Use of a seaweed habitat by red deer (*Cervus elaphus* L.)

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Abstract
The use of a seaweed habitat by red deer *Cervus elaphus* L. on the Isle of Rum, Scotland, was examined in detail. New information is provided on diet selection, timing of seaweed use relative to tides, inter-individual differences in seaweed use, and sex differences in site use within the seaweed habitat (‘site segregation’). Interestingly, seaweed use by adult males and females was closely correlated to that of their mothers. This implies that deer ‘learn’ early in life to include seaweed into their diet. Formerly, it has been suggested that male inferiority in indirect competitive ability relative to females causes site segregation in dimorphic ungulates (‘indirect competition hypothesis’). The observed pattern of site segregation within the seaweed habitat was used to test the hypothesis, which predicts that males should be found at sites where they can achieve higher intake rates, but where forage quality is lower than at female sites. With respect to seaweed use, the hypothesis further predicts that segregation should be lower within the seaweed habitat than within terrestrial vegetation communities, and that males should time seaweed use earlier (relative to the tide) than females. This is because seaweed availability is more subject to tidal rhythm than to indirect competition in comparison to terrestrial habitats. Males and females used different bays, and within bays they used different fractions of seaweed. However, male-preferred sites did not yield higher intake rates and were not of lower forage quality than sites preferred by females. Moreover, segregation was not lower within the seaweed habitat than within terrestrial vegetation communities, and males did not time their seaweed use earlier relative to the tide than did females. The indirect competition hypothesis could not explain the observed pattern of site segregation. Other factors, such as sex differences in sheltering or anti-predator behaviour, or social harassment, could be responsible instead.

Key words: grazing competition, habitat segregation, habitat use, inter-sexual segregation, ungulates, *Cervus elaphus*

INTRODUCTION
To most ruminants, seaweed is inaccessible. Nevertheless, many ruminant species include seaweed readily in their diet, wherever it becomes available. Sheep in Iceland, cattle in France (Chapman & Chapman, 1980) and reindeer on the Isle of South Georgia (Leader-Williams, 1988) have all been reported to use seaweed in their winter diets. A special breed of sheep on North Ronaldsay and Linga-Holme on the Orkney Isles in Scotland lives almost exclusively on seaweeds (Hall, 1975; Paterson, 1984). In addition, red deer (Clutton-Brock, Guinness & Albon, 1982), cattle and feral goats (pers. obs.) on the Isle of Rum, Scotland, can regularly be seen to forage on the sea shore for seaweed in winter. For red deer in the north block of Rum, seaweed is an important part of their winter diet: adult males average 18.3% of their time in the seaweed habitat and adult females 11.9% in winter (Clutton-Brock, Guinness *et al.*, 1982), although this habitat covers < 1% of the available area (Ferreira, 1970). Nevertheless, the use of the seaweed habitat by ruminants has rarely been studied or described in the accessible literature (see Paterson, 1984 for a review). The first purpose of the present study is to provide new and detailed information on the use of the seaweed habitat by red deer on the Isle of Rum, including data on seaweed availability, diet selection, relative intake rates, timing of seaweed use relative to tides and inheritance of the mother’s preference for the seaweed habitat by offspring. Particular attention is given to the pattern of inter-sexual site segregation within the seaweed habitat. The second purpose is to test whether the pattern of inter-sexual site segregation within the seaweed habitat supports the following prevalent hypothesis concerning foraging competition between the sexes in dimorphic ungulates (Clutton-Brock, Guinness *et al.*, 1982).

In many sexually dimorphic ungulate species, the
sexes differ with respect to forage habitat use (‘habitat segregation’), so that males use lower quality forage habitat and females use habitats with lower forage quantity (e.g. Geist & Petocz, 1977; Watson & Staines, 1978; Bowyer, 1984; Beier, 1987; Clutton-Brock, Iason & Guinness, 1987). Clutton-Brock, Guinness et al. (1982) have suggested that this habitat segregation is caused by male disadvantage in indirect foraging competition, relative to females (the ‘indirect competition hypothesis’). Their argument is that males, because of their larger body size, have higher forage requirements and, thus, need higher forage intake rates and a higher biomass, than females (Illius & Gordon, 1987, 1992). Therefore, if females graze preferred high quality forage habitats down to the minimum biomass viable for them, males cannot achieve sufficient intake rates in these habitats and are forced into marginal habitats of lower forage quality, but higher biomass (Clutton-Brock, Guinness et al., 1982). This argument can also be extended to segregation between sites within habitats (‘site segregation’: Clutton-Brock, Iason et al., 1987).

