

Hunting influences the diel patterns in habitat selection by northern pintails *Anas acuta*

Michael L. Casazza, Peter S. Coates, Michael R. Miller, Cory T. Overton & Daniel R. Yparraguirre

Northern pintail *Anas acuta* (hereafter pintail) populations wintering within Suisun Marsh, a large estuarine managed wetland near San Francisco Bay, California, USA, have declined markedly over the last four decades. The reasons for this decline are unclear. Information on how hunting and other factors influence the selection of vegetation types and sanctuaries would be beneficial to manage pintail populations in Suisun Marsh. During 1991-1993, we radio-marked and relocated female pintails (individuals: N = 203, relocations: N = 7,688) within Suisun Marsh to investigate habitat selection during the non-breeding months (winter). We calculated selection ratios for different vegetation types and for sanctuaries, and examined differences in those ratios between hunting season (i.e. hunting and non-hunting), age (hatch-year and after-hatch-year), and time of day (daylight or night hours). We found that diel patterns in selection were influenced by hunting disturbance. For example, prior to the hunting season and during daylight hours, pintails selected areas dominated by brass buttons *Cotula coronopifolia*, a potentially important food source, usually outside of sanctuary boundaries. However, during the hunting season, pintails did not select brass buttons during daylight hours, but instead highly selected permanent pools, mostly within sanctuaries. Also, during the hunting season, pintails showed strong selection for brass buttons at night. Sanctuaries provided more area of permanent water pools than within hunting areas and appeared to function as important refugia during daylight hours of the hunting season. Wildlife managers should encourage large protected permanent pools adjacent to hunted wetlands to increase pintail numbers within wetland environments and responsibly benefit hunting opportunities while improving pintail conservation.

Key words: *Anas acuta*, brass buttons, *Cotula coronopifolia*, ducks, habitat selection, northern pintail, radio-telemetry, sanctuary, waterfowl

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Northern pintail *Anas acuta* (hereafter pintail) populations within Suisun Marsh in California, the largest brackish water marsh in the western United States, have experienced substantial declines since the 1970s. Although no single causative factor explains these declines within Suisun Marsh, one hypothesis is that severe loss of seed sources within wetland habitat has limited the opportunities for pintails to feed during the winter (Frayer et al. 1989),

largely as the result of urban expansion and agricultural practices (Central Valley Joint Venture 2006). This marshland plays a critical role as a wintering area for pintail populations, especially during earlier months prior to the onset of winter rains when flooded habitats may be limited.

Pintails exhibit distinct diel patterns of spatial distribution (Cox & Afton 1997, Fleskes et al. 2002). For example, pintails have been observed using

different areas during night hours than those during daylight, which has been associated with feeding at night and resting in flooded areas during the day (Lovvorn & Baldwin 1996). The three primary hypotheses that explain this behaviour are: 1) the preference hypothesis, 2) the supplementary hypothesis (McNeil et al. 1992) and 3) the functional unit hypothesis. The preference hypothesis proposes that feeding areas are selected during night hours because this is a time when it is profitable and safe to forage. The supplementary hypothesis indicates that additional food is sought only to satisfy a nutritional deficiency from daytime foraging. Alternatively, the functional unit hypothesis indicates that differences between day and night use of habitat is thought to be caused by different fundamental behaviours (Tamisier 1976). For example, pintails used areas for feeding during night and social gathering during daylight hours in Louisiana. These associations between areas and social behaviours that are not associated with feeding or roosting have been termed functional units (Tamisier 1985).

Disturbance from hunting temporarily displaces ducks from feeding areas at local (Bregnballe & Madsen 2004) and regional levels (Madsen & Fox 1995, Madsen 1998a,b) to the point of not reaching population carrying capacities. Although the effects of hunting disturbance on pintail populations are unclear, some evidence from a study in Louisiana, USA, suggests that hunting pressure influences pintail spatial distribution (Cox & Afton 1997). An understanding of how hunting influences diel patterns in selection of specific food sources is essential to wetland management within the Pacific Flyway, especially considering that approximately 70% of the remaining wintering wetlands in California are privately owned and are almost used exclusively for recreational hunting (Gilmer et al. 1982, Heitmeyer et al. 1989).

We developed four objectives regarding habitat selection, the disproportionate use in relation to availability, by wintering pintails. First, we identified and mapped vegetation types that were thought to be important food sources for pintail populations within Suisun Marsh. We categorized vegetation plant communities based on winter pintail food habits in Suisun Marsh and other nearby wetlands. Important food sources included areas dominated by seeds from alkali bulrush *Scirpus maritimus* and brass buttons *Cotula coronopifolia* (George et al. 1965, Mall 1969). Second, we examined differences in dominant vegetation communities between areas

within sanctuary boundaries and those that were in hunting zones. Third, we evaluated the effects of daylight and nighttime hours and hunting and non-hunting periods on habitat selection patterns by radio-marked pintails. We considered night locations as foraging habitats based on reports of pintails feeding primarily at night (Miller 1985, Euliss & Harris 1987, Palomares & Delibes 1992). The purpose of this objective was to evaluate evidence for the prevailing night foraging hypotheses: preference or supplementary. If the preference hypothesis was valid, then we would have expected to find differences in diel habitat selection patterns between hunting and non-hunting periods because pintails should prefer to feed at times of lower threat. Lastly, we evaluated differences of diel patterns in selection for sanctuaries between hunting and non-hunting periods. In these selection analyses, we also considered age effects. We predicted that older pintails would demonstrate a greater degree of selection for habitat and sanctuaries than younger pintails.

