Foraging home ranges of Black Brant *Branta bernicla nigricans* during spring stopover at Humboldt Bay, California, USA

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Abstract

Foraging home ranges of Black Brant *Branta bernicla nigricans* ($n = 8$) were quantified to determine proportional use of available intertidal habitat during spring migration stopover at Humboldt Bay, California, USA. The average foraging range area was 232 ha (s.d. $\pm$ 156 ha) of which 114 ha (s.d. $\pm$ 43 ha) was comprised of their primary food, eelgrass *Zostera marina*; the other habitats included mudflat/sandbar and deep water channels. This amounted to individuals using an average of 16% of the available eelgrass in the bay (716 ha). Potential consequences are discussed for Black Brant remaining faithful to a relatively small proportion of available habitat. Individual Black Brant may employ different foraging strategies in different parts of Humboldt Bay to obtain nutrients and body stores to fuel migration and subsequent breeding.

Key words: Black Brant, eelgrass, foraging habitat, home range, spring staging.

Traditional use of sites during the non-breeding season and migration is one of the hallmarks of migratory goose behaviour (Boyd 1955; Owen 1980). Quantifying which sites successfully attract and hold migratory birds has been a challenge to managers and goose biologists. Studies of Canada Geese *Branta canadensis* and Barnacle Geese *Branta leucopsis* were among the first to document that it was the same individual flock members that repeatedly returned to particular roosts in California and staging islands in Norway, respectively, and that these individuals returned daily, seasonally, and annually (Raveling 1969, 1979; Gullestad *et al.* 1984; Black *et al.* 2007). Similar findings were documented for wintering Bewick's Swans *Cygnus columbianus*

bewickii on ponds and pastures at Slimbridge, England (Evans 1980; Rees 1987).

Individuals use restricted space within wintering and staging habitats; for instance, individual Greenland White-fronted Geese *Anser albifrons flavirostris* in Ireland consistently foraged on 10% or less of the available 1,000 ha area of pastures and other agricultural fields that supported the local population (Wilson *et al*. 1991). Individually marked birds were faithful to relatively small parcels at opposite ends of the study area (Wilson *et al*. 1991). Foraging Barnacle Geese walked the same paths and approached the same small food patches within Norwegian staging habitats and did so daily and annually, deviating by a mean of only 4 m between years (Black *et al*. 2007). Foraging performance (*i.e*. intake rates) improved with increasing years that individuals returned to a site, leading to the conclusion that individuals may improve reproductive prospects by being faithful to sites over time. Improved foraging performance was achieved when experienced individuals found multiple rich food patches within a site (Black *et al*. 2007). This body of work supports the notion that returning to sites (*i.e*. homing, philopatry, or site fidelity) by individuals has evolved and is maintained by the adaptive advantage of cumulative experience gained through returning to sites (Rohwer & Anderson 1988; Owen & Black 1990). Returning to a few well known locations may be more productive than spending time in, and exploring for, new sites (Kanarek *et al*. 2008).

Faithfulness to foraging sites in geese has been quantified on the individual level in a variety of terrestrial habitats, including saltmarsh, pastures and crops (St. Joseph 1979; Percival 1991; Ganter 1994; Summers & Critchley 1990; Wilson *et al*. 1991; Hill & Frederick 1997). The amount of habitat used by individual geese varied in these studies, but it is a common finding that individuals use only a minority of the total that is available.

