Historical changes in black brant Branta bernicla nigricans use on Humboldt Bay, California

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Historical changes in black brant *Branta bernicla nigricans* use on Humboldt Bay, California

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We examined 70 years (1931-2000) of black brant *Branta bernicla nigricans* abundance on Humboldt Bay, California. We used linear regression to convert count data to a standard variable (use-days) for evaluating hypotheses that explain temporal trends in brant use. Winter and spring brant-days on Humboldt Bay declined sharply in the mid-1950s and continued to decline through the mid-1980s, but have since increased. Evidence suggests that this trend may have been driven largely by changes in temporal patterns of hunting pressure on Humboldt Bay. We found little convincing support for alternative hypotheses such as changes in eelgrass *Zostera marina* condition over time, effects of non-hunting disturbance, and correlation with trends in abundance at the flyway level. Our study affirms the appropriateness of current hunting regulations for brant in California, but poses a challenge to wildlife managers who wish to provide hunting opportunities without displacing brant from important staging and wintering areas.

Key words: abundance, Branta bernicla nigricans, distribution, disturbance, eelgrass, hunting, Zostera marina

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During spring migration, black brant *Branta bernicla nigricans* (in the following referred to as 'brant') feed on eelgrass *Zostera marina* in shallow bays and estuaries along west coast North America (Reed et al. 1998b, Moore et al. 2004), where they accumulate nutrient reserves critical for successful reproduction (Ankney 1984, Ebbinge & Spaans 1995). Humboldt Bay is the most important spring staging area in California based on peak use data, and the fourth most important site in the Pacific flyway (Moore et al. 2004). Lee (2001) estimated that approximately 60% of the flyway population used the bay in spring 2001, probably because of its high eelgrass abundance and relative isolation from other staging areas (Moore et al. 2004). Our goals in this paper are to: 1) use historic counts to describe trends in brant use of Humboldt Bay, 2) evaluate use-patterns in relation to variation in hunting disturbance or Pacific flyway population trends, and 3) recommend an annual protocol for monitoring brant use.

Single winter censuses for Humboldt Bay have been conducted since 1931, with more frequent fall-, winter- and spring-counts since the 1970s. Data indicate that winter and spring brant use declined suddenly in the mid-1950s, continued to decrease through the mid-1980s, and then increased through 2000. Midwinter survey data reveal similar declines at winter and spring sites in Oregon and Washington (Drut & Trost 2000). Proposed hypotheses to explain changes in brant use primarily include disturbance due to hunting and other human factors and eelgrass habitat degradation (Einarsen 1965, Smith & Jensen 1970, Henry 1980, Subcommittee on Pacific Brant 1992). Investigation of these hypotheses has been hampered, however, by the sporadic nature and inconsistent timing of surveys, and lack of historical data for eelgrass condition or non-hunting human disturbance. We found predictive relationships between seasonal use-day estimates and count data, thus enabling us to recreate a historical record of brant use-days on Humboldt Bay that could be used to empirically test two possible hypotheses concerning use at a key staging area.

Material and methods

Study area

Humboldt Bay, located on the northern California coast, is the second largest estuary in the state, with a water surface area of 62.4 km^2 at mean high water (MHW; Proctor et al. 1980). The bay has three main sections, two of which receive 99% of the bay's brant use, i.e. Arcata Bay and South Bay. These areas consist of extensive tidal flats, accounting for 65-70% of the total MHW area of the bay (Barnhart et al. 1992). Eelgrass, which varies in extent annually, occurs below about +0.3 to +0.4 m (relative to mean lower low water; MLLW). In 1997, eelgrass covered approximately 1,044 ha of which 309 ha were in Arcata Bay and 720 ha were in South Bay (Terra-Mar 1997). A long narrow channel (Arcata Channel) connecting two sections of the bay contains about 15 ha of eelgrass, and supports about 1% of annual brant use (Humboldt Bay National Wildlife Refuge (HBNWR), unpubl. data). Shoot and biomass densities are also consistently higher on South Bay than on Arcata Bay, where an estimated 78-90% of the total biomass occurs (Keller 1963, Waddell 1964, Harding & Butler 1979, Bixler 1982).

Sources of brant abundance data

Moffitt (1931-1941, 1943) conducted annual February brant surveys along the entire coast of California during 1931-1942. We used U.S. Fish and Wildlife Service (USFWS) mid-winter survey data for 1940-1974. Midwinter counts were usually conducted in January; however some were as late as February or March (Henry 1980; Marty Drut, USFWS, pers. comm.). We obtained additional count data from Bentley & Christianson (1957, cited in Henry 1980), Denson (1961), Denson & Murrell (1962), and Monroe (1973, cited in Henry 1980). During 1975-1978, Henry (1980) conducted weekly counts of brant on Humboldt Bay during fall, winter and spring, and estimated weekly, monthly and seasonal brant use (i.e. number of brant use-days). Since 1978, USFWS personnel at HBNWR used this protocol to continue the surveys. Except for USFWS mid-winter aerial surveys, counts were ground based.

Analysis of winter and spring brant use

Two factors made it impossible to directly compare all brant data. First, while data from 1975-2000 provided direct estimates of seasonal brant use-days, surveys in many of those years occurred on South Bay only (Table 1). We estimated total Humboldt Bay use-days in these years by dividing use on South Bay by 0.83, as this was the average proportion of total use that occurred on South Bay in 11 years between 1975 and 2000 (range: 0.78-0.94; Moore et al. 2004).

