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Research Papers

California's Endangered Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*): Tolerance of Pedestrian Disturbance

Le Bruant des prés de la sous-espèce Belding (*Passerculus sandwichensis beldingi*) en voie de disparition en Californie : tolérance au dérangement piétonnier

Esteban Fernández-Juricic [1], Eric F. Zahn [2], Taylor Parker [3], and Theodore Stankowich [4]

ABSTRACT. Salt marshes constitute habitat islands for many endemic animal species, particularly along the California coast, where urban sprawl has fragmented this habitat. Recreational activities in salt marshes have increased recently, posing an interesting problem: how do endemic species lacking alternative habitat modify their tolerance to humans? We assessed seasonal and site variations in three tolerance parameters (distances at which animals became alert, fled, and moved after fleeing) of California's endangered Belding's Savannah Sparrow ((*Passerculus sandwichensis beldingi*). We approached individuals on trails in three salt marshes with different levels of vehicle and pedestrian traffic. Belding's Savannah Sparrows became aware and fled at shorter distances in the salt marsh coincident with greater levels of recreational activity as a result of habituation or visual obstruction effects. Seasonal effects in tolerance varied between sites. Alert and flight initiation distances were higher in the pre-nesting than in the non-breeding season in the site with the highest levels of recreational use likely due to greater exposure of breeding individuals; however, the opposite seasonal trend was found in each of the two sites with relatively lower human use, probably because individuals were less spatially attached in the non-breeding season when they foraged in aggregations. Distance fled was greater in the non-breeding than in the breeding season. Our findings call for dynamic management of recreational activities in different salt marshes depending on the degree of exposure to humans and seasonal variations in tolerance. We recommend a minimum approaching distance of 63 m and buffer areas of 1.3 ha around Belding's Savannah Sparrows.

RÉSUMÉ. Les marais salés représentent des îlots d'habitat pour de nombreuses espèces animales endémiques, surtout le long de la côte californienne où l'étalement urbain a entraîné la fragmentation de cet habitat. La pratique d'activités récréatives dans les marais salés a récemment augmenté, soulevant un problème intéressant : comment les espèces endémiques, qui n'ont pas d'habitat de rechange, modifient-elles leur tolérance aux humains? Nous avons déterminé les variations relatives à la saison et au site selon trois paramètres de tolérance (distance à laquelle l'oiseau se met en état d'alerte, s'enfuit et se déplace après s'être enfuit) chez le Bruant des prés de la sous-espèce Belding (*Passerculus sandwichensis beldingi*), en voie de disparition en Californie. Nous nous sommes approchés d'individus à partir de sentiers dans trois marais salés ayant des degrés différents de circulation motorisée et piétonnière. Les Bruants des prés se mettaient en état d'alerte et s'enfuyaient à de plus courtes distances dans le marais salé où se pratiquait un degré élevé d'activités récréatives, à cause de l'accoutumance ou des effets de l'obstruction visuelle. Les effets saisonniers qui agissaient sur le degré de tolérance ont varié selon les sites. La distance à laquelle l'oiseau se mettait en alerte et celle à laquelle il amorçait son envol étaient plus grandes juste avant la nidification que durant la saison hors reproduction dans le site caractérisé par l'utilisation récréative la plus intensive, vraisemblablement en raison d'une exposition plus grande des individus nicheurs. Toutefois, la tendance saisonnière opposée a été observée dans les deux sites ayant une utilisation humaine relativement

[1]Purdue University, [2]California State University Long Beach, [3]Tidal Influence, [4]University of Massachusetts

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plus faible, probablement parce que les individus ne sont pas territoriaux hors de la saison de reproduction, quand ils s'alimentent en groupe. La distance de fuite était plus grande hors de la saison de reproduction qu'en saison de reproduction. À la lumière de nos résultats, nous préconisons une gestion dynamique des activités récréatives qui ont cours dans divers marais salés selon le degré d'exposition aux humains et les variations saisonnières de la tolérance. Nous recommandons une distance d'approche minimale de 63 m d'un territoire et une zone tampon de 1,3 ha autour d'individus, de couples ou de groupes de Bruants des prés de la sous-espèce Belding.

Key Words: *buffer areas; endangered species; human disturbance; recreational activities; saltmarsh birds*

INTRODUCTION

Approximately 75% of southern California coastal wetlands have been lost to urban development (Zedler 1982, Zedler et al. 2001). The net result is a system of marshes heavily fragmented and prone to human disturbance, leaving around 25–30 biological "islands" of salt marsh habitat located along a 160-km strip of coastline between Tijuana, Mexico, and Goleta, California (Zedler 2001, Powell 2006). Salt marshes can be deemed as key ecosystems that support relatively fewer terrestrial vertebrates than other ecosystems, but with a high proportion of endemic species or subspecies (Greenberg et al. 2006). Marshes that are degraded may fail to provide suitable habitat for salt-marsh plant and animal species (Wilson et al. 2007), such as the rare wandering skipper (*Panoquina errans*), the endangered California least tern (*Sterna antillarum browni*), and the salt-marsh bird's beak (*Cordylanthus maritimus*).