Brent Geese *Branta bernicla* frequently use intertidal seagrasses and algae before shifting to saltmarsh and inland pastures (Charman & Macey 1978; Summers & Critchley 1990; Vickery *et al*. 1995; Fox 1996; Clausen 1998; Percival & Evans 1997; Ganter 2000; Inger *et al*. 2006). The subspecies, Black Brant *B. b. nigricans* is strictly marine, using bays and estuaries along the western North American/Mexican coast, feeding almost exclusively on intertidal seagrasses (*Zostera* sp.)(Ward *et al*. 1997, 2005; Moore *et al*. 2004). This intertidal habitat varies in quantity, quality, and topography, yet it is completely covered by seawater twice per day during periods of high tide challenging geese to meet energy fuelling demands (Clausen 2000; Moore & Black 2006). Black Brant begin to feed on eelgrass *Z. marina* while swimming above submerged plants whose leaves reach toward the surface (Clausen 2000; Moore & Black 2006). Even though their food plants are regularly inaccessible because of high tides, flocks regularly return to meadows higher in density, biomass, and nutrient content (Moore & Black 2006), suggesting that individual geese may make decisions based on cues involved in food choice and previous foraging performance. At high tide Black Brant flocks were regularly observed floating above particular eelgrass meadows

as if queuing above their food and waiting for tides to recede (Moore & Black 2006). It is not known, however, whether these flocks are comprised of the same individuals returning to the same eelgrass meadows over several days or whether individuals mix and move throughout an estuary whilst staging or wintering at the site.

The objective of this study was to determine whether individually-marked Black Brant return repeatedly to particular foraging locations during the spring staging period at Humboldt Bay, California. In particular, whether individual Black Brant behave like terrestrial foraging geese and repeatedly make use of only small sections of their habitat was investigated. Conversely, it is possible that Black Brant distribute themselves randomly or uniformly across all available meadows due to the limited access to food plants because of high tides. These questions were examined by radio-tracking the movements of individual geese, to quantify stopover duration and provide foraging home range estimates for the radio-marked birds.

Methods

We conducted this study on South Bay (1,632 ha), part of Humboldt Bay National Wildlife Refuge (HBNWR) in northern California, USA (40°48'N, 124°07'W). Humboldt Bay is a 62.4 km² estuary (Barnhart *et al.* 1992) with 1,044 ha of eelgrass in discrete beds separated by channels (Moore *et al.* 2004). It is the only large estuary containing substantial eelgrass beds (*i.e.* totalling > 300 ha), along this section of coast, which extends for 350 km to the south and 600 km to the north

(Moore *et al.* 2004), providing a discrete study area with little potential for regional foraging movements away from the estuary. South Bay contains most of the eelgrass beds in Humboldt Bay (716 ha) and supports the majority of the transitory population of Black Brant each year (Moore *et al.* 2004), which was estimated at 28% of the population, or 37,600 birds in 2000, and 58% of the population, or 77,800 birds in 2001 (Lee *et al.* 2007).

In July 1999, 45 Black Brant were fitted with radio transmitters on the Yukon-Kuskokwim Delta, Alaska. The 26 g transmitters consisted of a crystal and battery encased in epoxy resin, with a 20 cm whip antenna, and were surgically implanted into the coelomic cavity of adults (Hupp *et al.* 2006). Thirty-four of these radio-marked birds were relocated alive with operational transmitters in Baja California, Mexico, in winter 1999–2000, prior to northward migration. During January–May 2000, we scanned for all 34 radio frequencies daily from two elevated (50–75 m) locations (Bell Hill and Table Bluff) overlooking South Bay, to collect presence/absence data for each radio-marked bird. Receivers identified transmitters at distances spanning the farthest extent of South Bay from the receiver sites (5 km and 8 km, respectively). Thus, all radio-marked birds present on the bay should have been detectable.

After a bird was detected as present on the bay, a series of foraging locations were estimated by measuring the angles to it from fixed points (*i.e.* triangulation) during daylight hours when tide levels were low enough to permit foraging access to eelgrass (4 h before and after lowest low tide, Moore