Material and methods

Study area

Our primary study area consisted of 230 km² of marshlands within Suisun Marsh. Our study area also consisted of 93 km² of bays and waterways located at the west end of the confluence of the Sacramento and San Joaquin Rivers (also referred to as the Delta) approximately 12 km east of San Francisco Bay (Fig. 1). Our study area included about 150 private duck hunting clubs and several State Wildlife Areas, the largest of which is Grizzly Island Wildlife Area encompassing approximately 40.5 km².

The marsh had a steady water supply for wetland management, although the quality (salinity) of the water varied annually and seasonally (Rollins 1981). The marsh consisted of fresh and salt water environments, which provided a productive habitat for pintails, but it was generally unsuitable for agriculture because of high salinity. Wetlands within Suisun Marsh are permanently and seasonally flooded to provide water and nutrients for plants that are thought to be preferred by waterfowl populations. A large portion of the permanent water pools were located within three primary hunting sanctuaries and multiple smaller sanctuaries, encompassing 15.3 km² (approximately 7% of the marsh). For example, > 28% of the sanctuaries consisted of

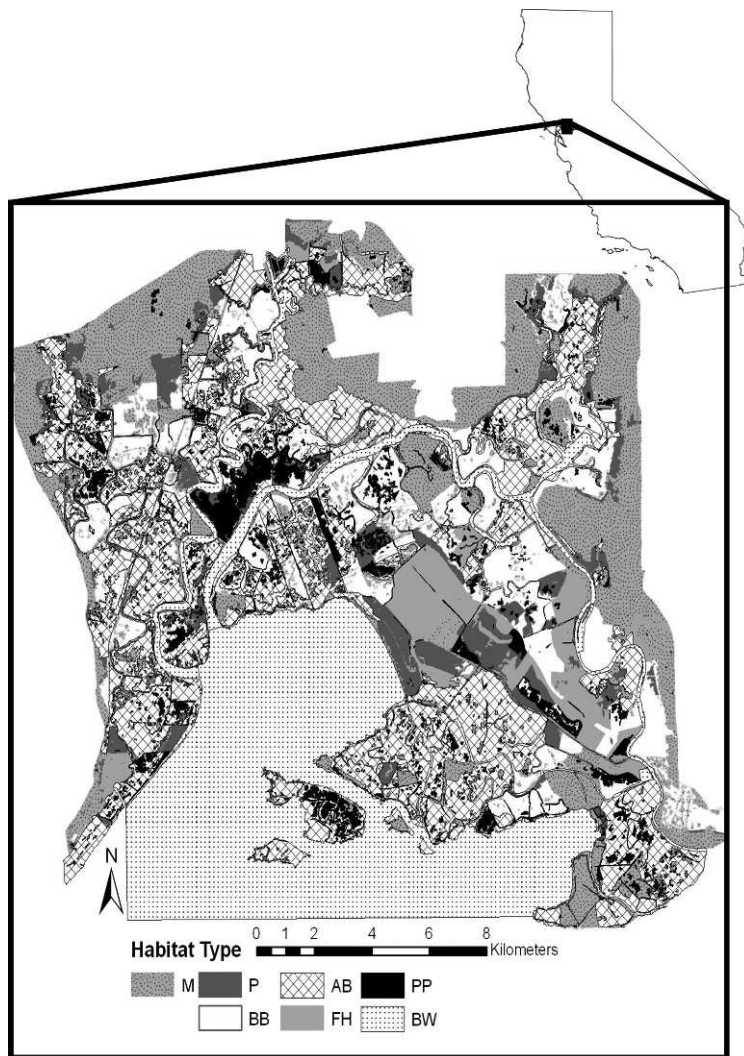


Figure 1. Study area and habitat map of Suisun Marsh based on important plants in waterfowl diet. PP = permanent pools, BB = brass buttons, P = pickleweed, FH = fat hen, AB = alkali bulrush, M = miscellaneous and BW = bays and waterways. Data were collected during 1991-1993.

permanent pools, whereas 4% of areas outside of sanctuaries consisted of permanent pools.

Vegetation types within sanctuaries usually differed from those outside of the sanctuaries. Areas outside the sanctuaries were characterized mostly by vegetation that was thought to provide a rich source of seeds for pintails, such as alkali bulrush, fat hen *Atriplex prostrata* and brass buttons. However, areas within the sanctuary were largely dominated by pickleweed *Salicornia virginica*. Bays and waterways were also found to be much less prevalent inside the boundaries of sanctuaries. The measurements of vegetation types are explained in detail later in the text.

Vegetation map

California Department Fish and Game (CDFG)

delineated Suisun Marsh vegetation types from true colour aerial photographs taken in June 1991 using a 1: 9,600 spatial resolution (CDFG, Bay Delta Division, Stockton, California, USA). Vegetation types were classified by the dominant plant species that have been reported or thought to be important to the diet of pintails (Mall 1969, Rollins 1981, Miller et al. 2009). Specifically, the plant species were identified within the photographs and the boundaries of the areas were delineated as distinct vegetation cover types where a change in plant species composition was detected. The species that covered the greatest amount of the delineated area was designated as the dominant vegetation type. For example, a vegetated area that consisted of 70% pickleweed, 15% brass buttons, 10% fat hen and 5% miscellaneous by visual observation of photographs would have been classi-

fied as a pickleweed vegetation type. The dominant vegetation types consisted of pickleweed, brass buttons, fat hen and alkali bulrush (Table 1, see Fig. 1). We classified areas with permanent wetland water (flooded at the time of aerial photography) as permanent pools and large open waterways and bays were also classified. We classified areas that were not thought to be important to pintails (primarily upland grasses) as miscellaneous. These areas were manually digitized from the delineated maps into Geographical Information System (GIS) map layers (polygons) for the habitat analyses. Verification of plant vegetation types on the ground was conducted by CDFG. In a separate GIS coverage, the boundaries of all sanctuaries throughout the marsh were also digitized. We conducted this mapping effort on a tri-annual basis, and thus, we assumed the spatial distribution of vegetation types to be the same during the years of pintail data collection.

