

Black Brant *Branta bernicla nigricans* forage at both tides on Humboldt Bay, California, USA

ELIZABETH ELKINTON¹, LONG LO¹ &
JEFFREY M. BLACK^{1*}

Waterfowl Ecology Research Group, Department of Wildlife,
Humboldt State University, 1 Harpst St., Arcata, California 95521, USA.

*Correspondence author. E-mail: Jeff.Black@humboldt.edu

Abstract

Black Brant *Branta bernicla nigricans* arrive at their breeding grounds in arctic and sub-arctic North America and eastern Russia in spring, a time when food resources are limited. They rely largely on energy stores, acquired at staging sites, for migration and to support egg laying and incubation. In California, Humboldt Bay is the most important staging site for Black Brant due to the abundance of Common Eelgrass *Zostera marina* along its shores. Access to Common Eelgrass has been assumed to be limited to low tides, when the plants are reachable, and that little feeding occurs at higher tides. We tested this assumption by quantifying Black Brant foraging behaviour throughout the tidal cycle, including in relation to factors that contribute to the occurrence of detached Common Eelgrass leaves, which float to the surface and thus become available to the birds at higher tides. Throughout the winter and spring periods (January–April 2011) Black Brant at Humboldt Bay foraged directly on Common Eelgrass beds during low tides and continued to feed on drifting leaves during higher tides. They switched from bed-feeding to drift-feeding at a mean tide height of 0.9 m. On average, 48% of flock members typically fed when Common Eelgrass beds were reachable during low tides, with 24% of birds feeding on drifting eelgrass during higher tides. The prevalence of drift-feeding declined as the tide level increased in the bay, ranging from 35% of birds at 1 m tides to 10% at 2.5 m tides. The amount of drifting Common Eelgrass available to Black Brant increased with higher maximum wind speeds and greater tidal range in the previous 24 h, and with greater numbers of Black Brant on the bay. By providing current information about foraging strategies and the use of high-tide feeding opportunities, this study can inform future projections of the carrying capacity of Humboldt Bay for staging Brant. This is particularly important in light of projected future impacts of sea level rises on food availability at staging habitats along the Pacific Flyway.

Key words: Brant, drifting eelgrass, foraging, Humboldt Bay, tide height, *Zostera marina*.

Long-distance migratory birds use staging areas during spring migration (Skagen 2006; Masero *et al.* 2011) to re-fuel and build energy stores necessary for breeding (Drent *et al.* 2006; Nolet 2006; Drent *et al.* 2007). Brent Geese *Branta bernicla*, which breed in arctic and sub-arctic regions, rely partially on body stores acquired at spring staging sites (Ankney 1984; Prop & Deerenberg 1991; Ebbinge & Spaans 1995; Inger *et al.* 2008). Black Brant *Branta bernicla nigricans* can travel up to 8,000 km between wintering areas in coastal Baja, Mexico and breeding grounds in northern Alaska and Canada, stopping to refuel primarily on Common Eelgrass *Zostera marina* found in Pacific Flyway bays and estuaries (Derksen & Ward 1993; Reed *et al.* 1998; Ward *et al.* 2005). A marine monocotyledon with extensive rhizomes, eelgrass *Zostera* sp. grows 3–5 slender leaves extending up to 1 m above the substrate (Hemminga & Duarte 2000). Clausen (2000) described how Light-bellied Brent *Branta bernicla brota* in Denmark reach down to 0.4 m into the water column to reach the vegetation. On the basis of this work, Moore & Black (2006) estimated that once the tides rise above 0.9 m mean low low water (MLLW) and the leaves have bent with the current, brant can no longer reach the leaves of rooted plants. Recent work attempting to quantify daily energy needs for Brent/Brant geese assume that little or no food is obtained during high tides (Moore 2002; Mason *et al.* 2006; Ladin *et al.* 2011; Clausen *et al.* 2013). Moore's (2002) calculations for Humboldt Bay suggested that Black Brant would suffer an energy deficit if they were limited to feeding only at low tides when the Common Eelgrass beds were "in reach".

This limitation due to tide has been emphasised in several studies on this species (Baldwin & Lovvorn 1994; Clausen 2000; Mason *et al.* 2006; Moore & Black 2006). In some study areas Brant (or Brent) fly to alternative foods in adjacent habitats during high tides (Charman & Macey 1978; Vickery *et al.* 1995; Ward *et al.* 2005), but Black Brant remain on the water and reportedly pick at dislodged drifting leaves on the surface, albeit to an unknown extent (Einarsen 1965; Henry 1980; Moore 2002; Lee *et al.* 2004; Moore & Black 2006). The occurrence of drifting eelgrass leaves has been found to increase with high winds (Bach *et al.* 1986) and high water velocity during ebb tides (Fonseca & Bell 1998) in North Carolina estuaries. It is also possible that Black Brant make use of dropped leaves that "escape" during intense foraging sessions on eelgrass beds (*sensu* Moore 2002).

This study aims to examine the extent of feeding on drifting eelgrass leaves during high tide, when eelgrass beds are inaccessible on Humboldt Bay. In particular, we determined the tide height at which Black Brant switch from bed- to drift-feeding, and compare this with the 0.9 m tide height proposed by Moore and Black (2006). The proportion of birds that engaged in feeding behaviour at both low and high tides was quantified and the conditions under which drifting eelgrass leaves became available in this dynamic habitat was investigated.