& Black 2006). Repeated estimation of locations for a given bird within a day were 20–180 min apart to allow some independence of locations, and locations were obtained every 2–3 days. Thus, we maximised data for each bird while assuming minimal serial spatial autocorrelation. Location error was estimated by triangulating on transmitters at seven known locations around South Humboldt Bay and calculating the linear distance between known and estimated locations (error estimate = 155 m, s.e. ± 46 m, 95% C.I. = 41–268 m). Estimated foraging locations were entered into a geographic information system (GIS) using ArcView 3.2 (ESRI, Inc., 3200 New York St., Redlands, CA, USA). Home ranges were estimated using the Kernel method in the Animal Movement extension in ArcView (Hooge & Eichenlaub 1997). We used the 75% kernel to define our estimate of individual bird foraging ranges as a compromise between using the 95% kernel to estimate a maximal range and the 50% kernel to estimate a core use area. Additionally, the 75% kernel was midway between the area described by point location estimate error buffers of 155 m (mean) and 268 m (upper 95% C.I.) around each estimated foraging location. Kernel Home Range calculates a fixed kernel home range utilisation distribution (Worton 1989) using least squares cross validation (Silverman 1986). Home ranges were used to clip data layers of habitat types in the bay and to determine overlap between birds. Amount (ha) of mudflat, eelgrass, and water at mean low tide were computed for each home range using imagery data from November 1997 (Terra-Mar 1997). Upland areas of home ranges (sand dunes) were excluded from analysis.

Results

We detected 12 of the 34 radio-marked Black Brant on South Bay. The first record was on 20 February and the last radio-marked bird in the study area departed on 14 April. Four birds were removed from the data set because they only remained at South Bay for 1–2 days located at the birds' main roost (sand bar) and were not detected at eelgrass foraging locations. The remaining eight birds (five males and three females, including one pair) had an average stopover duration of 11 days (range = 1–29 days) producing an average of 18 estimated foraging locations (range = 4–50 locations) per bird (Table 1). Table 1 provides a summary of data from these eight radio-tagged geese including minimum bird age (y), stopover duration (d; length of stay on South Bay), number of data points (foraging locations), area of foraging range from kernel estimate (ha), and area of foraging range that was eelgrass habitat (ha). Foraging range area was not correlated with the length of stay (linear regression: $t_7 = -1.11$, $P = 0.32$, n.s.), nor with number of bird locations ($t_7 = 0.71$, $P = 0.51$, n.s.), allowing us to consider each bird regardless of variation in amount of data.

The average foraging range area was 232 ha (s.d. ± 156 ha) with individual birds' foraging ranges distributed throughout the bay (1,632 ha), but with more use in the northern portion of the bay (Fig. 1). Foraging range area was on average 14% (s.d. ± 10%, range = 6–34%) of the total South Bay area. Each bird's foraging range

Table 1. Description of eight radio-tagged Black Brant tracked during migration stopover at south Humboldt Bay, California in spring 2000. Foraging ranges were defined by 75% adaptive kernel of triangulated foraging point location estimates (see text for details). Birds 5 and 6 were members of a breeding pair.

Bird identity	Sex	Minimum age (y)	Stopover duration (d)	No. of data points	Foraging range (ha)	Area of eelgrass (ha)
1	M	5	22	37	132	85
2	M	3	29	50	142	106
3	M	3	14	9	93	48
4	M	3	4	10	190	137
5	M	3	9	15	230	132
6	F	9	9	16	358	194
7	F	3	2	5	561	98
8	F	6	1	4	153	111

had 3 possible habitat types: eelgrass, mudflat, and deep water channels. The average foraging range was composed of 69% eelgrass (s.d. ± 6%), 14% mudflat/sandbar (s.d. ± 9%), and 17% deep water channels (s.d. ± 6%) compared to the entire South Bay which was 44% eelgrass, 39% mudflat/sandbar, and 17% deep water channels, which indicates selection for eelgrass, selection against mudflat, and use of deep water channels in proportion to availability. The average area of eelgrass in Black Brant foraging ranges was 114 ha (s.d. ± 43 ha, range 48–194 ha) and the average proportion of total eelgrass in South Humboldt Bay (716 ha) that was used by individual Black Brant was 16% (s.d. ± 6%, range = 7–27%). Amount of overlap among

individual foraging ranges averaged 41 ha (s.d. ± 25, range = 0–179 ha), or 18% (s.d. = 8%, range 8–29%) of a given bird's range. The overlap between members of the breeding pair was more pronounced; 78% of the male's foraging range overlapped with that of the female, and 50% of the female's overlapped with that of the male. The site where the pair members were both detected in the far north of the study area (Fig. 1a) was an important roost and grit ingestion site.

