Behaviour of wintering Tundra Swans *Cygnus columbianus columbianus* at the Eel River delta and Humboldt Bay, California, USA

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Abstract

Tundra Swan *Cygnus columbianus columbinanus* phenology and behaviour at the Eel River delta and southern Humboldt Bay in northern California, USA, is described. Counts made each January from 1963 onwards peaked at 1,502 swans in 1988. Monthly counts recorded during the 2006/07 and 2008/09 winters peaked in February, at 1,033 and 772 swans respectively. Swans roosted on ephemeral ponds at the Humboldt Bay National Wildlife Refuge, on ephemeral ponds within grassland pastures in the vicinity of the Refuge, and perhaps also used the Eel River as a roost. Flights between Refuge roosts and the pastures and ponds occurred in the two hours after sunrise and before dark. In winters 2008/09 and 2009/10, the percentage of cygnets in the flocks was 10.6% and 21.4% respectively, and increased to ≥31% cygnets each year after most swans had departed from the area in March. Average brood size in 2009/10 was 2.1 cygnets. Daily activities consisted of foraging (44.9% of activities recorded), comfort behaviour (22.1%), locomotion (16.2%) and vigilance (15.5%). Eight neck-collared swans identified in the wintering flock were marked at four locations in different parts of Alaska, up to 1,300 km apart.

Key words: activity budgets, movements, Tundra Swan, wintering behaviour.

Tundra Swans are amongst the largest and most esteemed of waterfowl, with their beauty and annual migration capturing the human imagination (Scott & The Wildfowl Trust 1971; Todd 1997; Kear 1990), yet in North America they are amongst the least studied (Limpert & Earnst 1994), particularly in the non-breeding period (*sensu* Owen & Cadbury 1975; D.K. Scott 1980; Black & Rees 1984; but see Earnst 1994). This paper contributes to improving the understanding of the wintering behaviour

of Tundra Swans *Cygnus columbianus columbianus* within traditionally-used northern California habitat in the coastal Pacific Flyway. Fidelity to non-breeding season sites is a feature of migratory swans (Evans 1980; Munro 1981; Rees 1987). Petrie & Wilcox (2003) reported that satellite-tracked Tundra Swans spend 20% of the annual cycle in the wintering range, 51% at staging sites and 29% on the breeding grounds. However, to better understand an animal's relationship with its habitat, a description is required of patterns in numbers, distribution and how individuals spend their time (Owen & Black 1990; Baldassarre & Bolen 2006). To that end, this paper describes: 1) historical use of the study site, 2) location of the main areas used, 3) seasonal and daily use of sites, 4) flock composition, and 5) the diurnal activity patterns of the swans. It also aims to identify the breeding and moulting areas for swans from this southwest part of the wintering range, which have not been described in earlier Tundra Swan marking and re-sightings programmes (Ely *et al.* 1997; Moermond & Spindler 1997; Dau & Sarvis 2002; Petrie & Wilcox 2003).

Methods

Tundra Swans were studied in the Eel River delta near Ferndale (known locally as Centerville; 40°06'N, 124°03'W) and at Humboldt Bay National Wildlife Refuge (1,600 ha; hereafter referred to as the Refuge), Humboldt County, California (40°45'N, 124°13'W). The Refuge is at the southeast corner of Humboldt Bay, 16 km from Ferndale and separated from it by Table Bluff Hill (97 m elevation). The Eel River delta (~13,365 ha) is south of Humboldt Bay (Fig. 1) and adjacent to agricultural pastureland used for dairy and beef cattle (Monroe & Reynolds 1974). The delta, the fourth largest in California, includes a network of sloughs and side channels which reach into the pastureland in the lower 11 km of the river (CDFG 1997; Schlosser 2007). Typical pasture grasses of the region include Velvet Grass *Holcus lanatus*, Marsh Grass *Heleochloa schoenoides*, Rye Grass *Lolium perenne*, Tall Fescue *Festuca arundinacea*, meadow grasses *Poa* sp. and bent grasses *Agrostis* sp., with White Clover *Trifolium repens* and buttercups *Ranunculus* sp. also commonly occurring (Verhey 1992; Long 1993). In response to winter heavy rains and flooding, ephemeral ponds of various sizes form in the fields, where swan flocks can be observed undisturbed from public roads and farm tracks. For instance, Ponds A and B (Fig. 1) were of 5.5 ha and 3.9 ha in area and up to 1.2 m deep (Combs & Botzler 1991). Dominant pond vegetation included rush *Juncus* sp., dock *Rumex* sp., blackberry *Rubus* sp., bull rush *Scirpus* sp., pondweed *Potamogeton* sp., ditchgrass *Ruppia* sp., duckweed *Lemna* sp. and assorted Gramineae (Combs 1988). The Refuge consists of a complex mosaic of fresh, brackish and saltwater wetlands in response to tidal influence, freshwater inputs and the residual salinity of old saltmarsh soils (HBNWR 2010).

