

SLAVE TO THE TIDES: SPATIOTEMPORAL FORAGING DYNAMICS OF SPRING STAGING BLACK BRANT

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Abstract. Arctic-nesting geese depend on nutrients acquired during spring migration for reproduction, and thus should attempt to maximize nutrient intake while on staging areas. We investigated site use of Black Brant (*Branta bernicla nigricans*) at an important staging location—Humboldt Bay, California—to determine whether birds selected the most profitable feeding areas available. Migrating Brant feed almost exclusively on eelgrass (*Zostera marina*), which is restricted in availability due to daily and seasonal tidal cycles. We mapped foraging Brant locations during low tides and collected eelgrass samples to describe food resources in 31 areas in the bay. We used negative binomial regression to evaluate goose densities during different tidal levels and times of season as a function of food biomass and nutrient content, distance from grit sites, and substrate elevation. Results varied by time of season and tidal depth, but Brant densities were positively correlated with eelgrass protein, calcium, and biomass in most analyses. Brant usually fed in the deepest possible areas permitted by tides, and closer to tidal channels, where biomass and nutrient content of eelgrass were greater and where depletion from grazing was probably less. During higher low tides, Brant fed closer to previously visited grit sites. Tide cycles change over the course of the Brant's staging period on the bay, enabling longer and more frequent access to deeper eelgrass meadows as spring progresses. These seasonal changes in tidal pattern coincide with seasonal changes in Brant use of the bay. Thus, migration patterns for estuarine bird species might be shaped by latitudinal gradients in both food phenology and seasonal tidal patterns.

Key words: *Brant*, *eelgrass*, *food availability*, *Humboldt Bay*, *staging*, *tides*.

Esclavos de las Mareas: Dinámica Espacio-Temporal del Forrajeo de Gansos *Branta bernicla nigricans* en Áreas de Escala Durante la Migración de Primavera

Resumen. Los gansos que nidifican en el Ártico dependen de nutrientes adquiridos durante la migración de la primavera para reproducirse, por lo que deberían intentar maximizar la adquisición de nutrientes cuando se encuentran en áreas de escala migratoria. Investigamos el uso de sitios por parte de *Branta bernicla nigricans* en una localidad de escala migratoria importante—la Bahía de Humboldt, California—para determinar si las aves seleccionan las áreas de alimentación disponibles que resultan más provechosas. Durante la migración, estas aves se alimentan casi exclusivamente del pasto *Zostera marina*, un alimento cuya disponibilidad está restringida por los ciclos diarios y estacionales de las mareas. Mapeamos la ubicación de los sitios de forrajeo durante las mareas bajas y recolectamos muestras de *Z. marina* para describir los recursos alimenticios en 31 áreas de la bahía. Usamos análisis de regresión binomial para evaluar las densidades de gansos en momentos con distintos niveles de la marea y en distintos períodos de la estación como una función de la biomasa de alimento y su contenido nutricional, la distancia a sitios con gravilla y la elevación del sustrato. Los resultados variaron de acuerdo al período de la estación y la profundidad de la marea, pero las densidades de gansos se correlacionaron positivamente con el contenido de proteína y de calcio en *Z. marina* y con su biomasa. Los gansos usualmente se alimentaron en las áreas de mayor profundidad permitida por las mareas, y más cerca de los canales mareales, en donde la biomasa y el contenido nutricional de *Z. marina* fueron mayores, y donde la disminución en la disponibilidad de alimento como consecuencia del forrajeo fue probablemente menos marcada. Durante las mareas bajas más altas, los gansos se alimentaron más cerca de lugares con gravilla que habían sido visitados previamente. Los ciclos de las mareas cambian durante la estadía de los gansos en la bahía, lo que permite el acceso por períodos más prolongados y con mayor frecuencia a los prados más profundos de *Z. marina* a medida que transcurre la primavera. Estos cambios estacionales en los patrones de la marea coinciden con cambios estacionales en el uso de la bahía por parte de los gansos.

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Por lo tanto, los patrones de migración de las especies de aves estuarinas podrían estar moldeados por gradientes latitudinales en la fenología del alimento y en los patrones estacionales de las mareas.

INTRODUCTION

For arctic-nesting geese, successful reproduction depends in part on acquiring nutrient reserves at spring staging sites. Deposits of fat, protein, and minerals are used to complete costly migrations (Ebbinge 1989, Reed et al. 1995, Prop et al. 2003), maintain body condition during the prelaying period when little or no food is available (Ankney 1984, Prop and de Vries 1993), and invest in egg laying and incubation (Raveling 1979, Ankney 1984, Ebbinge and Spaans 1995). Insufficient nutrient storage during spring migration results in lower breeding success (Ebbinge and Spaans 1995, Madsen 1995, Prop and Black 1998, Prop et al. 2003, Black et al. 2006).

Several factors affect the rate of nutrient store accumulation by geese in nonbreeding areas, including habitat selection (Gauthier et al. 1984, Madsen 1985, Prop and Black 1998), foraging behavior (Ydenberg and Prins 1981, Fox 1993), and social status (Teunissen et al. 1985, Black et al. 1992). Within a given feeding habitat, birds benefit from selecting areas of higher food quality and availability (Summers and Critchley 1990, Percival et al. 1996, Clausen 1998). We investigated this sort of 'microhabitat' selection in Black Brant (*Branta bernicla nigricans*), a goose whose feeding ecology outside the breeding season has received less attention than other goose taxa.

On their way to breeding areas in western and northern Alaska, Brant use several staging areas where they feed predominantly on eelgrass (*Zostera marina*, Reed et al. 1998, Ganter 2000, Ward et al. 2005). However, feeding on eelgrass poses ecological challenges to Brant. The protein content of eelgrass in spring is typically near or below 15% (Einarsen 1965, Harrison and Mann 1975, Ward 1983, Buchsbaum and Valiela 1987, this study), lower than that of most terrestrial graminoids used by geese (~25%; Prop & Vulink 1992). Furthermore, eelgrass grows in lower intertidal environments, so access to it is severely restricted by tidal cycles. Thus, nutritive and spatiotemporal constraints on feeding may limit the ability of Brant to meet energetic

requirements and store nutrient reserves during migration.