Discussion

The use of radio transmitters allowed us for the first time to follow individual Black Brant across their aquatic habitat. Prior to this study individual marks on this taxa were
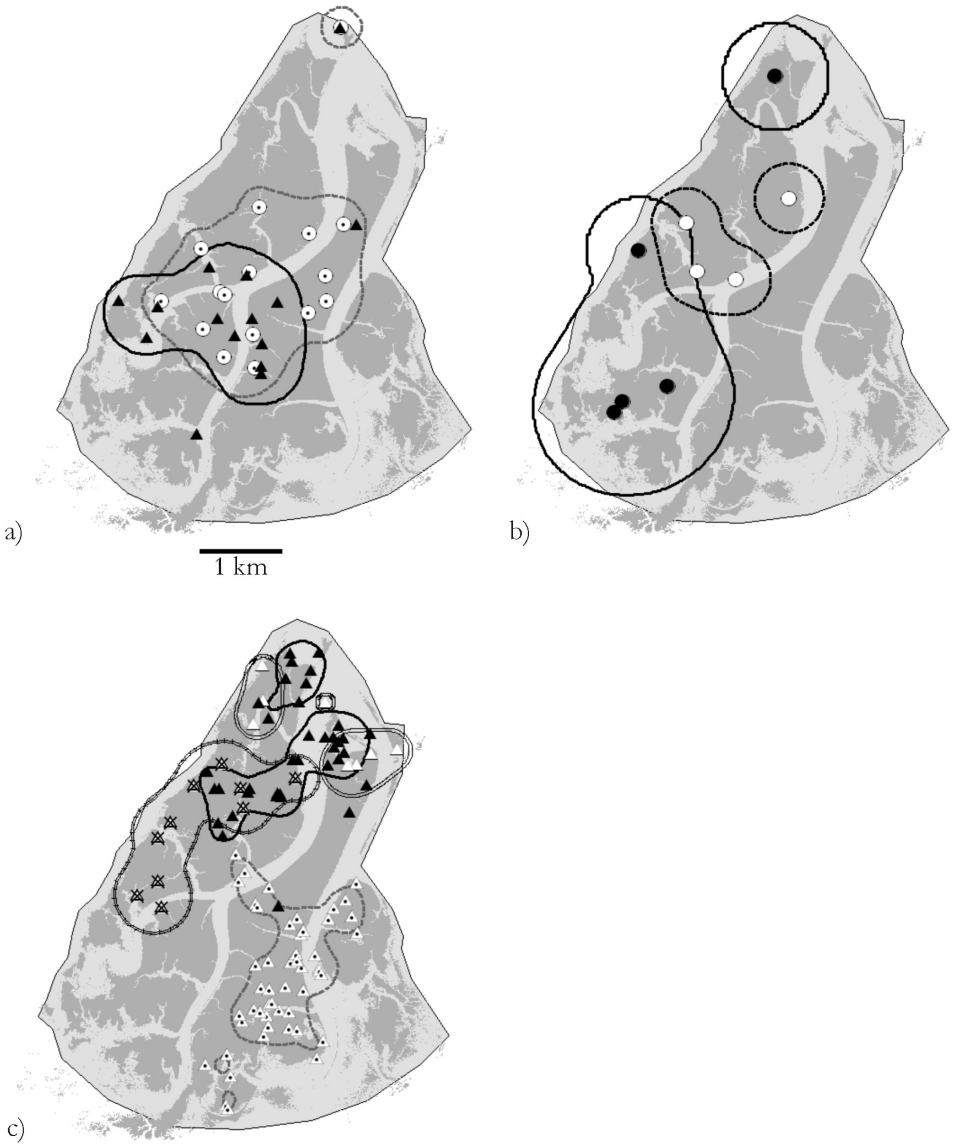
Figure 1. Foraging ranges of eight radio-tracked Black Brant during migration stopover at south Humboldt Bay, California, in spring 2000. (a) shows data points for members of a breeding pair (black triangle = male, open circle = female), (b) shows data points for two female geese, and (c) shows data points for four male geese. Foraging ranges were defined by 75% adaptive kernel of triangulated foraging point location estimates. Eelgrass beds are in dark grey, water and mudflats in light grey. Maximum E–W width of the bay is 4.3 km, and maximum N–S length is 6.2 km.