Attendance patterns and occurrence of all bird species in this study area have been observed and recorded by volunteer bird watchers over many years. Harris's (2006) study, based on 17,097 observations of Tundra Swans at the site, found that the

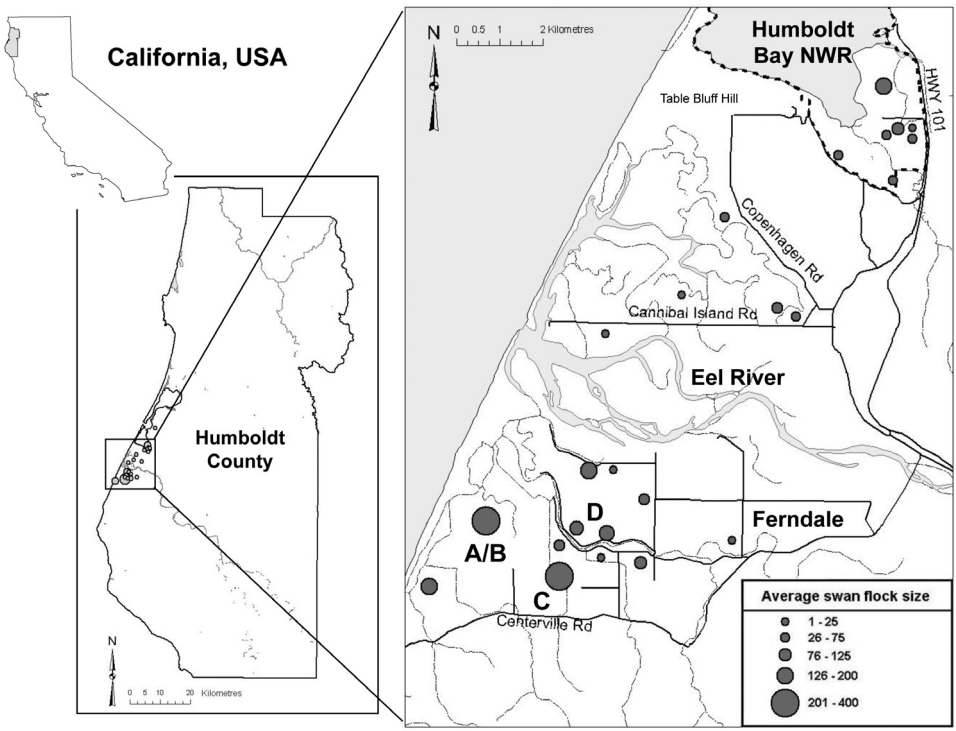

Figure 1. Map of study area showing the Eel River delta, including the Humboldt Bay National Wildlife Refuge (dotted line) and the town of Ferndale, Humboldt County, California, USA. Key pastures and ponds used by Tundra Swans in winters 2006/07–2009/10 are labelled, including Ponds A & B (historically known as Centerville Gun Club, Russ Ranch), Pond C (Damon Road), and Pond D (Riverside Ranch).

majority of birds were present from mid-November to mid-March, with few records from October and April, suggesting birds seen outside these dates were probably sick or injured.

Historical Tundra Swan records were collected from Christmas Bird Counts made at the site, conducted by volunteers in early January each winter for the years 1963–2009 (National Audubon Society 2002). The Christmas Bird Counts (ground counts) do not differ significantly from numbers of swans recorded during the aerial surveys of waterfowl in the area made by the California Department of Fish and Game in mid-winter (D. Lancaster pers. comm., CDFG, Eureka, California, USA)(t_8 = 2.31, P = 0.876, n.s.). We checked for linear trends in Christmas Bird Counts with Spearman Rank Correlation (Siegel 1956).