To date, the indirect competition hypothesis has been widely cited (see Conradt, 1997 for a review), but evidence relating to it is equivocal (Main & Coblentz, 1990; Bleich Bowyer & Wehausen, 1997; Conradt, 1997 for a review), but evidence relating to it is equivocal (Main & Coblentz, 1990; Bleich Bowyer & Wehausen, 1997; Conradt, 1997).

The use of saltwater seaweed by red deer Cervus elaphus L. offers a good opportunity to test the indirect competition hypothesis, because the seaweed habitat differs from terrestrial habitats with respect to indirect competition. This is because ruminants forage on washed-up seaweed (Clutton-Brock, Guinness et al., 1982; Paterson, 1984), the amount of which depends largely on tidal movements and storms (Paterson, 1984). Thus, availability of seaweed (unlike that of terrestrial vegetation) is less dependent on indirect grazing competition, at least at the time when tidal water starts to retreat (Paterson, 1984). Therefore, specific predictions of the indirect competition hypothesis for the seaweed habitat differ from those for terrestrial vegetation habitats, as follows. First, because indirect competition is reduced when animals are eating seaweed, degree of segregation should be less within the seaweed habitat by comparison with habitats with terrestrial vegetation. Second, since the seaweed habitat becomes depleted with increasing time after the tidal water has started to retreat and animals have started to forage (Paterson, 1984), males, if they are more sensitive to low forage biomass than females, should arrive at and leave the seaweed habitat earlier (relative to tidal times) than females. To test whether observed site segregation within the seaweed habitat can be explained by the indirect competition hypothesis, I examined whether (a) any observed spatial segregation within the seaweed habitat can be explained in terms of males using sites with higher forage quantity (i.e. yielding higher intake rates) but lower quality than females; (b) the degree of inter-sexual spatial segregation in the seaweed habitat is smaller than in terrestrial habitats; (c) males time their use of the seaweed habitat earlier, relative to tidal times, than females. Since seaweed on Rum was available in discrete bays, which differed in physical accessibility and exposure to weather, it was not possible to keep these factors constant. However, if the indirect competition hypothesis is the crucial explanation for inter-sexual site segregation, these factors should not have substantial influence.

METHODS

Study area and population

The study was conducted in the 12 km² north block of the Isle of Rum, Scotland (see Clutton-Brock, Guinness et al., 1982 for a detailed description of the area and the red deer population). Approximately 300–400 individually recognizable red deer were resident in the area and their life histories known (Clutton-Brock, Guinness et al., 1982). Seaweed was available to deer in several discrete bays, but for logistic reasons, observations concentrated on 5 bays: Rocky Bay (RB), Kilmory Main Bay (KM), Kilmory Side Bay (KS), Aristoteles Bay (AB) and Shanham Insir Bay (SI). Since deer feed on seaweed mainly in winter (Clutton-Brock, Guinness et al., 1982), data were collected between January and March. The observed bays differed most probably with respect to weather exposure and accessibility to predators (see Results and Discussion). These differences between bays should not confound the test of the indirect competition hypothesis (Clutton-Brock, Iason et al., 1987): if the hypothesis is the main explanation for inter-sexual site segregation within the seaweed habitat, the related factors, such as weather and predation, should at most play a secondary role. Thus, the results of the present test will give insight into the relevance and importance of the indirect competition hypothesis for segregation within the seaweed habitat.

Seaweed species availability

The availability of seaweed was determined in 3 bays (RB, KM and KS) during winters 1994–95 and 1995–96, using a point sampling method (Reich, Bonham & Remington, 1994; grid size, 10 cm). Transects through the bays ran from shore to low tide line, with 200–350 sampling points per bay, depending on bay size.

Census data

T. H. Clutton-Brock and F. E. Guinness provided census data on habitat use (including seaweed use) and spatial distribution of individual deer for winters 1974–93. Each census was conducted on foot by 1 observer within 1 day (5 times per month each year between January and March), and the observer tried to cover the resident deer population of the study area as
completely as possible (see Clutton-Brock, Guinness et al., 1982 for a description of censusing methods). The data also included information on the time of day of each observation. I used these data to examine the use of seaweed by individuals, to determine degree of spatial segregation within the seaweed habitat and within terrestrial habitats, and to examine the timing of seaweed use by deer. Further, I investigated whether adult sons and daughters resembled their mothers with respect to preference for the seaweed habitat by looking for correlations between adult offspring’s and mother’s proportion of time spent within the seaweed habitat in winter. Only deer that had access to seaweed and mothers that had been observed at least once in the seaweed habitat were included in the analysis. Information about kinship relations was also kindly provided by T. H. Clutton-Brock and F. E. Guinness.