Study area and methods

Humboldt Bay study site

Humboldt Bay (40°43'N, 124°14'E), on the north Californian coast (Fig. 1), is the

second largest coastal estuary in California and includes two wide and shallow bays (Arcata Bay and South Bay), and a narrow and deep entrance channel (Barnhart *et al.* 1992). Humboldt Bay covers *c.* 62.4 km² at mean high tide and 28.0 km² at mean low tide (Proctor *et al.* 1980 in Barnhart *et al.* 1992). Humboldt Bay tides are characterised by semidiurnal inequity, often with a large tidal range within one tide cycle, and *c.* 60%

of the total volume returns to the Pacific Ocean during ebb tide, indicating rapid water velocities within the bay during these periods (Barnhart *et al.* 1992). During the present study, tide height ranged from -0.4–2.5 m MLLW. Strong northwest winds result in high wave action and coastal upwelling during spring, which may affect the integrity of Common Eelgrass beds in Humboldt Bay. Wind speeds ranged from

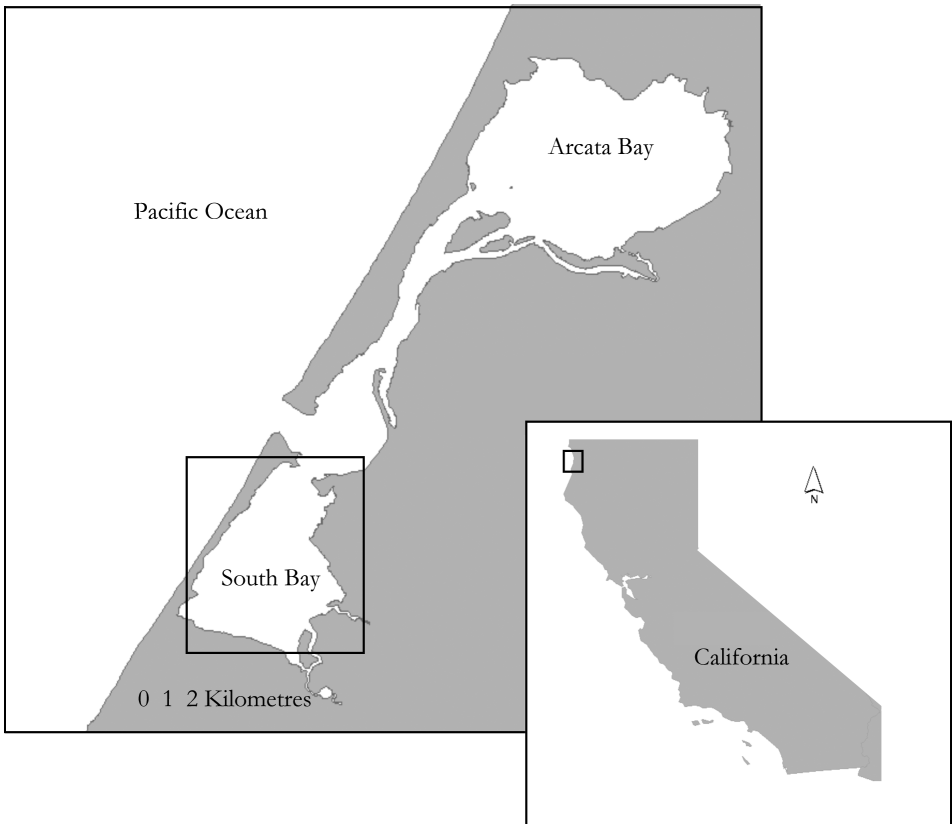


Figure 1. Location of South Bay relative to Arcata Bay and the narrow entrance channel that joins them, Humboldt County, California (Sources: Esri, TomTom, Department of Commerce, Census Bureau, U.S. Department of Agriculture (USDA), National Agricultural Statistical Service (NASS), accessed April 2013).

3.9–17.0 m sec⁻¹ during this study. Mean air temperatures vary by 5.2°C annually with lowest mean monthly temperatures in January (8.5°C; Barnhart *et al.* 1992). Peak numbers of Black Brant range from 15,000–25,000 geese, typically in mid-March (Moore & Black 2006), though the peak during 2011 was ~17,000 on 4 February (USFWS, unpubl. data).

The study site, on South Bay, supports *c.* 80% of the Black Brant population on Humboldt Bay, likely due to the 888 ha of eelgrass beds in the area (Shaughnessy *et al.* 2012). The above ground eelgrass biomass (standing stock) for South Bay was 0.71 × 10⁶ kg (dry) in winter and 1.8 × 10⁶ kg (dry) in summer (Moore 2002), the largest stand of Common Eelgrass between Mexico and Washington (Moore *et al.* 2004). Moore & Black (2006) reported leaves ranging in length between 0.2–0.8 m. The South Bay is encompassed within Humboldt Bay National Wildlife Refuge and supports the largest population of spring staging Black Brant in California (Einarsen 1965; Pacific Flyway Council 2002; Moore *et al.* 2004). Hunting of Black Brant on Humboldt Bay occurred from 7 November to 6 December 2010, prior to our study, followed by a Youth Hunt on 5–6 February 2011 (CWA 2010) which occurred during the 25 January–22 April 2011 study period.