Field methods

We captured female pintails using rocket nets and baited funnel traps (Schemnitz 1994) on Grizzly Island Wildlife Area during late August and early September in 1991 (N = 102) and 1992 (N = 101). We aged each captured individual as hatch-year (HY; N = 79) and after-hatch-year (AHY; N = 124) based on bird plumage (Duncan 1985, Carney 1992). We fitted pintails with 18-g (approximately 2% of the body weight) VHF backpack style radio-transmitters (Dwyer 1972) that included motion sensitive mortality switches (Advanced Telemetry Systems of Isanti, Minnesota, USA). Tagging of pintails resulted in handling for < 30 minutes, and we released all ducks at the location of capture.

We attempted to relocate pintails remaining in our primary study area of Suisun Marsh ≥ 5 times per week during daylight (relocations: N = 4,409, individuals: N = 201) and night hours (relocations: N = 3,279, individuals: N = 165) using radio-telemetry during September - March of 1991/92 and 1992/93. Dual vehicle-mounted yagi antennas were used with a null-peak system (Cochran & Lord 1963; Advanced Telemetry Systems of Isanti, Minnesota, USA). Vehicle alignment azimuth, location (Universal Transversal Mercator (UTM) units) and bird azimuths were keyed into a modified version of the XYLOG and UTMTEL programs (Dodge & Steiner 1986) to determine all pintail locations. We sought to minimize the time spent traveling between locations to prevent location bias based on movement of

Table 1. Cover types delineated and classified based on aerial photos within the minimum convex polygon (MCP) of relocations of all individual radio-marked pintails in the Suisun Marsh during 1991-1993.

Abbreviation	Description	Area (ha)	Area (%)
M	Consisted of no dominant plant species that were reported as important to pintails	7555	22.3
P	Pickleweed <i>Salicornia virginica</i> dominated	1901	5.6
BB	Brass buttons <i>Cotula coronopifolia</i> dominated	4666	13.7
FH	Fat hen <i>Atriplex prostrata</i> dominated	1576	4.7
AB	Bulrush <i>Scirpus</i> spp. dominated	8886	26.2
PP	Permanent water pools	1830	5.4
BW	Large open waterways and bays	7469	22.1

pintails (Schmutz & White 1990). This was partially accomplished by obtaining two or more azimuths at approximately 90° angles from the pintail location. We did not approach pintails within 100 m and sought to avoid measurements > 1.5 km away from actual pintail locations. The average error distance to test transmitters for our telemetry system was 58 ± 35 m.

Statistical analyses

Differences in vegetation proportions

Within a GIS, we intersected sanctuary boundaries and the vegetation map layers, and then, calculated the proportion of each vegetation type within sanctuaries and non-sanctuaries. Each vegetation type was tested separately for equality of proportions (Newcombe 1998). We reported proportions with the 95% confidence interval (CI) of the estimated difference. We considered proportions different if CIs did not include zero.

Habitat selection

We employed a design II habitat analysis, as described in Manly et al. (2002), because habitats that were used by individual pintails were known, and the available habitats were assumed to be the same for each pintail of the population. This design was appropriate because pintails often have home ranges that are large and overlap, and our study questions were specifically related to habitat selection within a distinct wetland area. Selection analysis requires a measure of available habitat to all individuals (Aebischer et al. 1993, Manly et al. 2002). Since studies that assign a predefined area may bias

selection (Aebischer et al. 1993), available habitat was calculated using radio-location data. We first imported relocations as points into a GIS (ArcGIS 9.3; ESRI software, Redlands, California, USA). We used Hawth's Analysis Tools (Beyer 2004) to generate a minimum convex polygon (MCP) on all the locations of tagged pintails. The overall MCP accounted for 92.4% of the Suisun Marsh legal boundaries. We calculated the area (ha) and proportion of each habitat type within the overall MCP using XTools Pro (DeLaune 2000).

We categorized relocation points by day and night to examine the hypothesis that habitat selection differs between daylight and nighttime hours. We defined daylight as the period from 30 minutes before sunrise to 30 minutes after sunset.

We also divided the study duration into two periods of time, pre-hunting and hunting, to examine the hypothesis that hunting activity influences habitat selection. We defined hunting seasons as 26 October - 5 January 1991/92 and 24 October - 10 January 1992/93. We classified all relocations obtained before the onset of the hunting season as during non-hunting. A split period of no duck hunting (17 - 29 November 1991 and 14 November - 5 December 1992) was still classified as hunting because other species (e.g. Canada geese *Branta canadensis* and ring-necked pheasants *Phasianus colchicus*) were open to hunt within Suisun Marsh, thereby still resulting in potential human disturbance.