**Observation sessions**

Since the census data did not include information on use of seaweed species or on use of the two fractions of seaweed (washed-up and growing fraction of seaweed), detailed observation sessions were carried out at 3 of the bays (RB, KM and KS) in winters 1994–95 and 1995–96. These 3 bays were < 500 m apart from each other and therefore accessible to the same subpopulation of deer. During 57 observation sessions on different days, lasting between 1 and 5 h each, all seaweed species that were eaten by the deer and, at the beginning of each session, which seaweed fraction was used by individuals were noted. Grazing and chewing rates of deer were also measured to estimate intake rates (see later).

**Spatial segregation**

The degree of spatial segregation was determined based on 100 × 100 m spatial quadrats within seaweed and terrestrial habitats in the north block on Rum, using Conradt’s (1998a) segregation coefficient as a measure:

$$SC = \sqrt{1 - \frac{\sum_{i=1}^{k} \frac{x_{i} \cdot y_{i}}{n_{i} - 1}}{X \cdot Y - \frac{X}{X} \cdot \frac{Y}{Y} \cdot \left(\frac{N}{N} - 1\right)}}$$

$X$: total number of observed males

$Y$: total number of observed females

$N$: total number of observed animals ($X + Y$)

$x_{i}$: number of males in $i$-th spatial quadrat

$y_{i}$: number of females in $i$-th spatial quadrat

$n_{i}$: number of animals in $i$-th spatial quadrat ($x_{i} + y_{i}$)

$k$: number of spatial quadrats

This measure can range from ‘0’ (no segregation) to ‘1’ (complete segregation) and is stochastically independent of sex ratio and deer density (Conradt, 1998a). Only adult males ($\geq$ 5 years) and adult females ($\geq$ 2 years) were considered. Data were pooled for each winter in each year to increase sample sizes. Only winters in which at least 60 males and 60 females were observed were included in the analysis (as recommended by Conradt, 1998a).

**Timing of seaweed use**

The proportions of males and females in the seaweed habitat were determined in each bay at different times of the day on different census days. Tidal time tables for Mallaig (20 km from Rum) were used to convert the day times into times relative to the tide, so that ‘0’ and ‘1’ referred to high tide and ‘0.5’ to low tide. I predicted that the proportion of deer foraging on seaweed should increase as the tidal water leaves each bay and should decrease when the water moves back in. Thus, the proportion of deer should follow a sinusoid curve with period 1 (1 tidal circle) which has been shifted along the time axis so that the maximum lies close to low tide. This was tested by fitting separate sinusoid curves for males and females within 5 bays (RB, KM, KS, AB and SI) to the data, as follows:

$$y = \beta + \gamma \cdot \sin(2\pi \cdot (t - 0.25 + \alpha))$$

$$= \beta + \gamma \cdot \cos(2\pi \cdot (-0.25 + \alpha)) \cdot \sin(2\pi \cdot t) + \gamma \cdot \sin(2\pi \cdot (-0.25 + \alpha)) \cdot \cos(2\pi \cdot t)$$

$$= \beta + A \cdot \sin(2\pi \cdot t) + B \cdot \cos(2\pi \cdot t)$$

$$= \beta + A \cdot t_{1} + B \cdot t_{2}$$

$y$: proportion of males (or females, respectively) in seaweed at time $t$; dependent variable

$t$: time relative to tide; independent variable

$\beta$: mean proportion of males (or females, respectively) in seaweed during the course of a tidal circle; regression coefficient

$\beta + \gamma$: maximum proportion of males (or females, respectively) in seaweed during the course of a tidal circle; regression coefficient

$\alpha$: time difference between time at which a maximum proportion of males (or females, respectively) is in seaweed and the time of minimum low tide; if $\alpha$ is positive, the maximum proportion of males/females uses seaweed before all the water has left the bay, if $\alpha$ is negative, the maximum proportion of males/females is found in the bay after minimum low tide; regression coefficient

$A$: first transformed regression coefficient

$B$: second transformed regression coefficient

$t_{1}$: transformed time $t$; first new independent variable

$t_{2}$: transformed time $t$; second new independent variable

Linear regressions with $t_{1}$ and $t_{2}$ were used as independent variables, $y$ as dependent variable and $\beta$, $A$ and $B$ as regression coefficients. If the proportion of males (or females, respectively) in seaweed followed a periodic curve with period 1, either $A$ or $B$ should be significantly different from 0. If the maximum proportion of males (or females, respectively) used seaweed at minimum low tide, $A$ should not be significantly different from 0.
(since \( \alpha = 0 \) and \( \cos(2\pi(-0.25 + \alpha)) = 0 \)) and \( B \) should be significantly smaller than \( 0 \) (since \( \alpha = 0 \) and \( \gamma \cdot \sin(2\pi(-0.25 + \alpha)) = -\gamma \)). If males timed their seaweeds to be used earlier than females, \( \alpha \) should be larger for males than females. Since \( A \) and \( B \) both depend not only on \( \alpha \), but also on \( \gamma \), I first estimated \( \gamma \) and \( \beta \) in separate regressions for each sex and then transformed the proportion of males (or females, respectively) in seaweed to: 

