Snowy Plovers select wide beaches for nesting

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Patrick, A.M. & Colwell, M.A. 2014. Snowy Plovers select wide beaches for nesting. *Wader Study Group Bull.* 121(2): 17–20.

Key words: beach width, Charadrius nivosus, habitat suitability, nest-site selection, Snowy Plover, threatened species

The Snowy Plover *Charadrius nivosus* is listed as threatened along the Pacific coast of North America where it breeds amidst sparsely vegetated (i.e. 'open') habitats on ocean-fronting beaches, salt pans, and riverine gravel bars. Habitat management to increase the Snowy Plover population has emphasized restoring coastal dunes and beaches by removing invasive plants; few studies, however, have quantified second order habitat selection by Snowy Plovers (i.e. choice of a breeding site from amongst habitats within the species' range). Consequently, we used three years of data on 109 nests to show that plovers nested on wider beaches compared with random locations; some nests, however, occurred on narrow beaches. Our findings may be useful in guiding restoration efforts aimed at improving the suitability of habitats for breeding Snowy Plovers. However, the weak explanatory power of beach width suggests that other unmeasured features of habitat or social factors may also influence how individuals select breeding sites.

INTRODUCTION

Efforts to improve the suitability and quality of wildlife habitats often require comparatively simple information to guide restoration efforts. In many cases, however, data are insufficient to understand how specific habitat features influence species' distributions. This may be especially true for threatened and endangered (i.e. rare) taxa for which the application of this knowledge may be directly applied to a species' recovery (e.g. MacDonald *et al.* 2010). For birds, resolving habitat relationships often involves comparing known breeding locations (as represented by nests, for instance) with random locations in a habitat-selection function (Manly *et al.* 2002, Morrison *et al.* 2006). The results of such analyses can inform conservation actions, such as the restoration of habitats to provide elements attractive to breeding birds.

The Snowy Plover *Charadrius nivosus* was listed as threatened by the U.S. government in 1993 (U.S. Dept. of Interior 1993). Three main factors are thought to limit recovery of the listed population segment (U.S. Fish and Wildlife Service 2007), including: 1) predation of eggs and chicks by native and introduced vertebrates; 2) disturbance and direct mortality associated with human recreational activities; and 3) loss and degradation of suitable habitat resulting from introduced plants, notably European beach grass *Ammophila arenaria*, which was established to stabilize drifting sands of coastal dunes (Buell *et al.* 1995). Along the Pacific coast, one outcome of establishment and spread of *Ammophila* is a reduction in suitability of habitats year-round. In winter, Snowy Plovers prefer to roost in open, sparsely vegetated habitats that facilitate early detection of danger posed by approaching avian predators (Brindock & Colwell 2011). Similar findings have been reported for breeding Snowy Plovers: they nest on wide beaches (MacDonald *et al.* 2010), amidst habitats that are comparatively free of vegetation (Muir & Colwell 2010, Powell 2001). Findings such as this inform habitat restoration in coastal regions in an attempt to improve habitat suitability for Snowy Plovers. However, precise information regarding Snowy Plover occurrence and easily manipulated habitat features are insufficient or have been derived from studies conducted at a spatial scale that is too small (e.g. nest-site selection: Powell 2001). Here, we analyze second order habitat selection (i.e. the home range of an animal within its geographical range; Johnson 1980) of Snowy Plovers in coastal northern California to determine whether there was an association between Snowy Plover nest-site selection and beach width. We predicted that Snowy Plovers would select wide beaches to benefit from early detection of predators.

STUDY AREA AND METHODS

We have studied a population of individually marked Snowy Plovers for 12 years (2001–2012) in Humboldt County, California. During this time, population size varied (19–64 breeding adults annually) with an increasing proportion breeding on sandy, ocean-fronting beaches (Colwell *et al.* 2010). A detailed description of habitats used by wintering and breeding Snowy Plovers in our study area is provided elsewhere (Brindock & Colwell 2011, Colwell *et al.* 2010, Muir & Colwell 2010). Ocean-fronting beaches extended along 79.5 km, from Centerville Beach in the south to Gold Bluffs Beach in the north (Fig. 1a).