Secondly, data prior to 1975 typically consisted of 1-4 counts during winter or spring, but they have not been used to estimate seasonal use-days. We used linear regression on South Bay data during 1975-2000 (N = 24 years) to identify predictive relationships between individual counts conducted at different times during winter and spring, with seasonal and total use-days in the same year. For example, we examined whether a single count conducted in the second week of February (as per Moffitt's protocol through the 1930s) could predict the estimate of use-days occurring in the same winter or spring. If a strong relationship existed, we extrapolated pre-1975 winter or spring brant use-days by entering available count values into a regression equation with slope coefficients that were estimated using the post-1975 data. We defined a strong relationship to be the regressions in which > 50% of the variation in use-days was explained by count data (i.e. adjusted $R^2 > 0.50$). Presumably, we could have used a slightly different cut-off (e.g. $R^2 > 0.40$ or 0.60) with similar results. We defined winter use as that occurring during January and February, and spring use as that occurring from March through May. We excluded December in winter use-day estimates because: 1) several of the years used to identify regression relationships (1975-2000) contained no December data, 2) pre-1975 December counts provided little additional predictive power to estimate winter use-days because they were conducted in years when both January and/or February were also counted, 3) it is not clear from historical counts whether brant in December were late-fall migrants, winter residents or early-spring migrants, and 4) relative to brant numbers in January

Table 1. Individual counts of black brant during winter and spring on Humboldt Bay (Arcata and South bays). In months when multiple counts were conducted, the peak count is reported.

Year	December	January	February	March	April	May	Source
1930/31			4200				Moffitt 1931
1931/32		3000	29415				Moffitt 1932
1932/33			5000	13000	3000		Moffitt 1933
1933/34	10000		16860				Moffitt 1934
1934/35	2000		105000				Moffitt 1935
1935/36			50000				Moffitt 1936
1936/37			22500	30000			Moffitt 1937
1937/38			45000	100000			Moffitt 1938
1938/39			29000	100000	25000		Moffitt 1939
1939/40		15385	56375				Moffitt 1940
1940/41		16300	50000				Moffitt 1941
1941/42		20000	48000				Moffitt 1943
1942/43		8000					USFWS winter survey
1943/44		2500					USFWS winter survey
1944/45		16000					USFWS winter survey
1945/46							USFWS winter survey
1946/47		25000					USFWS winter survey
1947/48		27120					USFWS winter survey
1948/49		27505					USFWS winter survey
1949/50		32500					USFWS winter survey
1950/51		36000					USFWS winter survey
1951/52		25000					USFWS winter survey
1952/53	28000						USFWS winter survey
1953/54			7500				USFWS winter survey
1954/55			11870				USFWS winter survey
1955/56			7000	19010			USFWS winter survey
1956/57	1700	6900	18800	37000	25000		Denson & Bentley 1962 Denson & Murrell 1962
1957/58		57		11300			Denson & Murrell 1962
1958/59		113	4850				Denson & Murrell 1962
1959/60	100	62	10000	35000	30000	300	Denson 1961 Denson & Murrell 1962
1960/61	600	2000	15000	40000	40000	30000	Denson 1961, Denson & Murrell 1962
1961/62			55800				USFWS winter survey
1962/63		383					USFWS winter survey
1963/64		2695					USFWS winter survey
1964/65		1					USFWS winter survey
1965/66		0					USFWS winter survey
1966/67		0					USFWS winter survey
1967/68	38	0	420	10900	39140	44	Monroe 1973
1968/69	0	6	0	12700	13425	900	Monroe 1973
1969/70	0	47	1170	12600	11000	400	Monroe 1973
1970/71		0					USFWS winter survey
1971/72		0					USFWS winter survey
1972/73	0	200	12000	33600	10500		HBNWR survey
1973/74		0					USFWS winter survey
1974/75[a]		7	3000	15000	37500	1200	Henry 1980
1975/76	80	140	4375	16810	22275	463	Henry 1980
1976/77	46	70	2760	21628	18030	692	Henry 1980
1977/78[a]	80	150	2500	20950	11680	950	Henry 1980
1978/79[a]	7	52	185	17250	20580	463	HBNWR survey
1979/80[a]	60	49	1295	15270	11760	901	HBNWR survey
1980/81[a]	400	59	1203	8880	11080	1340	HBNWR survey
1981/82[a]	57	80	1025	10860	5050	1430	HBNWR survey
1982/83[a]	37	30	450	6100	13450	250	HBNWR survey
1983/84[a]	18	201	490	10100	7000	615	HBNWR survey

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... Table 1 continued

Year	December	January	February	March	April	May	Source
1984/85[a]	25	50	2076	5200	7386	1060	HBNWR survey
1985/86							
1986/87[a]	43	86	600	4255	12460	400	HBNWR survey
1987/88[a]	109	161	3000	8000	8390	508	HBNWR survey
1988/89							
1989/90[a]	50	500	3400	10095	16375	5823	HBNWR survey
1990/91[a]	123	750	1638	12380	10095	2070	HBNWR survey
1991/92[b]		2000	9050	24710	24720	3757	HBNWR survey
1992/93[b]		3950	10660	23755	18415	2655	HBNWR survey
1993/94[b]		4100	11535	31870	26530	585	HBNWR survey
1994/95[b]		5825	20570	19504	24053		HBNWR survey
1995/96[b]	580	5094	19281	19605	16043	2373	HBNWR survey
1996/97[b]	334	6636	12319	14683	11561	1452	HBNWR survey
1997/98[c]		9119	10300	31400	14853	6300	HBNWR survey
1998/99[b]		4368	17812	23412	19406	474	HBNWR survey
1999/2000[b]	1144	6220	18490	24455	15330	2715	HBNWR survey

[a] Counts include brant on South Bay only.
[b] Counts also include the Arcata Channel.
[c] Counts also include brant in pastures surrounding Humboldt Bay.

and February, numbers in December have been low since the mid-1950s (see Table 1), and were typically low before 1975 also (Moffitt 1932, 1935, 1936); therefore, December use-days probably contributed relatively little to the number of use-days each year.