One of the conservation concerns for salt marshes is the reduction of tidal flushing, with a concomitant influx of freshwater runoff from urban centers, which can promote the establishment and spread of invasive plants by altering soil salinities (Kuhn and Zedler 1997, Zedler and Kercher 2004, Callaway 2005). The invasion of invasive plants (e.g., *Spartina alterniflora*) into barren mudflats can potentially create ecological traps by attracting marsh-specialist birds to nest in areas with high chances of flooding (Greenberg et al. 2006). Additionally, wetlands are popular places for recreational activities (e.g., fishing, birding, hiking, biking), which have increased due to urban sprawl in coastal areas (Burger et al. 1995, Burger 2000). Recreational activities could potentially influence breeding behavior and habitat use of salt-marsh species of conservation concern, such as the Belding's Savannah Sparrow, *Passerculus sandwichensis beldingi* (e.g., White 1986). Little attention has been devoted to assessing the seasonal patterns of tolerance of this species between locations subject to different levels of recreational activities. This information is important to establish how specialists without alternative habitats adjust their tolerance to human disturbance, and to develop strategies to minimize the effects of recreational activities.

Our goal was to study patterns of tolerance (distance at which individuals become alert and vacate breeding or foraging patches) and space use (distance fled after a bird–recreationist interaction) in relation to human approaches in three different salt marshes in southern California during the pre-nesting and non-breeding seasons. Based on our estimates of tolerance, we also calculated variations in minimum approaching distances (distance at which humans should be separated from wildlife to minimize behavioral disturbance) and buffer areas (areas where humans should not encroach to avoid displacing wildlife) of Belding's Savannah Sparrows. This information can be used in the zoning of marshes and habitat-restoration projects to enhance the protection of this endemic species.

In this study, we aimed to test two main hypotheses. First, as evidenced in other species (reviewed in Stankowich and Blumstein 2005), individuals living in areas where interactions with humans are less frequent tend to be less tolerant of human disturbance. We predicted that Belding's Savannah Sparrows would become alert, flee, and move greater distances at a site with minimal human presence compared with sites with more frequent human interactions, particularly because of the lack of alternative habitat nearby, which would require rapid adjustments to minimize breeding or energetic costs associated with human disturbance (e.g., Müllner et al. 2004, Beale and Monaghan 2005). Second, we expected seasonal variation in tolerance behavior; that is, animals would be more tolerant of approaches during the pre-nesting season as they would need to maintain their territories (Rodgers and Smith 1997, Díaz-Uriarte 1999). However, we predicted that this effect would be more pronounced at sites where interactions with humans are more frequent because experienced individuals may better assess the risk posed by human approaches and avoid unnecessary flights that would increase the probability of losing their territories.

METHODS

Study Species

The Belding's Savannah Sparrow is a resident salt-marsh obligate and endemic subspecies (Massey 1979) that has been categorized as endangered in the State of California since 1974. It nests in the mid- and upper-littoral zones of coastal salt marshes (Powell 1993), where males actively defend territories around dry, non-inundated substrates (Wheelwright and Rising 1993). However, Belding's Savannah Sparrows forage throughout the marsh, within the vegetation, along intertidal mudflats, and sometimes on neighboring sand dunes (Bradley 1973, Zedler 1982, Zembal et al. 1988). This subspecies has undergone physiological changes to live in salt marshes, such as an excretory system adapted to salty conditions (Goldstein et al. 1990). During the winter, individuals may form loose flocks (James and Stadtlander 1991), which appear to be aggregations around food-rich patches rather than social groups (Wheelwright and Rising 1993). Inter-population dispersal is deemed to be low (Powell and Collier 1998, Powell 2006), which may account for the degree of isolation between populations (Bradley 1994, Burnell 1996). Only in marshes larger than 10 ha do successful breeding attempts seem to occur (Powell and Collier 1998).

Study Areas

The study was conducted at three southern California coastal salt marshes: Los Cerritos (33º 45'48.55''N, 118º06'28.20''W), Anaheim Bay (33º 44'03.67''N, 118º03'55.53''W), and Bolsa Chica (33º42'17.25''N, 118º02'24.07''W). These wetlands are located in the middle of the southern California salt-marsh system, with Anaheim Bay falling between Bolsa Chica to the south (4.5 km) and Los Cerritos to the north (4.5 km). The area of these wetlands has been reduced by oil operations, residential and commercial developments, marinas, and highways.

The salt-marsh vegetation is divided into four types. First, the lower marsh gets fully inundated twice daily and is dominated by cordgrass (*Spartina foliosa*; 35–130 cm high). The diversity of the lower marsh is comparatively low (one or two native plant species). Belding's Savannah Sparrows use this area for foraging during low tides. Second, the middle marsh gets fully inundated twice daily but not as long as the lower marsh and is dominated by the pickleweed (*Salicornia virginica*; 20–100 cm high). Conditions are less anoxic in the middle marsh and the plant community is thus relatively more diverse (approximately 10 species). Belding's Savannah Sparrows use this area at low tides for foraging. Third, the upper marsh rarely gets fully inundated, which leads to drier conditions, and is dominated by woody subshrub glasswort (*Salicornia subterminalis*; 10–50 cm high). Approximately five to eight different native plant species can be found in this area. Belding's Savannah Sparrows use the upper marsh to nest and defend territories. Fourth, the transition zone is composed of shrubby plants that do not grow in the salt marsh or in the upland. The transition zone has less salty soils than the upper marsh, making it more prone to invasion by non-native plants, which offer high perches (>150 cm) for Belding's Savannah Sparrows.