\[
y' = \frac{\gamma - \beta}{\gamma} = \sin(2\pi(t - 0.25 + \alpha))
\]

\[
= \cos(2\pi(-0.25 + \alpha)) \cdot \sin(2\pi \cdot t)
\]

\[
+ \sin(\pi(-0.25 + \alpha)) \cdot \cos(2\pi \cdot t)
\]

\[
= A' \cdot \sin(2\pi \cdot t) + B' \cdot \cos(2\pi \cdot t) = A' \cdot t_1 + B' \cdot t_2
\]

Linear regressions with \( t_1 \) and \( t_2 \) were used as independent variables, \( y' \) as dependent variable and \( A' \) and \( B' \) as regression coefficients. If males terminated feeding on seaweed earlier than females, \( A' \) should be significantly larger in the regression for males than in that for females.

### Intake rates

Available biomass of growing seaweed was determined in bays RB, KM and KS by ripping as much seaweed off by hand within a fixed period, as possible. The collected seaweed was then dried and weighed. This method has been employed before for terrestrial forages and is thought to give a good estimate of available biomass (Clutton-Brock, Guinness et al., 1982). The grazing rate (number of bites/min) of deer on growing seaweed was counted for 1–5 min. Intake rate was estimated to scale to grazing rate \( \times \) available biomass (since at low biomass, bite size is proportional to available biomass; Illius & Gordon, 1987, 1992). Intake rate of washed-up seaweed was estimated by counting the chewing-rate (number of chews/min) of deer for 5–10 min. When deer foraged within the washed-up fraction, they tended to spend a lot of time searching until they picked up quite large pieces of seaweed (far exceeding the size of their buccal cavity), which they then started to chew. Since deer seemed to fill their entire buccal cavity for each chewing bout, chew-size was relatively constant. The rate of chewing bouts was therefore considered to scale directly with intake rate. Since no significant differences between the sexes were observed for chewing rate (Mann–Whitney test: \( n = 14 \) males, \( m = 29 \) females, \( P > 0.15 \)) or grazing rate (Mann–Whitney test: \( n = 14 \) males, \( m = 8 \) females, \( P > 0.10 \)), data for adult males, immature males and adult females were pooled for comparisons of chewing rates and grazing rates between bays.

### Rumen content

The rumen content of a newly deceased adult hind, whose rumen was filled with seaweed forage, was examined. The rumen content was mixed to make it as homogeneous as possible, a 0.25 l sample was sorted into different seaweed species and other plant material, and each component was dried in an electrical oven at 40 °C for 72 h and weighed. The rest of the rumen content was more superficially searched for additional seaweed species.

### Statistics

To determine whether males and females differed in their use of seaweed fractions, individual animals in groups were treated as independent of each other. This was justified, since both fractions were available to deer on a relatively small scale and individuals seemed to move independently of each other between the 2 fractions, so that part of a group was often in 1 fraction while the other part was in the other fraction.

Parametric tests (2-tailed) were used whenever data distributions permitted.

### RESULTS

#### The seaweed habitat

The habitat consisted of a washed-up fraction of seaweed justbelow the high tide line and a fraction of growing seaweed further from the shore. The three bays that were examined differed in morphology, seaweed composition and relative biomass of growing seaweed (Table 1). Kilmore Main Bay lay in a large, level delta of a freshwater stream, relatively exposed to the sea and wind. Rocky Bay and Kilmore Side Bay were steeper, better sheltered, more rocky and less accessible than Kilmore Main Bay. *Ascophyllum nodosum* and *Pelvetia caniculata* were common in Rocky Bay and Kilmore Side Bay but did not grow within Kilmore Main Bay. All other algal species were available in all three bays. Phenotypic size of growing seaweeds, and consequently their availability (i.e., biomass), was lower in Kilmore Main Bay than in the other two bays.

#### Use of seaweed species by red deer

During direct observations, animals within the washed-up fraction of seaweed foraged mainly on washed-up *Laminaria saccharina*, *L. digitata* and *L. hyperborea* fronds and stipes in the three bays. They also took a red alga (probably *Rhodymenia palmata*) and a few small, torn pieces of *Fucus* spp. In the fraction with growing seaweed, the deer grazed mainly on *P. caniculata* and a little on *Fucus* spp. in Rocky Bay and Kilmore Side Bay, and on *Fucus spiralis*, *F. vesiculosus* and to a lesser extent *F. serratus* in Kilmore Main Bay. They were not seen eating *A. nodosum*, which was abundant in two of the bays (Table 1). On three occasions, deer were...
observed eating a Porphyra sp. When the tide was exceptionally low (low spring tide), many deer foraged on the deepest growing Laminaria-fraction, which was not available at other times.