Different regression models were used to estimate brant use-days in different years, with independent variables defined by the dates for which pre-1975 count data were available (Appendix I). To estimate use-days from Moffitt's data in the 1930s and 1940s, our independent variable was the number of brant recorded during the second week of February. If only monthly peak numbers were reported in a particular pre-1975 year, we described the relationship between monthly peak counts and brant use-days in post-1975 years. In some instances, we did not know the exact date on which a pre-1975 count was conducted, nor whether it was a peak estimate. So, we assumed that such a count was a peak estimate if it exceeded peak values in post-1975 years. When the number of brant on a pre-1975 survey equaled zero, and we only knew which month the survey was conducted, we assumed this count was from the first week of the month, when numbers would be at their lowest (zero-counts were always from January or February). When multiple counts were available to predict use-days in a particular pre-1975 year, we used stepwise regression to select the combinations of counts that produced the best predictive model (i.e. that which maximized the adjusted R^2).

Once we had estimated historical brant use-days for each year, we used linear regression to determine whether annual variation on Humboldt Bay corresponded with the historical timing of hunting seasons or annual harvest estimates based on post hunting-season interviews with hunters (M. Drut, pers. comm., California Department of Fish and Game, unpubl. data). We also used regression to investigate whether annual trends in brant use-days on Humboldt Bay correlated with annual Pacific flyway population estimates (Drut & Trost 2000).

Analysis of fall brant use

Single counts were conducted on Humboldt Bay during fall migration (October-November) in seven years during 1956-1975. Weekly counts were used to estimate brant use-days on South Bay in 17 years during 1976-2000. We estimated bay-wide use (Arcata Bay and South Bay combined) in years following 1975 by dividing use-days on South Bay by 0.96, since the average percentage-use for that area ranged within 94-97% in fall (HBNWR, unpubl. data). Using the same methods as for winter and spring data, we identified linear relationships between fall use-days and peak counts from October and November in post-1975 data, from which we estimated fall use-days for the seven years prior to 1975 (Adjusted $R^2 = 0.62$, $F_{2,13} = 13.17$, $P < 0.001$). We used a Mann-Whitney test to examine whether fall use-days were lower in years when hunting seasons took place in fall.

Results

Winter and spring brant use

Strong relationships existed between estimates of winter brant use-days and individual brant counts conducted in

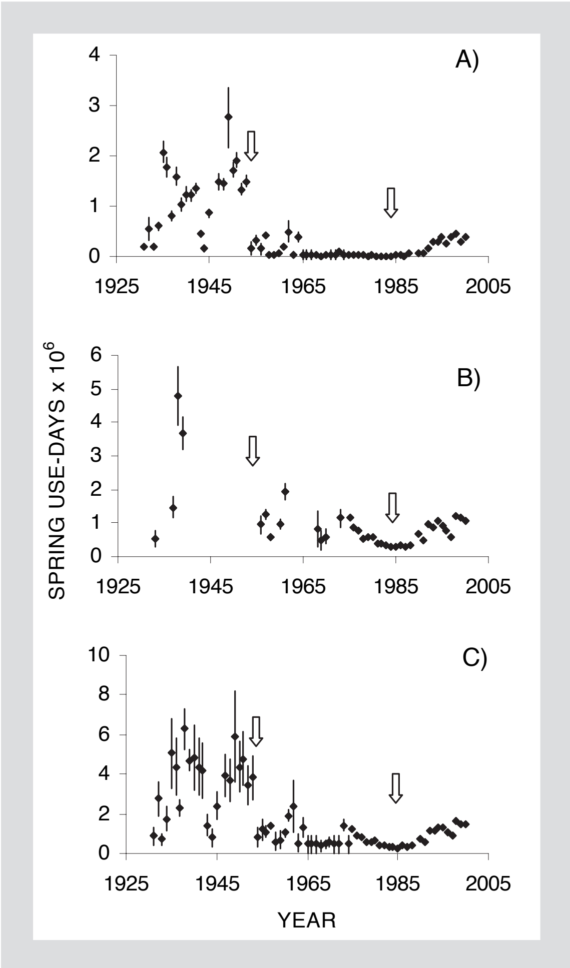

Figure 1. Estimated brant use on Humboldt Bay from 1931 to 2000 during (A) winter (January-February), (B) spring (March-May), and (C) both periods combined. For predicted estimates 95% confidence intervals are shown. Arrows indicate initiation of winter hunting seasons that lasted until late January or mid-February (1954), and cessation of winter hunts (1984).

January or February (Adjusted $R^2 = 0.74\text{-}0.99$, $F_{1\text{-}2,\ 18\text{-}22} > 54.0$, $P < 0.001$; see Appendix I), enabling extrapolation of winter brant use in all pre-1975 years with count data (Fig. 1). Winter brant use-days were much greater prior to the 1950s than in the decades following, with estimated use-days before 1954 commonly ranging within 1-2 million. By contrast, winter use-days since then have frequently measured below 100,000 use-days and reached a winter low of about 2,500 use-days in 1979.

January and February count data did not correlate well with spring use-days estimates, so we could only estimate spring use-days in 13 years between 1931 and 1974 when March or April data were available. Like winter use-day estimates, confidence intervals were relatively narrow for these 13 spring use-day estimates because regression relationships between March-April counts and spring use-days were strong (Adjusted $R^2 = 0.72\text{-}0.95$, $F_{1\text{-}4,\ 18\text{-}22} > 29.9$, $P < 0.001$; see Fig. 1). Unfortunately, only four of the 13 years pre-date 1954, which makes long-term evaluation of spring use-days in relation to hunting-season timing difficult. However, inspection of available spring counts (see Table 1) and use-day estimates (see Fig. 1) suggests that spring use-days on Humboldt Bay may have commonly exceeded 1 million use-days before 1954 (see Fig. 1), with estimates as high as 4-5 million use-days during this time.