Belding's Savannah Sparrows have been found to nest in all of the three marshes studied (Zembal et al. 2006), which have been subject to different levels of human disturbance. We conducted our approaches in the pre-nesting (from February to May) and non-breeding (from September to November) seasons between 2006 and 2008. Each site was studied only once per season; hence, we did not analyze between-year variation within each study site.

Los Cerritos is a wetland complex located in a densely urbanized portion of the city of Long Beach. Our data were collected in a 17.81-ha slough of tidal salt marsh with lower-, middle-, and upper-marsh zones transitioning into highly degraded upland areas. The slough area exceeds the proposed minimum habitat size needed to sustain viable populations of Belding's Savannah Sparrows (Powell and Collier 1998). The slough was diked in the 1940s along its perimeters to keep it from flooding adjacent oil operations. Belding's Savannah Sparrows here are exposed to regular foot and vehicle traffic as the dike has become a popular recreation trail and vehicles constantly drive along the oil-field roads. We used the dike trail for the human approaches.

Anaheim Bay is 206.5 ha and managed by the U.S. Fish and Wildlife Service, but protected as a National Wildlife Refuge. The site contains large continuous swaths of lower-marsh cordgrass habitat. The full tidal flushing at Anaheim Bay comes directly from the Pacific Ocean and feeds a diverse assemblage of plants in the lower and middle marsh zones; however, the extent of the upper marsh and transition zones is limited. Because this area is located on the Seal Beach Naval Weapons Station, access to the refuge is restricted to naval personnel and researchers; thus, disturbance from pedestrians is minimal (Zembal et al. 2006). Our study was conducted in the southeast portion of the refuge. There are roadways along the marsh perimeter; however, car traffic is infrequent (K. Gilligan, personal communication). We used these roads for the human approaches due to their close proximity to habitat used by Belding's Savannah Sparrows.

Bolsa Chica (134.3 ha) has been recently restored to keep the tidal influence. A 1 km wide tidal channel now connects the wetlands to the Pacific Ocean. This flooding created an over 150-ha tidal basin adjoined by several tide gates. Our study was conducted in a 20-ha northwestern portion of the muted tidal marsh that is dominated by middle marsh habitat with limited upper marsh and no lower marsh or upland transition zone. The California Department of Fish and Game manages this site as an ecological reserve, reducing pedestrian traffic by excluding public access. However, this study area receives heavy vehicular traffic due to a network of roadways that fragment the marsh habitat and connect extensive oil operations. Vehicular, along with pedestrian, traffic has increased recently as a result of restoration activities. We used the roads and other foot paths to conduct our human approaches.

We were not able to quantify the rates of pedestrians in each study site; however, we established a ranking of pedestrian loads based on field observations before and during this study and we confirmed this ranking with local wildlife managers. Overall, recreational activity levels increased in the following order in our study sites: Anaheim Bay, Bolsa Chica, and Los Cerritos.

Human Approaches

The most common type of recreational activity in our study areas was low-impact walking/hiking. We simulated this type of disturbance by walking and approaching birds in the same areas used by recreationists. Given the endangered nature of the Belding's Savannah Sparrow, we did not approach the animals directly as it is usually done in studies assessing tolerance (e.g., Blumstein et al. 2004). Instead, we measured tolerance while walking along the maintenance trails and dirt roadways (see above), never stepping into the native vegetation trying to reach the spot where the individual was first detected. Approaches were conducted in the morning (0700–1100 h) and afternoon (1500–1800 h), coinciding with the periods of high activity of this subspecies. After locating individuals with binoculars, we began walking with a steady pace (1 step/sec—approximately 0.45 m/s) on the pathway, if the subject did not show alert behavior toward us. We measured starting distance (SD, the distance at which approaches were initiated), alert distance (AD, the distance between the observer and the bird at the point where the bird modified its initial behavior in response to the approaching human, e. g., increasing vigilance), flight-initiation distance (FID, point at which the subject flushed or otherwise moved away from the approaching human), and distance fled (DF, the distance between the points where the bird flushed and landed) with a Bushnell Yardage Pro Sport 450 digital laser rangefinder. We measured starting distance because it can be a confounding factor in FID estimates (Blumstein 2003), and may also be useful in determining buffer areas. Approaches were conducted by a single observer (EZ or TP).

We measured other potential confounding factors that could influence tolerance: flock size (number of conspecifics in a 10-m radius circular plot), perching height, temperature, wind speed, humidity, percent cloud cover, initial behavior (whether the animal was perching or foraging on the ground), and type of substrate. Perching height was estimated visually after training, and categorized as 0 – 0.49 m or 0.50 – 1 m. Temperature, humidity, and wind speed were measured with a Speedtech SM-28 Skymaster handheld weather station. Type of substrate used by Belding's Savannah Sparrows before flushing was categorized as native plant, non-native plant, or others (barren ground, fence posts, fencing wire, etc.). Because approaches were not strictly direct, we also measured approaching angle (from 0° to 90°) with a protractor. In approaches that happened to be direct, the angle was 0°, whereas the angle increased in more tangential approaches.

