Density-dependent resource selection by a terrestrial herbivore in response to sea-to-land nutrient transfer by seals

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Abstract. Sea-to-land nutrient transfers can connect marine food webs to those on land, creating a dependence on marine webs by opportunistic species. We show how nitrogen, imported by gray seals, *Halichoerus grypus*, and traced through stable isotope (δ^{15}N) measurements in marram grass, *Ammophila breviligulata*, significantly alters foraging behavior of a free-roaming megaherbivore (feral horses, *Equus ferus caballus*) on Sable Island, Canada. Values of δ^{15}N correlated with protein content of marram and strongly related to pupping-seal densities, and positively influenced selective foraging by horses. The latter was density dependent, consistent with optimal foraging theory. We present the first demonstration of how sea-to-land nutrient transfers can affect the behavioral process of resource selection (resource use relative to availability) of terrestrial consumers. We hypothesize that persistence of horses on Sable Island is being facilitated by N subsidies. Our results have relevance to advancing theory on trophic dynamics in island biogeography and metaecosystem ecology.

Key words: density-dependent resource selection; feral horse (Equus ferus caballus); *food web; gray seal* (Halichoerus grypus); *isodar; marine-derived nutrient; marram grass* (Ammophila breviligulata); *Sable Island; stable isotope; trophic dynamics.*

Introduction

The transfer of matter and nutrients from richer to less-productive environments can occur across ecosystem boundaries, where physical processes and mobile consumers link the dynamics of seemingly distinct systems (Stapp et al. 1999). The role of biotic vectors in facilitating the flow of nutrients from aquatic to terrestrial systems has been especially well documented (see the review in Massol et al. [2011]). Interesting examples exist for roosting and nesting seabirds (Polis and Hurd 1995, Sánchez-Piñero and Polis 2000); basking sea lions, *Zalophus wollebaecki* (Farina et al. 2003); nesting sea turtles, *Caretta caretta* and *Chelonia mydas* (Hannan et al. 2007); and spawning salmon, *Oncorhynchus* spp., and brown bears, *Ursus arctos*, feeding on salmon (Hilderbrand et al. 1999). Terrestrial trophodynamics have further been shown to be affected by these allochthonous inputs, creating a dependence on aquatic food webs by opportunistic species, particularly within small-island oceanic systems (Stapp et al. 1999).

Warren et al. (2015) recently highlighted a need to take new approaches to using island systems to further our understanding of ecology and evolution, pointing to recent work by Gravel et al. (2011) as an example. In developing a trophic extension of island biogeography theory to predict community composition of food webs, Gravel et al. (2011)

concluded that greater attention must be paid to insular dynamics. In particular, "processes related to generalist/specialist distinctions, such as increased colonization rates, behavioral plasticity or the ability to feed on allochthonous inputs (Polis and Hurd 1995, Massol et al. 2011)…[p. 6]." This statement builds on a recent call by Massol et al. (2011) to link community and ecosystem dynamics through explicit incorporation of spatial ecology (metaecosystem theory), including the spatial flow of nutrients, organisms, and detritus to affect spatial dynamics of organisms under different trophic organizations.

Turning to behavioral ecology to advance our understanding of food webs in a metaecosystem context is inherently appealing given the wide body of theory available to predict animal movements. For example, Massol et al. (2011) makes reference to source–sink dynamics (Pulliam 1988) as one effector of how movements of individuals may potentially connect food webs. Here, we suggest applying concepts of optimal foraging theory as it relates to density-dependent habitat (resource) selection (Fretwell and Lucas 1969, Rosenzweig 1981, 1991, Morris 2003) within spatially structured populations (Appendix S1) to further the study of food-web connectivity across aquatic-terrestrial ecosystem boundaries. Whereas some studies have documented differences in use of foods or habitat by consumers near or far from areas with allochthonous inputs (Iason et al. 1986, Barrett et al. 2005, McLoughlin et al. 2006, Jakubas et al. 2008, Briggs et al. 2012, McCauley et al. 2012), no study has yet demonstrated how behavioral selectivity by

terrestrial consumers for resources might actually change with the addition or loss of these inputs to a system. That is, quantitative demonstration of changes in resource selectivity (greater use of a resource relative to its abundance or use of a resource more than expected from random) in response to nutrient subsidization is lacking.