To meet daily and migratory nutritive requirements, Brant should maximize their net rate of nutritive intake during the brief low tide periods when they can reach eelgrass. This may be accomplished by selecting the highest-quality food available, by feeding on the most nutritious plant parts, or by feeding in areas containing more nutritious plants (Summers and Critchley 1990, Fox 1993, Alonso and Herrera 2000, Black et al. 2006). Alternatively (or additionally), birds may simply attempt to maximize rates of total food intake up to their digestive capacity (Prop and Deerenberg 1991). This may be important for geese, which have relatively inefficient digestive capabilities and depend on rapid digestion of large quantities of food to meet their nutritive requirements (Owen 1972, Prop and Vulink 1992). One way to increase total food intake rate is to feed in areas of high food availability (Crawley 1983, Prop and Deerenberg 1991, Prop et al. 1998). For some terrestrial grazers, this may simply mean selecting areas with high above-ground standing stock (Short 1985, Sutherland and Allport 1994), and Charman (1979) found that Dark-bellied Brant (*B. b. bernicla*) walking on exposed beds of *Z. noltii* achieved higher daily consumption rates as plant density increased. In intertidal environments, however, rapidly changing water levels impose spatially heterogeneous access to food. Eelgrass growing lower in the intertidal zone has higher biomass (Keller and Harris 1966, Kentula and McIntire 1986, Thom 1990) and possibly protein content (Ward 1983), but is also submerged longer throughout the tidal cycle and therefore available less often than eelgrass in higher areas. Consequently, feeding in higher locations with less biomass may be the only option for Brant when tides are relatively high. For example, in Boundary Bay, *Z. japonica* constituted over half of the diet of Brant during winter and spring (Baldwin and Lovvorn 1994). This plant has lower growth rates and biomass densities than *Z. marina* (Phillips 1984, Thom 1990), but it grows higher in the intertidal zone, and therefore may have provided the most biomass

to Brant since it may have been available for longer periods during the tidal cycle.

One additional limitation to where Brant feed concerns their ability to find gizzard grit that enables the mechanical breakdown of their food (Lee et al. 2004). Therefore, the spatial relationship between grit sites and foraging sites may be important.

In this study, we examined the distributions of spring staging Black Brant in Humboldt Bay, California, in relation to availability and quality of *Z. marina* (hereafter, eelgrass), which the birds feed on almost exclusively. Eelgrass availability varies spatially and temporally as a function of eelgrass growth rates and standing stock, depletion by Brant, substrate elevation, and tidal cycles. We hypothesized that for Brant to maximize nutritive intake during the spring staging period, their distributions should shift in response to the continually changing food supply, so they could consistently feed in areas where available food biomass or food quality was greatest. Specifically, we predicted that: (1) Brant use would be positively correlated with eelgrass biomass, protein, and Ca^+ ; (2) Brant would feed closer to recently visited grit sites that they depend on for food processing; and (3) during higher low tides, Brant would feed in higher elevation eelgrass beds, whereas during lower low tides, lower beds would be preferred. To evaluate these predictions, we mapped locations of foraging Brant during daytime low tides from January to May 2000 and collected eelgrass samples from throughout the bay to describe spatial variation in biomass and nutrient quality. We describe the chronology of tidal cycles in Humboldt Bay and how this affects temporal variation in food access, and present multiple analyses that evaluate the importance of measured predictors during different tidal conditions and different periods of the spring staging season.

METHODS

STUDY AREA

Humboldt Bay ($40^{\circ}45'N$, $124^{\circ}10'W$; Fig. 1) is the most important spring staging site for Brant in California (U.S. Fish and Wildlife Service Subcommittee on Pacific Brant, unpubl. data), and the fourth most utilized on the west coast of North America (Moore et al. 2004; Moore and Black, in press). Peak counts and use-day

estimates between January and May averaged over 25 000 and 1.2×10^6 , respectively, during the last 9 years (1992–2000; Humboldt Bay National Wildlife Refuge, unpubl. data).

Humboldt Bay is influenced by mixed semi-diurnal tides (two highs and lows of differing height), and consists of two main sections: Arcata Bay and South Bay (Fig. 1). Intertidal flats cover $\sim 80\%$ in total of their mean high-water areas (Barnhart et al. 1992). The lowest flats are at a substrate elevation approximately 0.6 m below mean lower low water level (i.e., -0.6 m MLLW). Flats below about $+0.3$ m in elevation (i.e., $+0.3$ m MLLW) support extensive beds of eelgrass, which, based on November 1997 imagery data (Terra-Mar 1997), cover approximately 309 ha in Arcata Bay and 720 ha in South Bay. We conducted this study in South Bay, which contains 78%–95% of the total biomass of eelgrass (Harding and Butler 1979) and also 78%–94% of the Brant use recorded in Humboldt Bay each year (Moore et al. 2004).

MEASURING EELGRASS CONDITION

Originally, our intent was to measure initial eelgrass condition in the winter, prior to Brant arrival, and model eelgrass growth throughout the spring staging period. However, the condition of eelgrass in December–January follows months of slow growth (Sand-Jensen 1975, Bixler 1982) and principally reflects spatially stochastic loss processes such as leaf senescence (Harrison and Mann 1975, Kentula and McIntire 1986), winter storm damage, grazing depletion by American Wigeon (*Anas americana*, Yocum and Keller 1961), and leaf removal by diving ducks feeding on herring eggs (Rodway et al. 2003). Thus, we found that winter samples did not accurately represent spatial patterns of eelgrass development. We did not sample eelgrass while Brant were staging because this effort required ≥ 15 person-days at very low tides, during which we prioritized mapping surveys. Consequently, we compared spring Brant distributions with the condition of eelgrass measured the following summer. We reasoned that spatial variation in summer condition should reflect recent growth patterns of eelgrass because leaves only remain on shoots for about 38–65 days (Sand-Jensen 1975, Bixler 1982, Kentula and McIntire 1986).