Thirteen adult hinds and 15 adult stags who used the seaweed habitat were monitored individually in direct observations. All 28 deer fed on the growing and the washed-up fraction of seaweed, and usually ate both fractions within a single session. Sample sizes were too small to compare the use of different seaweed species between individuals or between sexes, but no differences were immediately apparent. However, inter-individual differences in the acceptance *per se* of seaweed as a forage seemed to be large (range of percentage of time spent in the seaweed habitat in winter: males 0–47%; females 0–28%; see also Fig. 1). Some individual deer seemed to be keen on seaweed. They observed the coast long before low tide, even when foraging far up a hill in terrestrial habitats, and moved quickly and straight down into the seaweed habitat as soon as the tide had regressed far enough. On the other hand, not all individual deer who had access to the seaweed habitat made use of it. Some deer who lived around the coast were never observed within the seaweed habitat, and some individuals seemed even to detest seaweed. In winter 1993–94, a 3-year-old male arrived within Rocky Bay together with two other young males, and wandered around the bay watching other deer eating algae, now and then picking up odd pieces of seaweed himself, chewing them a bit, but invariably spitting them out again, until he finally left the bay after nearly 2 h without having eaten a single piece. This implies that seaweed use requires ‘learning’. Therefore, the ‘inheritance’ of preference for seaweed use between mothers and offspring was investigated: in both sexes the proportion of time that an adult spent in seaweed in winter was significantly correlated to seaweed use by its mother (sons: $F_{1,70} = 18.8$, $n = 72$, $P < 0.001$, 21% of variance explained; daughters: $F_{1,206} = 60.8$, $n = 208$, $P < 0.001$, 23% of variance explained; see Fig. 1). This suggests that preferences for seaweed are learned early in life.

Examination of the rumen content of an adult hind confirmed the above observations of predominantly chosen seaweed species. Of the dry matter of the rumen content, 17.3% was seaweed; 39% of the seaweed was *Laminaria* spp. (mainly stalks), 34% *P. caniculata*, 21% *Fucus* spp. and 5% unidentified seaweed particles. A grosser examination of a larger portion of the rumen content added *R. palmata* to the species list. *Ascophyllum nodosum* was not found within the rumen sample.

**Did males use sites of higher forage quantity but lower quality than females?**

**Sex differences in use of bays and seaweed fractions**

Males and females segregated between sites within the seaweed habitat: the degree of inter-sexual spatial segregation within seaweed in January–March was 0.74 ± 0.11 ($n = 17$ years) and was significantly larger than 0 (Wilcoxon-test: $Z = 4.11$, $n = 17$, $P < 0.001$). The sexes differed in their use of bays: females used mainly KM (73% of their time in the three bays; see Fig. 2), while males used RB most (92% of their time in the three bays); numbers of deer of both sexes in KS were relatively small (see Fig. 2), and KS was therefore excluded from the present comparison. Males and females segregated also between the two seaweed fractions, so that males were

### Table 1. Proportion of ground covered by stones, sand and different seaweed species (in %) in each of three bays; mean (± SD) simulated offtake rates (i.e. relative biomass), grazing rates on growing seaweed and chewing rates of washed-up seaweed are given at the bottom

<table>
<thead>
<tr>
<th>Bay</th>
<th>Stones</th>
<th>Sand</th>
<th>Washed-up seaweed fraction</th>
<th>Growing seaweed fraction</th>
<th>Sample size</th>
<th>Mean chewing rate within washed-up seaweed fraction</th>
<th>Mean grazing rate within growing seaweed fraction</th>
<th>Simulated offtake (in g/s) of growing seaweed</th>
</tr>
</thead>
<tbody>
<tr>
<td>KM</td>
<td>19.5</td>
<td>25.7</td>
<td><em>Laminaria</em> spp. 8.4</td>
<td><em>Pelvetia caniculata</em> 1.5</td>
<td>300</td>
<td>4.1 ± 1.4; $n = 10$</td>
<td>49.9 ± 12.7; $n = 24$</td>
<td>0.16 ± 0.04; $n = 4$</td>
</tr>
<tr>
<td>KS</td>
<td>18.6</td>
<td>4.7</td>
<td><em>Ascophyllum nodosum</em> 1.0</td>
<td><em>Ascophyllum nodosum</em> 20.9</td>
<td>200</td>
<td>4.3 ± 1.4; $n = 6$</td>
<td>34.7 ± 8.3; $n = 3$</td>
<td>1.67 ± 0.56; $n = 4$</td>
</tr>
<tr>
<td>RB</td>
<td>15.3</td>
<td>28.4</td>
<td>Others 6.5</td>
<td><em>Fucus vesiculosus</em> 14.3</td>
<td>350</td>
<td>4.4 ± 1.2; $n = 6$</td>
<td>38.7 ± 9.0; $n = 20$</td>
<td>9.25 ± 4.90; $n = 4$</td>
</tr>
</tbody>
</table>