Distinguishing resource use by organisms (e.g., diet composition or habitat occupancy) from selection is important. Resource selection implies choice in the matter of acquisition: it is the behavioral process whereby individuals preferentially use a non-random set of available resources and is a trait expected to be under natural selection (Morris 2003). Differential resource selection and partitioning is a key facet of behavioral and evolutionary ecology as it is one of the principal relationships that permit species to coexist (Rosenzweig 1981). We hypothesize that spatial heterogeneity in population processes arising from variability in allochthonous inputs, due to density-dependent resource selection by terrestrial consumers, may be broadly relevant to insular dynamics with consequences to trophic dynamics of island biogeography (Gravel et al. 2011; Appendix S1: Fig. S1) and metaecosystem theory (Massol et al. 2011). It may also account for a few of our more enigmatic observations of persistence of species on islands, notwithstanding higher-than-expected abundances due to density compensation and lack of predation (MacArthur et al. 1972, Whittaker and Fernández-Palacios 2007).

Sable Island National Park Reserve, Nova Scotia, Canada (Fig. 1), presents a model system to test predictions associated with the above. A population of feral horses was introduced to Sable Island in the mid-1700s (Welsh 1975) that today exists free from predation, human interference, and guild competition (the horses are the only terrestrial mammal). The horses were formally protected as unmanaged wildlife by legislation in 1961 (Welsh 1975). What is notable about the structure of the horse population is that trends in movement and population growth along the length of Sable Island (Fig. 1) follow expectations of density-dependent habitat selection (Rosenzweig 1981, 1991, Morris 2003). Using fitness isodars (Appendix S1: Fig. S1), van Beest et al. (2014) recently showed that changes in regional densities from 2008 to 2012 (results updated to 2014 in Appendix S2: Fig. S1) conformed to density-dependent but generally non-ideal free distribution. Selection for grasslands over other vegetation associations was also conclusively density dependent, with erosion of selectivity with increasing local density due to competition (van Beest et al. 2014). The basis for these coarse- and fine-scaled density-dependent responses was not known; however, it was suspected that the influence of pupping gray seals on vegetation (gray seals return each January–February to pup on the island [Bowen et al. 2007]) may have been responsible by means of nutrient transfers from sea to land. Sable Island supports the world's largest colony of gray seals, which was estimated to number 394,000
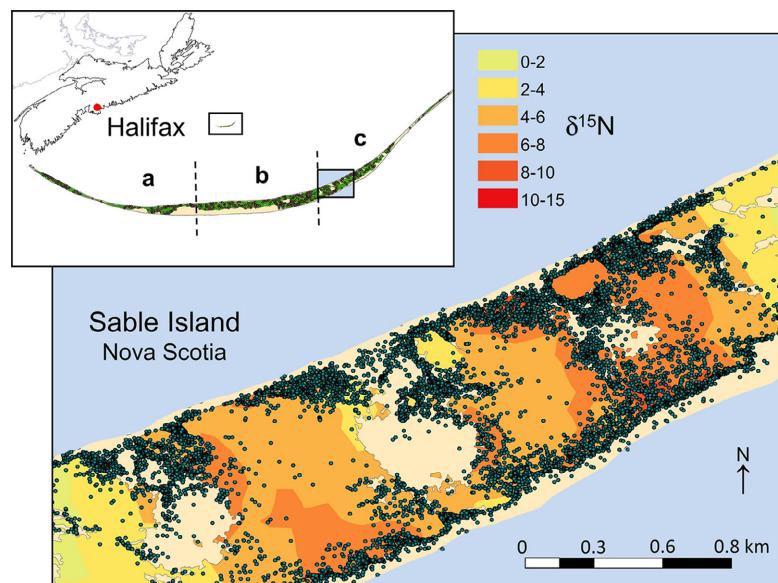

Fig. 1. Sable Island is located approximately 275 km east and south of Halifax, Nova Scotia, Canada (inset). Horizontal lines delineate west-central-east habitat zones (a–c) as identified by Contasti et al. (2012). The main figure shows the $\delta^{15}N$ isoscape (kriged surface of the distribution of $\delta^{15}N$ values in parts per thousand [‰] from sampled sites) within a representative section of eastern Sable Island. Point estimates of marram $\delta^{15}N$ were interpolated to construct the map using an anisotropic semivariogram incorporating second-order polynomial trend removal. More enriched sites are represented by warmer colors. Blue points represent individual gray seal pups used to compute relative seal densities for analysis (seal pups were counted from air photos during the whelping season in winter to index gray seal density). Unvegetated areas (i.e., beige [lightest shading]) within the center of the island indicate exposed sand dunes to >20 m in height. See online version for color image.

individuals in 2014 (Hammill et al. 2014). The west and the east regions of Sable Island (Fig. 1) are where the highest densities of gray seals occur in winter. During the period of data collection for this study, regional subpopulation (Contasti et al. 2012) densities were 49.0, 20.2, and 30.8 horses/km^2 of vegetated habitat for west, central, and east Sable Island (Fig. 1; Appendix S2: Fig. S1), while seal pup densities in 2010 were 3,121, 1,518, and 3,093 pups/km^2, respectively.