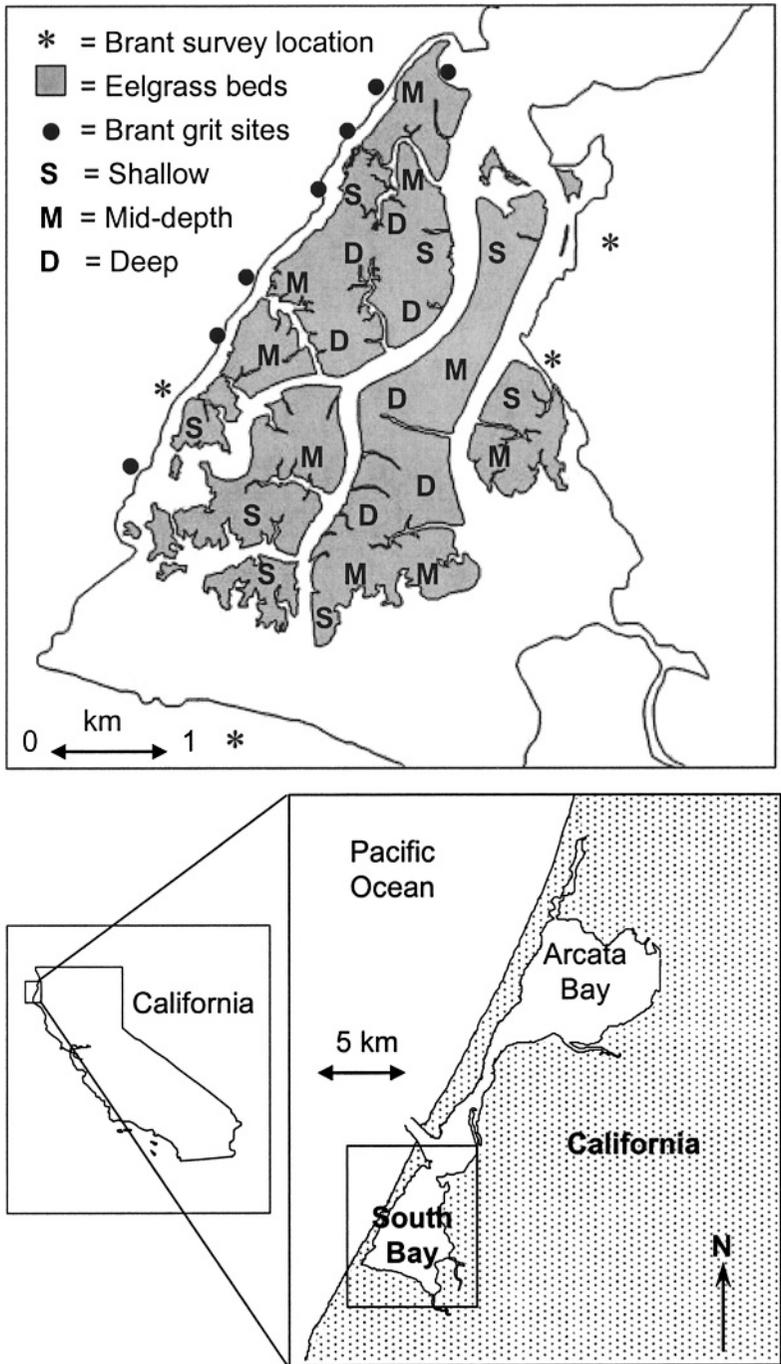


FIGURE 1. Map of Humboldt Bay, California (lower right), which comprises Arcata Bay and South Bay. S = "shallow" areas (>0.0 m relative to mean lower low water; MLLW); M = "mid-depth" areas (0.0 to -0.3 m); D = "deep" areas (less than -0.3 m).

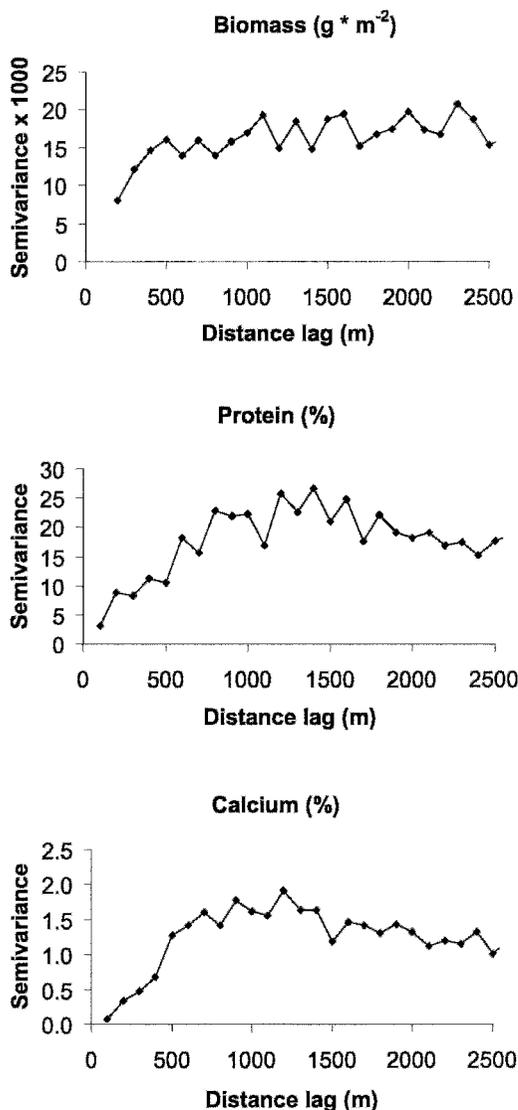


FIGURE 2. Semivariances of three eelgrass attributes as a function of distance between sample locations (lag), based on 133 samples collected in south Humboldt Bay, California, during July 2000. Samples separated by less than about 500–1000 m display positive spatial autocorrelative structure useful for kriging interpolation.

From 2 to 6 July 2000, we collected 133 samples of eelgrass throughout South Bay. We selected sampling locations systematically to ensure even coverage of the bay. We placed a 0.1 m^2 square quadrat on the substrate at each sampling location, and clipped all shoots that grew from within the square at ground

level. We counted the number of shoots in each sample and multiplied by 10 to estimate density (shoots m^{-2}). We dried each sample at 90°C and weighed all leaf material. We analyzed leaf material of each sample for percentage ash, total nitrogen (multiplied by 6.25 to estimate crude protein), and calcium (Ca^+)—an important mineral for eggshell formation and successful reproduction (Graveland and Drent 1997). Ash was measured to calculate ash-free percentages for protein. We used least-squares regression to determine whether biomass and nutrient content were related to tidal elevation, and to distance from nearest major ($\geq 50 \text{ m}$ wide) tidal channels. Values of eelgrass attributes from the 133 samples contained spatial autocovariance structure (Fig. 2), so to facilitate subsequent analyses, we used kriging interpolation (Burrough and McDonnell 1998) in ArcInfo 8.0.2 (ESRI, Redlands, California) to generate raster surface maps (1 ha resolution) for South Bay of biomass (sample biomass multiplied by 10 = g dry m^{-2}), percentage protein, and percentage Ca^+ .

BRANT SURVEYS

From 28 January to 5 May, we conducted low-tide surveys to count and map Brant feeding on eelgrass beds. Each survey lasted up to 4 hr, beginning 2 hr before and ending 2 hr after predicted low tide, depending on weather and lighting conditions. Observed water level data were obtained from the National Oceanic and Atmospheric Administration (NOAA) Center for Operational Oceanographic Products and Services (<http://tidesandcurrents.noaa.gov>). Surveys comprised up to six counts, beginning every 40 min during the survey period. Four observers stationed at different locations around South Bay (Fig. 1) simultaneously conducted counts in nonoverlapping survey areas that covered all eelgrass beds in the bay. During each count, observers used 20–60 \times spotting scopes to map the location, size (number of birds), and shape of Brant flocks on tracing sheets that were overlaid on U.S. Geological Survey Digital Orthophoto Quadrangles (DOQ) of Humboldt Bay. The DOQs provided 1 m resolution of the bay's topography and landmarks, thereby facilitating mapping accuracy. We digitized the hand-drawn Brant flocks in ArcView[®] (ESRI, Redlands, California) GIS as vector polygons, with all

flocks from an individual count entered into a single polygon layer. We then converted each layer into a raster grid, with each grid cell indicating the number of Brant in a particular 1 ha area during the count. For flocks >1 ha, we estimated the number of birds in each constituent cell as total flock size (number of birds) divided by the number of 1 ha cells spanned by the flock.

STATISTICAL METHODS

We used negative binomial regression in Stata 8.0 (StataCorp 1997) to analyze Brant densities (number per ha) in each of 31 “regions” of the bay (see below) as a function of environmental predictors. The negative binomial distribution is appropriate for overdispersed (variance > mean) count data (Long 1997). We divided the 15-week survey period into three five-week periods and defined four tidal ranges relative to MLLW: +0.60 to +0.90 m, +0.31 to +0.60 m, +0.01 to +0.30 m, and ≤0.0 m. Brant cannot reach eelgrass anywhere in the bay at water levels greater than +0.90 MLLW. We performed separate analyses for each period-tide combination because we expected relationships between Brant use and predictor variables to differ across the season and with different water depths.