Tundra Swan flock composition, distribution and behaviour was monitored in the agricultural pastures and ponds of the Eel River delta and at the Refuge in

winters 2006/07, 2008/09 and 2009/10. In 2006/07 and 2008/09 we counted Tundra Swans in the study area on driving to all sites within a 3 h morning period to determine distribution on Refuge and non-Refuge sites. Cygnets (first winter birds) were distinguished from adults by their grey plumage during counts made in winters 2008/09 and 2009/10. In winter 2009/10, the time and direction of daily flights of flocks were noted on 23 days between 26 January and 7 March 2010. Behavioural activities were also assessed in winter 2009/10, for flocks at Ponds C and D in the Eel River delta (Fig. 1). The behaviour of each individual in the flock was recorded during flock scans made at 15 min intervals, with no more than three scans recorded per daylight hour (07:30–18:30 h), during 18 days between 5 February 2010 and 7 March 2010. Individuals were recorded as grazing (obtaining food on land), aquatic feeding (obtaining food in water), sleeping, loafing, preening, head-up, extended head-up (*i.e.* vigilant or pre-flight signalling), swimming and walking (D.K. Scott 1980; Black & Rees 1984). Preening included pecking or scratching at plumage and shaking feathers. Loafing was defined as sitting without head extended or any other sign of vigilance or foraging. Head-up was defined as sitting or standing on land with a raised head. Extended head-up was defined as when the head and neck were extended to the full extent when on land or water. Comfort behaviour was the composite of sleeping, loafing and preening. The mean proportion of individuals exhibiting each behaviour was calculated for each hour of the day based on seven scans for 07:30–08:00 h, 10 scans for 18:00–18:30 h and 20–24 scans per hour (mean = 21.5, s.e. = 1.4) for the remainder of the day.

The swans' moulting and/or breeding areas were determined from sightings made of individuals fitted with neck collars on being caught during the moult in summers 2006–2009 at five sites in Alaska: the Izembek National Wildlife Refuge, southern Alaska Peninsula (55°32'N, 162°80'W); the Becharof National Wildlife Refuge, near King Salmon, northern Alaska Peninsula (58°39'N, 156°48'W); the Yukon-Kuskokwim River delta (61°22'N, 163°00'W); Kotzebue Sound, including the lower reaches of the Koyukuk and Kobuk Rivers (67°00'N, 161°00'W); and the Colville River delta, North Slope Alaska (70°23'N, 150°23'W) (Ely 2008). The swans were caught by using helicopters, planes, inflatable boats and dedicated biologists to corral the birds into a netted area for aging, sexing, measuring and marking (with neck collars and metal leg-rings), prior to release back on to the moult site (Ely *et al.* 1997).

Results

Maximum annual numbers of Tundra Swans counted in the Eel River delta and south Humboldt Bay area in early January 1963–2010 are shown in Fig. 2; numbers during the week of the annual Christmas Bird Count ranged from 36–1,502 birds. Numbers reached or exceeded 1,000 swans in seven years and the highest January count was in 1988. Consistently low numbers were recorded during the 1960s, with intermediate numbers in the early 1980s and since 1996. The number of swans declined between the early high count made in 1971

