habitats dominated by devil’s club (*Oplopanax horridus*) comprised approximately 32% of Channel Island (the understory of those habitats frequently contained *Dryopteris* ferns of which rhizomes were an important winter food for deer; Gillingham et al. 2000); (3) skunk cabbage (*Lysichiton americanum*) habitats (~17% of the island) occupied wetter sites (skunk cabbage provided large amounts of biomass in spring, enabling deer to achieve high intake rates while foraging; Gillingham et al. 1997, Parker et al. 1999); and (4) the remaining 3% of the island consisted of beach habitat (with grasses, forbs [e.g., *Glaux* spp., *Plantago* spp.], and *Carex* spp.), which was extensively used by deer. The first 3 habitats were greatly interspersed throughout the island, but the beach habitat was clearly distinctive (nonforest) and occurred only around the edge of the island.

Climate on Channel Island during our 2-year study was cool and wet, which was typical of coastal rainforests in Southeast Alaska. During winter, mean minimum and maximum monthly ambient temperatures were lowest during February (-1.3 and -3.0° C, respectively); and were highest in October (7.4 and 6.1° C, respectively). During winter 1989, snow covered the ground from mid December through late March (20-30 cm in forested habitats and < 10 cm on the beach). Snow depths were much greater in 1990 with > 80 cm in some forest habitats in February; snow cover persisted from early December through late March. During summer, mean minimum and maximum monthly temperatures were lowest in April of both years (8.4 and 6.1° C, respectively) and high in July and August (15.6 and 14.1° C, respectively).

METHODS

Observations

We bottle raised 2 cohorts of young black-tailed deer in small pens (1.2 m by 2.4 m) located in the natural environment as part of a larger study of forage intake and energy expenditure (Gillingham et al. 1997, Parker et al. 1999). Animals were weaned onto natural vegetation. Once weaned, deer were completely dependent on natural forage for survival. During this continuous 2-year study, we observed 9 free-ranging deer (2 males and 2 females born in 1987; 2 males and 3 females born in 1988). Using a system of plant units (average-sized species-specific units for estimating intake; Parker et al. 1993b), we recorded forage intake by species, in addition to the habitat in which the intake occurred and all animal behaviors (standing, lying, walking, running, playing, drinking, grooming, nursing, cud-chewing, urinating, defecating) on clock-equipped computers that were waterproof (Husky Hunter; Northwest Signal Supply, Lake Oswego, Oregon, USA) (Gillingham et al. 1997, Parker et al. 1999). Animals were followed throughout 2- to 8-h observation periods over the 2-year study. For-
aging behavior was defined in subsequent analyses as that time in which animals ingested or sought food so long as food intake did not cease for > 2 min (Gillingham et al. 1997).

We grouped habitat types by their dominant vegetation component for purposes of analyses: Vaccinium, Lysichiton, Oplopanax, and beach. Although habitats were not equally distributed, all were available to any animal on the island. In winter, Lysichiton-dominated habitats had no available forage when covered with snow. Further, absence of observable Lysichiton meant that those habitats were not readily recognizable by the observer. Our winter analyses, therefore, are based on only 3 habitat types: Vaccinium, Oplopanax, and beach. Parker et al. (1999) provides a detailed explanation of how intake rates of digestible dry matter, digestible protein, and metabolizable energy per minute foraging were calculated.

**Analyses of Habitat Use**

We assumed that black-tailed deer should only allocate their foraging time differentially among habitats if they obtain different intake rates while foraging in those habitats. To identify months for which intake rate differed significantly among habitats, we compared average intake rates of digestible dry matter, digestible protein, and metabolizable energy per min foraging for each month and animal. Following application of appropriate transformations to correct for heteroscedasticity as necessary, we used analysis of variance (ANOVA, Statsoft 1999) for each month and intake type, with animals as replicates, to determine when significant differences in intake rates occurred among habitats. Based on those analyses, we examined our hypotheses relative to habitat use only for data in winter (December - February) and in summer (June and July). We used least significant difference (LSD) tests for planned comparisons (Statsoft 1999) to contrast individual mean values following each ANOVA.