In spite of the relative lack of March and April count data, we estimated the number of annual brant use-days for the entire goose season (January-May) from 1931 (see Fig. 1). However, the precision and apparent accuracy of use-day estimates depended on the number of counts available in a given year. In years when both winter and spring counts were available (see Table 1), estimates were generated from regression models with high adjusted R^2 values (see Appendix I), and thus had relatively narrow confidence intervals (see Fig. 1). By contrast, when only winter counts (January or February) were available, total use-day estimates were generated from regression equations with lower adjusted R^2 (see Appendix I), and had wider confidence intervals (see Fig. 1). Further, when only one or two counts were available, estimation accuracy may be sensitive to annual variation in the timing of migration. Annual estimates of total use-days (see Fig. 1) ranged within 1-6 million use-days before 1954. By contrast, the total number of use-days following 1953 have usually been < 1 million, and reached a low of about 285,000 total use-days in 1985.

The timing of a major decline in brant use coincides with the initiation of winter hunting seasons on brant in California that ran from November or December through the end of January or mid-February (Subcommittee on

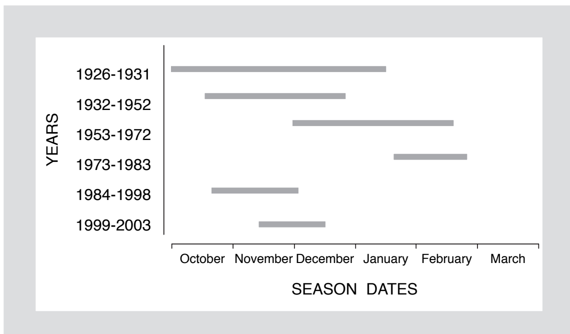

Figure 2. Approximate brant hunting-season dates in California during 1926-2003 based on data from Subcommittee on Pacific Brant (1992) and M. Drut (U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Portland, Oregon, pers. comm.).

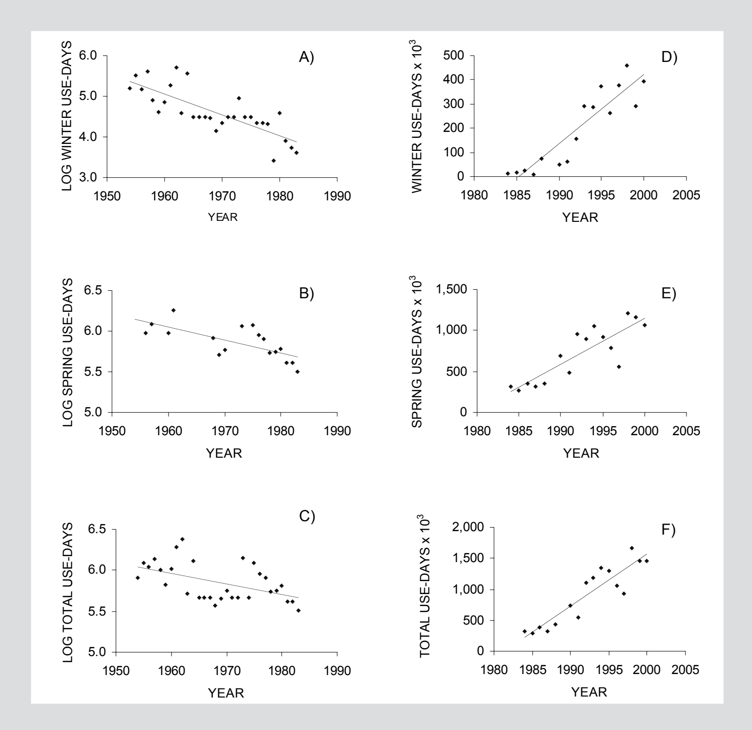

Figure 3. Panels A-C: Winter, spring, and total brant use from 1954-1983 (log-transformed to meet normality assumptions of regression analysis), while brant hunting through January or mid-February took place on Humboldt Bay. For winter (A), $R^2 = 0.62$, $F_{1, 28} = 45.24$, $P < 0.001$. For spring (B), $R^2 = 0.49$, $F_{1, 15} = 14.28$, $P = 0.002$. For total (C; winter and spring combined), $R^2 = 0.26$, $F_{1, 28} = 9.81$, $P = 0.004$. Panels D-F: Increasing brant use from 1984-2000, during which time January and February hunts have not taken place on the bay. For winter (D), $R^2 = 0.84$, $F_{1, 14} = 72.66$, $P < 0.001$. For spring (E), $R^2 = 0.73$, $F_{1, 14} = 38.25$, $P < 0.001$. For total use (F), $R^2 = 0.83$, $F_{1, 14} = 68.38$, $P < 0.001$.

Pacific Brant 1992). Prior to 1953, hunting seasons usually ran from October or November through mid to late December, although they did occasionally run through the first week of January, and until 20 January in 1946 (Fig. 2). From 1954 to 1983, winter and spring brant use on Humboldt Bay steadily declined (Fig. 3). Then, in the winter-spring of 1983/84, the hunting season reverted to the fall (see Fig. 2). Winter and spring use has steadily increased since then (see Fig. 3), peaking in 1998 at about 461,000 and 1,207,000 use-days, respectively. However, these estimates are still short of estimated pre-1950 levels. Harvest estimates were not available prior to 1958, so we could not directly relate harvest levels to the sudden decline in brant use in the mid-1950s. However, for the period 1958-1983, we found no relationship between winter harvest and winter use-day estimates in the same year ($R^2 = 0.08$, $F_{1,14} = 1.25$, $P = 0.28$; Fig. 4), nor between harvest in one year and change in winter use-days in the following year ($R^2 = 0.03$, $F_{1,14} = 0.46$, $P = 0.51$).