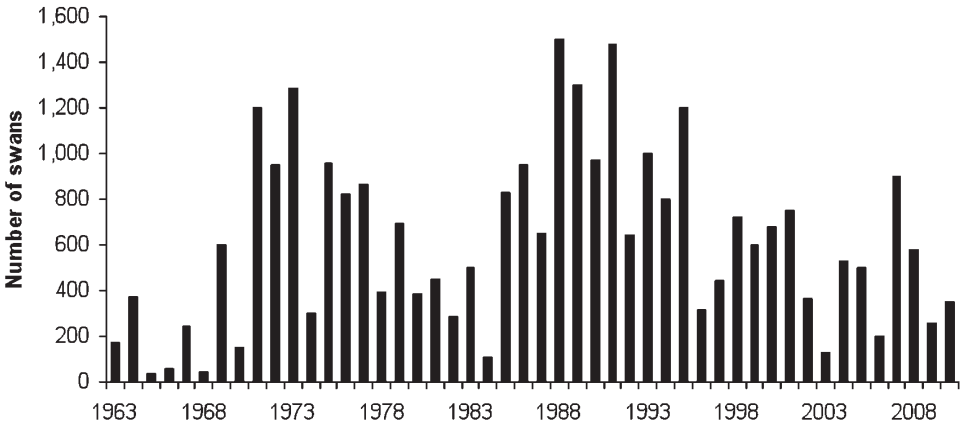

Figure 2. Maximum Tundra Swan numbers recorded during Christmas Bird Counts (January 1963–January 2009) made from the southern Humboldt Bay habitats to the mouth of the Eel River.

and the present (r_s = 0.315, n = 40, $P < 0.05$), particularly between the highest count (made in 1988), and the present (r_s = 0.708, n = 23, $P < 0.001$). The average Christmas Bird Count for the entire period was 614 swans (s.e. = 56).

Within-season peak numbers during winters 2006/07–2008/09 occurred on 6 February 2007 (1,033 swans), 8 February 2009 (772 swans) and 5 February 2010 (475 swans using Eel River delta only, excluding the Refuge), after which numbers declined until the last birds departed in mid to late March. Based on days when swans were counted in all areas in the same morning, about half of the birds were recorded on the Refuge and the other half on non-Refuge ponds and pastures (mean = 51.1% on the Refuge, s.e. = 12.1%, range = 15.6–84.6%, n = 6 mid-season counts). Birds began moving from the Refuge roost pond soon after sunrise, flying either to pastures or to other flooded fields on the Refuge, or directly to pastures in the surrounding area. Peak flight activity took place from 08:00–10:30 h and 16:00–18:15 h (Fig. 3). Evening flights decreased sharply after 18:15 h; few flights occurred after twilight (Fig. 3). Whereas most flights in the middle of the day were between fields and ponds within the Eel River delta study area, morning and evening flights were of flocks moving from and to the Refuge (Fig. 3). Swans flying into Eel River delta sites in the morning from the Refuge arrived 1 h later than those coming from local roosts. The slight increase in flights at 14:00 h involved swans moving exclusively among Eel River delta sites and the peak at 18:00 h involved birds moving between Ponds A/B, C and D, where some swans were presumed to have spent the night. Re-sightings of birds, identified by reading their neck collar codes, confirmed that individuals may use several ponds in the study area (see below). Average size of all flying flocks was 6.4 swans (s.e. = 0.4, range = 1–53 swans, n = 299 flocks).

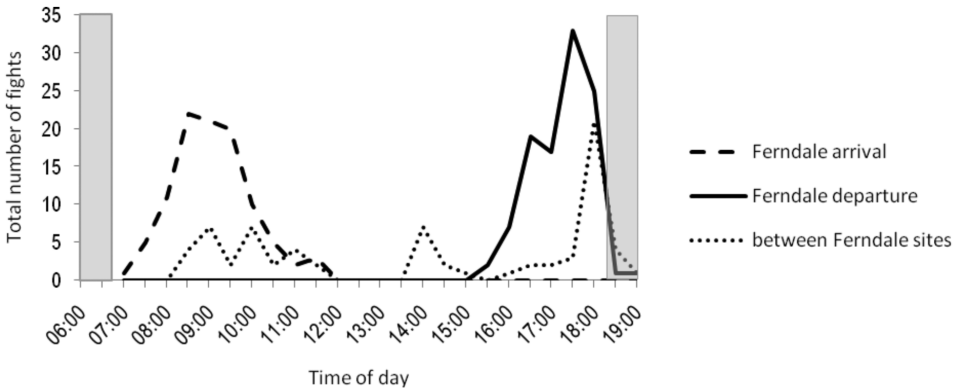

Figure 3. Frequency of swan flights in relation to time of day from and to roost sites and pastures within the Eel River delta and Humboldt Bay National Wildlife Refuge, recorded at Ferndale, California, USA, on 23 days between 26 January and 7 March 2010. Flights may be made by a group of swans or a single bird. Shaded regions indicate periods of darkness.