Because predictor and dependent variables were positively autocorrelated across 1 ha grid cells, and because the accuracy of mapping Brant flocks at 1 ha resolution was uncertain, we used *K*-means cluster analysis (Hartigan and Wong 1979) in NCSS 2000 (NCSS, Kaysville, Utah) to group all 1 ha grid cells throughout the bay into 31 larger contiguous regions (4–63 ha in size) of similar elevation. Analyses were then performed at this spatial scale, i.e., we defined the density of Brant in a given region as the observational unit. For each variable in our analysis, the value for a region equaled the average of its constituent 1 ha grid cell values. We were also concerned with temporal autocorrelation in the data, since spatial counts conducted on the same day, or even within the same several-day period, may have been positively related. Therefore, we averaged all Brant-distribution grids from the same week and tidal range into a single grid. We used NOAA observed water level data for Humboldt Bay, corrected for time lags and estimated water level variations for different

areas of the bay, to determine which Brant-distribution grids fell within a given tidal range. Thus, for a given analysis, *n* equaled 31 (number of regions) times the number of weeks for which there were data (maximum possible *n* = 155). For each period-tide analysis, multiple observations came from each region in the bay. To deal with this potential lack of independence, we used the ‘cluster’ option in Stata 8.0, which uses a robust variance estimator and adjusts standard errors for repeated observations on the same region (StataCorp. 1997).

We fit a finite set of models to the data in each analysis, and performed model selection based on Akaike’s (1973) information criterion with a bias-correction term for small sample size (AIC_c; Hurvich and Tsai 1989). We constructed a “confidence set” of models (those with ΔAIC_c < 4), and scaled Akaike weights (*w_i*; Burnham and Anderson 2002) to models in this set. We performed model averaging to estimate parameters $\tilde{\beta}_j$:

$$\tilde{\beta}_j = \sum_{i=1}^R w_i I_j(g_i) \hat{\beta}_{j,i}$$

where

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)}$$

and

$$I_j(g_i) = \begin{cases} 1 & \text{If predictor } x_j \text{ is in model } g_i, \\ 0 & \text{otherwise.} \end{cases}$$

This estimator reduces estimation bias associated with model selection uncertainty and spurious effects, and helps stabilize inference (Burnham and Anderson 2002). We evaluated the relative importance of variables by summing Akaike weights (*w_{+[j]}*) for all models in the confidence set where variable *j* occurred (Burnham and Anderson 2002). We standardized continuous predictor variables for analysis, so each $\tilde{\beta}_j$ could be interpreted as the amount of change in the log of expected density (log[μ]) following a one SD change in the predictor variable from its mean. AIC_c model selection results are implicit in estimates of $\tilde{\beta}_j$ (± SE) and

associated $w_+(j)$, which reflect Akaike weights of candidate models.

Potential predictors of Brant density in each region included: eelgrass biomass (Mass), crude protein and Ca^+ content, distance to nearest grit site (Grit), substrate elevation (modeled as a linear [Elev] or quadratic [Elev + Elev²] effect), Brant use recorded in each region during previous five-week periods (Prev1 and Prev2 = average of all counts conducted during the first and second five weeks, respectively), and average daily number of Brant in South Bay each week (Number). The latter was to control for the effect of total Brant numbers on region-specific Brant density.

RESULTS

VARIATION IN EELGRASS CONDITION

Values are presented as mean \pm SD. Crude protein (ash-free) content of July eelgrass samples was $12.7\% \pm 4.2\%$, but this probably underestimated that of eelgrass consumed by geese in earlier months. Leaf nitrogen declines from winter to summer (Pedersen and Borum 1993, Clausen 1994); crude protein of 74 samples we collected the previous winter (December–January) was $15.9\% \pm 2.3\%$. Protein content was higher closer to large tidal channels ($R^2 = 0.31$, $F_{1,130} = 59.4$, $P < 0.001$), but in contrast to the finding of Ward (1983), did not vary with elevation ($R^2 = 0.03$, $P = 0.96$). Biomass (234 ± 123 g dry m^{-2}) varied inversely with tidal elevation ($R^2 = 0.16$, $F_{1,131} = 24.0$, $P < 0.001$). Calcium content ($1.4\% \pm 1.0\%$) increased with distance from major tidal channels and was higher in lower-elevation eelgrass beds (Adj $R^2 = 0.34$, $F_{2,130} = 34.9$, $P < 0.001$).

TIDAL RESTRICTIONS ON FORAGING

Eelgrass shoot length in Humboldt Bay varies in summer from ~ 0.3 m on average (max ~ 0.6 m) near its upper intertidal limit to ~ 1.3 m on average (max. >2 m) in the deepest areas (Keller 1963). However, shoot lengths in winter and spring are only about 55%–75% of those in summer (Bixler 1982, Moore 2002), and thus vary along the elevation gradient from ~ 0.25 m to 0.8 m on average when Brant are staging. Since leaves are not suspended vertically in the water column (because they bend with tidal currents and lose buoyancy with age

and damage), most of these plants only reach <0.2 – 0.6 m above the substrate. Brant can reach 0.4 m into the water column (Clausen 2000), but some overlap is required with plant height for a bird to obtain younger leaves, which are shorter and more desirable than older leaves (Fox 1993, Moore 2002; J. Prop and JMB, unpubl. data). Therefore, we approximated that water depth must typically be less than ~ 0.6 m for Brant to feed over the shallowest eelgrass beds, and less than ~ 1 m for Brant to feed over the deepest beds. Thus, a tidal depth of <0.9 m (0.3 m elevation + 0.6 m depth) is required before Brant can reach eelgrass growing in the highest-elevation areas.

Based on the above estimates, only $\sim 33\%$ of all days before early March would have permitted Brant to forage on eelgrass beds during both daily tides, and the higher of the two low tides was typically very restrictive (Fig. 3). In contrast, on $\sim 66\%$ of all days after 5 March, tides permitted two feeding opportunities, both of which were relatively long in many cases (Fig. 3). Lower tides increased overall access to eelgrass in the bay and generally permitted more prolonged foraging periods (Fig. 4). Lower low tides (the lower of the two each day) also were lower after (0.00 ± 0.18 m) than prior to early March (0.23 ± 0.30 m; Fig. 3). Thus, foraging opportunities in the latter two-thirds of the season were not only more frequent, but consistently were longer and included access to a greater proportion of the bay's eelgrass habitat.

BRANT DISTRIBUTIONS

We mapped and counted Brant 153 times during 34 surveys. The seasonal pattern of use-days was typical for Humboldt Bay; Brant numbers increased gradually from late December through March, peaked near the month's end (17 809 on 24 March), then decreased rapidly until most migrants had left by mid-May.