We used the $R^2_{\text{PRED}}$ (Langvatn and Hanley 1993), given by:

$$R^2_{\text{PRED}} = 1 - \left[ \frac{\sum (Y_{\text{OBS}} - Y_{\text{PRED}})^2}{\sum Y_{\text{OBS}}^2} \right]$$

to evaluate the relative fit of data to the different hypotheses of forage intake. The $R^2_{\text{PRED}}$ value is similar to a coefficient of determination ($r^2$) from regression analysis (i.e., percentage of variation explained by the regression, or in this instance the prediction). If each observation matched each prediction perfectly, the quantity in brackets, the residual error, would be zero and the $R^2_{\text{PRED}}$ value would be 1. In evaluating whether deer used available habitats in proportion to intake rates of dry matter, protein, or energy in each habitat, our predicted use was the total amount of active time multiplied by the cumulative distribution of each specific intake rate per minute foraging. For example, if the digestible dry matter intake rates in Lysichiton habitats were twice as high as the other 3 habitats in summer, then animals should have allocated 40% of their time active in Lysichiton habitats compared with 20% in each of the other 3 habitats. We used the relative proportion of the Vaccinium, Lysichiton (summer only), Oplopanax, and beach habitats available on the island multiplied by the total time active for each combination of animal and season to evaluate use relative to habitat availability.

Because the statistical distribution of $R^2_{\text{PRED}}$ is unknown, we combined our use of the $R^2_{\text{PRED}}$ values with a distributional test of the same hypotheses. We constructed a cumulative frequency distribution for each intake hypothesis and the observed active time. For example, the cumulative distribu
tion of habitat use was the percentage of each available habitat. We then used a Kolmogorov-Smirnov 2-sample test (Sokal and Rohlf 1995) to evaluate significance of our observed and predicted values. Sample size (n) for each Kolmogorov-Smirnov test of habitat use was conservatively taken to be the total number of behavioral trials (days) for each test period (2 winters and 2 summers). This approach necessarily used the same animals for multiple comparisons within the same season, but we believe does not inflate sample size substantially with nonindependent choices of habitat. Instead, this approach assumes that on a given day the habitats encountered by an animal, and the foraging decisions made within them, are independent of choices made by animals on another day. Given the complex juxtaposition of habitats on Channel Island (Parker et al. 1999), we believe this to be a reasonable assumption.

Analyses of Pellet Index

Instead of sampling for pellet groups, we recorded every defecation event throughout our observations and the habitat in which the deposition of pellet groups took place. The estimate of ‘habitat use’ from pellet groups was then compared with the actual time animals spent active in each habitat. To examine the distribution of pellet groups deposited during active bouts, we considered only those bouts that were complete, (i.e., those trials for which we observed an animal from the start of an active bout after bedding until the animal bedded again, n = 450). Data were expressed in terms of percentage of the complete foraging bout that had elapsed whenever defecation occurred because active bouts differed in length. We pooled data for males and females for all analyses because sex of animal that deposited the pellet group cannot be reliably determined from plot-based sampling of pellet groups.

To evaluate accuracy with which deposited pellet groups predicted actual habitat use by deer, we grouped data for all observed active bouts into spring (April - May), summer (June - August), autumn (September - November), and winter (December - March). For each period, we constructed cumulative frequency distributions of habitat use based on time active and defecation events in each habitat; distributions were compared with a Kolmogorov-Smirnov 2-sample test. For those analyses, we considered the sample size to be number of active bouts that we observed (n = 944). Finally, we assumed that pellets would persist for an entire year and repeated the previous analyses after pooling all active bouts and pellet data into a single ‘yearly’ sample to assess efficacy of an annual survey of pellet groups.

RESULTS

Habitat Use Relative to Intake Rate

Intake rates of digestible dry matter, digestible protein, and metabolizable energy by black-tailed deer in both summers (June and July) were significantly higher in Lysichiton-dominated habitats than in Vaccinium, Oplopanax, or beach habitats (Table 1). In both summers, intake rates of digestible protein were lower on the beach than in other habitats. This outcome also held for intake rates of metabolizable energy in 1989. In winter, when Lysichiton was not available to deer, all 3 rates of intake were more similar among available habitats (Table 1). In 1989, intake rate of metabolizable energy was lowest in Oplopanax-dominated habitats, protein intake was similar among all habitats, and intake of digestible dry matter was higher on beach than in Oplopanax habitats. By contrast, intake rates of digestible dry matter and metabolizable energy in 1990 were similar in all habitats and intake rates of digestible protein were higher on beach.
Table 1. Intake rates of digestible dry matter, digestible protein, and metabolizable energy (Met. energy) by black-tailed deer in Vaccinium, Lysichiton, Otopanax, and beach habitats. Data were collected on Channel Island in Southeast Alaska from June 1989 through September 1990. For each season, \( n \) represents the number of animal-months of data that were considered in analyses. \( P \) values correspond to the test of the hypothesis of equal intake rates among habitats by ANOVA.