In 2009, the mean percentage of cygnets was 10.6% (s.e. = 0.02%) for three counts when peak numbers were present. As numbers of swans in declined in March, the proportion of cygnets increased to 31.7% (s.e. = 0.01%, n = 2 counts). In 2010, the proportion of cygnets averaged 21.4% (s.e. = 1.2%, n =11 counts when peak numbers were present) with the percentage of cygnets again increasing to 31.0% (s.e. = 1.3%, n = 3 counts) as numbers present declined at the end of the winter. Numbers of cygnets counted in each brood over 13 days between 9 January and 5 March 2010 gave a mean brood size of 2.1 cygnets (s.e. = 0.1): 80 broods with 1 cygnet, 83 with 2 cygnets, 56 with 3 cygnets, 16 with 4 cygnets and 4 with 5 cygnets.

The swans' primary activity during the study period in 2010 was foraging (44.9% of activities recorded in 233 flock scans); the remainder of the day was spent preening, loafing or sleeping (combined as comfort behaviour; 22.1%), swimming and walking (combined as locomotion; 16.2%), or being vigilant (head-up and extreme head-up; 15.5%). Peak grazing effort occurred at 16:00 h, with a smaller peak between 09:00–10:30 h (Fig. 4a). Peak aquatic feeding occurred prior to 08:00 h, when more birds were on the ponds and grazing was at its daily minimum (Fig. 4a). Aquatic feeding effort declined throughout the remainder of the day. Most comfort activity occurred between 10:00–15:30 h; about 25% of activities in the middle of the day were comfort movements (Fig. 4b). A peak in sleeping (18.2%) occurred at 14:00 h. Locomotion on land or water occurred at 07:00–08:00 h and again at 18:00 h, remaining low at other times of day (Fig. 4c). This was concurrent with the morning and evening flights (Fig. 3, Fig. 4c) and with extreme head-up postures (Fig. 4d). Regular head-up postures were at a minimum in the morning hours, and increased throughout the day (Fig. 4d).