If seal and horse abundances are at least spatially correlated, and selection for grasslands by horses is density dependent (van Beest et al. 2014), we might expect selective foraging by horses to relate to spatial heterogeneity in sea-to-land nutrient inputs by seals in a density-dependent manner. Here, we first demonstrate links between stable isotope values (δ^{15}N) in terrestrial plant tissues among sampling plots on Sable Island and local densities of pupping gray seals. Then, we incorporate these data into a resource-selection function (Manly et al. 2002) to show how selective browsing among plots by horses is fundamentally altered by δ^{15}N values in forage. Bump et al. (2009) concluded that increased δ^{15}N values in soils and foliage at sites of biotic nutrient deposition is indicative of higher available nitrogen in soils, resulting in increased plant N assimilation. Crude protein and N content in vegetation are in direct relation (Owusu-Apenten 2005), and crude protein content is critical for growth and maintenance in horses (Saastamoinen et al. 2012); hence, we predicted that feeding behavior of horses would be positively affected by ^{15}N enrichment of forage. We also predicted that plot selection based on forage δ^{15}N values would be density-dependent following van Beest et al. (2014): selection for plots with increased forage δ^{15}N values would be greater at lower local horse densities when intraspecific competition is low, but relatively weaker at higher horse densities when competition (and browsing pressure among plots) is high. Our results suggest that sea-to-land nutrient transfer by seals has the potential to play an important role in the population and behavioral ecology of Sable Island horses indirectly through effects on forage vegetation, leading to predictive patterns of density-dependent space-use. This may be broadly relevant to trophic dynamics of insular systems in consideration of the spatial flow of nutrients and organisms (Gravel et al. 2011, Massol et al. 2011).

MATERIALS AND METHODS

Study area

We conducted our study at Sable Island National Park Reserve (43°55′ N, 60°00′ W), a long (49 km) and narrow (1.25 km at its widest), crescent-shaped sand bar located approximately 275 km southeast of Halifax, Nova Scotia, Canada (Fig. 1). Vegetation associations have been recorded by several authors (Catling et al. 1984, Stalter and Lamont 2006, Tissier et al. 2013) indicating American beach grass, or marram (*Ammophila breviligulata*), as a dominant perennial species throughout the island. Shores and edges are relatively barren except for established halophytic or sand-tolerant plants, including marram and sandwort (*Honckenya peploides*). Symbiotic nitrogen fixation is primarily attributed to the herbaceous, perennial, beach pea (*Lathyrus maritimus*), which is heterogeneously distributed across the island (Contasti et al. 2012).

There are two primary biotic groupings for the transfer of marine-derived nutrients onto Sable Island: (1) seabirds, including Greater Black-backed (*Larus marinus*) and Herring Gulls (*L. argentatus*) and colonies of Common (*Sterna hirundo*) and Arctic (*S. paradisaea*) Terns; and (2) gray seals. The island supports 3,300–4,200 and 2,400–3,960 breeding pairs of gulls and terns, respectively (Toms et al. 2006). Gray seals spend their time hauled out on beaches in summer but use most inland areas during the winter breeding season, with local concentrations around colonies (Bowen et al. 2007, Breed et al. 2006, Beck et al. 2007). Transfer of nutrients occurs primarily through either defecation or decay of carcasses from dead seals. Since 2007, the population of horses on Sable Island has been the focus of a long-term, individual-based study of ecology and evolution, whereby individual movements and life histories for nearly all living horses are recorded in summer (July–September) during a systematic walking census. Horses are identified by their unique markings using digital photography, with mark–resight detection probability for years 2008–2013 averaging 0.992 (sampling protocols in Contasti et al. 2012, van Beest et al. 2014, and Richard et al. 2014).

Sampling

In 2011, between July and August (corresponding with the primary period for plant growth [Tissier et al. 2013]), we visited 480 randomly distributed plot sites within the vegetated portion of the island. We placed a 1-m^2 quadrat at each site (Fig. 1). Tissier et al. (2013) presented an analysis of plant community assembly on Sable Island and its biotic and abiotic drivers (from 134 independently sampled circular plots with 2 m radius, data collected in 2010). They identified three different vegetation assemblages using hierarchical cluster analysis and nonmetric multidimensional scaling associated with predictor variables of distance from shore (m) and slope (degrees). For each of our plots, we quantified these two variables and percent cover of species with the highest summed abundances across vegetated plots of Tissier et al. (2013), including: marram, beach pea, yarrow (*Achillea millefolium*), red fescue (*Festuca rubra*), *Poa* spp. (not identifiable below genus level in the field), and common wild rose (*Rosa virginiana*). We also documented percent cover of the rare, but important, indicator species sandwort (Contasti et al. 2012). We recorded whether a plot showed any evidence of horse browsing (bitten stems). All species but rose were commonly browsed by horses.