<table>
<thead>
<tr>
<th></th>
<th>Vaccinium</th>
<th>Lysichiton</th>
<th>Otopanax</th>
<th>Beach</th>
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<tr>
<td></td>
<td>( \bar{X} )</td>
<td>SE</td>
<td>( \bar{X} )</td>
<td>SE</td>
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<tr>
<td>Summer 1989 (( n = 13 ))</td>
<td>1.15&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.42</td>
<td>1.74&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.69</td>
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<tr>
<td>Digestible dry matter (g/min)</td>
<td>0.41&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.31</td>
<td>0.70&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.44</td>
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<tr>
<td>Digestible protein (g/min)</td>
<td>4.44&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.82</td>
<td>6.68&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.35</td>
</tr>
<tr>
<td>Met. energy (kcal/kg/min)</td>
<td>1.07&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.56</td>
<td>1.09&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.51</td>
</tr>
<tr>
<td>Summer 1990 (( n = 17 ))</td>
<td>1.09&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.40</td>
<td>1.42&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.53</td>
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<tr>
<td>Digestible dry matter (g/min)</td>
<td>0.32&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.29</td>
<td>0.54&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.35</td>
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<tr>
<td>Digestible protein (g/min)</td>
<td>4.17&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.79</td>
<td>5.44&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.05</td>
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<tr>
<td>Met. energy (kcal/kg/min)</td>
<td>0.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.27</td>
<td>0.32&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.35</td>
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<tr>
<td>Winter 1989 (( n = 18 ))</td>
<td>0.29&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.22</td>
<td>0.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.27</td>
</tr>
<tr>
<td>Digestible dry matter (g/min)</td>
<td>0.02</td>
<td>0.10</td>
<td>0.02</td>
<td>0.12</td>
</tr>
<tr>
<td>Digestible protein (g/min)</td>
<td>1.10&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.40</td>
<td>0.88&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.53</td>
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<tr>
<td>Met. energy (kcal/kg/min)</td>
<td>0.34</td>
<td>0.30</td>
<td>0.52</td>
<td>0.71</td>
</tr>
<tr>
<td>Winter 1990 (( n = 26 ))</td>
<td>0.34</td>
<td>0.30</td>
<td>0.52</td>
<td>0.71</td>
</tr>
<tr>
<td>Digestible dry matter (g/min)</td>
<td>0.02&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.10</td>
<td>0.02&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.17</td>
</tr>
<tr>
<td>Digestible protein (g/min)</td>
<td>1.29</td>
<td>0.58</td>
<td>1.90</td>
<td>1.34</td>
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<sup>1</sup>Means within a row sharing a common superscript are not significantly different according to a LSD test for planned comparisons.

than in Otopanax habitats (Table 1).

Habitat use by both male and female black-tailed deer during the first summer (Fig. 1; 1989) was best explained by use of habitats based on their availability rather than use of habitats proportional to intake of digestible dry matter, digestible protein, or metabolizable energy that deer experienced in those habitats. Comparisons of distributions of observed use while active (Fig. 1; time active) with hypothesized distributions based on habitat availability and the 3 nutritional hypotheses leads us to reject the nutritional hypotheses for both males and females. The \( R^2_{\text{pred}} \) values (Fig. 1) indicate that 80% for females and 83% for males of the observed habitat use was explained by habitat availability. Nutritional hypotheses were rejected because animals appeared to 'overuse' Vaccinium and beach habitats while 'underusing' (compared with availability) Lysichiton and Otopanax habitats: highest rates of intake occurred in the Lysichiton and Otopanax habitats.

Conversely, in summer 1990 the time male and female black-tailed deer spent in the 4 available habitats was not related to habitat availability (Fig. 1; 1990); none of those nutritional-intake hypotheses were significantly different from observed distri-
Fig. 1. Comparison of observed summer (June and July) habitat use by female (top panels) and male (bottom panels) black-tailed deer when active with hypothesized use based on habitat availability and intake rates of digestible dry matter (DDM), digestible protein, and metabolizable energy (ME) for 1989 (left panels) and 1990 (right panels) on Channel Island, ~20 km southeast of Wrangell, Alaska, USA. The cumulative proportion of observed time active is shown at the left of each panel. Significance values (ns or *) at the top of each cumulative distribution represent the outcome of comparing hypotheses of use based on habitat availability, digestible dry matter intake, digestible protein intake, and metabolizable energy intake, with the observed distribution of active time in Beach, Oplopanax, Lysichiton, and Vaccinium habitats, from a Kolmogorov-Smirnov test. Percentage of variation explained by each hypothesis ($R^2_{pred}$ values) is presented at the bottom of each bar.