Model goodness of fit. Relatively high values of the overdispersion parameter (α) verified the appropriateness of using negative binomial regression for our data, which contained a much greater number of zero observations than would have been predicted by a Poisson count process. Our models fitted the observed proportion of eelgrass regions with density = 0 well (~ 0.15 – 0.65 ; Fig. 5). During the first 10 weeks,

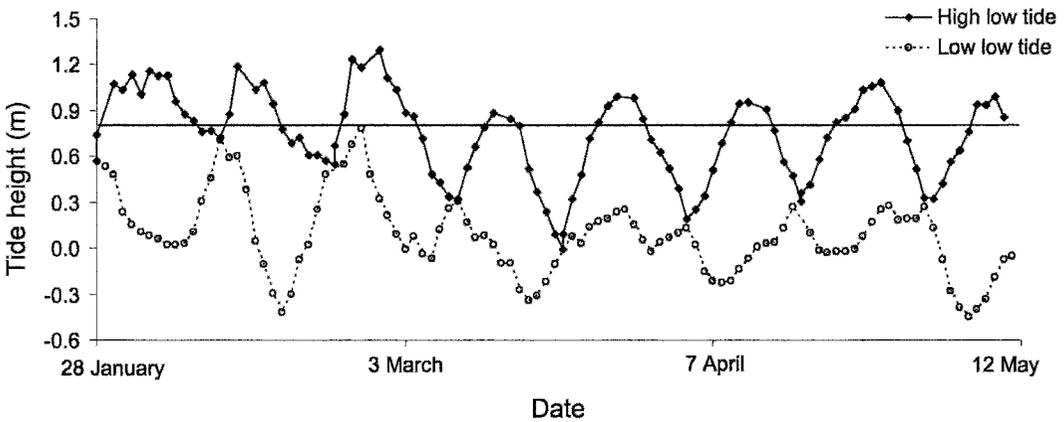


FIGURE 3. Low-tide heights (relative to mean lower low water; MLLW) for North Spit, Humboldt Bay, California, on all dates between 28 January and 11 May 2000. Horizontal line depicts the approximate maximum tide height (+0.8 m) that allows Brant to reach eelgrass in the shallowest areas of the bay.

the proportion of eelgrass regions with zero counts increased as tide levels decreased (Fig. 5), indicating that Brant selectively fed in relatively few areas when they had full access to all areas of the bay. The fit of models to nonzero data was more variable, but appeared adequate for most analyses.

28 January–2 March. During the first five survey weeks, daily Brant numbers in South Bay increased steadily from ~3500–10 000 birds. During the highest water levels that allowed Brant to feed (+0.6 to +0.9 m), Brant densities were positively correlated with substrate elevation and negatively correlated with distance from grit sites (Table 1). Sandy grit

sites, submerged most of the day, are the first resources to become available as tides retreat, as they occur relatively high in the intertidal zone (Lee et al. 2004). Large numbers of Brant congregate at grit sites at their earliest opportunity, and subsequently depart to feed on eelgrass beds as soon as they become available. Holding grit and elevation variables constant, Brant selected eelgrass beds with higher biomass and protein content (Table 1, Fig. 6). Trends were similar during slightly lower water levels (+0.3 to +0.6 m), but smaller $w_+(j)$ and slope coefficients for grit-site distance and biomass indicated that these variables were less important predictors of Brant density (Table 1),

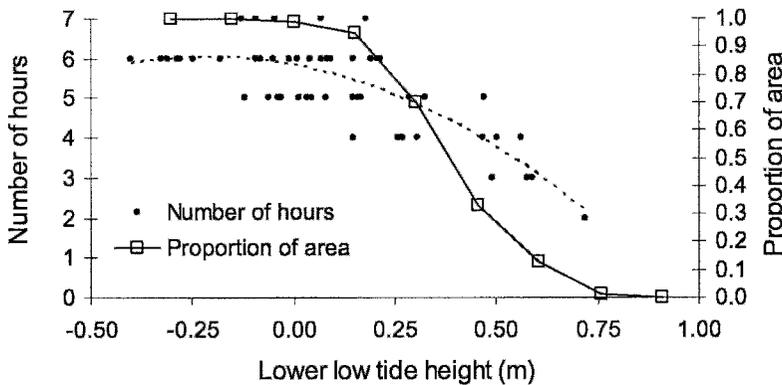


FIGURE 4. Temporal and spatial access to eelgrass by Black Brant in south Humboldt Bay, California, as a function of tide height. Dotted line is fit to the number of consecutive hours surrounding a tidal minima (x -axis) when water level is less than +0.8 m ($n = 53$ lower low tides between 28 January and 11 May). Solid line depicts the approximate relationship between tide height and proportion of habitat area accessible to Brant, based on estimates of elevation-specific plant length.

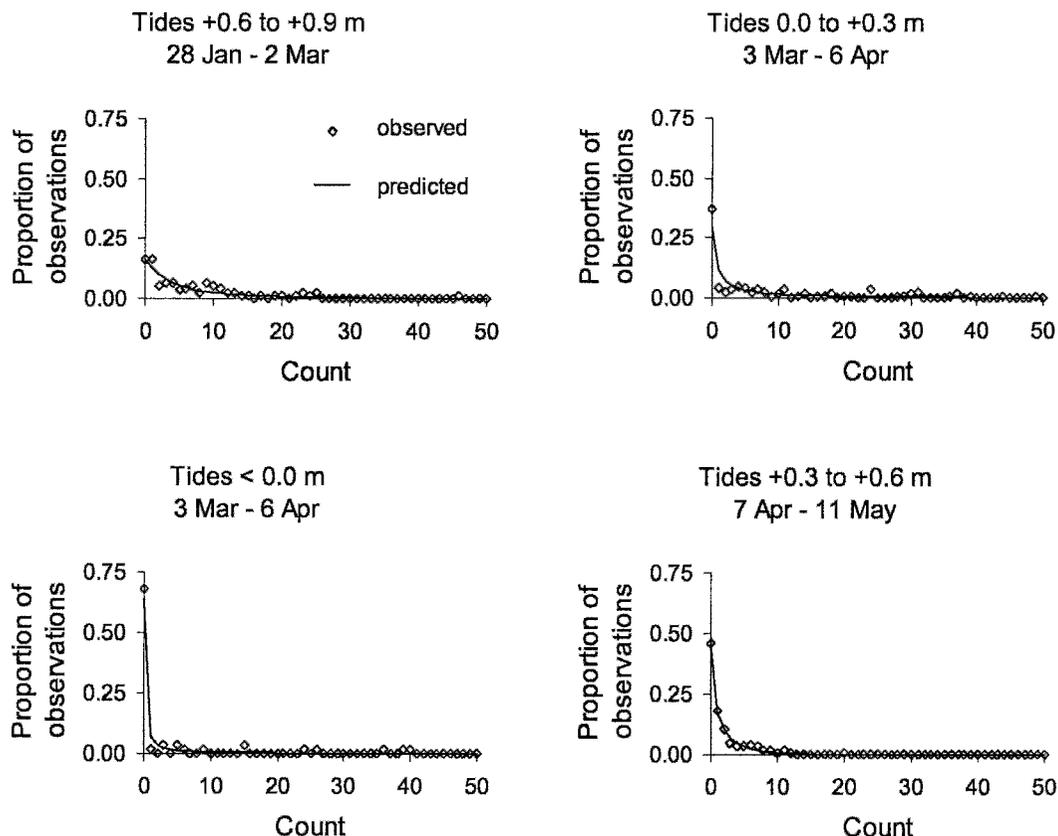


FIGURE 5. Observed and predicted densities of Brant (count per ha) in Humboldt Bay, California, from negative binomial regression models for four period-tide analyses.