Identifying foraging strategies

Individual Black Brant were recorded as bed- or drift-feeding during 2–3 min focal bird observations on 52 days between 25 January and 22 April 2011. Observers stood on shore, 1–2 metres above the high tide line, with one-third of South Bay visible on

clear days. Observations were conducted *c.* every 20 minutes during favourable weather conditions and timed to ensure that behavioural data were recorded for each hour of the day throughout the tidal cycle during all daylight hours each month. Only the behaviour of actively feeding Black Brant was followed, determined by watching individuals for 20–30 s then, if the majority of that time was spent foraging, the focal observation commenced. Observations were timed for two minutes with a stop watch, and if the focal individual continued to actively feed beyond two minutes, observation continued for another one minute. During this time the observer dictated the behaviours of the focal individuals to an assistant. Focal birds were considered bed-feeding when leaves were visible or birds close by, presumably feeding at similar depths, were up-ending to reach leaves suspended in the water column. Birds were considered drift-feeding when leaves were not visible or the tide was high and nearby individuals were not up-ending.

Determining tide threshold

To determine the tide height at which foraging focal individuals switched from bed- to drift-feeding, a simple logistic model was developed based on the focal bird observations described above:

$$p(d) = \frac{1}{1 + e^{-(\alpha + (\beta * \chi))}}$$

where $p(d)$ was the probability of drift-feeding, the y-intercept and the slope of the curve due to tide height χ . This model defines the probability of drift-feeding

between 0.0 and 1.0 and assumes an asymptotic relationship between tide height and $p(d)$ such that at the highest tide height χ , the probability of drift-feeding is exactly 1.0 and conversely the probability of bed-feeding is exactly 0.0. From this model we calculated the tide height (m) at which the probability of drift-feeding was 50% and thus when Black Brant switched from bed to drift-feeding. Tide data was retrieved from the nearest National Oceanographic and Atmospheric Administration tide buoy no. 9418767, located *c.* 4 km north of the centre of South Bay (NOAA 2011).

Quantifying bed- and drift-feeding

To quantify the proportion of Black Brant bed- and drift-feeding, instantaneous flock scans were conducted on 49 days from 31 January–22 April. Scans occurred on good weather days made at *c.* 20 min intervals and were timed to ensure that data were recorded for each hour of the day throughout the tidal cycle during all daylight hours. Flock size and number of foraging Brant were recorded. Birds were considered to be foraging when they were: a) swimming or standing with head in the water, b) swimming or standing with head raised and food in bill, or c) up-ending. Foraging birds were categorised as bed- and drift-feeding in the same way as described above. We calculated a mean of all hourly proportions to determine the proportion a typical flock foraged hr^{-1} using scans of flocks of > 50 Brant. The maximum flock size scanned was 155 Brant. Given that large flocks have been shown to behave differently than small flocks (Inglis & Lazarus 1981), only flocks of at least one-third the maximum size were

included in the analysis to obtain a representative sample.

Non-parametric Wilcoxon signed-rank tests were used to compare the proportion of birds bed- and drift-feeding and across months. Appropriate Bonferroni adjustments for multiple comparisons were applied to these analyses ($\alpha = 0.025$). To evaluate the influence of tide on bed- and drift-feeding, we created a simple linear model for each group with the proportion of the flock foraging as the response variable and tide height (m) as the predictor variable. For the drift-feeding model, the proportion feeding was square-root transformed to control for the non-normal data distribution.

Determining factors influencing drifting eelgrass

To explore potential factors influencing the amount of drifting eelgrass on South Bay, we weighed samples of washed up detrital eelgrass, collected along the South Bay shoreline on 29 occasions between 25 February and 10 April 2011. Sample weights were used as an index of the biomass of drifting eelgrass available to the geese during the previous tidal cycle. All debris was cleared from 15 sample plots (0.5×5 m), which were measured using a metre stick and marked with stakes and natural land marks along the 5 km sand spit that makes the northwest shore line of South Bay. Access to the shoreline was difficult, so to minimize habitat damage the spacing of plots was based on locations of hunter access roads and thus was non-systematic. The amount of eelgrass (wet, kg) that had accumulated was measured at all 15 plots

each sample day after an interval of 24 h. Samples were nearly entirely composed of eelgrass, confirmed by observation of only negligible amounts of algal and other seagrass species drifting on the water surface during out-going tides. A mean daily sample weight was calculated to provide an index of detrital eelgrass washed ashore. Samples were measured in the field so some variation in dampness will have occurred due to weather conditions. Eelgrass along the northwest shore was measured because the tide flows north during ebb tide, and due to the angle and curvature of the shoreline, large amounts of eelgrass regularly wash ashore in *c.* 0.5 m wide detrital mats. Wind and tidal information was obtained from the same buoy mentioned above (NOAA 2011).