We did not tag individuals because of the endangered nature of this subspecies. To reduce the chances of estimating the tolerance behavior of the same individuals more than once on a given day, we sampled birds from different areas of the marsh (e. g., avoiding individuals in contiguous areas). Although this design runs the risk of a certain degree of pseudoreplication (the same individuals may have been approached more than once), Runyan and Blumstein (2004) concluded that the bias introduced in tolerance studies with unmarked individuals is very limited. Particular attention was paid during the non-breeding season to ensure that each bird approached was from the *beldingi* subspecies. Several Large-billed Savannah Sparrows (*rostratus* subspecies) were observed but not sampled.

In the pre-nesting season, we conducted 46 approaches over 4 non-consecutive days at Los Cerritos, 69 approaches at Anaheim Bay over 4 non-consecutive days, and 68 approaches at Bolsa Chica over 4 non-consecutive days. In the non-breeding season, we conducted 36 approaches at Los Cerritos over 7 non-consecutive days, 44 approaches at Anaheim Bay over 4 non-consecutive days, and 42 at Bolsa Chica over 4 non-consecutive days. Visual determination of AD proved difficult at times due to the variability in angle of approach, so AD was not recorded for every single approach.

Statistical Analysis

To satisfy normality assumptions, AD was natural log transformed and DF was $\log_{10}$ transformed. SD, lnAD, FID, and $\log_{10}$DF were subjected to curvilinear regressions to test potential non-linear relationships between SD and AD, SD and FID, and FID and DF (Blumstein 2003). Although AD is a better predictor of FID than SD, some approaches were missing AD measurements, so we decided to use SD instead. Following Stankowich and Coss (2006), we fit all three relationships to linear, quadratic, and logarithmic models sequentially. If the quadratic term (e.g., SD^2) achieved significance ($P < 0.05$), the term was retained in the model, and all future models contained both the linear and quadratic terms. If the quadratic term did not achieve significance, the relationship was fit to linear and logarithmic functions (Blumstein 2003), and the best-fitted function was judged by the R^2 statistic. All models contained intercepts.

We were interested in the effects of site, season, and starting distance, so we included these factors in all models. Preliminary ANOVAs showed temperature, humidity, wind speed, and group size to be highly correlated with season (all F_{1303} varied from 6.62 to 37.87; $P \leq 0.032$): in the non-breeding season, temperature and group size were higher whereas humidity and wind speed were lower in relation to the pre-nesting season. Therefore, we excluded these variables in the main models and included season as a composite variable. Similarly, initial behavior was highly associated with substrate and height (substrate: $\chi^2 = 275.676$, df = 2, $P < 0.001$; height: $\chi^2 = 292.832$, df = 3, $P < 0.001$); therefore, only initial behavior was included in the list of candidate predictors in the model. We winnowed our list of other candidate predictors (approach angle, initial behavior, percent cloud cover) for each model using stepwise linear regressions. In the first stage, site, season, and SD (and SD^2 for AD and FID) were entered into the model; in the second stage, approach angle, initial behavior, and cloud cover were entered into the model in a stepwise fashion, where at each step, the factor with the lowest P value less than 0.10 was entered into the model until only factors with $P > 0.1$ were excluded from the model. The factors that were selected for the model were then entered into a general linear model that included site, season, the appropriate distance (SD or FID), the interaction between site and season, and any other interaction of interest (e. g., initial behavior x site).

To compare levels of a factor, we used planned comparisons. All effect sizes (η^2) were calculated by hand according to Cohen (1973) due to mislabeling in SPSS (Levine and Hullett 2002). Two-tailed significance was reached at $\alpha = 0.05$ and all statistical analyses were run in SPSS 10.0 and Statistica 8.0. We present most of the model results in tables and the planned comparisons in the text.

A recent study (Fernández-Juricic et al. 2005) evaluated the different methods (and their assumptions) to estimate minimum approaching distances (MAD) and buffer areas based on their degree of conservatism and their ability to establish the difference between direct and tangential approaches. We used two of those methods, the first one because of its high performance in these two criteria (Fernández-Juricic et al. 2005), and the second one because of its high degree of conservatism in the estimates, which is important for a State-classfied endangered species based on the precautionary principle (Groom et al. 2006; e.g., overestimating buffer areas may be recommended despite the fact that the effects of human disturbance on this subspecies' breeding and survival parameters have not been fully established):

M1- based on Rodgers and Smith (1995, 1997), and Rodgers and Schwikert (2002). MAD = (AFID+1.6495*SD)+AAD, where AFID is the mean FID, SD is the standard deviation of AFID, and AAD is the mean AD. Buffer areas are calculated as Π * MAD^2.

M2- based on Vos et al. (1985). MAD correspond to the maximum FID recorded +AAD, where AAD is the mean AD. Buffer areas are estimated as Π * MAD^2.

RESULTS

Alert Distance

The distance at which Belding's Savannah Sparrows became alert to the observer was correlated linearly with SD ($R^2 = 0.675$, $P < 0.001$), where individuals became alert at greater distances when the observer started approaching from greater distances, but the quadratic function provided the best fit ($R^2 = 0.695$, quadratic term: $t = -4.123$, $P < 0.001$). Although extrapolation outside the range of measured values may not be advisable, the curve is described by the function: lnAD = 1.98 + 0.04(SD) – (1.8 x 10^{-4})(SD^2); with the peak of the function at a SD of 111 m, where the predicted AD is 67 m.