whereas protein and Ca^+ content became stronger predictors (Fig. 6). During water levels less than +0.3 m, when Brant could access eelgrass in most areas of the bay (Fig. 4), protein and Ca^+ content were the strongest predictors of bird densities (Fig. 6). These two nutrient variables were in all candidate models for the two lowest tidal ranges, and their associated slope coefficients increased with decreasing tide heights (Table 1). The relationship between Brant density and elevation switched from linearly positive to a convex quadratic during lower tide conditions (Table 1), indicating that higher Brant densities occurred on intermediate-to-lowest elevation beds (Fig. 7). However, the importance of elevation as a predictor of Brant density was weaker during lowest low ($w_+[j] = 0.45$) than highest low tides ($w_+[j] = 1.00$).

3 March–6 April. The second five weeks of Brant surveys represented the period of peak

Brant use, with daily Brant counts on South Bay increasing from $\sim 10\,000$ – $18\,000$. During this period, minimum low tides were consistently low (Fig. 3), thus none of our surveys were during water levels greater than +0.6 m, and most surveys during +0.3 to +0.6 m merely captured transitions to lower tide heights (less than +0.3 m) an hour or two later. Because of this, we did not observe a positive relationship between Brant density and substrate elevation during medium-high (+0.3 to +0.6 m) tides. In fact, there was a weak negative relationship between elevation and Brant density during these water levels (Table 2). This suggests that Brant were queuing over deeper eelgrass beds, i.e., they anticipated the imminent availability of low-elevation eelgrass. During lower tides (less than +0.3 m), we observed an even stronger quadratic relationship between density and elevation than in the previous five weeks (Table 2, Fig. 7), indicating that Brant used

TABLE 1. Model-averaged estimates of slope parameters from negative binomial regressions of Brant density (number per ha) in each of 31 "regions" within Humboldt Bay, California, from 28 Jan to 2 Mar 2000, during four different tidal height ranges (relative to mean lower low water level). Intercept is the $\log(\mu)$ when each covariate equals its standardized mean of zero. Other $\tilde{\beta}_j$ predict change in $\log(\mu)$ with one SD change in the covariate. Sample size (n) = 31 * number of weeks with data. $w_+(j)$ is the sum of weights (w_i) for models containing covariate j . The overdispersion parameter (α) reflects the amount of variation in counts around the expected values.

Tide level	+0.6 to +0.9 m		+0.3 to +0.6 m		0.0 to +0.3 m		<0.0 m	
n	93		93		62		31	
Model covariate ^a	$\tilde{\beta}_j \pm SE$	$w_+(j)$						
Intercept	1.68 ± 0.13	1.00	1.60 ± 0.16	1.00	1.44 ± 0.22	1.00	0.58 ± 0.39	1.00
Number	0.47 ± 0.09	1.00	0.54 ± 0.10	1.00	0.39 ± 0.15	1.00		
Mass	0.63 ± 0.21	1.00	0.21 ± 0.28	0.37				
Grit	-0.40 ± 0.17	1.00	-0.28 ± 0.25	0.63				
Elev	0.33 ± 0.20	1.00	0.31 ± 0.20	0.81	0.80 ± 0.93	0.51	0.75 ± 1.04	0.45
Elev ²					-1.00 ± 1.14	0.51	-1.22 ± 1.54	0.45
Protein	0.16 ± 0.15	0.73	0.79 ± 0.27	1.00	1.15 ± 0.32	1.00	1.83 ± 0.49	1.00
Ca ⁺			0.58 ± 0.29	0.91	1.61 ± 0.39	1.00	2.16 ± 0.57	1.00
α	0.75 ± 0.17	1.00	1.59 ± 0.39	1.00			3.10 ± 1.12	1.00

^a Number = the number of birds on the bay at time of survey; Mass = eelgrass biomass density; Grit = distance from nearest grit site; Elev = elevation of eelgrass bed, relative to mean lower low water (MLLW); protein and Ca⁺ = percentage nutrient content of eelgrass (ash-free dry weight).

deeper eelgrass beds in the latter period. Proximity to grit sites was a weak predictor of Brant densities during tides less than +0.3 m. As during the first five weeks, protein and Ca⁺ were positively related to Brant densities during tides less than +0.3 m; however, the importance of these predictors was lower in this time period than during the first five weeks, as evidenced by smaller slope coefficients and $w_+(j)$ in the second five weeks (compare Table 1, 2). Brant distributions were positively correlated between the first and second five-week periods (Table 2), indicating that Brant densities in March were higher in eelgrass regions that had also received higher use in February. This relationship was strongest during tides less than +0.3 m (Fig. 8), probably because Brant had little opportunity to deplete low-elevation areas during the first five weeks.

7 April–11 May. This period was characterized by rapid decline in Brant use of Humboldt Bay, with numbers dropping from peak levels to <1000 birds. The distribution of low tides was similar to the second five-week period (Fig. 3); thus, we consistently observed Brant over deeper eelgrass beds and, during the lowest water levels, the relationship between substrate elevation and Brant density was similar to the previous five-week period (Fig. 7). Even during

the highest water levels that we surveyed (greater than +0.6 m), Brant densities were negatively correlated with substrate elevation (Table 3), such that many birds were in areas with water depth >1 m. Eelgrass biomass was a consistent predictor of Brant densities during this period (Table 3). Protein and Ca⁺ were weakly positively related to Brant densities during the highest low tides, and protein was also correlated with Brant densities during tides between 0.0 and +0.3 m. During the highest low tides only, Brant densities were higher in areas that received higher use in the first five weeks but lower use in the second five weeks (Table 3).

DISCUSSION

Optimally foraging individuals behave in a manner that maximizes their long-term average intake rate of energy or limiting nutrients (Stephens and Krebs 1986). Brant in Europe are known to feed in the most profitable of available habitats, switching in response to changes induced by differences in plant species' phenologies, or depletion from grazing (Boudewijn 1984, Vickery et al. 1995, Clausen 1998). Clausen (2000) found that Light-bellied Brant (*B. b. hrota*) abandoned their preferred food, eelgrass, when water levels increased to the