We sought to test whether a larger quantity of drifting leaves occurred on days with higher winds, which potentially influence currents and wave action over eelgrass beds, and during days when larger tidal ranges may result in faster currents and a larger volume of water crossing the beds. A set of *post hoc* linear models therefore were used to test potential factors influencing the amount of drifting eelgrass. Drift sample weight (wet, kg) was the response variable and predictors were maximum wind speed during the prior 24 h (MWS; $m\ sec^{-1}$), maximum tidal range during the prior 24 h (MTR; highest high – lowest low, in metres), and the number of Black Brant on South Bay determined from the most recent count (BC). This last variable was included to assess whether the number of Black Brant foraging on the bay at any given time may increase the amount of drifting leaves due to breakage by foraging birds. Interactions

between predictor variables were not anticipated and therefore no interaction terms were included in the candidate model set. Moore (2001) reported that Black Brant dropped or discarded about 25% of the leaves that they harvested from eelgrass beds. This led us to consider whether more birds feeding on the bay during low tide dislodge a greater number of leaves which are then available for drift-feeding during high tides.

The models were evaluated using Akaike's Information Criterion and corrected for small sample sizes (AICc). Models with the lowest AICc value best describe the data relative to the other candidate models. The best models were averaged and model fit tested for each by calculating an R^2 and deviance R^2 value. The response variable, drift sample weight, was cube-root transformed to control for non-normality in the data.

Results

Foraging strategies: probability of drift-feeding

A total of 319 focal bird observations were conducted at South Humboldt Bay during the study, covering all daylight hours, of which 146 were on bed-feeding individuals and 173 on drift-feeding individuals. The logistic model predicted that as tide height increased, Black Brant were more likely to drift-feed than bed-feed. The resulting equation for this model was:

$$p(d) = \frac{1}{1 + e^{-(13.461 + (15.023 * tideht))}}$$

The model suggests that the probability of drift-feeding was near 0.0 at the lowest

tides and increased as tide heights increased (Fig. 2). At an average tide height of 0.9 m the probability of Black Brant bed-feeding or drift-feeding was 0.5 (50%), and thus they likely made the switch from bed- to drift-feeding at that point. The model provides mathematical support for the proposal that these birds are physically limited in their reach length and that at \approx 0.9 m tide height eelgrass leaves are out

of reach (Clausen 2000; Moore & Black 2006).

Quantifying drift-feeding

Overall, 115 flock scans were carried out at South Humboldt Bay during the study, again covering all daylight hours: 62 on bed-feeding flocks and 53 on drift-feeding flocks. Results of a Wilcoxon signed-rank test indicated that on average (\pm s.e.), $48 \pm$

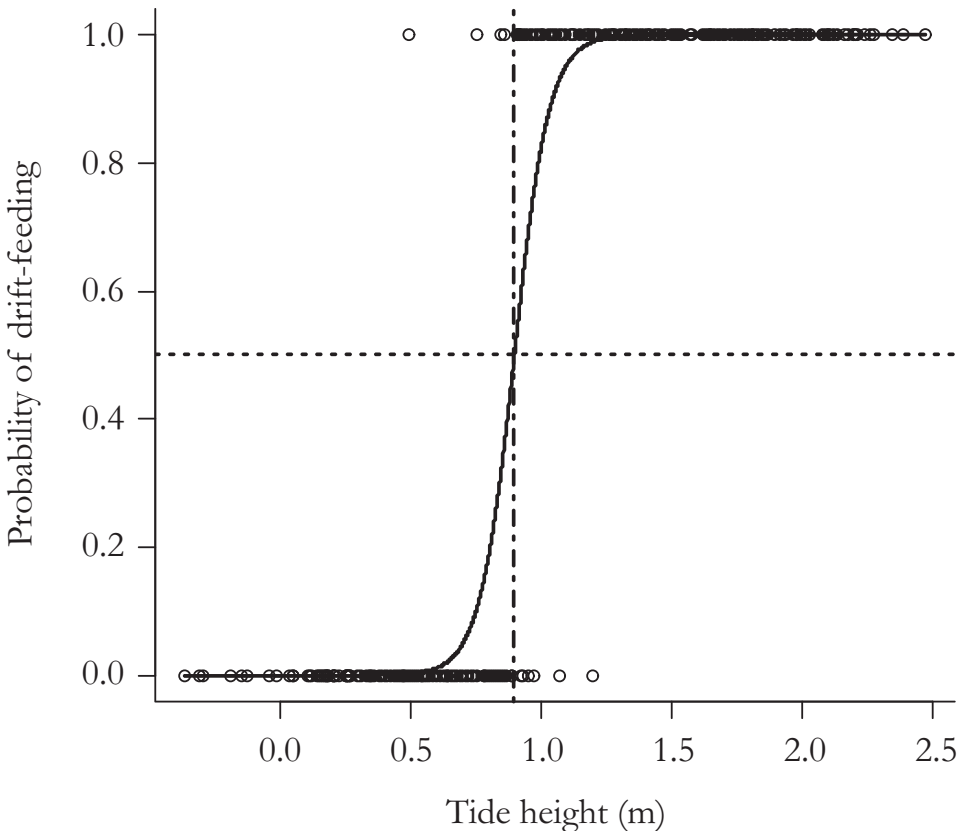


Figure 2. Logistic model predicting the probability of drift-feeding based on tide height (m) on South Humboldt Bay, California, January – April 2011. Intersection of the dashed lines indicates the tide height at which the probability of drift-feeding is 0.5.