Because marram occurred in nearly all plots (98%), we selected marram as our indicator species for isotopic and subsequent analyses. Marram is also the most important forage species for horses in terms of biomass consumed and time spent feeding (Welsh 1975). At each plot, we clipped the center-most marram plant, which we cleaned to remove excess debris, placed in a paper envelope, and stored at –20°C prior to isotopic analysis.

In addition to sampling vegetation plots, we collected samples from candidate vector species on Sable Island (also in 2011) to determine their isotopic values. We obtained skin samples from the rear flipper of adult beached (dead) seals ($n = 14$), which we froze at –20°C in sealed plastic bags until analysis. We collected adult tern ($n = 20$) covert feathers from found-dead birds or nest sites, which we stored dry until needed. We also collected horse hair ($n = 60$ individuals) by passive and opportunistic snagging of tail hair, following University of Saskatchewan Animal Care Protocol 2009032.

Preparation of samples and isotopic analysis

We traced $\delta^{15}N$ values in our system to evaluate sea-to-land nutrient transfer by seals into marram vegetation (Dawson et al. 2002). We dried our samples of marram in an oven at 65°C for 24 h before crushing into a powder. Since marram possessed relatively low amounts of N and high C, we measured out 12-mg and 1-mg aliquots (±0.05 mg) into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis, respectively. We freeze-dried samples of gray seal tissue, which we then repeatedly rinsed in a 2:1 chloroform:methanol solvent for lipid removal (Ramsay and Hobson 1991). We sectioned tips of each tern feather to a maximum of 5 cm, and retained tips for analysis. Average hair growth for mammals is 1 cm per month (Bol and Pflieger 2002); therefore, we sectioned 4-cm subsamples of horse tail hair from the follicle upward to account for nutrient integration within tissues during the vegetation growing (spring/summer) season. Feather and horse hair samples were cleaned of surface oils using a solvent with a 2:1 mixture of chloroform:methanol, which we then dried under a fume hood for 24 h. We homogenized and powdered animal samples to 1-mg aliquots, which we weighed into tin capsules for analysis.

We combusted samples in a Europa Scientific Robo-Prep elemental analyzer (Sercon Limited, Crewe, Cheshire, UK) and the resulting CO_2 and N_2 within samples were analyzed by a Europa Scientific 20–20 continuous-flow isotope ratio mass spectrometer. We compared samples to ratio standards for both ^{13}C and ^{15}N in the form of Vienna PeeDee Belemnite limestone and atmospheric N_2, respectively, following lab protocols of Ramsay and Hobson (1991). We expressed isotope values in a ratio of heavy-to-light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) on a delta scale (δ), which indicates the deviation (in parts per thousand [‰]) of the isotopic composition of a sample from the standard. We constructed a $\delta^{13}C$ and $\delta^{15}N$ biplot (means with SD) to demonstrate isotopic

discrimination among trophic levels (Appendix S2: Fig. S2). We also related $\delta^{15}N$ values of marram grass to their crude protein content as determined from the mass fraction of N (%) and the Kjeldahl conversion for livestock forage and feeds (Owusu-Apenten 2005).

Preliminary considerations

Terns occupied two principal colonies on Sable Island (Toms et al. 2006; which we also confirmed during our 2011 walking census), and horses were not observed to venture into active tern colonies (which corresponded to much of our sampling season). Further, the eastern tern colony on Sable Island was largely enclosed by a fence that excluded horses. Due to the relatively confined effects of terns on vegetation to within bounds of effectively "unavailable" habitat ($n = 20$ plots), and inability to monitor gull densities, we restricted all further analyses to the role of seals on shaping the $\delta^{15}N$ isoscape (Rascher et al. 2012) of Sable Island (Fig. 1). Accounting for non-complete cases, our data set was reduced to $n = 389$ plots. Values of $\delta^{15}N$ in marram of these plots ranged as high as 15.2‰ ($\bar{x} = 2.7$‰, SD = 4.3‰). We mapped $\delta^{15}N$ as a kriged surface to visualize the isoscape in relation to the occurrence of gray seals (Fig. 1). In terms of island divisions previously used to describe seal and horse densities (Fig. 1; *Introduction*), values of $\delta^{15}N$ ($\bar{x} \pm$ SE) in marram varied as 2.9‰ ± 0.4‰, 2.0‰ ± 0.3‰, and 3.9‰ ± 0.4‰, for west, central, and east Sable Island, respectively.

To reduce the number of variables included for modelling, we applied a PCA analysis (R package ade4 [Dray and Dufour 2007]) to compile our descriptive data of plots into two common variables, including the first and second axes of the PCA (Appendix S2: Table S1, Figs. S3 and S4). These two axes (PC_1 and PC_2) accounted for 40.3% of the variation in our plots, with PC_1 facing species associated with sparse, dry grasslands and hummocks (rose, red fescue, *Poa* spp.) against marram grasslands and plots associated with higher slope. PC_2 faced increasing distance from shore with percent cover of beach pea and sandwort.