Starting distance and its square had significant effects in all models of AD (Table 1). We found significant differences in ADs between sites (Fig. 1a), where AD was greater at Anaheim Bay than at Los Cerritos and Bolsa Chica, with marginally significant differences between the latter two. Although season had no significant effect on AD (Table 1), there was a significant interaction between season and site on AD (Table 1; Fig. 1a), where AD was lower in the non-breeding than in the pre-nesting season at Los Cerritos, but this seasonal effect reversed at Bolsa Chica and was not significant in Anaheim Bay (Fig. 1a). We also found that perched individuals at Los Cerritos and Bolsa Chica became alert at greater distances than individuals foraging; however, there was no such effect at Anaheim Bay (Table 1; Fig. 2a).

Flight-Initiation Distance

The distance at which Belding's Savannah Sparrows fled was correlated linearly with SD ($R^2 = 0.383$, $P < 0.0001$), but the quadratic function provided the best fit ($R^2 = 0.392$, quadratic term: $t = -2.05$, $P = 0.0412$). The curve is described by the function: FID = 2.26 + 0.50(SD) – (2.2 x 10^{-3})(SD^2); with the peak of the function at a SD of 114 m where the predicted FID is 31 m.

Starting distance had significant effects in FID (Table 1); however, the square of SD did not achieve significance (Table 1). We found significant differences in FID among sites (Table 1; Fig. 1b), where FID was greater at Anaheim Bay than at Los Cerritos and Bolsa Chica, with no significant differences between the former two (Fig. 1b). Although season had no direct effect on FID (Table 1), there was a significant interaction between season and site on FID (Table 1; Fig. 1b), where FID was significantly lower in the non-breeding than in the pre-nesting season at Los Cerritos, but the opposite significant seasonal effect was found at Anaheim Bay (Fig. 1b). There was no significant seasonal effect at Bolsa Chica (Fig. 1b). We also found a significant interaction effect between site and initial behavior (Table 1), by which perched individuals tended to flee at greater distances than individuals foraging on the ground at Bolsa Chica (Fig. 2b). However, this effect was not significant Los Cerritos and Anaheim Bay (Fig. 2b).

Distance Fled

The distance sparrows fled from the observer was correlated positively and linearly with FID ($R^2 = 0.134$, $P < 0.0001$), and neither the quadratic nor the logarithmic functions provided a better fit to the data. The relationship is described by the function: $\log_{10}$DF = 1.27 + 0.01(FID).

Flight-initiation distance significantly influenced DF (Table 1). Belding's Savannah Sparrows moved greater distances after fleeing in the non-breeding compared with the pre-nesting season (Table 1; Fig.

Table 1. Effects of starting distance, site, season, initial behavior, and some of their interactions on Belding's Savannah Sparrows (a) alert distance, (b) flight-initiation distance, and (c) distance fled.

	df	F	*P*	η^2
(a) Alert distance				
Starting Distance	1, 251	99.05	<0.001	0.239
Starting Distance^2	1, 251	15.25	<0.001	0.037
Site	2, 251	8.77	<0.001	0.042
Season	1, 251	0.06	0.809	<0.001
Initial Behavior	1, 251	13.07	<0.001	<0.001
Season x Site	2, 251	4.31	0.014	0.021
Site x Initial Behavior	2, 251	4.96	0.008	0.024
(b) Flight-initiation distance				
Starting Distance	1, 294	23.98	<0.001	0.064
Starting Distance^2	1, 294	2.54	0.112	0.007
Site	2, 294	16.14	<0.001	0.086
Season	1, 294	0.01	0.923	<0.001
Initial Behavior	1, 294	3.41	0.066	0.009
Season x Site	2, 294	6.42	0.002	0.034
Site x Initial Behavior	2, 294	3.79	0.024	0.020
(c) Distance fled				
Flight-Initiation Distance	1, 298	47.867	<0.001	0.134
Site	2, 298	1.741	0.177	0.010
Season	1, 298	4.858	0.028	0.014
Season x Site	2, 298	2.098	0.125	0.012

1c), but neither site nor the site x season interaction influenced significantly DF (Table 1).

Minimum Approaching Distances and Buffer Areas

Given that perched birds were warier of human approaches than those foraging, we used AD and FID of perching individuals for the calculation of minimum approaching distances and buffer areas. Using both methods, minimum approaching distances were slightly higher at Anaheim Bay than at Bolsa Chica and Los Cerritos, and in general were higher in the pre-nesting season around pairs than in the non-breeding season around groups (Table 2). Minimum approaching distances varied between 59 and 63 m at Anaheim Bay, 47 and 52 m at Bolsa

Fig. 1. Mean (±SE) effects of site (Los Cerritos, Bolsa Chica, Anaheim Bay) and season (pre-nesting, black bars; non-breeding, white bars) on (a) alert distance, (b) flight-initiation distance, and (c) distance fled of Belding's Savannah Sparrows. Intensity of recreational activities (e.g., pedestrians) varied among sites: Los Cerritos (higher intensity), Bolsa Chica (intermediate intensity), Anaheim Bay (lower intensity).