1.7% of a typical flock of Black Brant fed on eelgrass beds during tides of < 0.9 m and $24 \pm 1.9\%$ fed on drifting eelgrass during tides of > 0.9 m during spring staging ($W = 3050$, $P < 0.001$). The proportion of the flock bed-feeding and drift-feeding did not vary across months ($W = 369$ and $W = 115$ respectively, n.s. in each case). As tide height

increased to 0.9 m, there was no significant influence on the proportion of the flock bed-feeding during low tides ($R^2 = 0.006$, $F_{1,60} = 0.38$, $p = 0.54$); however, as tide height increased above 0.9 m, a smaller and smaller proportion of the flock drift-fed ($R^2 = 0.32$, $F_{1,51} = 24.31$, $p < 0.001$; Fig. 3). The trend in Figure 3 depicts a decline in

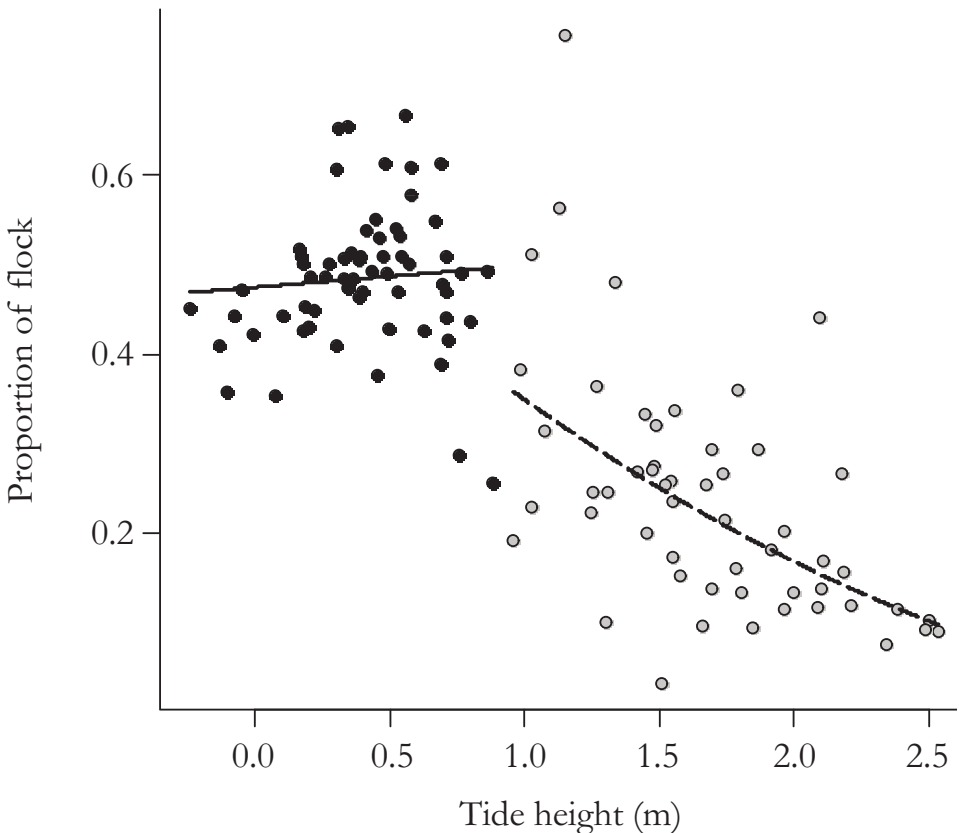


Figure 3. Proportion of the flock bed-feeding and drift-feeding hr^{-1} throughout the tide cycle on South Humboldt Bay, California, January – April 2011. Black circles with solid line = the proportion bed-feeding (during tides < 0.9 m; equation for the regression line is $y = 0.475 + 0.024x$; $R^2 = 0.006$, $F_{1,60} = 0.38$, $P = 0.54$). Grey circles with dashed line = the proportion drift-feeding (during tides > 0.9 m; equation for the regression line is $y = (0.772 - 0.180x)^2$; $R^2 = 0.32$, $F_{1,51} = 24.31$, $P < 0.001$). Bed- and drift-feeding data were split at 0.9 m tides based on the logistic model in Fig. 1.

proportion foraging from *c.* 35% at 1 m, *c.* 20% at 1.75 m, and *c.* 10% at 2.5 m tides.

Factors influencing drifting eelgrass

The mean drift sample collected along the northwest shore of South Bay weighed 2.31 ± 0.72 kg per plot (2.5 m^2), with a range of 0–16.5 kg per plot (2.5 m^2 ; $n = 29$ sample days). Mean maximum wind speed during the 24 hours prior to drift sampling was $9.14 \pm 0.53 \text{ m sec}^{-1}$ with a range of 3.86–16.98 m sec^{-1} ($n = 29$ sample days). Mean maximum tidal range during the 24 hours prior to sampling was $1.97 \pm 0.05 \text{ m}$ with a range of 1.55–2.79 m ($n = 29$ sample days). Number of Black Brant counted on South Bay during the drift collection periods ranged from 975 on 15 March to 13,200 on 1 March ($n = 13$ counts).