Sea-to-land transfer of N

We were initially interested in understanding the extent to which variation in $\delta^{15}N$ in marram, controlling for plot characteristics and excluding tern-influenced sites, could be explained by gray seal activity. For this, we created an index of local seal density to assign to each plot, based on georeferenced locations of individual seal pups digitized by the Bedford Institute of Oceanography using high resolution air-photo composites of Sable Island taken in January 2010 (Bowen et al. 2007, Hammill et al. 2014). Using a Geographical Information System (ArcMap 10.3.1; ESRI, Redlands, California, USA), we quantified seal densities at plot sites by summing the number of pups within 25 m of a plot. We assumed a positive relationship between density of pups within colonies and deposition

of feces and carcasses of pups and adults. Colony bounds were primarily limited by topography (Fig. 1), which we expected to change little from 2010 to when we collected vegetation data in 2011. This delay (approximately 18 months) also allowed for a time lag to be included with respect to deposition of carcasses to affect N assimilation in surrounding vegetation: elevated soil $\delta^{15}N$ attributed to mammal carcasses at Isle Royale, Michigan, USA, was recently shown by Bump et al. (2009) to peak after 16 months, with $\delta^{15}N$ values in plant foliage (large-leaf aster, *Aster macrophyllus*) peaking at 26 months.

We then used linear regression to relate marram $\delta^{15}N$ values to predictors of the first two axes of our PCA (PC_1 and PC_2), seal density, and all interaction terms. We square-root-transformed $\delta^{15}N$ values to achieve normality of model residuals. We compared candidate models using AIC corrected for small sample size (AIC_c; Burnham and Anderson 2002), selecting the model with the smallest AIC_c including interactions; however, when the difference in AIC_c was <2.0 units between competing models, we applied the parsimony principle and selected the model with fewest parameters (Burnham and Anderson 2002). We only included main effects with Spearman-rank correlations of $r_S < 0.6$.

Effects of $\delta^{15}N$ on horse foraging behavior

A powerful yet simple approach to quantifying how animals select habitat and resources therein is the Resource Selection Function (RSF; Manly et al. 2002). An RSF is typically defined as any function describing the use of resource units (e.g., points, pixels, or plots in space) that is proportional to the probability of unit use by an organism (Manly et al. 2002). We solved an RSF to estimate the influence of marram $\delta^{15}N$ values assigned to plots and the extent to which plot characteristics predicted the proportional probability of horse foraging (browsing; coded as occurring [1] from observation of bitten stems or not [0] in any of our plots; $n = 148$ and 241, respectively). Although our analysis was closely framed as a presence/absence design (in which case a resource selection probability function [RSPF] may be directly computed; Manly et al. 2002), we did not assume this as our study period was not instantaneous, and some plots may have become browsed after sampling (our analysis better corresponded to a used/available design, fit by a RSF). We thus assumed a function between the relative probability of use, $w(\cdot)$, and a vector of n predictor variables, $x = x_1, x_2, x_3, \ldots, x_n$, using the log-linear form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n) \qquad (1)$$

Due to the mathematical relationship between the Poisson and binomial distributions, we estimated coefficients (β) using those of a logistic regression (Boyce et al. 2002, Manly et al. 2002).

We included PC_1 and PC_2 as composite variables describing vegetation associations and abiotic descriptors in our RSF model. During the summer of 2011, we observed

448 unique horses on Sable Island as part of our weekly walking censuses. To account for effects of horse density on probability of browsing, we assigned to each plot the total number of horses that had centroids of annual movement located within a 4,000 m radius of the plot, and included this variable in our model. Our choice of radius to use around plots corresponded roughly to the 95th percentile of the within-summer range of movements of horses on Sable Island (4,438 m, 2008–2010; as used in Rozen-Rechels et al. 2015). Density, in this case, was a measure of the count of horses that were likely to have the plot located within their normal range of movement (i.e., possibility of browsing the plot). Our global model to predict relative probability of browsing included as additive effects vectors of PC_1 and PC_2, $\delta^{15}N$ in marram of plots, horse density, and up to three-way interactions. We again used AIC_c for model selection in the manner described previously for predicting $\delta^{15}N$ in marram at each plot.

Evaluation

We evaluated predictive success of our RSF using the k-fold cross-validation procedure as proposed by Boyce et al. (2002). For this we calculated cross-validated correlations (r_S) between 10 RSF-bin ranks and area-adjusted frequencies for four test-training sets, each with $n \approx 100$ observations (i.e., four random sets from the 389 cases available). As a confirmatory analysis of observed relationships for tests above, we also conducted a final PCA including the main variables of interest arising from our regressions: distance to shore, slope, percent cover of marram, and $\delta^{15}N$ of marram, whether a plot was browsed or not, seal density, and horse density (the latter computed as number of horses within 4,000 m of a plot, but also as animals per square kilometer of vegetated habitat). We performed all statistical analyses with R v. 3.0.3 (R Development Core Team 2010).