Each year, observers surveyed suitable breeding habitats for newly initiated nests of Snowy Plovers from mid-March until mid-July. Observers visited all sites a minimum of once a week and located nests by observing Snowy Plover behavior and by following tracks. When observers found a nest they recorded its location (i.e. UTM coordinates) using

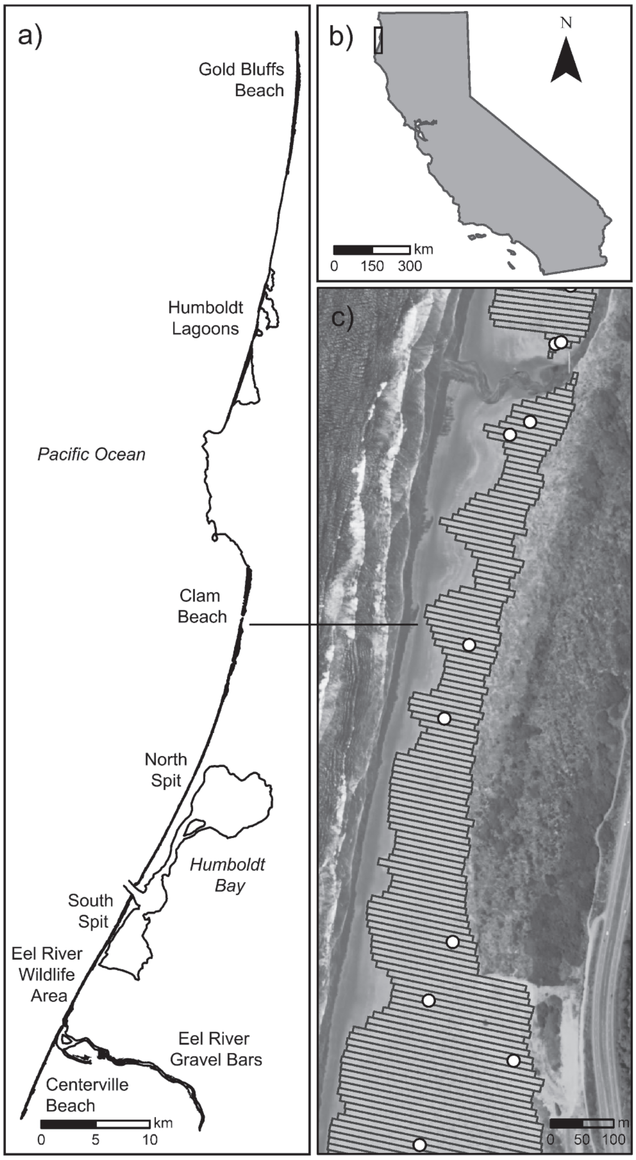

Fig. 1. Locations (a) where Snowy Plovers nested along ~80 km of sandy, ocean-fronting beaches in coastal northern California (b); (c) shows an example of the method of arranging sampling rectangles perpendicular to the long axis of the ocean-fronting beach as a means of measuring beach width at nest locations (open circles).

a global positioning system (GPS). To evaluate relationships between Snowy Plover breeding sites and habitat suitability as gauged by 'openness' (see Muir & Colwell 2010), we plotted the UTM coordinates of nests and compared beach width of this sample to the beach width of random locations. Random locations were generated in ArcMap 9.3 (ESRI, Redlands, CA) using the 'create-random-points' tool, which generates a specified number of random points within a polygon shapefile. To create the polygon shapefile, we delineated suitable habitat using a supervised classification in ERDAS Imagine 11 (ERDAS Inc., Norcross, GA) based on three images acquired by the National Agriculture Imagery Program (NAIP; 1 m resolution) in June 2005, 2009, and 2010. We used these images to represent the range of habitats within the study area, recognizing that beach topography varies annually under the influence of ocean conditions. With each image, we classified habitats into ten land-cover types, with 3–28 training polygons per type (Patrick 2013). We considered one of these land-cover types (sparsely vegetated, dry sand) to be suitable breeding habitat along ocean-fronting beaches. The area of suitable beach habitat varied annually (2005, 888 ha; 2009, 825 ha; 2010, 786 ha). The decrease in area was likely to be an artifact of the classification and not a reflection of habitat loss.