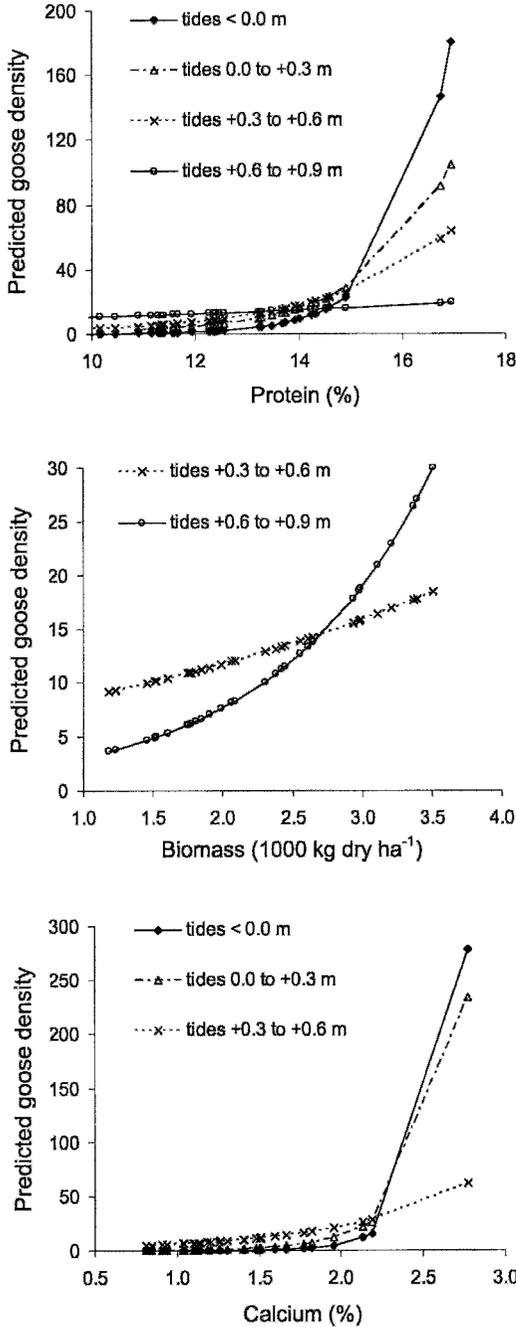


FIGURE 6. Fitted values for Brant densities (number per ha) in 31 eelgrass regions on south Humboldt Bay from 28 January to 2 Mar 2000, as a function of eelgrass percentage protein, biomass density, and percentage calcium. Predictions are based on model-averaged estimates of negative binomial regression parameters. Predictions for a given variable assume a population of 10 000 Brant and that other covariates are equal to the mean value

point that declining eelgrass availability made it more profitable to feed in higher saltmarsh areas where different foods were available. Brant in Humboldt Bay feed almost exclusively on eelgrass during the entire staging period—they do not switch to alternative foods during higher water levels—and we found that Brant distributions varied with patterns of food quality and availability in a manner consistent with our ‘optimality-based’ predictions.

Brant fed on lower-elevation eelgrass beds when tides permitted. Eelgrass biomass and Ca⁺ content increased in beds lower in the intertidal zone, and Ward (1983) found that protein content is also higher in deeper areas, although we did not find this latter relationship in our samples. Because tides permit shorter and less frequent access to deeper areas of the bay, lower-elevation beds might be depleted more slowly. Therefore, the preference of Brant for lower-elevation eelgrass beds when they are available probably reflects selection for areas with both higher food quality and abundance. Indeed, selection for areas with higher biomass, protein, and calcium content was reflected in our analyses.

Because we sampled vegetation after the staging period, it is possible that spatial variation in eelgrass condition was a consequence of bird use rather than vice versa, as geese are known to enhance plant condition in some terrestrial systems (Prins et al. 1980, Ydenberg and Prins 1981). Clausen (1994) found that 40 days following release from grazing pressure, eelgrass biomass was higher in grazed than ungrazed plots, but these differences no longer existed after another five weeks. We believe that since eelgrass exhibits high leaf turnover rate, and since our samples were collected 3–4 months after the two periods of highest Brant use, it is unlikely that our samples principally reflected Brant-induced effects on biomass. Rather, our samples should have reflected spatial variation in growth patterns that would have affected Brant use throughout the season. Grazing could have longer-term enhancing effects on plant protein

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for all regions. Tide heights are in relation to mean lower low water level (MLLW).

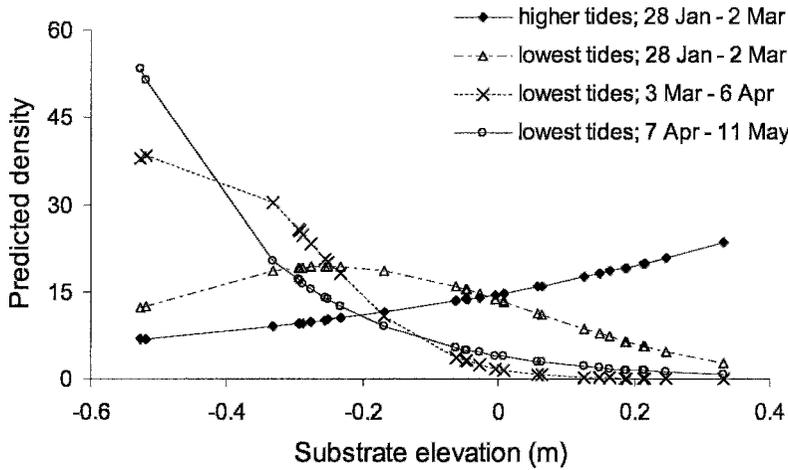


FIGURE 7. Fitted values for Brant densities (number per ha) in 31 eelgrass regions on south Humboldt Bay (winter–spring 2000) as a function of substrate elevation. Predictions are based on model-averaged estimates of negative binomial regression parameters. Predictions assume a population of 10 000 Brant and that other covariates are equal to the mean value for all regions. “Higher tides” are +0.6 to +0.9 m in relation to mean lower low water level (MLLW). “Lowest tides” are <0.0 m (MLLW).

content if goose droppings enrich sediment nitrogen (sensu Bazley and Jefferies 1985), particularly if eelgrass beds are nitrogen-limited, so we cannot conclude whether protein distribution affected goose distributions or vice versa. Both may be true, such that nitrogen enrichment and goose use create a positive

feedback loop, resulting in areas receiving traditionally high use. Longer-term studies would elucidate whether Brant favor the same areas every year.

We frequently observed dense aggregations of Brant feeding along the edges of tidal channels that weaved through eelgrass beds.

TABLE 2. Model-averaged estimates of slope parameters from negative binomial regressions of Brant density (number per ha) in each of 31 “regions” within Humboldt Bay, California, from 3 Mar to 6 Apr 2000, during four different tidal height ranges (relative to mean lower low water level). Intercept is the $\log(\mu)$ when each covariate equals its standardized mean of zero. Other $\tilde{\beta}_j$ predict change in $\log(\mu)$ with one SD change in the covariate. Sample size (n) = 31 * number of weeks with data. $w_+(j)$ is the sum of weights (w_j) for models containing covariate j . The overdispersion parameter (α) reflects the amount of variation in counts around the expected values.