Within the hunting season, all areas were accessible to hunters except those within sanctuaries. Although it was likely that some areas were more accessible than others, we were not capable of accounting for this source of variation in the habitat selection analyses. However, because pintails were actively managed for hunting in non-sanctuary areas, we are confident that an effect of variation in accessibility was negligible. Wildlife management areas allowed hunting at least three days per week (i.e. Wednesday, Saturday and Sunday), and most hunting clubs followed these standards voluntarily, resulting in a minimum of 25 hunt days and a maximum of 59 per season. It is possible that hunting clubs allowed > 3 hunt days per week, which presented challenges in collecting and analyzing data of hunting effects on a day-to-day basis with respect to the relatively large spatial scale of our study. Therefore, we categorized hunting period based on waterfowl hunting season because of the strong potential for lag effects from hunting disturbance to confound

non-hunting days during the hunting season. Daily bag limits during the years of our study were set at one pintail during both years, and we made the assumption that hunting pressure across the season and landscape was constant. Adult survival was estimated at 78% based on radio-telemetry data (Fleskes et al. 2007).

We calculated the proportional use of each habitat type for each pintail by day-night period separately within each hunting category. To estimate proportionate use of habitat by pintails, we buffered relocation points 60 m to account for triangulation error (i.e. 58 ± 35 m). We calculated the area and proportion of the buffer that intersected each habitat type using XTools Pro (DeLaune 2000), and we averaged proportions for each individual.

We conducted the habitat analyses in two steps. During step one, we investigated sources of variation in the disproportionate use of vegetation types using a multivariate mixed effect model approach. We first generated Napierian logarithmic ratios (i.e. $\ln(a_i/b)$; Aebischer et al. 1993) by dividing each habitat proportion (a) by the proportion of alkali bulrush, the most dominant habitat type (b). This step was necessary to remove the unit sum constraint (Aebischer et al. 1993) and normalize compositions (Aitchison 1986). We replaced zero values with 0.005 to reduce Type I error rate (Bingham & Brennan 2004). We then developed log-ratios for available habitat using the same method. We used the differences between the six log-ratios for used and available habitats as response variables (Aebischer et al. 1993) in the models. This approach was taken to identify differences in any one log-ratio (i.e. response variable) as a function of the independent variables.

To evaluate evidence for different hypotheses of variation in disproportionate use, we developed a candidate set of seven *a priori* models (Table 2). The models consisted of age, hunting season and day-night period as fixed effects. We included random effects of year and repeated measurements for individual birds because variation in disproportionate use may only be partly explained by the fixed effects (Gillies et al. 2006, Koper & Manseau 2009).

We used Akaike's Information Criterion (Akaike 1973) to evaluate evidence of support for each model. We compared models by calculating the difference in support (ΔAIC). We also calculated model probabilities (w ; Anderson 2008). Parameter estimation and model fit were performed using the package 'lme4' (Bates et al. 2008) in Program R (R Development Core Team 2008).

Table 2. A candidate set of *a priori* mixed effects models used to investigate habitat selection of pintails within the Suisun Marsh, California. Each model included year as a random effect and individual bird as a repeated measures effect. Hypothesis is the one represented by the model, and it is supported if the model has greatest support among the candidate set.

Model covariates	Description of covariates	Hypothesis
AGE	Age (hatch-year and after-hatch-year)	Age alone influences selection
DN	Day vs night	Diel patterns in selection alone
HS	Hunting vs non-hunting	Hunting alone influences selection
AGE, DN (additive)	Additive effect (age and day period)	Age effects and daylight independently influence selection
AGE, HS (additive)	Additive effect (age and hunt period)	Age effects and hunting independently influence selection
DN, HS (additive)	Additive effect (day and hunt period)	Daylight and hunting independently influence selection
DN, HS (interaction)	Interactive effect (day and hunt period)	Diel patterns in selection are influenced by hunting

During step two, we investigated the disproportionate use of vegetation types by pintails within each of four groups: 1) hunting season and daylight, 2) hunting season and night, 3) non-hunting season and daylight and 4) non-hunting season and night. These groups were based on the most parsimonious model identified in step one. For each group, we conducted a compositional analysis (Aebischer et al. 1993) and calculated selection ratios (SR) for each vegetation type. SR represent the proportion of used habitat to available habitat, with a 95% CI based on Bonferroni inequality (Manly et al. 2002) using individual pintails as the unit of replication. If the CIs of a habitat type included the value one, we scored the habitat type as no selection or avoidance (Manly et al. 2002). $CI > 1$ suggested habitat selection, and $CI < 1$ suggested avoidance. We estimated differences between SR (Manly et al. 2002) of the vegetation types (e.g. brass buttons vs permanent pools) within each group. Selection between habitats was considered different if the CI did not include zero (Manly et al. 2002). We conducted the SR analyses using the software package 'adehabitat' (Calenge 2006) in Program R (R Development Core Team 2008).

The relatively low number of pintail relocations subsequent to the hunting seasons precluded post-hunting data to be included in the mixed model habitat selection analyses. However, we carried out a *post hoc* examination to evaluate differences in proportional use of permanent pools and the most selected food type between three periods: pre-hunting, hunting and post-hunting. These analyses were carried out for day and night categories. For example, we calculated the proportion of points found in permanent pools vs other habitat types in six categories during pre-hunt daylight hours. We obtained 156 locations from 21 pintails in the daylight hours and 106 locations from 15 pintails at night during the post-hunting period.