limited to engraved leg bands which are viewable in this location only when the birds come out of the water to preen and obtain grit from sand bars (Lee *et al*. 2004, 2007). Neck collars are not appropriate for Black Brant, which regularly upend (tip) to reach submerged food (Lensink 1968).

Individual Black Brant have the opportunity to become familiar with intricacies of their staging area, for instance its tidal patterns, predation risks (notably from birds of prey, foxes and hunters), and the location of eelgrass beds and gritting sites. Radio-marked birds were present on South Humboldt Bay for an average of 11 days (range 1–29 days, $n = 12$) during spring migration. Lee *et al*. (2007) compare the stopover duration based on the radio-marked birds with estimates derived from capture-mark-recapture probabilities of birds with engraved leg-bands. Evidence from Boundary Bay and Qualicum, British Columbia, Canada, indicate high annual return rates by spring staging Black Brant, estimated at 82% and 89%, respectively (Reed *et al*. 1998).

Based on records of the eight radio-marked Black Brant staging at Humboldt Bay, individual foraging areas were on average 16% of the total available eelgrass (716 ha). On average therefore an individual Black Brant used only a small portion of the available habitat, which is similar to that reported for Greenland White-fronted Geese in Ireland (Wilson *et al*. 1991). The extent of the foraging home range that was comprised of eelgrass was 48–194 ha (mean = 114 ha). Birds with smaller foraging ranges visited fewer eelgrass meadows during their time on the bay, whereas birds with larger ranges visited multiple eelgrass meadows across the expanse of the bay. Moore & Black (2006) quantified variation of eelgrass quality and quantity in relation to elevation, location within the bay, and distance from deep water channels suggesting that geese with larger foraging home ranges visited eelgrass meadows with a larger range of forage qualities. When tides moved quickly we observed flocks move along the length of a meadow and from meadow to meadow down an elevational gradient. When tides moved slowly we observed flocks remain and forage on single beds for longer periods of time.

Geese may gain access to safe foraging areas through accumulated experience when returning to sites within and across seasons (Rohwer & Anderson 1988; Owen & Black 1990). Revisiting small areas of available habitat may also yield advantages from reduced interruptions while foraging due to improved dominance among familiar individuals or kin, and by enabling family members to reunite (Raveling 1979; Owen & Black 1990; Robertson & Cooke 1999; Black *et al*. 2007). The breeding pair that we monitored visited many of the same eelgrass meadows while foraging and they were located together on the gritting site (Fig. 1a).

This study provides evidence that individuals (and possibly pairs) repeatedly make use of different sections of Humboldt Bay, which leads to the possibility that individuals are pursuing different foraging strategies with respect to the size, number, and quality of meadows they visit (see also Ganter 1994; Phillips *et al*. 2003). We suspect that these strategies result in a range of

abilities in acquiring nutrients and body stores that can be achieved at Humboldt Bay, similar to the range of abilities reported for individual Brent and Barnacle Geese foraging in terrestrial staging habitats (Teunissen *et al.* 1985; Prop & Deerenberg 1991; Prop *et al.* 2003; Black *et al.* 2007). The ontogeny of foraging strategies in geese, achieved from the combination of genetic predisposition and learning from parents or other social groups, is an exciting subject that remains largely untouched by workers.

Acknowledgements

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