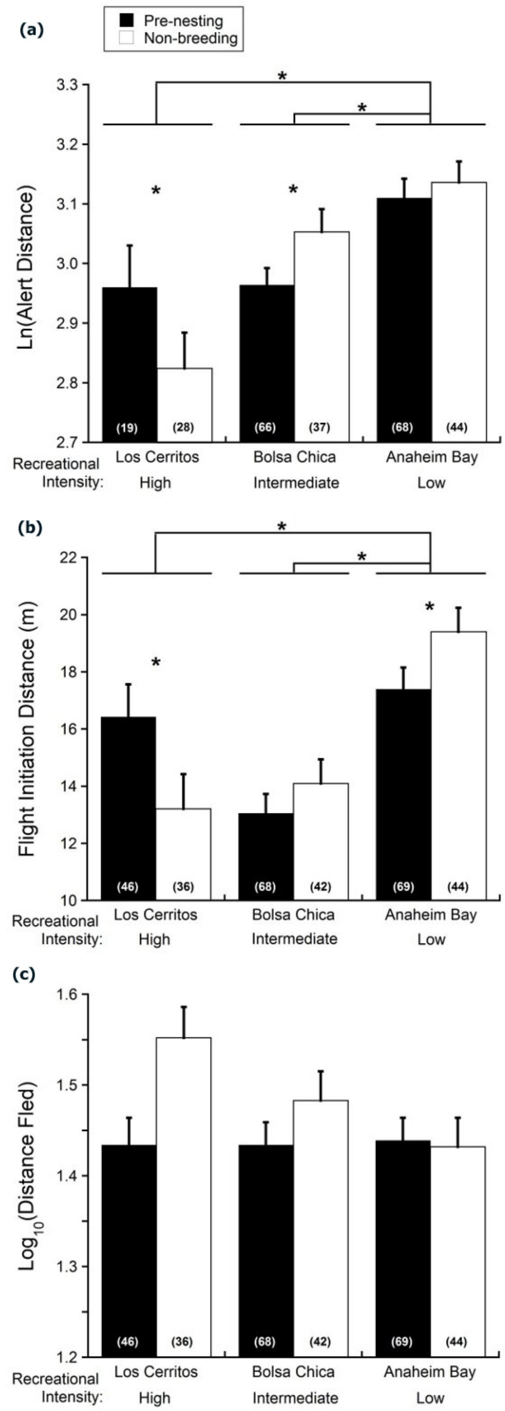
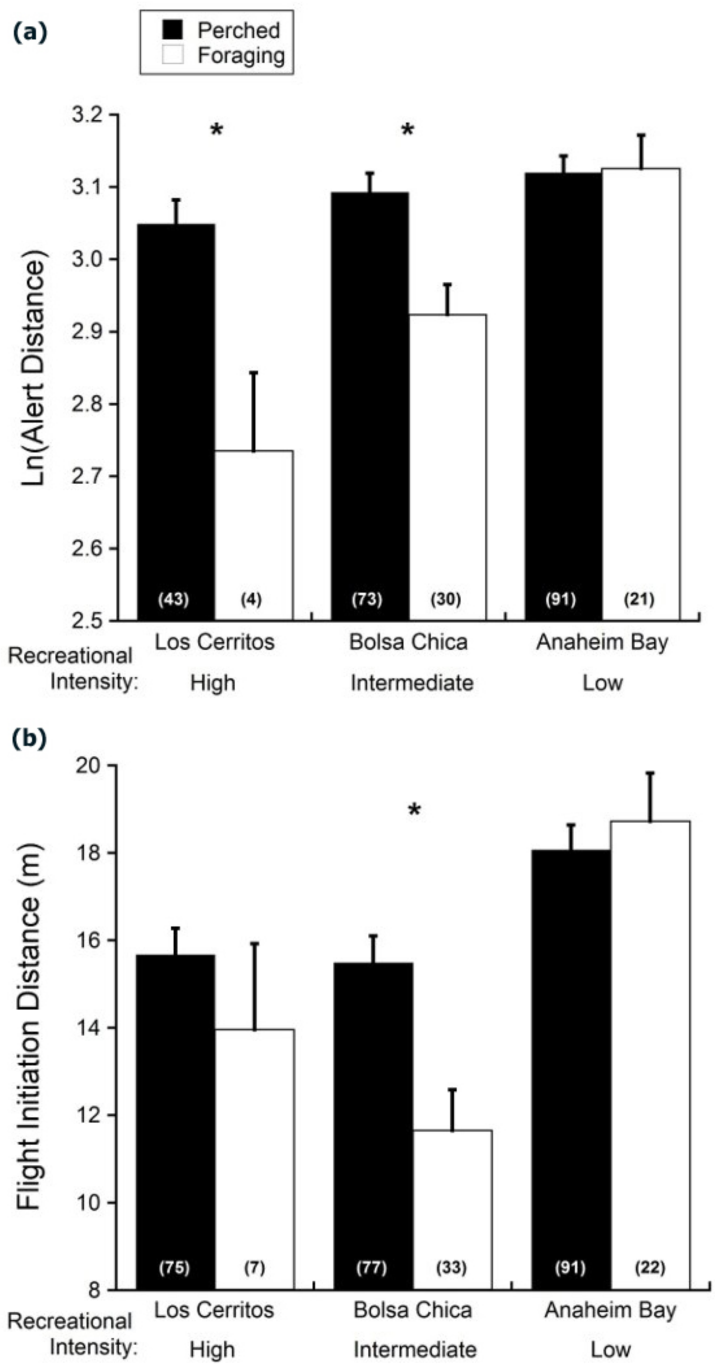


Fig. 2. Mean (±SE) effects of initial behavior (perched, black bars; foraging, white bars) within sites on (a) alert distance, and (b) flight-initiation distance of Belding's Savannah Sparrows. Intensity of recreational activities (e.g., pedestrians) varied among sites: Los Cerritos (higher intensity), Bolsa Chica (intermediate intensity), Anaheim Bay (lower intensity).