Distributions of habitat use. For both males and females, however, hypothesized use based on intake rates of digestible protein explained slightly less variation in those data than the other 2 nutritional-intake hypotheses (Fig 1.; $R^2_{pred}$ values). We observed an increased use of both Lysichiton and beach habitats in 1990; the habitats in which intake rates were highest.

We compared use of only 3 habitats by deer in winter: Vaccinium, Oplopanax, and beach. In the first winter of study (Fig. 2; 1989), deer used habitats in proportion to their availability and not relative to the intake rates that they achieved when in them. In addition to being significantly different from the distribution of active time in habitats, hypotheses based on intake rates did not explain much variation ($R^2_{pred}$ values). Vaccinium habitats were used in greater proportion than would be predicted by intake hypotheses, whereas Oplopanax habitats were underutilized.

The pattern of use relative to availability was even more pronounced for male and female black-tailed deer in the second winter of study, when habitat availability explained 85 and 94%, respectively, of the
observed variation in habitat use for males and females (Fig. 2; $R^2_{\text{pred}}$ values). Nutritional hypotheses did not fit the observed use of habitats. A characteristic of the $R^2_{\text{pred}}$ values is that they may be negative when fit is poor, which occurred for females in the winter 1990 for intake of digestible protein.

**Accuracy of Fecal-pellet Indices**

Using data from only those active bouts in which the animal was observed continuously from the start of an active bout until the animal bedded, we noted that animals were 2.5 times more likely to defecate shortly after beginning an active bout than at any other time during the bout (Fig. 3). Consequently, pellet groups were biased towards the habitats in which animals bedded. If animals bedded wherever they finished foraging, then that bias would be unimportant. Our observations (M.P. Gillingham and K.L. Parker, unpublished data) indicated that deer exhibited a bias toward moving toward bedding in *Vaccinium* habitats (as compared with wet *Lysichiton*.

Fig. 2. Comparison of observed winter (December - February) habitat use by female (top panels) and male (bottom panels) black-tailed deer when active with hypothesized use based on habitat availability and intake rates of digestible dry matter (DDM), digestible protein, and metabolizable energy (ME) for 1989 (left panels) and 1990 (right panels) on Channel Island, ~20 km southeast of Wrangell, Alaska, USA. The cumulative proportion of observed time active is shown at the left of each panel. Significance values (ns or *) at the top of each cumulative distribution represent the outcome of comparing each hypothesis of use based on habitat availability, digestible dry matter intake, digestible protein intake, and metabolizable energy intake, with the observed distribution of active time in Beach, *Oplopanax*, and *Vaccinium* habitats, from a Kolmogorov-Smirnov test. Percentage of variation explained by each hypothesis ($R^2_{\text{pred}}$ values) is presented at the bottom of each bar.
and Oplopanax habitats), but that in 93.6% of 944 observations, animals began feeding in the same habitat in which they had just bedded.

Observed distribution of depositions of pellet groups within habitats did not accurately predict the distribution of active time that deer spent in those habitats throughout spring and summer (Fig. 4). From April through May, pellet groups significantly underestimated use of Oplopanax habitats and underestimated use of beach habitats by deer. Similarly, fecal-group distribution significantly underestimated use of beach by deer during summer (June - August). From September through November and from December through March, however, the distribution of habitat use predicted by observed pellet group deposition was not significantly different from observed use of habitat by deer (Fig. 4). To simulate a single annual survey of pellet groups, we pooled data from our observations during active bouts. On an annual basis, distribution of pellet groups significantly overestimated the use of Vaccinium habitats and underestimated use of beach habitats.