Maximum wind speed, tidal range, and number of Black Brant all influenced the amount of drifting eelgrass (Table 1). The two best models, MWS + MTR + BC (55.9% of the model weight, $R^2 = 0.51$, deviance $R^2 = 0.76$) and MWS + MTR (32.4% of the model weight, $R^2 = 0.71$, deviance $R^2 = 0.70$), were averaged (Table 2). The averaged model indicates that the amount of drift eelgrass on South Bay increased with greater maximum wind speeds and greater tidal ranges during the prior 24 h (Fig. 4). The number of birds on South Bay also had a positive influence on the amount of drifting eelgrass recorded.

Discussion

Arctic-breeding geese often make fine adjustments to maximize intake and meet

Table 1. Candidate models predicting amount of drifting eelgrass washed ashore from South Humboldt Bay, California from 25 February–10 April, 2011. MWR = maximum wind speed during the previous 24 h; MTR = maximum tidal range during the previous 24 h, BC = the number of Black Brant on South Bay, determined from the most recent count.

Model	Deviance	K^a	AICc ^b	w^c
MWS+BC+MTR	20.17	5	84.38	0.63
MWS+MTR	23.18	4	85.47	0.37
MWS+BC	25.89	4	88.67	0.07
MWS	29.11	3	89.36	0.05
BC	33.91	3	93.79	0.01
MTR	38.19	3	97.24	0.00
NULL	47.38	2	100.99	0.00

^aNumber of parameters.

^bAkaike's Information Criterion corrected for small sample size.

^cRelative model weight.

Table 2. Model averaged coefficient estimates describing factors influencing drifting eelgrass washed ashore from South Humboldt Bay, California from 25 February–10 April, 2011.

Parameter	Averaged estimate	Unconditional s.e.
Intercept	-5.1882	1.4325
Max tidal range (MTR)	1.8525	0.7051
Max wind speed (MWS)	0.2200	0.0744
Numbers of Brant (BC)	0.0001	0.0001

energy demands (Prop & Loonen 1989; Prop and Deerenberg 1991; Black *et al.* 2007; Inger *et al.* 2008). Recent studies investigating energy balance models for Brant (Brent) foraging in aquatic habitats have documented movements to alternative foraging areas (*e.g.* inland) or to roost sites when the primary food (eelgrass) is no longer reachable due to high tides (Mason *et al.* 2006; Ladin *et al.* 2011; Clausen *et al.* 2013). These models have assumed that Black Brant feed only when direct access to eelgrass is possible during low tide. On Humboldt Bay, Black Brant remain on the water during high tides after Eelgrass beds are covered, and any feeding at this time was assumed negligible (Moore & Black 2006). Our findings, however, indicate that Black Brant at Humboldt Bay feed substantially during *both* tides, employing drift-feeding when the beds are out of reach. Derived from Clausen's work (2000), Moore and Black (2006) proposed a foraging threshold of 0.9 m based on the reach limit of the birds and the length of Common Eelgrass leaves. Our logistic model, based on close observation of individuals, confirms this threshold but also provides new insights

into the behavioural switch Black Brant make as soon as eelgrass leaves are out of reach.

Whereas an average of 48% of Black Brant flock members were foraging when eelgrass beds were 'reachable' (below 0.9 m), 24% were foraging at higher tides on drifting eelgrass. As tides continued to rise, the proportion foraging declined from 35% at 1 m to 10% at 2.5 m tides. The decline may be due to satiation, depletion, or dispersal of drifting leaves. Leaves that become dislodged during low tides, particularly during periods of high winds, waves and large tidal fluctuations, likely float directly above the beds initially. With time leaves disperse. As tides continue to rise Black Brant feeding on drifting leaves also disperse, resulting in greater distances between flock members than when feeding directly over the eelgrass beds (EE & JMB pers. obs.).

Previous studies on Humboldt Bay have only accounted for foraging during low tide, suggesting that Black Brant may suffer a 'shortfall' in energy acquired during spring staging (Moore 2002). However, it is clear that drift-feeding occurs during high tide,