Chica, and 44 and 58 m at Los Cerritos, depending on the method (Table 2). We recommend minimum approaching distances of 63 m for Belding's Savannah Sparrows.

Using both methods, buffer areas were higher at Anaheim Bay than at Bolsa Chica and at Los Cerritos, and slightly higher in the pre-nesting season around pairs than in the non-breeding season around groups (Table 2). Buffer areas varied between 1.01 and 1.27 ha in Anaheim Bay, 0.70 and 0.84 ha in Bolsa Chica Wetlands, and 0.62 and 1.06 ha in Los Cerritos Wetlands (Table 2). We recommend buffer areas of 1.3 ha around Belding's Savannah Sparrows.

DISCUSSION

We found that Belding's Savannah Sparrow's overall tolerance to human approaches varied among sites and between seasons. We were unable to distinguish between sexes (e.g., this is not a sexually dimorphic species) and we only approached individuals on trails, which may somehow limit the generality of our findings to off-trail scenarios. Given the endangered nature of this subspecies, we could not tag individuals nor increase disturbance levels unnecessarily by stepping into the native vegetation because of ethical concerns. Nevertheless, most of the pedestrian disturbance that these populations are exposed to comes from hikers who generally stay on trails; thus, our treatments mimicked the recreationists' behavior. We discuss plausible explanations for our results and we derive specific management implications.

Regardless of season, alert and flight responses were greater at Anaheim Bay, where Belding's Savannah Sparrows rarely encounter humans, than at Los Cerritos and Bolsa Chica, where the human visitation rate is relatively higher. According to previous studies (reviewed in Stankowich and Blumstein 2005), this finding can be interpreted as a result of habituation effects, by which a given source of disturbance is no longer regarded as dangerous following repeated exposures to it (Mirza et al. 2006, Thompson and Spencer 1966). Risk allocation can also explain this result (Lima and Bednekoff 1999, Rodriguez-Prieto et al. 2009), as individuals are expected to decrease their allocation of anti-predator effort to frequent high-risk encounters with predators to allow animals to use the necessary resources without vacating patches so frequently. The combined effects of habituation and risk allocation are supported by the differences in alert and flight-initiation distances between perched and foraging individuals. These differences were stronger at the two sites where human activity was more frequent (Los Cerritos, Bolsa Chica), suggesting that animals may be willing to accept greater risks while foraging given limited opportunities to do so undisturbed. In contrast, Belding's Savannah Sparrows responded at equal distances at the site with the lowest disturbance (Anaheim Bay), where opportunities for undisturbed foraging may be more frequent. An alternative interpretation for the site differences can be related to habitat structure: non-native plants are more abundant and taller in the marsh–upland transition zone at Los Cerritos and Bolsa Chica than at Anaheim Bay. Visual obstruction could then reduce the distance at which Belding's Savannah Sparrows detect, and consequently flee from, an approaching human.

There was a trend for alert distance and flight-initiation distance to be greater in the non-breeding than in the pre-nesting season at the sites with relatively lower visitation rates (Bolsa Chica and Anaheim Bay). Vegetation structure did not change substantially seasonally within each site. Furthermore, in both Bolsa Chica and Anaheim Bay, the roads used for the approaches were at the marsh level. Animals may be less tolerant in the non-breeding season because they are less attached to a particular spot (e.g., breeding territory) or because while foraging in aggregations the chances of any individual detecting a threat increase (e.g., collective detection; Lima 1994, Roberts 1996). Actually, the increase in flight-initiation distance when Belding's Savannah Sparrows aggregated in the non-breeding season runs counter to previous studies that found that individuals in groups actually increase the delay between detection and reaction (Fernández-Juricic et al. 2002, Boland 2003). This suggests that risk at these sites may be heightened by the detection responses of conspecifics.

In the highly visited site (Los Cerritos), tolerance was actually lower (greater alert and flight-initiation distances) in the pre-nesting season. This could be related to the fact that perched birds were more aware of approaching threats than foraging individuals, whose attention was likely occupied in the search for food on the ground. Indeed, detection distances may have been greater during the pre-nesting season at Los Cerritos due to the fact that Belding's Savannah Sparrows were more likely to

Table 2. Estimated minimum approaching distances (MAD) and buffer areas (BA) for the three study areas and seasons following two methods. Method 1 (Rodgers and Smith 1995, 1997) estimates MAD as (AFID+1.6495*SD)+AAD, where AFID is the mean FID, SD is the standard deviation of AFID, and AAD is the mean AD. Method 2 (Vos et al. 1985) estimates MAD as the maximum FID recorded +AAD, where AAD is the mean AD. Buffer areas for both methods are calculated as Π * MAD2.