**DISCUSSION**

Intake rates of digestible dry matter, digestible protein, and metabolizable energy achieved by black-tailed deer in Oplopanax, Lysichiton, Vaccinium, and beach habitats varied considerably between summer and winter in both years of study. During both summers, intake rates in Lysichiton habitats, on average, often were greater than twice those in Vaccinium, Oplopanax, or beach habitats (as much as 4.3 times higher for intake rates of digestible protein in beach habitats in the first summer; Table 1). With Lysichiton unavailable in winter, intake rates in Vaccinium, Oplopanax, and beach habitats did not differ consistently. Even when intake rates differed significantly among habitats, absolute differences often were small (e.g., 0.02 g digestible protein per min in winter 1990; Table 1). At the same time, a difference of 0.02 g digestible protein per min meant that animals realized twice the
intake rate of digestible protein on the beach compared with Vaccinium and Oplopanax habitats, presumably because of denser available biomass.

Given seasonal differences in intake rates, we expected that habitat use by black-tailed deer would be much more responsive to intake rates in summer than to those achieved in winter. Results of our analyses, however, were not completely consistent with those predictions. In the first summer of study, we rejected all 3 nutritional-intake hypotheses; observed use of all 4 habitats by male and female black-tailed deer was consistent with use of habitats based on their availability (Fig. 1; 1989). For both male and female deer, rejection of the nutritional hypotheses resulted from the animals greatly overusing Vaccinium and underutilizing Lysichiton habitats relative to predictions of nutritional hypotheses. In contrast, in the second summer of study (Fig. 1; 1990), use of available habitats by black-tailed deer was best explained by intake rates of digestible dry matter and metabolizable energy (Fig. 1; $R^2_{\text{pred}}$ values), but data did not support habitat use based on habitat availability. In 1990, deer use of Lysichiton and beach habitats increased, and was much more consistent with the predictions of nutritional hypotheses. This outcome may have been because, during the second summer of study, animals were likely under greater pressure to forage efficiently. Summer is a critical time for weight gain (Parker et al. 1993a) given that these black-tailed deer live in a negative energy balance throughout winter (Klein 1979, Parker 1988, Parker et al. 1996). In the second year of study, animals were larger with greater absolute intake requirements; all but 1 female had young (2 of them had twins). Males were not only larger (Parker et al. 1993a), but older animals gained condition in preparation for the upcoming rut (Parker et al. 1993a). Therefore, during summer 1990, animals may have responded more to differences in habitat-specific rates of intake than during the first summer of study.

If animals responded only to intake rate, deer would spend all of their time in the habitat with the highest potential intake. Nutritional factors requiring a more mixed diet likely preclude this simple approach to foraging. For example, the highest intake rates of skunk cabbage sustained during foraging bouts that we observed in free-ranging black-tailed deer approached the short-term maxima achieved by captive animals (Gillingham et al. 1997). The secondary metabolites of this species, however, likely dictates that it be mixed with other foods in the diet of deer (Hanley and McKendrick 1983, Robbins et al. 1987, Bryant et al. 1991, McArthur et al. 1993).

For both winters of study (Fig. 2), we rejected all 3 nutritional hypotheses; black-tailed deer use of the 3 habitat types was consistent with the hypothesized use based on habitat availability. From 74 to 94% of variation in habitat use was explained by habitat availability (Fig. 2; $R^2_{\text{pred}}$ values). In all instances, use of Vaccinium habitats by deer greatly exceeded the use predicted by all nutritional hypotheses (Fig. 2). During winter, deer often roamed across the island in search of wind-blown arboreal lichens after storms (Parker et al. 1999). Distribution of wind-blown lichens, however, was not associated with a specific habitat (Parker et al. 1999). Mild weather in winter that improved thermoregulatory costs for black-tailed deer (Parker 1988), also made fern rhizomes available when the top few centimeters of the ground thawed. Rhizomes were not limited to a single habitat and deer searching for rhizomes likely encountered habitats in proportion to their availability (Gillingham et al. 2000).

Whether a result of widely distributed and temporally available foods, or tempo-
rally available habitats, hypotheses based on nutritional intake did not explain habitat use by black-tailed deer in either winter of this study. In addition, given moderate snow depths, deer likely benefited from searching widely for temporarily available foods such as fern rhizomes and lichens. Shrub stems such as Vaccinium could be encountered readily across the island. Many times we observed that if a foraging animal was successful in finding large amounts of arboreal lichen during 1 foraging bout, they were likely to search for them again after bedding (Gillingham et al. 1997; M. P. Gillingham and K. L. Parker, unpublished data). If, however, deer traveled long distances and located few lichens, they appeared to concentrate at large Vaccinium shrubs and foraged very intensively. Given that animals are in a negative energy balance throughout winter, an animal that is processing a rumen full of shrub twigs probably can afford to be ‘risk prone’ (sensu Stephens and Krebs 1986) and search for rare but nutritionally beneficial foods across habitats, provided that the snow depths do not greatly increase locomotory costs (Parker et al. 1984).