Tide level	+0.3 to +0.6 m		0.0 to +0.3 m		<0.0 m	
	n	93	124	62		
Model covariate ^a	$\tilde{\beta}_j \pm SE$	$w_+(j)$	$\tilde{\beta}_j \pm SE$	$w_+(j)$	$\tilde{\beta}_j \pm SE$	$w_+(j)$
Intercept	2.66 ± 0.12	1.00	1.82 ± 0.15	1.00	-0.10 ± 0.52	1.00
Mass					0.55 ± 0.67	0.52
Grit	-0.13 ± 0.17	0.44				
Elev	-0.28 ± 0.16	0.86	0.63 ± 0.59	1.00	0.36 ± 1.31	1.00
Elev ²			-1.72 ± 0.67	1.00	-2.91 ± 1.88	1.00
Protein			0.42 ± 0.13	1.00	0.99 ± 0.93	0.64
Ca ⁺			0.57 ± 0.22	1.00	0.47 ± 0.70	0.31
Prev1	0.13 ± 0.16	0.46	0.36 ± 0.27	1.00	1.22 ± 0.59	0.89
α	1.47 ± 0.23	1.00	1.72 ± 0.38	1.00	4.67 ± 1.83	1.00

^a Prev1 = average of all counts conducted during the first five weeks. See Table 1 for description of other covariates.

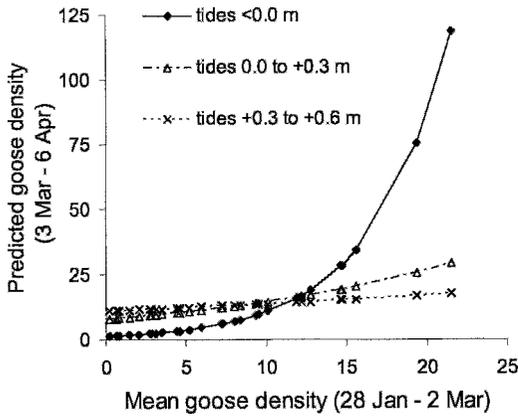


FIGURE 8. Fitted values for Brant densities (number per ha) in 31 eelgrass regions on south Humboldt Bay from 3 March to 6 April 2000, as a function of mean densities observed during the prior five-week period (28 January to 2 March). Predictions are based on model-averaged estimates of negative binomial regression parameters. Predictions assume a population of 10 000 Brant and that other covariates are equal to the mean value for all regions. Tides are in relation to mean lower low water level (MLLW).

This also probably reflected selection for higher-protein plants on a more local scale (within eelgrass region), as protein content of

our samples increased with nearness to channel. Eelgrass acquires much of its nitrogen from the water column via uptake through its leaves (Pedersen and Borum 1993), and Thomas et al. (2000) showed for two seagrass species that ammonium uptake increased with current velocity, which is higher near the edges of seagrass beds (Fonseca et al. 1982, Peterson et al. 2004).

Although patterns of Brant use generally conformed to our expectations, there was some variation in which predictors were important during each analysis, and even in the relationship between a predictor and the response. For example, eelgrass biomass was positively related to Brant use during higher low tides in the first five weeks, during lower low tides in the second five weeks, and during all tide conditions in the third five weeks. Brant used deeper eelgrass beds on average as the season progressed. Some lack of concordance across analyses may be explained by the inability of a single index of eelgrass condition to account for dynamic processes, such as patterns of food depletion (sensu Percival et al. 1996, Rowcliffe et al. 2004). Depletion may explain why Brant densities in the third five weeks were positively related to Brant densities in the first five weeks,

TABLE 3. Model-averaged estimates of slope parameters from negative binomial regressions of Brant density (number per ha) in each of 31 “regions” within Humboldt Bay, California, from 7 Apr to 11 May 2000, during four different tidal height ranges (relative to mean lower low water level). Intercept is the $\log(\mu)$ when each covariate equals its standardized mean of zero. Other $\tilde{\beta}_j$ predict change in $\log(\mu)$ with one SD change in the covariate. Sample size (n) = 31 * number of weeks with data. $w_+(j)$ is the sum of weights (w_j) for models containing covariate j . The overdispersion parameter (α) reflects the amount of variation in counts around the expected values.

Tide level	+0.6 to +0.9 m		+0.3 to +0.6 m		0.0 to +0.3 m		<0.0 m	
n	62		124		124		31	
Model covariate ^a	$\tilde{\beta}_j \pm SE$	$w_+(j)$						
Intercept	-0.47 ± 0.28	1.00	0.68 ± 0.18	1.00	0.69 ± 0.21	1.00	-0.02 ± 0.31	1.00
Number					0.17 ± 0.17	0.66		
Mass	0.14 ± 0.20	0.37	0.36 ± 0.18	1.00	0.21 ± 0.24	0.67	0.86 ± 0.31	1.00
Grit								
Elev	-1.23 ± 0.23	1.00			0.71 ± 0.61	1.00	-1.13 ± 0.29	1.00
Elev ²					-1.50 ± 0.69	1.00		
Protein	0.18 ± 0.31	0.27			0.42 ± 0.25	1.00		
Ca ⁺	0.20 ± 0.32	0.27						
Prev1	0.74 ± 0.31	0.95						
Prev2	-0.50 ± 0.21	0.94						
α	0.66 ± 0.31	1.00	2.04 ± 0.50	1.00	1.57 ± 0.41	1.00	0.99 ± 0.44	1.00

^a Prev1 and Prev2 = average of all counts conducted during the first and second five weeks, respectively. See Table 1 for description of other covariates.

but negatively related to densities in the immediately preceding (second) five weeks at higher low tides. Eelgrass depletion may also explain why Brant use progressively shifted to lower-elevation eelgrass beds through time, and why the strength of the relationship between Brant densities in the first vs. second five-week periods decreased from the lowest tide conditions to tides between +0.3 and +0.6 m. During the first five weeks, grazing intensity was highest in higher-elevation areas, and tides during this time did not permit Brant to heavily deplete the lowest-elevation eelgrass beds.

Tides govern feeding opportunities for Brant in Humboldt Bay and other Pacific coast staging areas. The distribution of biomass and nutrients in the bay may dictate where Brant prefer to feed, but it is the cycle of rising and falling water levels that determine when and where they may actually do so. D. Lee et al. (Humboldt State University, unpubl. data) found that most Brant arriving on the bay in January and February stay ~30–50 days, compared to ~15–30 days for birds arriving in March or April. A likely explanation for this is the relative frequency with which tides allow Brant to forage during these respective periods. Feeding opportunities are shorter and less frequent in January and February, which may explain why fewer birds make use of the bay at that time of year (Moore et al. 2004; D. Lee et al., unpubl. data). In contrast, Brant arriving at Humboldt Bay later in the season should be able to accumulate nutrient reserves much more quickly.

Models describing bird migration strategies are based on timing for gaining access to preferred food (Drent et al. 2003). For geese, the time of arrival and departure from migratory stopover sites has been linked to the phenology of plants, mediated by weather conditions (Drent et al. 1980, Prop et al. 2003). We suggest that migration patterns for estuarine bird species might also be shaped by seasonal tidal patterns and how these vary along latitudinal gradients. Tidal patterns will vary at each staging area and their effect on the availability of intertidal foods will also be governed by the depth and elevation of each estuary or bay. Migratory species, like Brant Geese, may be doubly challenged with learning how the availability and quality of favored food

plants are shaped by multiple global phenomena (Ward et al. 2005).

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