We investigated an alternative explanation for the downward trend in brant use of Humboldt Bay, which is that the flyway population simply decreased during this time. During the period of brant decline on Humboldt Bay (1960-1983), we found no significant relationship between the total number of brant use-days on the bay and the Pacific flyway brant population index (log transformed with one outlier

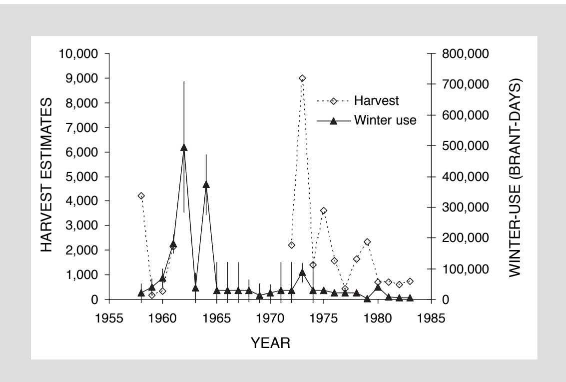

Figure 4. Winter brant-day (January-February) and harvest estimates on Humboldt Bay during 1958-1983, i.e. the period of winter hunting seasons. For use-day estimates 95% confidence intervals are shown for Humboldt Bay in years prior to 1975.

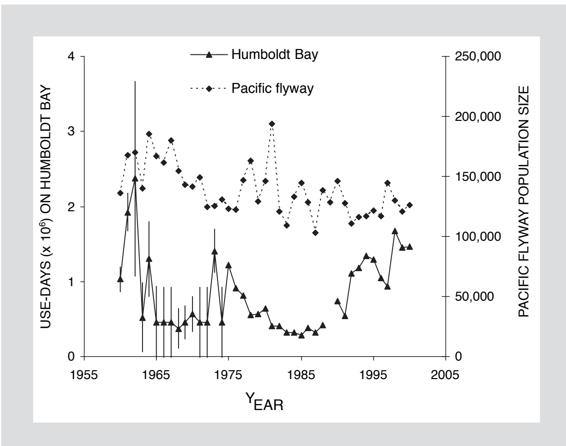

Figure 5. Number of brant-days during January-May estimated annually on Humboldt Bay since 1960, and the Pacific flyway population size for black brant during that time, as indexed by USFWS mid-winter survey data (Drut & Trost 2000). For use-day estimates 95% confidence intervals are shown for Humboldt Bay in years prior to 1975.

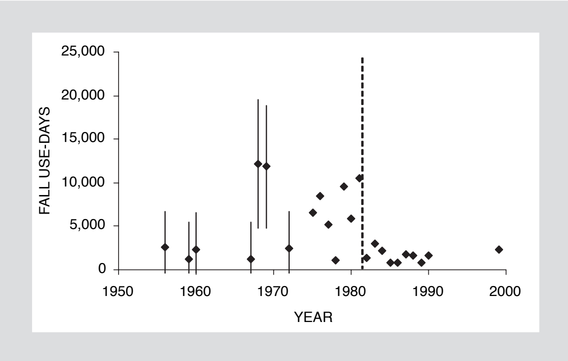

Figure 6. Brant use on south Humboldt Bay from 1956 to 2000 during fall migration (October-November). For predicted estimates 95% confidence intervals are shown. The dashed line divides the periods when fall hunting did (right) and did not (left) occur.

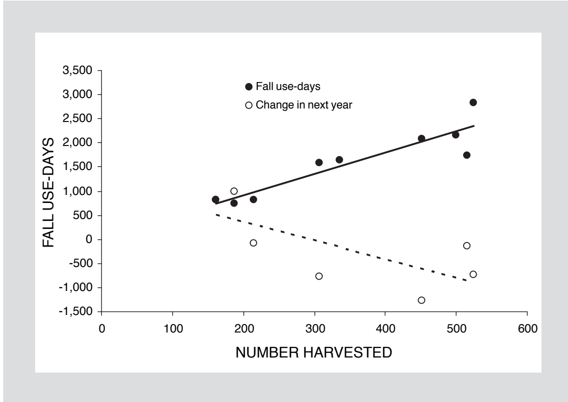

Figure 7. Relationships between harvest and fall brant-day estimates during October-November on Humboldt Bay for the years 1983-1990 and 1999 (period of fall hunting seasons). Solid circles represent plot of harvest against same-year use-estimates; $R^2 = 0.84$, $F_{1,7} = 35.1$, $P < 0.001$. Open circles represent plot of harvest again the change in use-day from harvest-year to subsequent year; $R^2 = 0.51$, $F_{1,5} = 5.30$, $P = 0.07$.

removed; $R^2 = 0.002$, $F_{1,22} = 0.04$, $P = 0.85$; Fig. 5). Similarly, no relationship existed between population size and number of brant use-days during the period of increasing brant use on Humboldt Bay, which occurred from 1984 to 2000 ($R^2 = 0.08$, $F_{1,14} = 1.29$, $P = 0.27$). Unfortunately, flyway data are not complete prior to 1960, so we could not test whether the dramatic decrease in use of Humboldt Bay in the early 1950s was associated with a flyway level decline.

Fall brant use

We compared data collected during 1956-1982 when hunting took place in January and February but not in October or November, with data collected during 1983-1999 when fall-hunting took place (see Fig. 2). In years when fall-hunting was absent, brant use was variable, but higher on average than during years when brant were hunted (Mann-Whitney test: $\bar{x}_{nohunt} = 5{,}507$, $\bar{x}_{hunt} = 1{,}671$, $Z = -2.42$, $P = 0.016$, $N = 24$; Fig. 6). Fall harvest was positively correlated with fall use-day estimates, indicating that hunters were more successful in years with more birds (Fig. 7). More interestingly, fall harvest was negatively related to fall use-days in the subsequent year with marginal statistical significance (see Fig. 7), suggesting that harvest intensity (either by number reduction or by related disturbance) may have a direct effect on fall brant use.

During 1975-1999 (the years when observed use-day estimates were available), the majority of the fall use occurred in November (mean = 91%, range: 76-100%, N = 16). This information is consistent with reported departure dates from Izembek Lagoon (Dau 1992), and early reports suggesting that brant rarely arrived on Humboldt Bay before November (Moffitt 1932, 1935, 1938, 1940, 1941, 1943).