When defining habitat use by black-tailed deer, researchers must also consider if the animals are aware of the habitat distinctions implicit in our system of habitat classification. Deer are likely cognizant of those habitats regardless of cues that they use to apportion foraging effort. Large differences in intake rate in Lysichiton habitats in summer, and the distinctive ecological characteristics of wet Lysichiton habitats, support our contention. In winter, we observed specific periods when deer were searching for rhizomes or for arboreal lichens, but those behaviors were temperature and snow dependent (Gillingham et al. 2000). When deer were not searching for those specific foods, the relatively small differences in intake rate among habitats may mean that deer did not distinguish between Oplopanax and Vaccinium habitats but, rather, searched at a more fine-grained level, such as that of the plant rather than the patch.

Habitat classification is a question of scale. From our perspective, Channel Island consisted of 4 distinct habitats in summer and 3 in winter. To wildlife managers, however, the island might represent a single stand type, possibly with 2 aspects at low elevation (< 400 m; Kirchhoff and Schoen 1987). At the other extreme is the fine scale of the individual plant, or even parts within a plant. Patches of habitats that we considered in our analyses are highly intermixed on the island. Consequently, our animals might not have distinguished between our habitat types. Juxtaposition of habitats also meant relatively low energetic costs to move among them and may have enabled deer to be, for example, in relatively dry Vaccinium areas after feeding in Lysichiton. Although those habitats were typical of those used by deer in Southeast Alaska, our results are likely scale dependent. If our patches were larger (e.g., differences between north- and south-facing slopes), then the time and energy costs of traveling between them would be much higher. At a large scale, we might have seen stronger correlations with nutritional hypotheses.

During this study, we had the unique opportunity to follow tractable animals closely for extended periods of time in a natural environment that was not predator free. Predators of black-tailed deer on the islands surrounding Channel Island included wolves (Canis lupus), brown bears (Ursus arctos), and black bears (U. americanus). Although we encountered neither wolves nor grizzly bears on Channel Island, black bears (or their sign) were observed on a number of occasions. Therefore, although we could not measure risk of predation
directly, we believe that predation risk is incorporated into our observations.

Use of habitats by black-tailed deer in coastal environments has been studied by radio telemetry (Schoen and Kirchhoff 1990, Yeo and Peek 1992), but often was assessed by sampling fecal pellet groups. In this study, distribution of observed pellet deposition within habitats did not predict the use of habitat by black-tailed deer, which were active throughout spring and summer. Habitat use based on pellet deposition did not differ from observed use from September through March. When we pooled all data from our observations of active bouts on an annual basis (to simulate a single annual extensive survey), use of habitats based on observations differed significantly from distribution of habitat use predicted by fecal deposition. This conclusion is based on the comparison of the cumulative distributions of time active and pellet deposition. The rank order of pellet groups has been suggested as an alternative to assessing relative use of habitats (Leopold et al. 1984).

In all months (Fig. 4), while pellets overestimated the total use of Vaccinium habitats, Vaccinium was correctly ranked as the most-used habitat. Less-used habitats, however, would have been incorrectly ranked by pellet data in this study in April-May and June-August, but not in September-November and December-March (Fig. 4). Ranking of pellet-use data also incorrectly identified close to 50% of the habitats in other studies (11 of 24; Collins 1984).

Our approach does not consider additional concerns regarding counts of pellet groups. We compared actual habitat use to pellet deposition, and our results did not incorporate any sampling bias associated with pellet-group transects including varying decay rates (Lehmkuhl et al. 1994), spatial distribution of pellet groups (Neff 1968), plot size (Smith 1968), and observer effects (Van Etten and Bennett 1965).

Additionally, pellet groups do not persist indefinitely (Harestad and Bunnell 1987). After 1 year, 16-48% of the original complement of pellets persisted in wet environments (Harestad and Bunnell 1987); this degradation is likely even higher in beach environments that are frequently flooded with high tides. Even without biases associated with sampling, persistence, and defecation rates (Sawyer et al. 1990), pellet groups neither accurately predicted habitat use by black-tailed deer during spring and summer nor on an annual basis. These new findings need to be considered in addition to cautions offered by others concerning the use of fecal groups (Collins and Urness 1981, Leopold et al. 1984).

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