(i.e. relative biomass)
observed significantly more often on the washed-up fraction and females on the growing fraction (males on washed-up fraction: 60% of total observations; females on washed-up fraction: 42% of total observations; \( \chi^2 \)-test: \( \chi^2 = 9.5, \) d.f. = 1, \( P < 0.01, n = 381 \) females, \( m = 89 \) males). The same tendency was observed separately within each of the three bays (see Fig. 2).

**Differences in forage quantity between bays and seaweed fractions**

Within the growing seaweed fraction, the grazing rate in Rocky Bay was significantly lower than in Kilmory Main Bay (0.78 times as high in Rocky Bay as in Kilmory Main Bay; Mann-Whitney test: \( Z = 2.58, n = 24 \) animals in Kilmory Main Bay, \( m = 20 \) animals in Rocky Bay, \( P = 0.01; \) Table 1), but forage biomass was so much higher in Rocky Bay (i.e. 58 higher; see Table 1), that grazing rate in Rocky Bay was probably limited by forage handling time and not by biomass, so that relative intake rates were higher in Rocky Bay than in Kilmory Main Bay (note that grazing rate biomass is \( 0.78 \times 58 = 45.2 \) as high in RB as in KM). Within the washed-up fraction, Rocky Bay and Kilmory Main Bay did not seem to differ in intake rates: chewing rates were not significantly different between Rocky Bay and Kilmory Main Bay (Mann-Whitney test: \( U = 71, n = 10 \) animals in Kilmory Main Bay, \( m = 6 \) animals in Rocky Bay, \( P > 0.3; \) see Table 1). The washed-up fraction of seaweed of all bays seemed to yield lower intake rates than the growing fraction: although grazing rate within the growing fraction and chewing rate within the washed-up fraction are not directly comparable to each other, chewing rates were so much lower than grazing rates (Table 1) and, thus, handling time of washed-up seaweed so much longer than that of growing seaweed, that it is very probable that intake rates were lower in the washed-up fraction.

**Differences in forage quality between bays and seaweed fractions**

Within the washed-up fraction of seaweed, mainly *Laminaria* spp. were eaten, while in the growing seaweed fraction *P. caniculata* was eaten in Rocky Bay.
Use of a seaweed habitat by red deer

Table 2. Relative nitrogen content, fibre content and in vitro dry matter digestibility of different algae species in winter (January–March); source: Paterson (1984) and Conradt (1997)

<table>
<thead>
<tr>
<th>Algae species</th>
<th>Relative nitrogen content (%)</th>
<th>Relative fibre content (%)</th>
<th>In vitro dry matter digestibility (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhodymenia palmata</td>
<td>3.7</td>
<td>2.1</td>
<td>66.4</td>
</tr>
<tr>
<td>Laminaria saccharina</td>
<td>1.7</td>
<td>5.9</td>
<td>56.4</td>
</tr>
<tr>
<td>L. digitata</td>
<td>–</td>
<td>–</td>
<td>58.7</td>
</tr>
<tr>
<td>L. hyperborea (frond)</td>
<td>2.0</td>
<td>5.0</td>
<td>–</td>
</tr>
<tr>
<td>L. hyperborea (stipe)</td>
<td>1.3</td>
<td>9.6</td>
<td>–</td>
</tr>
<tr>
<td>Ascophyllum nodosum</td>
<td>1.2</td>
<td>8.4</td>
<td>32.1</td>
</tr>
<tr>
<td>Pelvetia caniculata</td>
<td>1.7</td>
<td>–</td>
<td>52.5</td>
</tr>
<tr>
<td>Fucus spiralis</td>
<td>2.2</td>
<td>–</td>
<td>47.5</td>
</tr>
<tr>
<td>F. serratus</td>
<td>–</td>
<td>–</td>
<td>14.6</td>
</tr>
<tr>
<td>F. vesiculosus</td>
<td>–</td>
<td>–</td>
<td>22.7</td>
</tr>
</tbody>
</table>