Sanctuary selection

We manually digitized waterfowl sanctuary boundaries in a GIS. We classified these areas into sanctuary (SC) and non-sanctuary (NSC). Similar to the methods described above, pintail relocations were buffered and the proportion of sanctuary within the buffer was computed as used. Napierian log-ratios of use and available sanctuary (i.e. $\ln(SC/NSC)$) were developed, replacing zero values with 0.005 (Bingham & Brennan 2004). Difference between use and available was calculated as a response variable. We used the same seven *a priori* mixed effects models (hypotheses) as described for selection of vegetation types to investigate factors that influence selection for sanctuaries. We estimated model parameters (package 'lme4'; Bates et al. 2008, R Development Core Team 2008) and used information theory to evaluate the models (Anderson 2008). As with the analyses of habitat types, we computed SR for sanctuaries and recorded their 95% CIs based on Bonferroni inequality (Manly et al. 2002) (package 'adehabitat'; Calenge 2006, R Development Core Team 2008) for each of four groups: 1) hunting season and daylight, 2) hunting season and night, 3) non-hunting season and daylight and 4) non-hunting season and night.

Results

Sanctuary habitat proportions

Over 75% of the sanctuary consisted of permanent pools (28%), pickleweed (21%) and alkali bulrush (28%; Table 3). The proportion of sanctuary that consisted of permanent pools (0.28) was substantially greater than the proportion of non-sanctuary that consisted of permanent pools (0.04). The proportion of sanctuary that consisted of pickleweed (0.21) was also greater than the proportion of non-sanctuary that consisted of pickleweed (0.05). However, pro-

Table 3. Tests of equal proportions of available habitat types within sanctuary and non-sanctuary areas in Suisun Marsh, California during 1991-1993. The degrees of freedom for each proportional tests was one and the number of hectare was used as the sample unit. Difference indicates a significantly lesser (-), greater (+), or no difference (ND) in the proportion of available habitat in sanctuary than in non-sanctuary areas. Alkali bulrush was the only habitat type with CI that did not include zero.

Habitat type	Sanctuary	Non-sanctuary	χ^2	95% CI		Difference
				Lower	Upper	
Permanent pool	0.28	0.04	1473.5	0.21	0.26	+
Pickleweed	0.21	0.05	680.1	0.14	0.18	+
Fat hen	0.08	0.04	44.6	0.02	0.05	+
Alkali bulrush	0.28	0.26	1.8	-0.01	0.04	ND
Brass buttons	0.03	0.14	136.1	-0.12	-0.10	-
Bays and waterways	0.03	0.23	301.5	-0.21	-0.18	-
Miscellaneous	0.08	0.23	172.4	-0.16	-0.13	-

portions of alkali bulrush in sanctuary (0.28) and non-sanctuary areas were similar (0.26). The proportion of non-sanctuary that consisted of brass buttons (0.14) was significantly greater than the proportion within the sanctuaries (0.03).

Habitat selection

Our data demonstrate a distinct difference in the selection of habitat types between day-night periods in relation to hunting season. The most parsimonious model consisted of an interaction between day-night period and hunting season (Model 1; Table 4), which had strong support from the data ($w_1 = 1.00$). Because the response consisted of multiple habitat types, this result indicated that selection for at least one of the habitat types was influenced by day-night and hunting. A second model, with substantially less support (Model 3; see Table 4), included day-night period and hunting season as an additive effect. An intercept-only model was not supported by these data (see Table 4).

The top-ranked habitat type during three of the four light/hunt groups (day-night period by hunting season) was permanent pools (Fig. 2). During the daylight hours for hunting and non-hunting seasons, pintails showed substantially greater selection for permanent pools than the other habitat types (see Fig. 2). Selection for permanent pools during hunting season ($SR = 8.6 \pm 1.6$) was greater than non-hunting season ($SR = 4.4 \pm 0.6$) during those times (see Fig. 2).

During the night hours, pintails showed selection for permanent pools during the non-hunting season ($SR = 2.9 \pm 0.7$) but avoidance ($SR = 0.5 \pm 0.2$) during the hunting season. Therefore, the difference in selection for permanent pools between day and night was much greater during the hunting season than the non-hunting season (see Fig. 2).

Brass buttons was the most selected habitat type during hunting season at night (see Fig. 2). No difference was found in selection for brass buttons between day and night during the non-hunting season (day: $SR = 2.3 \pm 0.3$, night: $SR = 2.0 \pm 0.3$), but a substantial difference occurred during the hunting season, when brass buttons was selected during the night ($SR = 3.2 \pm 0.6$) but not during the day ($SR = 1.1 \pm 0.5$; see Fig. 2). Pickleweed was also selected at night during the non-hunting season ($SR = 2.1 \pm 0.5$; see Fig. 2). SR during this time were significantly different between pickleweed and all other habitat types, except permanent pools and brass buttons (see Fig. 2). However, no evidence of selection was found during daylight hours of the non-hunting season ($SR = 0.8 \pm 0.2$; see Fig. 2). During daylight hours of the hunting season, no evidence was found for selection of pickleweed ($SR = 1.5 \pm 0.9$).

Table 4. Analysis of Akaike's information criteria for assessing multivariate mixed models of six log-ratios (i.e. use to available) of vegetation types as a function of multiple covariates for pintail in Suisun Marsh, California during 1991-1993. K = number of model parameters, LL = model log-likelihood, ΔAIC = difference in AIC units between the model of interest and the most parsimonious model, w = model probability (Anderson 2008). DN = day-night and HS = hunting season. Random components in models were not listed in the table but included year and repeated measures of individual birds. Main effects were included in the model with an interaction term.