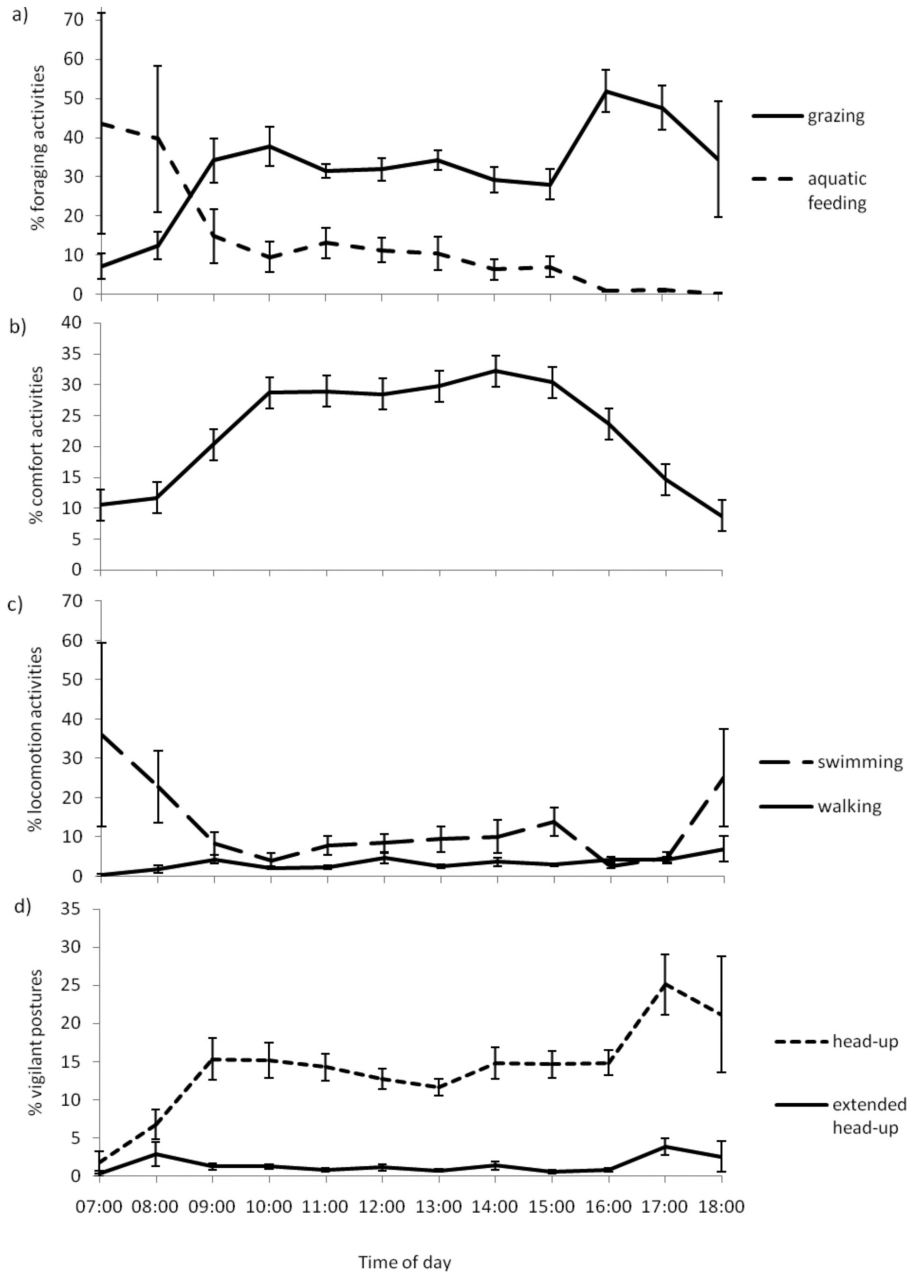

Figure 4. Mean proportion (± s.e., n = 233 flock scans) of swans in: a) foraging activities, b) comfort activities (preening, sleeping and loafing), c) locomotion activities, and d) vigilant postures, at the Eel River delta, California, USA from January–March 2010.

Four adult swans fitted with neck collars on the North Alaska Peninsula in July 2006 were observed at the Refuge on Humboldt Bay in winter 2006/07. These were P733 (female) seen on 5 January; P753 (male) seen on 18 December after being recorded at Everett, Washington, on 27 November; and two birds, P734 (male) and P738 (female), recorded in the same flock at the Refuge on 15 March before being re-sighted back on the Northern Alaska Peninsula at Rapids Camp Lagoon on 25 April 2007.

Four more adult swans with neck collars were identified in the study area in winter 2009/10. Female P942 (caught on the Northern Alaska Peninsula in July 2009) was observed at the Refuge (on 11 February 2010) and Pond D (12 February 2010). Male U076 (caught at Koyukuk River in July 2008) used Pond A (on 22 February 2010) and Pond C (28 February 2010). Female K384 (caught on the Yukon-Kuskokwim River delta in July 2009) used Pond A (on 22 February 2010) and Pond C (28 February and 5 March 2010). Finally, male U565 (caught at the Kobuk River delta in July 2008) was seen at Pond A (on 22 February 2010) and the Refuge (1 March 2010).

Discussion

The Christmas Bird Counts revealed long-term variability in the number of swans found in the Eel River–Humboldt Bay area in early January, with the highest number (1,500 swans) occurring in 1988. It is difficult to determine from the Christmas Bird Counts alone whether overall use of the site by the swans has declined, because these counts do not reflect the peak number of birds occurring in the area each winter. More frequent counting effort between November and March can be used to describe arrival, peak and departure patterns, and in 2007 and 2009 the highest number of swans occurred in early February. In those two years, numbers increased from 902 to 1,133 birds and from 258 to 772 birds between the January (Christmas Bird) and February counts. Peak numbers in 2007 and 2009 persisted for just one week, indicating a pattern of arrival and departure of transient swans on their way elsewhere. For example, the neck-collared pair (P734/P738) was seen at the Refuge on 15 March 2007 and then back on the breeding grounds in Alaska on 25 April 2007. Tundra Swans are known to stop at numerous sites during migration, spending more time at the northerly staging areas than wintering sites further to the south (Ely *et al.* 1997; Dau & Sarvis 2002; Petrie & Wilcox 2003).