Table 3. Significance tests for sinusoid curve regressions of seaweed use on tidal time for each sex in five different bays in the north block of the Isle of Rum. In the male/female columns the first F-values (bold) test the significance of fitting a sinusoid curve to the data, and the second F-values test whether peak use of seaweed was at a significantly different time from maximum low tide (i.e. from $t_{low\, tide} = 0.5$); last column, results of significance tests investigating whether males and females differed in their timing of seaweed use; *significant results

<table>
<thead>
<tr>
<th>Bay</th>
<th>Males Regression: $F_{1,339} = 4.8, P &lt; 0.05^<em>$ peak: $t = 0.27; F_{1,338} = 3.9, P &lt; 0.05^</em>$</th>
<th>Females Regression: $F_{1,418} = 9.9, P &lt; 0.01^*$ peak: $t = 0.46; F_{1,417} = 1.4, P &gt; 0.2, NS$</th>
<th>Sex difference in timing? $F_{1,751} = 1.5, P &gt; 0.2, NS$</th>
</tr>
</thead>
<tbody>
<tr>
<td>KM</td>
<td>Regression: $F_{1,265} = 2.6, P = 0.1, NS$ peak: $t = 0.55; F_{1,264} = 0.3, P &gt; 0.2, NS$</td>
<td>Regression: $F_{1,262} = 6.9, P &lt; 0.01^*$ peak: $t = 0.45; F_{1,261} = 0.8, P &gt; 0.2, NS$</td>
<td>$F_{1,521} = 0.9, P &gt; 0.2, NS$</td>
</tr>
<tr>
<td>KS</td>
<td>Regression: $F_{1,401} = 10.7, P &lt; 0.01^*$ peak: $t = 0.46; F_{1,402} = 0.9, P &gt; 0.2, NS$</td>
<td>Regression: $F_{1,388} = 8.2, P &lt; 0.01^*$ peak: $t = 0.50; F_{1,387} = 0.0, P &gt; 0.2, NS$</td>
<td>$F_{1,757} = 0.5, P &gt; 0.2, NS$</td>
</tr>
<tr>
<td>RB</td>
<td>Regression: $F_{1,260} = 3.0, P &gt; 0.05, NS$ peak: $t = 0.36; F_{1,261} = 2.8, P &gt; 0.05, NS$</td>
<td>Regression: $F_{1,446} = 19.0, P &lt; 0.01^*$ peak: $t = 0.46; F_{1,445} = 1.4, P &gt; 0.2, NS$</td>
<td>$F_{1,721} = 1.3, P &gt; 0.2, NS$</td>
</tr>
<tr>
<td>SI</td>
<td>Regression: $F_{1,327} = 8.8, P &lt; 0.01^*$ peak: $t = 0.54; F_{1,338} = 0.6, P &gt; 0.2, NS$</td>
<td>Regression: $F_{1,389} = 18.6, P &lt; 0.01^*$ peak: $t = 0.53; F_{1,388} = 0.6, P &gt; 0.2, NS$</td>
<td>$F_{1,682} = 0.0, P &gt; 0.2, NS$</td>
</tr>
<tr>
<td>AB</td>
<td>Regression: $F_{1,339} = 4.8, P &lt; 0.05^<em>$ peak: $t = 0.27; F_{1,338} = 3.9, P &lt; 0.05^</em>$</td>
<td>Regression: $F_{1,418} = 9.9, P &lt; 0.01^*$ peak: $t = 0.46; F_{1,417} = 1.4, P &gt; 0.2, NS$</td>
<td>$F_{1,751} = 1.5, P &gt; 0.2, NS$</td>
</tr>
</tbody>
</table>

and Kilmory Side Bay, and Fucus spp. in Kilmory Main Bay (see earlier). According to published literature (see Table 2), of the relevant seaweed species Laminaria spp. had the highest in vitro digestibility, followed next by P. caniculata, then F. spiralis and finally other Fucus spp.

Was degree of spatial segregation within the seaweed habitat lower than within terrestrial habitats?

Degree of spatial segregation was slightly lower within the seaweed habitat (including all bays within the study area) than within terrestrial habitats in the north block of Rum (degree of spatial segregation within the seaweed habitat: 0.74 ± 0.11, $n = 17$ years; within terrestrial habitats: 0.80 ± 0.05, $n = 17$ years). However, the difference was not significant (Wilcoxon-test: $Z = 1.43, n = 17, P > 0.15$; NS). It was unlikely that the existing patterns of neighbouring terrestrial habitat usage influenced the usage of the adjacent and fluctuating seaweed habitats: deer often moved straight into the seaweed habitat from terrestrial habitats much further away than the next bay. On the contrary, use of bays was likely to influence use of the neighbouring terrestrial habitats: when the deer left a bay they tended to start foraging on the adjacent areas of short grassland.