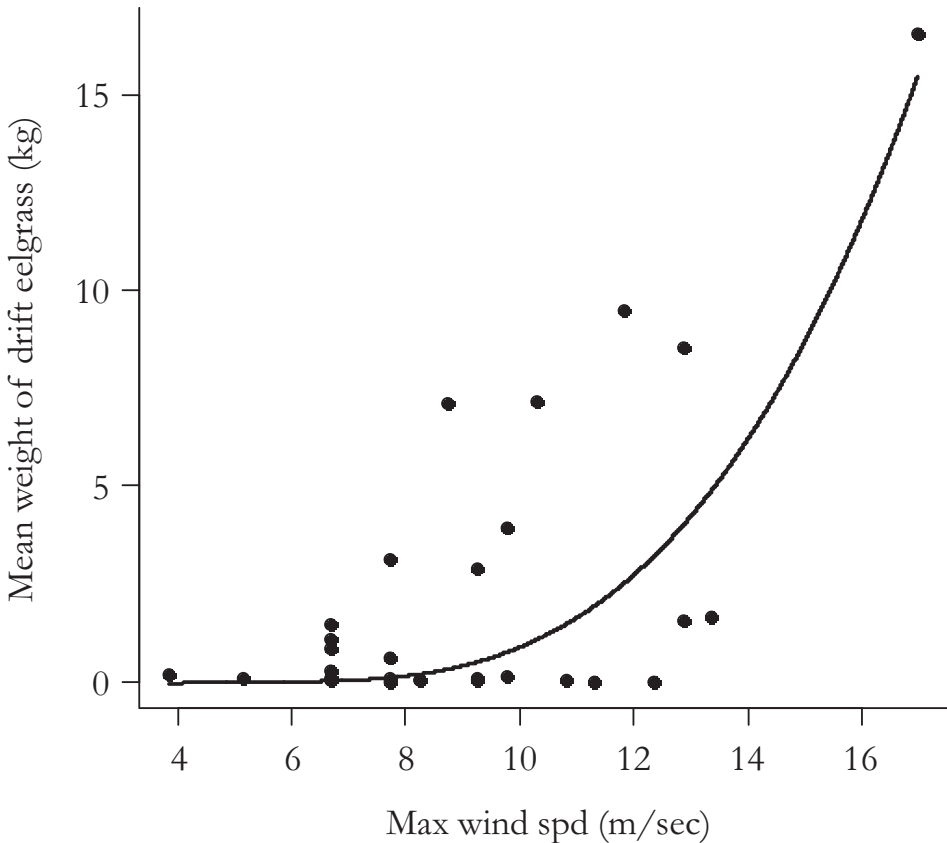


Figure 4. Averaged model showing the mean weight of eelgrass samples (wet, kg) collected along the northwestern shoreline of South Humboldt Bay, 25 February – 10 April, 2011 in relation to maximum wind speed (m sec^{-1}) during the prior 24 hrs (line shown), the maximum tidal range (m) during the prior 24 hrs, and the number of Black Brant on the Bay. The latter two variables were held constant to their means for plotting purposes. Equation of line is $y = -1.243 + 0.220x$.

and that the amount of drifting eelgrass is influenced by winds, tidal fluctuations, and the number of birds feeding on the Bay which may drop or discard leaves. Determining the amount of eelgrass consumed by Black Brant (g day^{-1}) while foraging on beds at low tide and on drifting leaves at high tide ($> 0.9 \text{ m}$) would be a valuable next step. Future research should

also focus on whether, how much, and how often Black Brant forage at night. Both types of studies would greatly enhance carrying capacity estimates for Humboldt Bay. This is important in light of projected future impacts of sea level rise on food availability for Black Brant at staging habitats along the Pacific Flyway (Shaughnessy *et al.* 2012).

Acknowledgements

We thank our field crews for their hard work on this project. A special thank you to R. Van Kirk and D. Barton for statistical feedback, and the Humboldt State University Wildlife Department for logistical support. We are grateful to the U.S. Fish and Wildlife Service and the Bureau of Land Management for providing special access to South Bay and South Spit. Funding was provided by the U.S. Fish and Wildlife Service.

References

- Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and molting Brant. *The Auk* 101: 361–370.
- Bach, S.D., Thayer, G.W. & LaCroix, M.W. 1986. Export of detritus from Eelgrass (*Zostera marina*) beds near Beaufort, North Carolina, USA. *Marine Ecology Progress Series* 28: 265–278.
- Baldwin, J.R. & Lovvorn, J.R. 1994. Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and Brant in Boundary Bay, British Columbia. *Marine Ecology Progress Series* 103: 119–127.
- Barnhart, R.A., Boyd, M. & Pequegnat, J.E. 1992. Ecology of Humboldt Bay: an estuarine profile. U.S. Fish and Wildlife Service Biological Report 1. Washington, D.C., USA.
- Black, J.M., Prop, J. & Larsson, K. 2007. *Wild Goose Dilemmas*. Branta Press, Groningen, the Netherlands.
- California Waterfowl Association [CWA]. 2010. CWA homepage. <http://www.calwaterfowl.org> (accessed 27 Sept 2010).
- Charman, K. & Macey, A. 1978. The winter grazing of saltmarsh vegetation by Dark-bellied Brent Geese. *Wildfowl* 29: 153–162.
- Clausen, K.K., Clausen, P., Fox, A.D., Fællø, C.C. & Madsen, J. 2013. Varying energetic costs of brent geese along a continuum from aquatic to agricultural habitats: the importance of habitat-specific energy expenditure. *Journal of Ornithology* 154: 155–162.
- Clausen, P. 2000. Modelling water level influence on habitat choice and food availability for *Zostera* feeding brent geese *Branta bernicla* in non-tidal areas. *Wildlife Biology* 6: 75–87.
- Derksen, D.V. & Ward, D.H. 1993. Life history and habitat needs of the Black Brant. U.S. Fish and Wildlife Service, Anchorage, Alaska, USA.
- Drent, R.H., Fox, A.D. & Stahl, J. 2006. Travelling to breed. *Journal of Ornithology* 147: 122–134.
- Drent, R.H., Eichhorn, G., Flagstad, A., Van der Graaf, A.J., Litvin, K.E. & Stahl, J. 2007. Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding. *Journal of Ornithology* 148 (Supplement 2): S501–S514.
- Ebbinge, B.S. 1989. A multifactorial explanation for variation in breeding performance of brent geese (*Branta bernicla*). *Ibis* 131: 135–143.
- Ebbinge, B.S. & Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied Brent Geese *Branta b. bernicla* in the highArctic. *Journal of Avian Biology* 26: 105–113.
- Einarsen, A.S. 1965. *Black Brant: sea goose of the Pacific*. University of Washington Press, Seattle, USA.
- Fonseca, M.S. & Bell, S.S. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series* 171: 109–121.
- Hemminga, M.A. & Duarte, C.M. 2000. *Seagrass ecology*. Cambridge University Press, Cambridge, UK.
- Henry, W.G. 1980. Populations and behaviour of Black Brant at Humboldt Bay, California.