Discussion

Historical brant use of Humboldt Bay

Historically, Humboldt Bay has been the most important area in California for wintering and migrating brant. During 1931-1942, Humboldt Bay accounted for 36-84% ($\bar{x} = 68\%$) of the brant observed in California during February (Moffitt 1943). Based on USFWS mid-winter inventories (Drut & Trost 2000), this value ranged within 12-100% during January 1941-1952 ($\bar{x} = 60\%$), and according to incomplete winter estimates of the entire flyway in 1951 and 1952 (Drut & Trost 2000, Leopold & Smith 1953), Humboldt Bay may have harboured as much as 15-20% of the Pacific flyway brant population in January. From the mid-1950s through the mid-1980s, however, winter and spring brant use declined precipitously on Humboldt Bay, then increased from the mid-1980s through 2000, but still remains below pre-1950s levels. Similar declines occurred at other winter- and spring-staging sites in Oregon and Washington (Drut & Trost 2000), and coincided with an increase in winter use at new sites along the western coast of mainland Mexico in the early 1960s (Smith & Jensen 1970, Drut & Trost 2000), and with initiation of winter hunting seasons that extended through mid-February rather than the end of December (Subcommittee on Pacific Brant 1992).

Pacific flyway mid-winter population size did not explain the historical variability in brant use of Humboldt Bay. No correlation was found between January-May brant use on Humboldt Bay and the flyway population size during any period in 1960-2000. Therefore, the decline in use on Humboldt Bay during 1954-1983, and the subsequent increase during 1984-2000, was not simply tracking any such trend in the population as a whole.

Eelgrass condition has been suggested as a factor affecting brant use of Humboldt Bay based on few empirical data and anecdotal data (Einarsen 1965, Henry 1980). In the winters/springs of 1937/38, 1940/41, 1951/52, 1952/53, 1957/58 and 1997/98, substantial numbers of brant fed in salt marshes and pastures surrounding Humboldt Bay (Moffitt 1938, Moffitt 1941, Leopold & Smith 1953, Murrell 1962; HBNWR unpubl. report 1998). In all cases, this behaviour was attributed to poor feeding conditions on the bay, where eelgrass was observed covered with slimy or silty deposits, and/or infected with *Labyrinthula* (implicated in the wasting disease of eelgrass on the Atlantic coast in the 1930s; Moffitt & Cottam 1941). Eelgrass in these years was greatly reduced in its extent and severely depleted by brant. However, in incidents prior to 1954, estimated brant use on Humboldt Bay remained high. Similarly, in the winter/spring of 1997/98, the greatest number of brant use-days in the last 25 years was recorded. Reduced food abundance on Humboldt Bay may thus affect brant feeding behaviour and habitat use, without reducing use of the overall area. The steady decline in brant use from the mid-1950s through the mid-1980s, if induced by poor eelgrass condition, would presumably have resulted from a long-term change in eelgrass habitat for which no evidence exists. In fact, several studies suggest that eelgrass was healthy and abundant from 1959 through 1962 (Murrell 1962, Keller 1963), in 1972 (Harding 1973), in 1975-1977 (Henry 1980), and in 1980-1981 (Bixler 1982). We therefore consider it unlikely that historical trends in brant use of Humboldt Bay could be explained by changes in quality or size of eelgrass habitat.

The most widely held view is that winter hunting disturbance from the 1950s to the 1980s reduced winter and spring brant use of Humboldt Bay and other sites in California, Oregon and Washington, and may have driven brant to new wintering sites in Mexico (Denson 1964, Smith & Jensen 1970, Henry 1980, Subcommittee on Pacific Brant 1992). During 1931-1953, when winter and spring brant use of Humboldt Bay was consistently high, the hunting season began in October or November, and typically ended by the end of December (see Fig. 2). This could have affected fall migrants, for which there are no data, but not spring migrants. During 1954-1983, the hunting season consistently ran through late January or mid-February (Subcommittee on Pacific Brant 1992), and declining winter and spring use of Humboldt Bay occurred during this time. Since 1983, hunting seasons in California have been limited to fall months, during which time winter/spring use-days have increased and fall use-days have decreased on Humboldt Bay. In Washington and Oregon also, hunting seasons have been more restrictive since 1983; during 1984-1986 there were no open seasons in these states, and since then seasons have been shorter and have ended earlier than before 1984 (Subcommittee on Pacific Brant 1992). Midwinter survey data (Drut & Trost 2000) suggest that winter brant numbers in Washington have increased since the mid-1980s.

We cannot definitively conclude whether decreased brant use of U.S. sites was a cause or consequence of increased use in Mexico. However, it is not surprising that hunting might have had such an impact on brant use on Humboldt Bay and other U.S sites in general. Shifts in local and flyway-wide distributions due to hunting pressure have been documented in several other waterfowl populations (references in Fox & Madsen 1997, Bechet et al. 2003). Hunting activities apparently interrupt foraging time, increase energetic costs due to extra flying time, and displace birds to less profitable feeding areas (Fox & Madsen 1997, Madsen 1998) such that birds are unable to build adequate fat and nutrient reserves (Madsen 1995, Madsen & Fox 1995, Feret et al. 2003), a prerequisite to successful breeding in brant (Prop & Deerenberg 1991, Ebbinge & Spaans 1995) and other northern geese (Madsen 1995, 2001, Black et al. 1991, Prop & Black 1998). In addition, disturbances near traditional grit sites and roosts may limit the birds' ability to replenish gizzard grit thus reducing digestive efficiency. Wild geese are thought to adjust their foraging routines on temporal and spatial scales to best achieve requisite fat and nutrient reserves (Owen & Black 1990, Prop et al. 2003). Geese that are unable to meet their daily energetic needs are more likely to initiate movements to new areas (e.g. younger birds; Black 1998, Black et al. 1991), thus establishing new migratory traditions (Black et al. in press).