Did males time their seaweed use earlier than females?

The proportion of males and females in seaweed fluctuated periodically with tidal times: the regression with sinusoid curves was significant for females and males in all five bays, apart from males in Shamhnan Insir Bay and Kilmory Side Bay (see Table 3, Fig. 3). The peak time in use of seaweed by males and females in all bays was not significantly different from the time of maximum low tide, apart from seaweed use by males in Kilmory Main Bay (Table 3). There was no significant difference between males and females in their timing of seaweed use within any of the five bays (Table 3).

DISCUSSION

The finding that adult sons and daughters adopted their mother’s extent of feeding on seaweed and, thus, seemed to ‘learn’ to use the seaweed habitat early in life is of
particular interest. Consequently, individuals differed widely in acceptance of seaweed as forage. The sexes were found to segregate significantly within the seaweed habitat: they segregated between separate bays, as well as between different fractions of seaweed (washed-up and growing fraction) within each bay. I found that males preferred a bay in which intake rates within the growing fraction were higher than in a nearby bay preferred by females. This agrees with the assumptions of the indirect competition hypothesis. However, in comparison with females, within each bay males preferred the washed-up fraction over the growing fraction, and the intake rates within the washed-up fraction did not differ between the preferred bays of males and females. Moreover, the washed-up fraction seemed to yield lower intake rates than the growing seaweed fraction. Thus, it is unlikely that males achieved higher intake rates in the seaweed sites which they preferred, than did females in their sites.

The digestibility of seaweed species fell within the range of digestibility for terrestrial forages on Rum (compare Table 2 to Gordon, 1989 and Conradt, 1997). The highest quality seaweed species (Laminaria spp.) was mainly eaten in the washed-up fraction, which males preferred relative to females. The seaweed species of second highest quality (Pelvetia caniculata) was abundant in the male-preferred bay, but was not found in the bay preferred by females. Fucus spiralis and other Fucus spp. which were mainly eaten in the female-preferred growing seaweed fraction in the female-preferred bay, had the lowest digestibility of seaweed species eaten by the deer. Therefore, contrary to predictions of the

Fig. 3. Fitted curves for the proportion of males (broken line) and females (solid line) eating seaweed at different times relative to the tide (0, 1: maximum high tide; 0.5: maximum low tide) in different bays: (a) KM, (b) KS, (c) RB, (d) SI, (e) AB; diagram (f) shows how much sea water had retreated out of each bay at any time.
indirect competition hypothesis, female deer did not seem to prefer seaweed sites (bays and seaweed fractions) of higher forage quality relative to males.

Further, degree of spatial segregation in the seaweed habitat was not significantly lower than degree of spatial segregation in terrestrial habitats. Also, males did not time their seaweed use earlier than females, but both sexes used the seaweed habitat most at minimum low tide. These results did not support the indirect competition hypothesis. However, unlike the earlier report (Clutton-Brock, Guinness et al., 1982), both sexes did not exclusively use seaweeds in the washed-up fraction, but used to a large extent the fraction of growing seaweed which is subject to grazing competition during low tide. This could have weakened the predicted difference in degree of spatial segregation between seaweed and terrestrial habitats. Nevertheless, this does not explain why seaweed sites preferred by males did not yield higher intake rates, sites preferred by females did not offer higher forage quality, and the sexes did not segregate for timing of seaweed use. Thus, the observed pattern of inter-sexual segregation between bays and seaweed fractions could not be explained by the indirect competition hypothesis. Because of the discrete and fragmented distribution of bays, the number of bays which could be examined was small. Therefore, it would be worthwhile to investigate inter-sexual site segregation within the seaweed habitat in other sexually dimorphic ungulate populations.

Alternative explanations of the observed site segregation within the seaweed habitat could be sex differences in sheltering behaviour (Jackes, 1973; Conradt, 1997; Conradt & Guinness, 1997) or sex differences in anti-predator behaviour (e.g. Miquelle et al., 1992). The bay which was preferred by females was more exposed to wind and weather than the bay preferred by males. Also, the bay preferred by females was more easily accessible and offered an unobstructed view, so that predators would find it harder to surprise or to cut off deer in the female-preferred than in the male-preferred bay. A further cause of segregation between bays could have been social conflicts between the sexes (Conradt, 1997, 1998b, 1999). The space of the seaweed habitat and the time for the seaweed habitat use was much more limited than in terrestrial vegetation habitats. Thus, deer interacted much more closely within the seaweed habitat (in particular within the washed-up fraction; Conradt, 1997) and direct competition could become important, so that females might avoid harassment by larger males through segregation to less preferred bays.

REFERENCES