RESULTS

Sea-to-land transfer of N

Gray seals were indicated as the top consumer followed closely by isotopic ratios for terns and gulls, while horse values were closer to ratios obtained directly from marram grass (Appendix S2: Fig. S2). Seal density was a significant and positive predictor of $\delta^{15}N$ values in marram grass (Table 1[a]). The selected model (Appendix S2: Table S2) included additive effects of PC_1 and seal density, and their interaction. Values of $\delta^{15}N$ in marram grass increased as density of seals increased and as the value on PC_1 increased (Table 1, Fig. 2); however, the positive effect of local seal density on $\delta^{15}N$ of marram was reduced (and eventually turned negative) if plots were located on steeper slopes and with higher percent cover of marram (interaction term). Values of $\delta^{15}N$ in marram significantly and positively related to crude protein content of samples ($R^2 = 0.24$, $F_{1,107} = 34.6$, $P < 0.00001$).

TABLE 1. Parameter estimates and standard errors (SE) from the selected models (a) explaining $\delta^{15}N$ values in marram grass (square-root-transformed) and (b) the proportional probability of plots being browsed in summer relative to their availability by feral horses on Sable Island, Nova Scotia, Canada (2011).

Factors	Coefficient	SE	t	P
Model a				
(Intercept)	3.237	0.033	97.62	<0.0001
PC_1	0.057	0.024	2.41	0.016
Seal density	0.042	0.004	9.35	<0.0001
$PC_1 \times$ Seal density	−0.010	0.004	−2.78	0.006
Model b				
(Intercept)	−2.023	0.389	−5.20	<0.0001
PC_1	0.187	0.085	2.20	0.028
PC_2	−0.354	0.092	−3.86	0.0001
Horse density	0.012	0.003	3.76	0.0002
$\delta^{15}N$	0.211	0.079	2.67	0.008
Horse density $\times \delta^{15}N$	0.001	0.001	−2.04	0.042

Notes: PC_1 and PC_2 refer to the first two principal components axes describing variation in plot units (Appendix S2: Table S1, Figs. S3 and S4). Seal density is a relative index of colony distribution computed as the count of seal pups within 25 m of a plot as recorded from air photos from the previous winter. Horse density is the count of horses with summer (July–August) movement centroids within 4,000 m of a plot. Percentage deviance explained (adjusted R^2) by model a was 0.202 (deviance of model [120.93] vs. null deviance [152.71]). Percentage deviance explained by model b was 0.092 (deviance of model [469.4] vs. null deviance [516.8]).

Effects of $\delta^{15}N$ on horse foraging behavior

The selected model predicting effects of marram $\delta^{15}N$ values on horse foraging behavior (Table 1[b]; Appendix S2: Table S3) included additive effects of PC_1 and PC_2, marram $\delta^{15}N$, and horse density, and the interaction between $\delta^{15}N$ in marram and horse density. Horses selected to feed in plots with greater coverage of marram compared to species associated with fescue grasslands and shrubs (rose), and browsed plots generally closer to shore in the presence of beach pea and sandwort. Holding all other variables constant, increasing $\delta^{15}N$ in marram positively related to proportional probability of browsing; however, the effect of $\delta^{15}N$ in marram on predicting browse occurrence was density dependent. At higher horse density, plots were predicted to be browsed with diminishing influence of $\delta^{15}N$ of marram, which had its greatest effect on feeding-site selection at lower horse density (Table 1, Fig. 3). More simply, selectivity of horses for ^{15}N-enriched marram was greatest when fewer horses had access to a sampled plot.

Our RSF had good predictive performance (across the four cross-validation sets, $r_S = 0.79$). Our confirmatory PCA of plot-assigned predictors explained 43.5% of variation on the first two axes (Appendix S2: Fig. S5). The first axis (26.7% of variation) faced $\delta^{15}N$ and seal density (in very close association) with browse occurrence and horse density against distance to shore. Percent cover of marram and slope described the second axis of the PCA.
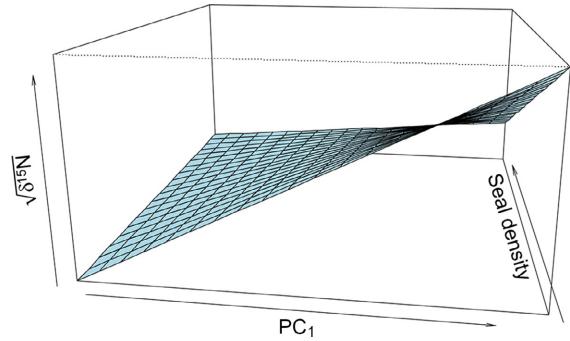

FIG. 2. Relationship predicted by the selected model between square-root-transformed $\delta^{15}N$ values in marram grass on Sable Island (2011) and the first axis of the PCA (PC_1) describing plots (Appendix S2: Table S1, Figs. S3 and S4 for details) and seal density (Fig. 1).