A site is considered to be important for the conservation of a population when ≥1% of the total population uses it, irrespective of the time of year (D.A. Scott 1980; Taylor *et al.* 2005). The swans wintering at Eel River–Humboldt Bay are part of the Western Population of Tundra Swans, which breed in southern Alaska and winter in the western USA (Limpert *et al.* 1991). Population size is currently estimated at 96,200 birds; USFWS 2009). The peak counts of 1,033 and 772 birds in 2007 and 2009 therefore represent 1.1% and 0.8% respectively (mean = 0.9%) of the population, indicating that the Eel River–Humboldt Bay wintering area is close to qualifying as a site of conservation

importance for the Western Population of Tundra Swans. Using maximum counts as an indicator of site use does, of course, underestimate the total number of birds that move through an area, particularly if there are wintering sites to the south. For example, Black Brant Goose *Branta bernicla nigricans* numbers at Humboldt Bay peaked at about 17,000 birds but mark-recapture probabilities estimate that 37,600–77,800 individuals pass through the site, depending on the year, where they stay for an average of 26 days (Lee *et al.* 2007).

The conservation status of a site is also assessed by considering the level of protection and potential threats to areas that are used by local populations (D.A. Scott 1980; Scott & Jones 1995; Black 1998). The swans in the Eel River–Humboldt Bay wintering area regularly roost and forage in pastures and ponds on the Refuge; as many as 85% of the birds (mean = 51%) were observed at the Refuge on days when swans were counted in all areas in the same morning. Two of the four collared swans seen in 2010 were observed on the Refuge and the Eel River delta ponds, confirming the connection between the fully protected Refuge roost sites and foraging areas on nearby private land.

The California Department of Fish and Game manages 862 ha of the Eel River Wildlife Area, adjacent to the mouth of the river, for hunting. No swans were observed in this area during our study but Miller *et al.* (1986) reported Tundra Swans swimming and preening near the mouth of the Eel River at dusk, suggesting that the estuary may be used as a night-time roost by some of the swans. All other regularly used ponds and flooded pastures were under private ownership; conversations with landowners indicated a long history of accepting swans at these sites. The Wildlands Conservancy recently purchased 445 ha of mainly dune habitat, which serves to buffer pastureland and Ponds A and B from prevailing winds.

Tundra Swans are protected in California and we are unaware of birds being taken illegally in our study area, but they are hunted legally under licence in other western states. Three of 88 local bird carcasses examined had signs of old wounds from shot and two birds had a single pellet in their gizzard grit; the carcasses were from 135 swans found drowned in 1984, apparently due to exceptionally high surf in the Eel River estuary (Miller *et al.* 1986). Three birds had unidentified nematodes under their gizzard linings, but there was no evidence that swans had ingested toxic substances (pesticides were not evident in the tissues) (Miller *et al.* 1986). Besides the presumed low threat of predation by local Grey Foxes *Urocyon cinereoargenteus* and Bald Eagles *Haliaeetus leucocephalus* in the area (1–5 eagles present in winters 2007/08–2009/10; Burton 2010), Avian Cholera *Pasteurella multocida* outbreaks have been recorded at Ponds A and B (Fig. 1) in eight winters prior to 1980. The first confirmed outbreak was in 1945 and the most recent was in 1979 (Botzler 2002). Workers found 16, 83 and seven swan carcasses at Ponds A and B in 1975, 1976 and 1978, respectively (Hazlewood *et al.* 1978; Oddo *et al.* 1978; Mensik & Botzler 1989). Of waterbirds in the area, Tundra Swans were reported to be the second-most susceptible to the disease, after American Coots *Fulica Americana*

(Botzler 1991; Mensik & Botzler 1989). Focusing on questions to do with susceptibility to Avian Cholera, Combs (1988) reported on activity budgets of swans and other waterfowl on Ponds A and B, but due to differences in field methodology and data treatment we could not make comparisons. Apparent absence of the disease since 1979 coincided with digging of a new well to feed Ponds A and B, but other potential explanations remain unexplored (Botzler 2002; R.B. Botzler, pers. comm.).