#	Model specification	K	LL	ΔAIC	w
1	DN, HS (interaction)	7	-655.9	0	1.00
2	DN	5	-665.7	15	0.00
3	DN, HS (additive)	6	-664.8	16	0.00
4	AGE, DN (additive)	6	-665.3	17	0.00
	Intercept-only	4	-672.7	29	0.00
5	HS	5	-672.7	29	0.00
6	AGE	5	-673.2	30	0.00
7	AGE, HS (additive)	6	-672.2	30	0.00

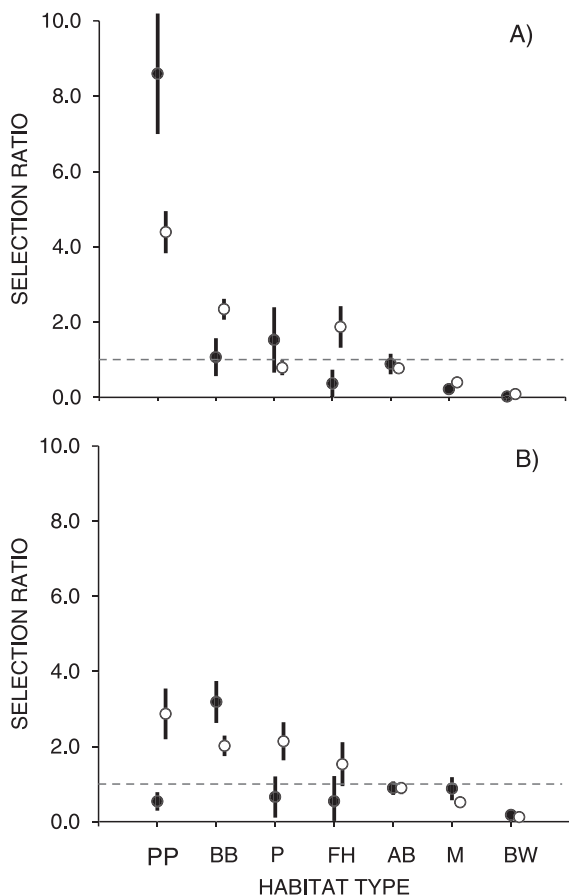


Figure 2. Comparison of selection ratios (calculated with proportions of use and availability; Manly et al. 2002) for habitat types within daylight (A) and night periods (B) during hunting seasons (●) and non-hunting seasons (○) by pintails at Suisun Marsh, California, USA. Bars represent 95% CIs. PP = permanent pools, BB = brass buttons, P = pickleweed, FH = fat hen, AB = alkali bulrush, M = miscellaneous and BW = bays and waterways. Data were collected during 1991-1993.

In the *post hoc* examination of habitat use during daylight hours, we found that the proportion of permanent pools used during the post-hunting period was similar to the proportion used during the pre-hunting period, and in both periods, permanent pools were used substantially less than during the hunting period (Fig. 3A). We also found that brass buttons was selected greater during the night hours of the hunting season than during night hours of the non-hunting season. For example, the proportion of relocation points in brass buttons at night during the pre-hunting and post-hunting periods were similar, and the proportion was substantially higher during the hunting period (see Fig. 3B).

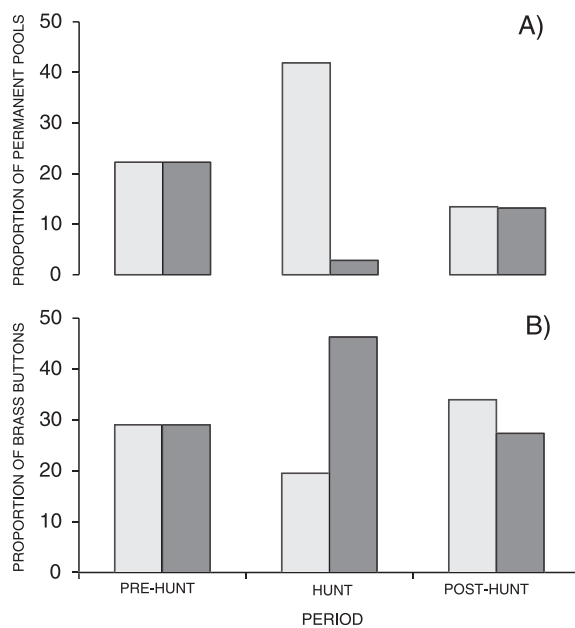


Figure 3. Proportion of permanent pools (A) and areas dominated by brass buttons (B) used by pintails during day (□) and night (■) hours of the pre-hunting, hunting and post-hunting period at Suisun Marsh during 1991-1993.

Sanctuary selection

We examined pintail habitat use of lands open to hunting and sanctuary lands. The most parsimonious model consisted of an interaction between day-night period and hunting season (Model 1; Table 5) and showed strong support from the data ($w_1 = 1.00$). No other models showed support (ΔAIC values were > 40 of all other models), nor did the intercept-only model (see Table 5).

Table 5. Analysis of Akaike's information criteria for assessing mixed models of the log-ratio (i.e. use to available) of sanctuary as a function of multiple covariates for pintail in Suisun Marsh, California during 1991-1993. K = number of model parameters, LL = model log-likelihood, ΔAIC = difference in AIC units between the model of interest and the most parsimonious model, w = model probability (Anderson 2008). DN = day-night and HS = hunting season. Random components in models were not listed in the table but included year and repeated measures of individual birds. Main effects were included in the model with an interaction term.