Detailed accounts of hunter disturbance (Murrell 1962, Henry 1980) describe south Humboldt Bay as being essentially unavailable to brant during a large portion of the hunting season. A narrow sand spit that separates South Bay from the ocean provides important roost and grit habitat to brant (Lee 2001), and is crossed by brant to enter the bay. Heavy hunting pressure along this spit prevents access to the bay and sand habitat, while intensive hunting from scull boats and offshore blinds precludes use of sanctuary areas within eelgrass habitat. Such disturbance effects in January, and especially in February, could have consequences for brant use in March and April as well, if winter residents make up a significant fraction of the spring population. Lee (2001) found that spring-staging birds arriving to Humboldt

Bay in late January through February stayed approximately 30-50 days on average. Alternatively, social facilitation may act such that brant on the bay in February attract later arrivals. This also seems plausible, given that later spring migrants are comprised of a greater fraction of juveniles (Henry 1980, Reed et al. 1998b, Lee 2001) who may need to learn the location of important staging areas from earlier arriving adults. Though unstudied in brant, related learning processes have been suggested for juvenile Canada geese *Branta canadensis* (Williams & Kalmbach 1943, Surrendi 1970, Raveling 1976).

Hunting, in addition to its disturbance effects, might also reduce the number of use-days in an area simply by reducing local population numbers through hunting mortality. Adult brant show high fidelity to winter and spring-staging sites (Reed et al. 1998a), so high hunting mortality as seen in some years during 1958-1983 (see Fig. 3) could have long-term negative impacts for the number of use-days on Humboldt Bay. Harvest data do not exist for Humboldt Bay prior to 1958, so we could not rigorously evaluate whether extreme harvest mortality caused the sudden drop in brant use-days in the early 1950s. However, for years when harvest data were available, we found no relationship between winter harvest intensity and winter use-day estimates, suggesting that overharvest may not have been the primary driver of winter or spring population trends on Humboldt Bay, at least since 1958. Furthermore, an 'overharvest hypothesis' does not predict increasing use of other areas in the flyway (i.e. Mexico). The coincident rise in use of Mexican sites in the 1960s therefore suggests that northbound migrants were not reduced by harvest on Humboldt Bay, but may have been displaced, so that for the past several decades brant have spent most of January and February in Mexico rather than in the U.S. For southbound migrants, data do suggest that fall harvest intensity may have affected fall use-days in the subsequent year. Why might there be a relationship between harvest intensity and brant use-days in fall, but not winter and spring? One possibility is that while brant use-days are much higher in winter than in fall, harvest intensity has been similar in these two seasons. Fall-harvest numbers during 1983-2000 (Median = 304; 1st-3rd quartiles: 290-440) were of comparable magnitude to winter harvest estimates between 1958 and 1983 (Median = 1,490; 1st-3rd quartiles: 684-2,235), whereas fall brant use during 1984-2000 (Median = 1,638, 1st-3rd quartiles: 819-2,086) was roughly 20 times lower than estimated winter use during 1958-1983 (Median = 30,028, 1st-3rd quartiles: 21,064-38,722). Thus, we might expect a given level of harvest to have a greater measurable effect on fall brant use-days.

Human population and industrialization surrounding Humboldt Bay has increased, as has related sources of non-hunting human disturbance to brant. These changes have been quantified by Henry (1980) and Schmidt (1999), who identified the activities of clam fishermen, recreational and commercial boaters, oyster culture, low-flying aircraft, and vehicle traffic (especially off-road vehicles) on the east shore of South Bay (South Spit) as the most significant contributors. In addition, a temporary camping settlement on South Spit was described as a major deterrent to brant use at roost and grit sites during the first half of the 1990s (HBNWR, unpubl. reports 1991-1995). We agree with previous authors that these factors are likely to have played a role in reducing winter and spring brant use-days following the early 1950s, and suggest that persistent human disturbance could prevent brant use-days from returning to historical levels. However, these non-hunting disturbances are probably not solely responsible for the overall trends in brant use-days observed over the past 70 years. Based on our historical estimates, Humboldt Bay suffered a steep drop in brant use in 1953 or 1954, which persisted and declined further through the mid-1980s. This decline definitely coincided with a change in timing of winter hunting seasons, whereas there is no indication that other sources of disturbance also occurred in a punctuated and then persistent manner. Furthermore, the number of winter and spring brant use-days have increased since the cessation of winter hunting in the mid-1980s, despite probable increases in non-hunting human disturbance.

While January and February brant use has increased in response to fall hunting seasons, December use (while hunting is occurring) has not similarly responded, having remained consistently low on Humboldt Bay since at least the 1960s. Occasional high counts in December during the 1930s and 1950s, along with large January counts during the 1940s, suggest that larger numbers of brant arrived earlier, at least in some years, than they do today. Increased winter use along the mainland coast of Mexico has presumably resulted in fewer brant moving up into California before January, so while winter use on Humboldt Bay has increased in the absence of hunting disturbance, the arrival of brant is still somewhat delayed each year.

Since 1956, fall use has been low and irregular on Humboldt Bay, although higher on average in years without fall hunting. During fall migration, most brant fly non-stop from Alaska to Mexico (Dau 1992), and early reports suggest that relatively few brant stopped at Humboldt Bay in fall (Moffitt 1932). The variability of fall use in non-hunting years can probably be explained by the fact that Humboldt Bay is not a major fall-staging ground, so numbers are more likely to depend on annual variation in weather patterns and the number of birds unable to make the otherwise non-stop migration (Dau 1992).

Management implications

Collection of long-term data on single species is valuable for management, but may be costly and difficult to maintain. Conversely, studies of shorter duration often preclude analysis of historical trends in population size, distribution and habitat condition and use. We suggest that accurate predictions of brant use-days ($R_a^2 > 0.90$) at Humboldt Bay can be derived from single mid-monthly counts from January through April, thus lowering the costs and facilitating the establishment of a long-term monitoring program, though such a protocol should be revalidated and calibrated periodically via thorough estimation of seasonal brant use-days.