We visited all sites to confirm classifications. We measured habitat width by overlaying a 10 x 10 m grid over suitable habitat (e.g. sparsely vegetated sand of the beach fore- and back-dunes) using the 'fishnet' tool in ArcMap. We removed the vertical lines of the grid, which yielded parallel lines spaced 10 m apart, and then rotated the lines so that they ran perpendicular to the long axis of the beach (Fig. 1c). We measured beach width as the length of those lines, which represented the distance between the high-water mark of the ocean and the beginning of vegetation upslope. For nine nests that occurred on the wet sand immediately adjacent to the area that we identified as suitable habitat, we used the 'ruler' tool to measure the extra distance between nests and the habitat polygon. We measured beach width for nests (2005, n=40; 2009, n=32; 2010, n=37) and an equal number of random locations. Results are presented as means ±SD.

We evaluated beach width as a predictor of nest location using a resource-selection function (Manly *et al.* 2002, Morrison *et al.* 2006) with an information theoretic approach (Burnham & Anderson 2002). We used logistic regression (1 = nest; 0 = random) to evaluate whether beach width predicted nest occurrence. The analysis included four candidate models with beach width, year, and null (i.e. intercept only) as predictors. We assessed the ranking of models using Akaike's Information Criterion, corrected for small sample size (AIC_c). We evaluated model fit by calculating the percent deviance explained by the top model (i.e. 100* (null dev-model dev)/null dev).

RESULTS

Our sample of 109 nests represents a subset (n = 37) of the ~125 males we have monitored over 12 years; some of these birds nested multiple times during the years from which the data originated. In particular, four males nested 7–14 times over the three years in which we quantified beach width. This was due to high rates of nest loss and re-nesting. Beach width at their nests (206 ± 90 m, range: 33–369 m) was similar to the remaining sample of males (245 ±116 m, range: 36–478 m) used in analyses. Hence, our analysis included all nests of all breeding males in each year.

Snowy Plover nests occurred on wider beaches (225 ± 112 m) compared with random locations (187 ± 116 m; Fig. 2). The top model, with 76% of the weight, had beach width as the only predictor variable (Table 1). This top model predicted that a beach width of roughly 205 m had an equal probability of having a nest or random location. And as beach width increased, the probability of finding a nest (versus a random location) increased (β= 0.003). The 95% confidence interval for beach width did not overlap zero (CI = 0.0005–0.0054). Percent deviance explained by the top model was 2%.

DISCUSSION

Our finding that Snowy Plovers nested on wide beaches corroborates results for this species from studies conducted at smaller (e.g. nest site; Powell 2001), similar (Muir &

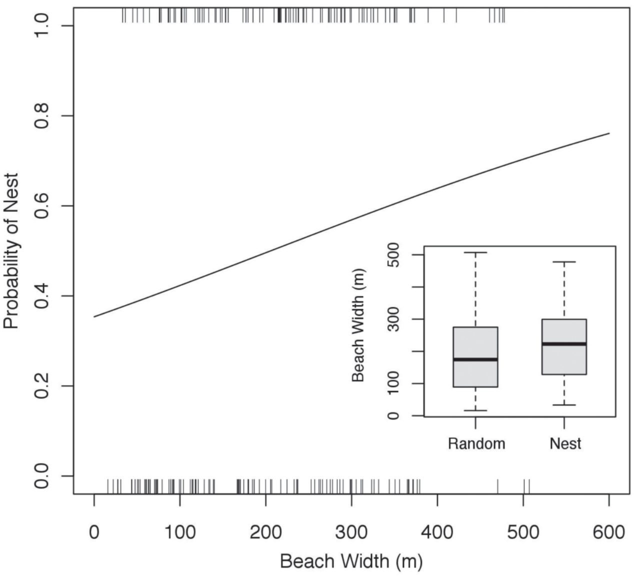

Fig. 2. Results of logistic regression showing variation in beach width at Snowy Plover nests (1.0) and random locations (0.0). Tick marks along top and bottom axes represent beach widths at nests and random locations, respectively. Inset graph shows a box plot with median (line), interquartile range (box) and minimum and maximum values (whiskers) for random locations and Snowy Plover nests.