#	Model specification	K	LL	ΔAIC	w
1	DN, HS (interaction)	7	-731.8	0	1.00
2	DN, HS (additive)	5	-768.0	41	0.00
3	DN	5	-767.8	43	0.00
4	AGE, DN (additive)	6	-783.2	70	0.00
5	HS	5	-794.8	93	0.00
6	AGE, HUNT (additive)	6	-794.6	94	0.00
	Intercept-only	4	-811.9	125	0.00
7	AGE	5	-811.6	124	0.00

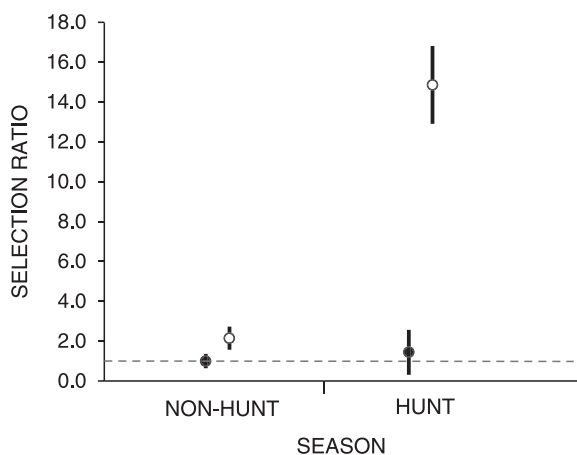


Figure 4. Comparison of selection ratios (calculated with proportions of use and availability; Manly et al. 2002) for sanctuaries within daylight (○) and night (●) periods during hunting and non-hunting seasons by pintails within Suisun Marsh, California, USA. Bars represent 95% CIs. Data were collected during 1991-1993.

Pintails highly selected sanctuaries during daylight hours of the hunting season ($SR = 14.9 \pm 2.0$) and during daylight hours of the non-hunting season (Fig. 4), although the relationship was not as strong during the non-hunting season ($SR = 2.1 \pm 0.6$). Pintails did not show selection for sanctuaries during night hours of the hunting ($SR = 1.4 \pm 1.1$) or the non-hunting ($SR = 1.0 \pm 0.4$) seasons (see Fig. 4).

Discussion

Pintails exhibited differential selection in habitat types between day and night that was influenced by hunting, a finding similar to results from Louisiana, USA (Cox & Afton 1997) and Mexico (Migoya et al. 1994). These results support the preference hypothesis (McNeil et al. 1992), which states that birds prefer to feed at night because it provides a safe feeding opportunity. Under the preference hypothesis, we expected to observe less selection for vegetation types related to feeding during the daylight hours and greater selection during night hours as potential threat to pintails increases. Indeed, during the hunting season pintails selected sanctuaries during the day that consisted of permanent pools rather than areas with feeding opportunities. In other words, the selection for permanent pools within sanctuaries during daylight, and feeding areas on hunting lands during night, was substantially greater during a time when pintails experienced hunting pressure. Our findings are also consistent with other

research showing that hunting causes local disturbances to pintails (Cox & Afton 1997) and other waterbird populations (Bell & Owen 1990, Madsen & Fox 1995).

Perhaps the most logical explanation for this finding is that sanctuaries provide areas that are relatively safe during daylight hours of the hunting season, which supports the high survival rates attributed to the use of sanctuaries (Miller et al. 1995). One study attributed high diurnal use of sanctuaries and nocturnal use of feeding areas of green-winged teal *Anas crecca* to avian predation (Tamisier 1974), suggesting that pintail habitat selection was not influenced by human disturbance (Tamisier 1976). However, the differential diel patterns of sanctuary use during the hunting season reported in other literature (Lovvorn & Baldwin 1996, Cox & Afton 1997), coupled with our findings, provide evidence that hunting disturbance is an important factor affecting habitat selection by female pintails.

Pintails also showed distinct differences in selection of habitats between day and night that did not always appear related to hunting. For example, during the non-hunting season, pintails selected permanent pools within sanctuaries, which may have been attributed to the establishment of functional units (Tamisier 1985). Pintails often formed large groups and exhibited gregarious daytime behaviours, roosted and preened within the open water at Suisun Marsh, similar to those diurnal behaviours reported elsewhere (Tamisier 1976). Permanent pools provide limited food for pintails (Rave 1999). During the night of non-hunting seasons, pintails selected habitat types with food sources that we classified based on data from the literature (Mall 1969, Burns 2003). Because pintails primarily forage at night (Miller 1985, Palomares & Delibes 1992), our findings also provide evidence for a functional unit hypothesis, in that pintails select different habitats during the day than night based on their diurnal gregarious behaviour (Tamisier 1976), independent of human disturbance.

The pre-hunting diel patterns here may be explained by an anti-predator adaptation in feeding at night to avoid predation. For example, the second greatest source of pintail mortality in the Central Valley and Suisun Marsh was predation (Fleskes et al. 2007), and most predation occurred in the fall before the hunting season. Although pintails have been reported to forage during daylight hours (Miller 1986), this feeding occurs in early autumn or late

winter and is not as frequent as nocturnal feeding (Tamisier 1976). Authors who studied pintails in agricultural settings have suggested that greater daytime use of sanctuaries during the non-hunting season resulted from other disturbance, such as agricultural operations (Cox & Afton 1997). However, during the non-hunting season in the Suisun Marsh, human disturbance by agriculture was not an issue.

It is possible that the results of hunting on diel patterns in habitat selection were confounded by seasonality. The limitations in post-hunting season telemetry data precluded our ability to differentiate between hunting and seasonality. Many of the pintails migrated away from Suisun Marsh during or immediately after the hunting season. Pintails might have chosen permanent pools more often in late winter, a time which coincided with hunting season. However, this was unlikely because these habitats probably had less available food, as did adjacent hunting areas, as winter advanced (Hamilton & Watt 1970). This resulted in pintails spending more time traveling to food sources and less time in sanctuaries (Cox & Afton 1997).