Using this method, we extrapolated historical brant use of Humboldt Bay, which enabled us to identify long-term trends and investigate factors thought to affect them. We suggest that 30 years of hunting disturbance during early spring migration resulted directly in declining brant use during 1953-1983. Other forms of disturbance and habitat conditions probably contributed relatively little to this decline. This conclusion has been assumed by wildlife managers, who have responded by maintaining a fall hunt in California since 1984. The results of our study empirically affirm the appropriateness of the current policy; relieving hunting pressure has increased brant use of Humboldt Bay. However, this poses a challenge to managers of how to provide hunting opportunities without driving brant away from important migration areas.

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Appendix I. Regression equations used to estimate winter, spring or total brant use-days during 1931-1974 (all $F_{1\text{-}5,\ 18\text{-}23} > 27$, $P < 0.001$). Equations were derived from 1975-2000 data, but were based on count dates from pre-1975 years. For example, in 1949 one count was conducted during the second week of January. Therefore 1975-2000 data were used to determine the relationship between winter use-days and a count conducted in this week. The regression relationship was then used to predict winter use-days in 1949 from that year's count.

Prediction variable	Years	Explanatory variables[a]	Regression equation	Adjusted R^2
Winter use-days	1964-67, 71-72, 74	1st week of January	Y = 30029 + 128 (Jan)	0.89
	1949	2nd week of January	Y = 24263 + 100 (Jan)	0.80
	1947	3rd week of January	Y = 25386 + 58 (Jan)	0.94
	1944	4th week of January	Y = 19851 + 53 (Jan)	0.95
	1943, 45, 48, 50-53, 58, 63	January peak	Y = 17491 + 53 (Jan)	0.97
	1931	1st week of February	Y = 12794 + 43 (Feb)	0.98
	1933-34, 36-39	2nd week of February	Y = 4783 + 35 (Feb)	0.94
	1935	Model 1: 1st week of February Model 2: 2nd week of February (averaged)	Model 1: Y = 12794 + 43 (Feb) Model 2: Y = 4783 + 35 (Feb)	0.96
	1955	3rd week of February	Y = 6505 + 27 (Feb)	0.87
	1954	4th week of February	Y = 4909 + 21 (Feb)	0.73
	1956	February peak	Y = 1418 + 21 (Feb)	0.78
	1968-69	1st week of January, 1st week of February	Y = 13492 + 24 (Jan) + 36 (Feb)	0.98
	1962, 70	1st week of January, February peak	Y = 7489 + 89 (Jan) + 9 (Feb)	0.95
	1932	3rd week of January, 2nd week of February	Y = 10213 + 42 (Jan) + 14 (Feb)	0.97
	1940-42	January peak, 2nd week of February	Y = 7848 + 43 (Jan) + 10 (Feb)	0.99
	1957, 59-61, 73	January and February peaks	Y = 4965 + 41 (Jan) + 6 (Feb)	0.99
Spring use-days	1933, 37-38, 56, 58	1-15 March	Y = 47217 + 47 (Mar)	0.80
	1970	1-15 March, April peak	Y = -67043 + 40 (Mar) + 15 (Apr)	0.85
	1973	February peak, March peak	Y = 95571 + 20 (Feb) + 24 (Mar)	0.82
	1968-69	March peak, April peak	Y = 6867 + 24 (Mar) + 14 (Apr)	0.69
	1939	2nd week of February, 16-31 March, 16-30 April	Y = -6251 + 28 (Feb) + 23 (Mar) + 24 (Apr)	0.89
	1957, 60, 61	February peak, 16-31 March, 16-30 April	Y = 3555 + 19 (Feb) +22 (Mar) + 22 (Apr)	0.94
Total use-days	1964-67, 71-72, 74	1st week of January	Y = 459878 + 312 (Jan)	0.66
	1949	2nd week of January	Y = 451577 + 198 (Jan)	0.52
	1947	3rd week of January	Y = 461033 + 139 (Jan)	0.66
	1944	4th week of January	Y = 478181 + 121 (Jan)	0.61
	1943, 45, 48, 50-53, 63	January peak	Y = 474309 + 120 (Jan)	0.62
	1931	1st week of February	Y = 460186 + 100 (Feb)	0.65
	1932, 34, 40-42	2nd week of February	Y = 438531 + 78 (Feb)	0.56
	1935	Model 1: 1st week of February Model 2: 2nd week February (averaged)	Model 1: Y = 460186 + 100 (Feb) Model 2: Y = 438531 + 78 (Feb)	0.60
	1955	3rd week of February	Y = 442475 + 65 (Feb)	0.56
	1954	4th week of February	Y = 400270 + 54 (Feb)	0.61
	1959	February peak	Y = 405249 + 54 (Feb)	0.64
	1962	1 January, February peak	Y = 367556 + 153 (Jan) + 36 (Feb)	0.75
	1958	January peak, 1-15 March	Y = 63720 + 57 (Jan) + 47 (Mar)	0.88
	1970	1st week of January, 1-15 March, April peak	Y = -47048 + 157 (Jan) + 36 (Mar) + 17 (Apr)	0.91
	1957, 60, 61	January peak, February peak, 16-31 March, 16-30 April	Y = 12881 + 39 (Jan) + 26 (Feb) + 21 (Mar) + 22 (Apr)	0.97
	1968, 69	1 February, March peak, April peak	Y = -1337 + 77 (Feb) + 17 (Mar) + 17 (Apr)	0.91
	1939	2 February, 16-31 March, 16-30 April	Y = 2649 + 63 (Feb) + 23 (Mar) + 23 (Apr)	0.92
	1933, 37-38	2 February, 1-15 March	Y = 63590 + 39 (Feb) + 45 (Mar)	0.87
	1956	February peak, 1-15 March	Y = 44817 + 25 (Feb) + 46 (Mar)	0.87
	1973	February peak, March peak	Y = 83882 + 40 (Feb) + 25 (Mar)	0.87

[a] indicates that count was either a monthly peak value, or that it was conducted within the particular 1 or 2-week period specified. If multiple counts were conducted within this time period, the largest one was used, both for deriving the regression equations (1975-2000 data) and for entering pre-1975 into these equations to estimate historical values.