- Unpublished M.S. Thesis, Humboldt State University, Arcata, USA.
- Inger, R., Gudmundsson, G.A., Ruxton, G.D., Newton, J., Colhoun, K., Auhage, S. & Bearhop, S. 2008. Habitat utilisation during staging affects body condition in a long distance migrant, *Branta bernicla brota*: potential impacts on fitness? *Journal of Avian Biology* 39: 704–708.
- Inglis, I. R. & Lazarus, J. 1981. Vigilance and flock size in brent geese: the edge effect. *Zeitschrift für Tierpsychologie* 57: 193–200.
- Ladin, Z.S., Castelli, P.M., McWilliams, S.R. & Williams, C.K. 2011. Time energy budgets and food use of Atlantic Brant across their wintering range. *Journal of Wildlife Management* 75: 273–282.
- Lee, D.E., Hamman, M.G. & Black, J.M. 2004. Grit-site selection of Black Brant: particle size or calcium content? *Wilson Bulletin* 116: 304–313.
- Masero, J.A., Santiago-Quesada, F., Sánchez-Guzmán, J.M., Villegas, A., Abad-Gómez, J.M., Lopes, R.J., Encarnação, V., Corbacho, C. & Morán, R. 2011. Long lengths of stay, large numbers, and trends of the Black-tailed Godwit *Limosa limosa* in rice fields during spring migration. *Bird Conservation International* 21: 12–24.
- Mason, D.D., Barboza, P.S. & Ward, D.H. 2006. Nutritional condition of Pacific Black Brant wintering at the extremes of their range. *Condor* 108: 678–690.
- Moore, J.E. 2002. Distribution of spring staging Black Brant *Branta bernicla nigricans* in relation to feeding opportunities on South Humboldt Bay, California. Unpublished M.S. Thesis, Humboldt State University, Arcata, CA, USA.
- Moore, J.E. & Black, J.M. 2006. Slave to the tides: spatiotemporal foraging dynamics of spring staging Black Brant. *Condor* 108: 661–677.
- Moore, J.E., Colwell, M.A., Mathis, R.L. & Black, J.M. 2004. Staging of Pacific flyway Brant in relation to Eelgrass abundance and site isolation, with special consideration of Humboldt Bay, California. *Biological Conservation* 115: 475–486.
- National Oceanic and Atmospheric Administration (NOAA). 2011. Center for Operational Oceanographic Products and Services. Tidal Station Locations and Ranges, Outer Coast, California. <http://tidesandcurrents.noaa.gov/tides09/tab2wc1a.html> (accessed on 10 Nov 2011).
- Nolet, B.A. 2006. Speed of spring migration of Tundra Swans *Cygnus columbianus* in accordance with income or capital breeding strategy? *Ardea* 94: 579–591.
- Pacific Flyway Council. 2002. Pacific Flyway Management Plan for Pacific Brant. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Prop, J. & Deerenberg, C. 1991. Spring staging in brent geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19–28.
- Prop, J. & Loonen, M. 1989. Goose flocks and food exploitation: the importance of being first. *Acta XIX Congressus Internationalis Ornithologici* (Ottawa): 1878–1887.
- R Development Core Team (2012). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Reed, A., Ward, D.H., Derksen, D.V. & Sedinger, J.S. 1998. Brant (*Branta bernicla*). In A. Poole (ed.), *The Birds of North America Online*. Cornell Laboratory of Ornithology, Ithaca, USA. <http://bna.birds.cornell.edu/bna/species/337/doi:10.2173/bna.337> (accessed 10 Sept 2010).
- Shaughnessy, F.J., Gilkerson, G., Black, J.M., Ward, D.H. & Petrie, M. 2012. Predicted

- Zostera marina* response to sea level rise and availability to foraging black brant in Pacific coast estuaries. *Ecological Applications* 22: 1743–1761.
- Skagen, S.K. 2006. Migration stopovers and the conservation of Arctic-breeding Calidridine sandpipers. *The Auk* 123: 313–322.
- Vickery, J.A., Sutherland, W.J., Watkinson, A.R., Lane, S.J. & Rowcliffe, J.M. 1995. Habitat switching by Dark-Bellied Brent Geese *Branta b. bernicla* in relation to food depletion. *Oecologia* 103: 499–508.
- Ward, D.H., Reed, A., Sedinger, J.S., Black, J.M., Derksen, D.V. & Castelli, P.M. 2005. North American Brant: effects of changes in habitat and climate on population dynamics. *Global Change Biology* 11: 869–880.