The average number of cygnets per family was 2.1 (range = 1–5 cygnets) for Tundra Swans wintering at Eel River–Humboldt Bay in winter 2009/10. For comparison, average brood size for 1999 was initially reported as being 2.3 cygnets on the breeding grounds (Kuparuk) in west-central Alaska (Ritchie *et al.* 2002), 1.9 cygnets at autumn staging areas on the upper Mississippi River (Thorson *et al.* 2002) and 1.6 cygnets on wintering grounds in coastal states of eastern USA (Serie *et al.* 2002). The Eastern Population of Tundra Swans, estimated at 100,200 in 2009 (USFWS 2009), nests in northern Alaska and travels across Canada to the Great Lakes and winters in eastern coastal states (Limpert *et al.* 1991). The average brood size for this population in north-central Alaska breeding grounds (in August) was 2.5 cygnets (range = 2.0–2.8, n = 11 years; Ritchie *et al.* 2002), and the average brood size on eastern wintering grounds was 1.5 cygnets (range 0.8–2.2, n = 17 years; Serie *et al.* 2002). The single value from the Eel River delta therefore is on the high end of the reported range for both Tundra Swan populations in winter; all but one of Serie *et al.*'s (2002) 17 winter assessments were less than our value of 2.1 cygnets per brood.

The percentage of cygnets in the wintering flock at Eel River–Humboldt Bay was 10.6% in 2009 and 21.4% in 2010. For comparison, the average percentage of cygnets recorded for Eastern Population Tundra Swans in late summer flocks in north-central Alaska was 25% (range = 13.8–33.9%, n = 11 years; Ritchie *et al.* 2002) and in winter flocks on the eastern seaboard the average was 12.6% (range = 4.1–23.6%, n = 17 years; Serie *et al.* 2002). The Eel River delta values of proportion of young therefore were within the range reported for wintering flocks. Evans (1979) was among the first to point out the usefulness of flock composition assessments, for enabling a comparison of the relative productivity between wintering locations, different years and across species. Although flock composition in the Eel River delta has yet to be compared with that for Tundra Swans elsewhere, calculations based on the proportion of cygnets and brood size estimates recorded in 2010 found that there were 102 cygnets and 49 successful breeding pairs in the flock of 475 swans at the site in this year.

Waterfowl are known to adjust foraging effort according to the types of foods consumed and amount of daylight available at different times of the year (Owen & Black 1990). The average proportion of Tundra Swans recorded as feeding in the Eel River delta was 44.9%, which amounts to just under 5 h of foraging time (in 11 h of daylight on 1 March). The swans' diet was not quantified during the study, but was

assumed to consist of the available seeds, leaves of terrestrial pasture grasses, and shoots and tubers of aquatic plants. Rees & Bowler (1991) reported a similar proportion of 48.4% (4.9 h) feeding in Bewick's Swan *Cygnus columbianus bewickii* flocks in England in late winter/spring. The diurnal pattern of Eel River delta Tundra Swans, with peaks in foraging activity at the beginning and end of the day, was also similar to that described for Bewick's Swans (Bowler 1996, described in Rees 2006). The late afternoon peak in feeding effectively extends the foraging day, as food continues to be digested in the gut during darkness (Owen 1972).

Peaks in locomotion on land and water, and extreme head-up postures coincided with morning and evening flights because of the swans' pre-flight ritual where the head and neck are pumped and calls are given prior to family and group take-off (Black 1988). The birds may also have become more head-up vigilant in the evenings due to an increased risk of predation as light levels decreased and a presumed increase in Grey Fox and Raccoon *Procyon lotor* activity in the area.

Swans in the Eel River–Humboldt Bay area originated from at least four of the five capture locations at breeding/moulting areas in Alaska. Five of the eight birds originated from the Northern Alaska Peninsula in the southern part of Alaska and one each from Yukon-Kuskokwim River delta, Koyukuk River, and Kobuk River in the western part of Alaska. These areas are separated by 1,300 km from the northern to the southern-most sites. It is surprising that birds in such a small flock in coastal California are comprised of birds from multiple breeding areas. We would expect mixing to occur in wintering areas with larger numbers but not for smaller flocks. Perhaps mixing is initiated at staging areas prior to leaving Alaska and again during frequent stops during migration (Ely *et al.* 1997; Moermond & Spindler 1997; but see Dau & Sarvis 2002). Bellrose (1980) suggested that the coastal migratory route was most likely used by swans coming from the Alaska Peninsula and Bristol Bay, Alaska. This suggestion is corroborated by five of our observations but it is possible that the three swans marked in western Alaska came to the coast after first travelling the inland Central Valley corridor (Fig. 2 and Fig. 3 in Ely *et al.* 1997; also see Moermond & Spindler 1997).

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