DISCUSSION

Gray seals clearly presented a nutrient subsidy to vegetation on Sable Island. Values of $\delta^{15}N$ in marram grass increased as local density of seals on land increased throughout most of the range of plots considered, although high values of $\delta^{15}N$ were also obtained on high slopes where seals were not present (which we speculate may be due to nutrient inputs of seabirds, especially gulls). Subsequently, horse foraging behavior was influenced by $\delta^{15}N$ values in marram, with plots exhibiting higher $\delta^{15}N$ having greater probability of being browsed relative to their availability, especially at low horse density. At higher horse densities, plots were browsed regardless of $\delta^{15}N$; indeed, use of additional plots and even avoidance of plots with high $\delta^{15}N$ could be expected where recovery of forage from browsing lags (van Beest et al. 2010). These observations fit our predictions, with the latter being especially notable in that it links foraging behavior (selectivity) of horses to nutrient subsidies provided by seals in a manner expected from optimal foraging theory; i.e., density-dependent resource selection.

Indirect effects of marine influences on consumers, as we show here, may account for some of the more fascinating observations in the literature for linked aquatic and terrestrial food webs. This includes observations of extraordinarily high densities of small predators on oceanic islands, including lizards (Case et al. 2002) and spiders (Polis and Hurd 1995), or unexpectedly high biomass of large-bodied consumers in resource-limited systems (e.g., increased densities of geese, *Branta bernicla* and *Anser brachyrhynchus*, and reindeer, *Rangifer tarandus*, foraging near colonies of Little Auk, *Alle alle*, on Spitsbergen [Jakubas et al. 2008]). Such effects should be expected to affect local population dynamics by affecting reproduction and survival, but also animal movements (as our data show). On the Isle of Rum, Scotland, Nussey et al. (2005) showed that during a period of population growth from 1978 to 2001, red deer, *Cervus elaphus*, were spatially distributed among three population
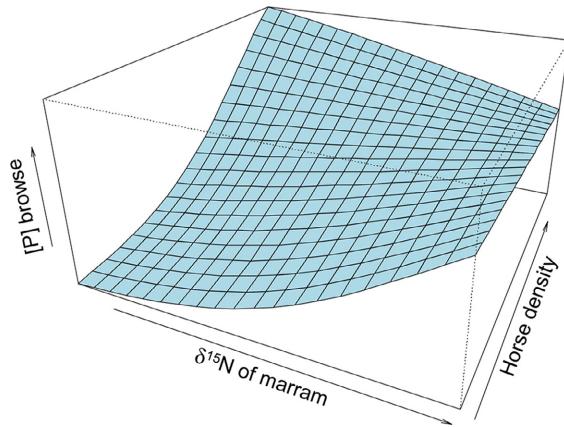
Fig. 3. Resource selection function indicating log-odds probability of plots being browsed ([P] browse) by Sable Island horses in relation to $\delta^{15}N$ values in marram grass of sample plots in interaction with horse density (count of horses with summer [July–August] 2011 movement centroids within 4,000 m of a plot).

subdivisions, one of which was concentrated on orthogenic pastures of *Agrostis*/*Festuca* spp. near the coastline (Iason et al. 1986). Effects of using gull-influenced *Agrostis*/*Festuca* grassland on lifetime reproductive success were positive at low density but negligible or even negative at high density (McLoughlin et al. 2006). Fortin et al. (2008) modelled the density effect, and concluded that red deer specialization on *Agrostis*/*Festuca* grassland was the best strategy at most densities, but at very high density a generalist strategy of habitat selection would convey greatest fitness. Erosion of habitat selectivity at high density due to intraspecific competition (density-dependent habitat selection) may help explain why differences in genetic relatedness (global F_{ST} [fixation index] estimates) for females of the three red deer subpopulations decreased over the study period with increasing population size.