(a) Method 1

Study area	Season	MAD (m)	BA (ha)
Anaheim Bay	Non-breeding	59.06	1.09
Anaheim Bay	Pre-nesting	56.76	1.01
Bolsa Chica Wetlands	Non-breeding	47.36	0.70
Bolsa Chica Wetlands	Pre-nesting	47.15	0.70
Los Cerritos Wetlands	Non-breeding	44.36	0.62
Los Cerritos Wetlands	Pre-nesting	48.39	0.74

(b) Method 2

Study area	Season	MAD (m)	BA (ha)
Anaheim Bay	Non-breeding	60.85	1.16
Anaheim Bay	Pre-nesting	63.48	1.27
Bolsa Chica Wetlands	Non-breeding	49.74	0.78
Bolsa Chica Wetlands	Pre-nesting	51.61	0.84
Los Cerritos Wetlands	Non-breeding	48.72	0.75
Los Cerritos Wetlands	Pre-nesting	58.06	1.06

be perched instead of foraging than at the other two sites ($X^2 = 8.33$, df = 2, $P = 0.015$). Another potential factor explaining this seasonal trend at Los Cerritos is that the trail used for the approaches is elevated above the marsh and native vegetation levels, where Belding's Savannah Sparrows hold their breeding territories, increasing exposure and potentially perception of risk.

Contrary to other studies (e.g., Burger and Gochfeld 1981, Fernández-Juricic et al. 2005), Belding's Savannah Sparrows did not modify their perception of risk depending on the angle of approach. The lack of angle effects could be also related to the fact that the observer stayed on the trail during the approach and did not encroach into native vegetation. A recent study, involving Vesper Sparrows (*Pooecetes gramineus*), Western Meadowlarks (*Sturnella neglecta*), and American Robins (*Turdus migratorius*), found that birds show more tolerance to on-trail than off-trail human approaches (Miller et al. 2001); the same result has been found in mule deer (*Odocoileus hemionus*; Miller et al. 2001, Taylor and Knight 2003).

Distances fled were generally greater in the non-breeding season, which could be explained by a higher site territoriality of males during nesting (White 1986). Larger distances fled suggest that animals may restrict the use of suitable habitat near the flushing point (Lima 1993, Fernández-Juricic et al. 2006), potentially reducing the availability of foraging or nesting sites.

The use of behavioral responses to humans to establish the degree to which a species is affected by human disturbance has been criticized on the grounds that species that show low tolerance might not be negatively affected at the population level if they have alternative areas with no disturbance to move to (Gill et al. 2001). However, the Belding's Savannah Sparrow is an endemic salt-marsh subspecies that does not use alternative habitat regularly for foraging or breeding (Massey 1979). Thus, behavioral responses can be used as a proxy to estimate distances that would minimize individuals vacating breeding or foraging patches in the presence of recreational activities. Actually, human disturbance has been implicated as a potential factor negatively influencing Belding's Savannah Sparrows directly (White 1986) and indirectly (Zembal and Hoffman 2002, Zembal et al. 2006). A previous study recommended minimum approaching distances of at least 30 m during the non-breeding season for this subspecies based on data collected in the Tijuana Estuary (White 1986). Furthermore, a regulatory agency approved a 7.5 m minimum approaching distance for Los Cerritos Wetlands (cited in Zedler 1996). However, these studies did not use any of the current methods to estimate minimum approaching distances (Fernández-Juricic et al. 2005), and greatly overestimated the tolerance of Belding's Savannah Sparrows.

Our findings provide three specific management implications. First, we recommend restricting human access to at least 63 m from breeding territories or heavily used spots during the non-breeding season, and to set aside areas of at least 1.3 ha around each individual, pair, or group. Future studies should establish the relationship between tolerance to recreationists and territory size, shape, and density (Powell 1993, Powell and Collier 1998), as these factors can be used to better estimate the amount of core habitat necessary to protect this species. Current estimates indicate that Belding's Savannah Sparrows need salt marshes larger than 10 ha to breed successfully (Powell and Collier 1998). Second, taking advantage of potential visual obstruction effects by plants may be a useful way of increasing tolerance; however, we recommend using native transition-zone vegetation (e.g., *Lycium californicum*, *Isocoma menziesii* var. *vernonioides*, *S. subterminalis*), which would minimize the negative effects of invasive plants in salt marshes. Third, seasonal variation in tolerance among sites needs to be taken into consideration. In the larger sites with relatively lower levels of visitation (Bolsa Chica and Anaheim Bay), a greater level of protection may be necessary in the non-breeding season, as individuals use space less restrictively and are less tolerant of human activity. However, in the highly visited salt marsh (Los Cerritos), greater levels of protection against human activities are necessary during the breeding season and could be achieved by restricting access through the breeding habitat. This is particularly important given the reduced area of this salt marsh, which could limit breeding success (Powell and Collier 1998). Our findings show high levels of intra-specific (e.g., between-population) variability in tolerance of recreationists, which prevents us from making generalizations to other species and calls for assessing the tolerance of recreational activities of other salt-marsh specialists, as the coexistence between humans and wildlife may require dynamic management strategies that vary in space and time.

Responses to this article can be read online at:
http://www.ace-eco.org/vol4/iss2/art1/responses/

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