Pintails strongly selected brass buttons habitats, as an overwhelming majority of night locations occurred on the < 5% of the private lands that contained a high proportion of brass buttons dominated habitat. Brass buttons produces a relatively small seed which often windrows along pond margins, making it readily available to waterfowl (Rollins 1981), and has been identified as an important food plant for waterfowl in Suisun Marsh (George et al. 1965, Mall 1969). Furthermore, the years of our study were in drought, which benefitted brass buttons because it tends to be relatively more salt-tolerant than other species in the marshland (Faber 1985), and during these years brass buttons may have provided an abundant food supply for pintails (George et al. 1965).

Although alkali bulrush is thought to be the most important food plant for pintails in Suisun Marsh (George et al. 1965, Mall 1969, Rollins 1981), we failed to detect a selection for this habitat type. One explanation is the widespread availability of alkali bulrush across the marshland. Alkali bulrush showed equal proportions within sanctuary and non-sanctuary areas. Another explanation for why alkali bulrush has been shown to be a relatively more important food source for pintails than brass buttons is that soft foods, such as brass buttons, often are undetected in gizzard samples as a consequence of

the increased digestibility (Swanson & Bartonek 1970). Recent methods using esophageal samples identified sea purslane *Sesuvium verrucosum* and alkali bulrush as the major food items in Suisun Marsh (Burns 2003). Sea purslane was relatively rare in Suisun Marsh during the years of our study and has only recently been established within the same areas as brass buttons (S. Chappell, pers. comm.).

We observed differences in daytime selection of brass buttons between hunting and non-hunting seasons. These observations can be explained by differences in the proportion of available brass buttons that were inside and outside sanctuary boundaries. For example, brass buttons made up a greater proportion of non-sanctuary than sanctuary areas. During the non-hunting season, pintails selected habitats dominated by brass buttons day and night, but these were mostly outside the sanctuaries. With the onset of hunting season, permanent pools were the only habitat selected throughout the day, but these were mostly inside sanctuaries. In southwestern Louisiana, pintails that used large sanctuaries with pools might have been disadvantaged (Rave 1999). This is due to the fact that pintails have been reported to forage during daylight hours (Miller 1986) and those permanent pools often lack important foods in useable quantities, which has been suggested for Canada geese (McLandress & Raveling 1981).

Perhaps the decline in population numbers within Suisun Marsh over the past couple of decades is related to pintails selecting agriculturally-related areas for wintering outside of the Suisun Marsh boundaries but within the Central Valley that provide a combination of feeding and safety benefits. For example, a large majority of land cover within the northern Central Valley of California consists of rice croplands (Miller et al. 1989), which has displaced vast amounts of original wetland habitats for wintering waterfowl (Eadie et al. 2008). Rice croplands often function similar to managed wetlands (Miller et al. 2010). Rice is also often flooded prior to the hunting season under normal agricultural procedures to decompose stubble following rice harvest, which often exposes food in the form of residual rice seeds (Miller et al. 2010). A large portion of the flooded rice croplands is not hunted, and these areas have fewer avian predators than marshlands (Elphick 2004), leading to increases in waterfowl survival (Fleskes et al. 2007). Feeding opportunities, coupled with increased safety benefits, appear to explain shifts in distribution of wintering ducks from

portions of the Central Valley into croplands following the flooding of rice (Fleskes et al. 2005a,b). Wildlife management areas may offer concentrated food sources for pintails by promoting the growth of specific plants favoured by pintails. However, those areas with increased hunting pressure, that lack well-designed and positioned sanctuaries, may result in pintails switching to rice cropland, where they might benefit from relatively greater safety and food accessibility.

Increasing the area and distribution of designated sanctuaries with permanent pools should be encouraged at Suisun Marsh and other wetlands. Studies indicate that the creation and design of refuges increases abundance of waterfowl populations (Fox & Madsen 1997). One experimental study demonstrated that hunting disturbance was a causal factor of lower population numbers, and creation of refuges was the single most important factor that influenced distribution and density of waterbirds (Madsen 1995). Providing additional refuges to adjacent hunted areas will likely increase feeding and safety opportunities for pintails and perhaps influence their abundance. In our study, permanent water pools provided necessary daytime refugia to support pintail populations during hunting periods, allowing them to feed in hunted areas at night. Without permanent pools within sanctuary boundaries, pintails likely would have abandoned the hunted and managed wetland areas. Further development of sanctuaries throughout the wetland may prevent pintails from leaving wetlands and moving to agricultural areas in the Central Valley. Perhaps, managing for plants that provide seed sources within sanctuaries would also increase the overall number of pintails within a marsh. However, one trade-off might be an increased probability of ducks remaining within the sanctuaries, thereby reducing hunting opportunities.

A large majority of the protected area at Suisun Marsh were within three primary sanctuaries. Larger and fewer sanctuaries support higher bird densities by providing lower ratios of buffer to core areas (Fox & Madsen 1997). Although some important information about design of refuge has been experimentally studied on other waterfowl (Madsen 1995, Fox & Madsen 1997), studies are needed that identify specific attributes of permanent pool sanctuaries that increase selection by pintails (e.g. pool size, perimeter to area ratio, water depth and distance to food sources). Large sanctuaries positioned near managed hunting areas likely reduces the time and energy

needed for pintails to travel between day and night sites, and those sanctuaries are likely to be most important during late winter when food is relatively scarce. Incorporating large protected permanent pools adjacent to hunted wetlands is perhaps an effective strategy to increase pintail numbers within wetland environments and responsibly benefit hunting opportunities while improving pintail conservation.

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