We believe that spatial heterogeneity in sea-to-land nutrient transfers, and associated structuring of populations and movements expected to arise from density-dependent habitat selection, may be particularly important for the dynamics of organisms under different trophic organizations (Massol et al. 2011). In this context, dispersal/colonization among patches would be a key variable (Hanski and Gilpin 1991). On Sable Island, fitness-optimizing selection of habitat by Sable Island horses was previously shown by van Beest et al. (2014) to explain movements and local population growth (expected and realized fitness as well as colonizing densities) along the length of Sable Island (Appendix S2: Fig. S1). Dispersal distance from the barycenters of breeding groups of horses (which have high home range overlap) can be short (<100 m) for adult females (Debeffe et al. 2015) but also distant (up to 18 km) for other age and sex strata, varying in positive relation with local density at the origin of a disperser (Marjamäki et al. 2013). Although we did not explicitly model effects of changes in allochthonous inputs on persistence probability of Sable Island horses (e.g.,

through changing abundance of seals), it is plausible that there may be a link between these inputs and horse population dynamics including maximum density. We believe that, given (1) heterogeneity in seal-mediated N inputs on the island, (2) demonstrative effects of these inputs on ^{15}N enrichment of marram grass, (3) dispersal and colonization abilities of horses along the length of Sable Island, and (4) selectivity for regions and grasslands (van Beest et al. 2014) and $\delta^{15}N$ values in marram of grasslands in a density-dependent manner, it is not unreasonable to conclude that without seal-mediated allochthonous inputs to the island the current population size of horses and thus prospects for persistence might be very different.

Since 1960, the size of the horse population has positively related to that of gray seals ($R^2 = 0.56$, $n = 22$, $P < 0.0001$; Appendix S2: Fig. S6). For reasons that remain largely unknown but possibly due to increases in biomass of small pelagic fishes, the seal herd is remarkable for having grown to astoundingly high abundance since the early 1960s (Bowen et al. 2007): from less than a few thousand animals to the estimated 394,000 individuals in 2014 (Hammill et al. 2014). Productivity of gray seals was just 615 ± 138 [56] (annualized $\bar{x} \pm SD$ [SE]) pups born on Sable Island from 1960 to 1969, compared with 62,000 and 71,000 pups counted as being born on the island (from air photos) in 2010 and 2014, respectively (Hammill et al. 2014). At the same time, the horse population increased from an annual mean of 199 ± 25 [9] horses from 1960 to 1969 (Welsh 1975) to an annual average of 488 ± 68 [26] horses from 2008 to 2014. The latter, which peaked at 559 horses in 2013, is the highest-known abundance in the population's 260-yr history (Welsh 1975). However, a cause-and-effect link between seal population dynamics and horse population dynamics remains to be established. Effects of climate change to positively affect horse abundance (e.g., by increasing the length of the growing season on Sable Island) may also factor into the observed changes in horse densities over time. A further influence leading to an increase in the average size of the horse population over the past 50 years may have been the enactment of protective measures for the horses (freedom from human interference) as part of the *Sable Island Regulations* of the *Canada Shipping Act* in 1961 (Welsh 1975). Testing the strength of linkages between seal and seabird population dynamics and that of the horse population will likely rest on future changes in population sizes of interacting species and additional treatment of isotopic and demographic data.

An additional area of future research for this system lies in modelling horse-facilitated nutrient cycling on Sable Island. Primary or secondary consumers are known to affect nutrient flows across ecosystem boundaries by directly moving subsidies or items (e.g., brown bears feeding on salmon, Hilderbrand et al. 1999), or (as would be the case for horses) by defecation after feeding on ^{15}N-enriched vegetation. In the case of Sable Island, 20.7% of sampled plots contained horse feces, and so we expect horse mobility to not be trivial in terms of nutrient

cycling. To generalize effects of motility of consumers on terrestrial communities in the context of allochthonous inputs requires additional work, but this is clearly a topic relevant to improving the link between community and ecosystem dynamics through explicit incorporation of spatial ecology (Massol et al. 2011).

Effects of marine subsidies by animal vectors on vegetation and hence terrestrial food webs will depend on how consumers behaviorally respond to nutrient enrichment and how they distribute themselves along gradients of allochthonous inputs (Havik et al. 2014). The nature of insular population dynamics, which may lead to generalist vs. specialist distinctions, dispersal dynamics, and feeding behavioral plasticity may be particularly important for incorporating trophic dynamics into island biogeography theory (Gravel et al. 2011). This may also help to bridge community and ecosystem dynamics through explicit incorporation of spatial ecology (Massol et al. 2011), including the spatial flow of nutrients, organisms, and detritus to affect spatial dynamics of organisms under different trophic organizations. Theoretical bridges must be strengthened, however, with empirical demonstration. Here we show, for the first time, that a large terrestrial herbivore responds to a gradient of seal-mediated, allochthonous inputs by positively selecting ^{15}N-enriched areas for feeding in a density-dependent manner. This may have consequences for population dynamics and persistence of the horses on Sable Island, and possibly nutrient flows deeper into the Sable Island system. Our results further our understanding of how sea-to-land nutrient transfer may affect population dynamics and community stability through consumer behavioral ecology.

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SUPPORTING INFORMATION