Colwell 2010) and larger (e.g. regional; MacDonald *et al.* 2010) spatial scales, which show that plovers prefer to nest in open (i.e. sparsely vegetated) areas. In our study area, many beaches were bordered to the east by dense stands of *Ammophila*, which often formed an abrupt boundary that defined unsuitable habitat for plovers and resulted in a narrow beach. In efforts to restore native dune ecosystems, it is this eastern edge of *Ammophila* that is often the target of restoration. Hence, results should be useful in justifying and guiding restoration efforts aimed at improving habitat for Snowy Plovers. In particular, success of restoration efforts aimed at improving coastal dune habitats for plovers (via removal of *Ammophila* and other invasives) may hinge, in part, on the extent of sparsely vegetated habitat created by a restoration project. Additionally, restoration may be unsuccessful if proposed restoration sites lack sufficient width in which to expand native dune communities.

Muir & Colwell (2010) suggested that restoration projects attempt to create open areas of sufficient size (~100 m radius) to attract breeding Snowy Plovers. Although we are tempted to prescribe some minimum beach width (e.g. ~200 m) necessary to attract Snowy Plovers, this seems unjustified given the wide range of beach widths at Snowy Plover nests (range: 33–478 m), which is related to the low explanatory power of our model (i.e. 2% deviance explained). In other words, some Snowy Plover nests occurred on narrow beaches (e.g. 17 nests occurred on stretches of beach <100 m wide). This suggests that other features influence habitat selection of breeding Snowy Plovers, and it highlights some inadequacies of our understanding of Snowy Plover breeding biology. We suspect the presence of conspecifics strongly influences individual choice of a nest site, as evidenced by social attraction (Nelson 2007) and the observation of breeding aggregations (i.e. loosely clustered nests; Patrick 2013, Saalfeld *et al.* 2012).

The observation that nests occurred on wide beaches may be in part due to the majority of nests occurring on a single wide beach (77%; 84/109 nests; Colwell *et al.* 2014). This site (i.e. Clam Beach) was also the only site continually occupied by breeding Snowy Plovers over the 12-year study (Colwell *et al.* 2012). These birds could have occupied the site because of its width, or because of other factors, such as social attraction.

Other shorebirds have been shown to benefit from the extent of open habitat around nests. Temminck's Stint *Calidris temminckii* nests were more likely to hatch on wide than on narrow shorelines (Koivula & Rönkä 1998). Wider (i.e. more open) habitats may allow birds to detect predators at a greater distance, and thus increase early departure of incubating adults, which results in improved nest crypsis. The close relative of the Snowy Plover in the old world, the Kentish Plover *Charadrius alexandrinus*, has been experimentally shown to benefit from nesting in areas with less cover (Amat & Masero 2004). Adult birds left their nests at a greater distance in more exposed areas.

An unanswered question concerns whether or not the same habitat features that are attractive to plovers also enhance their reproductive success and survival, especially within restored habitats. This latter question is critical to the success of restoration efforts aimed at ameliorating factors that limit population growth. Effective management decisions aimed at increasing the population size of the Snowy Plover would benefit from an understanding of how habitat affects reproductive success of individuals choosing to nest and rear young in habitats of varying quality, as defined by habitat features such as beach width.

ACKNOWLEDGEMENTS

The manuscript was greatly improved by the comments of two anonymous reviewers. We thank the many field assistants

Table 1. Results of model selection using logistic regression to compare beach width at Snowy Plover nests and random locations in coastal northern California.

Model	K	logL	AIC_c	$DAIC_c$	W_i
width	2	-148.12	300.29	0	0.76
null	1	-151.11	304.23	3.94	0.11
width + year	4	-148.07	304.33	4.04	0.1
width * year	6	-147.28	306.96	6.67	0.03

K = Number of parameters in model.
AIC_c = Akaike's Information Criterion adjusted for small sample size.
$DAIC_c$ is the difference in AIC_c value between the top model and each subsequent model.
AIC_c weight (W_i) is the proportion of total weight than can be attributed to each model.

who have worked on this project over the past 12 years, especially S.E. McAllister, K.G. Ross, and A.N. Transou. Support for our research came from the California Department of Fish and Wildlife, California Department of Parks and Recreation, Chevron Oil Corporation, Eureka Rotary Club, Humboldt County Fish and Game Advisory Commission, Humboldt County Planning Department, Humboldt State University Sponsored Programs Foundation, Mad River Biologists, Marin Rod and Gun Club, MRB Research, Inc., Redwood Region Audubon Society, Stockton Sportsmen's Club, Western Section of The Wildlife Society, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, and California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis.

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