

Annual variation in distance to nearest neighbor nest decreases with population size in snowy plovers

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In non-colonial species, the spatial pattern in which nests occur in a population often varies among years and with habitat quality and population size. In aggregated patterns nests occur nearer than expected by chance and apparently suitable habitat remains unoccupied. We assessed annual (12 years) and spatial (10–100 km) variation in nest dispersion using distance to nearest conspecific nests for a small, color-marked population (19–64 adults annually) of Snowy Plover *Charadrius nivosus* breeding in coastal northern California. Across 100 km of suitable habitat, average distance to conspecific nest was 1,284 m (median = 182 m, SD = 4,019 m, range = 20–41,519 m, $n = 210$ nests); 19% of nests were <100 m from a conspecific's nest. When we restricted analyses to a 10-km beach where more plovers consistently bred, average distance to nearest nest decreased. Plover nests were aggregated in 11 of 12 years; the one exception occurred when local population was lowest. For marked males ($n = 43$) that bred in multiple years (range: 2–10), there was no evidence that individuals consistently nested near conspecifics. These results suggest that breeding aggregations may be more prevalent near the core of the species' range where populations are larger, and they serve as a cautionary reminder of the challenges of estimating population size based on extrapolations derived from areas of high breeding density to unsampled, but seemingly suitable, habitat.

Keywords

aggregated
Charadrius nivosus
 nest dispersion
 nearest neighbor distance
 Snowy Plover
 threatened

INTRODUCTION

Quantifying a species' breeding dispersion (i.e., nearest neighbor distance) has both theoretical and applied value. In theory, understanding intraspecific variation in the spatial distribution of nests (or territories) offers insight into the role of conspecific attraction (Ward & Schlossberg 2004, Ahlering & Faaborg 2006) and habitat quality (Melles *et al.* 2009) in influencing selection of a breeding site. Additionally, breeding dispersion provides valuable information on mating systems (Pitelka *et al.* 1974, Casey *et al.* 2011). In conservation, evidence of a patchy breeding distribution has implications for methods of estimating total population size (Long *et al.* 2008), and it may direct management actions to ameliorate the negative effects of nest loss owing to predators in areas where individuals aggregate (Page *et al.* 1983).

Many bird species have been characterized as breeding in an aggregated pattern, which is defined as individuals nesting nearer conspecifics than expected by chance; a corollary of this pattern is that seemingly suitable habitat

remains unoccupied (Stamps 1988, Brown & Brown 2001). In some birds, variation in nest (or breeding) dispersion has been shown to be influenced by population size or density (McLandress 1983). However, a high density of birds may be confounded by an underlying relationship with habitat quality, since adults often return to sites where they bred successfully and young produced in a prior year may be philopatric (Oring & Lank 1984, Pearson & Colwell 2014). Moreover, evidence suggests that individuals may prospect for breeding sites based on evidence of successful breeding by conspecifics (Rioux *et al.* 2011). The most effective way to evaluate an hypothesis of aggregated breeding requires long-term study over a large study area such that the pattern is not merely associated with spatial scale.

The Pacific coast population of the Snowy Plover *Charadrius nivosus* (hereafter 'plover') is listed as threatened under the U.S. Endangered Species Act (USFWS 1993). In 2015, the population size was approximately 2,200 adults (11-yr mean \pm SD: 1821 \pm 214; USFWS 2017). Plovers breed on

ocean-fronting beaches, salt pans, riverine gravel bars, and other sparsely-vegetated habitats (Page *et al.* 2009). Across western North America, plovers have been characterized as ‘semi-colonial’ (Paton & Bachman 1996, Powell 2001, Saalfeld *et al.* 2012, Thomas *et al.* 2012), although this has not been rigorously quantified. The underlying reasons for aggregated breeding are poorly understood.

Snowy Plovers have a wide, but patchy distribution across western North America (Page *et al.* 2009). Along the Pacific coast, most plovers breed in southern California, with only smaller, isolated subpopulations further north (Eberhart-Phillips *et al.* 2015). At finer scales, plovers have been characterized as having aggregated nests or occurring at higher densities in some habitats (e.g., Page *et al.* 1983, Saalfeld *et al.* 2012). These conclusions, however, are affected by the temporal and spatial extent of a study. For instance, an aggregated pattern may arise by analysis of all nests within a breeding season. If nest failure is frequent, then nesting aggregations may stem from multiple nests of individuals replacing failed attempts. This issue can only be addressed by studying a color-marked population within a brief interval of peak breeding activity. Size of study area may also pose problems for the interpretation of spatial pattern (Krebs 1999). If researchers opt to investigate a species in an area of high density, which is often the case, then interpretation will be biased toward an aggregated pattern.

In northern California, where we have studied plovers since 2001, the amount and quality of habitat varies greatly. Breeding plovers favor sparsely vegetated habitats during the breeding (Muir & Colwell 2010) and non-breeding seasons (Brindock & Colwell 2011). Invasive plants, mainly European beach grass *Ammophila arenaria*, have degraded habitats (USFWS 2007), which affects selection of breeding sites (Patrick & Colwell 2014, Leja 2015). In addition to physical features of habitat, experience also influences selection of a breeding site. Adults tend to nest near where they successfully hatched eggs, whereas failed breeders disperse greater distances (Pearson & Colwell 2014). Furthermore, yearlings and immigrants (i.e., naïve breeders) are more likely to settle at sites occupied by older (i.e., experienced) plovers, and they nest nearer experienced adults than expected by chance (Nelson 2007). Over the study duration, plovers bred in two distinct habitats: sandy, ocean-fronting beaches and riverine gravel bars. These habitats differ greatly in quality, as measured by the per capita fledging success of males (Colwell *et al.* 2010, Herman & Colwell 2015). On gravel bars, heterogeneous substrates (varying from coarse sand to large rocks of different color) afford eggs and chicks camouflage from the principal visual predator (Common Raven *Corvus corax*; Colwell *et al.* 2007, 2011).

Here, we use detailed records of individually marked Snowy Plovers, collected over 12 years, to quantify the degree to which breeding dispersion (derived from nearest neighbor distance) varied annually. Furthermore, we evaluated the relationship between spatial pattern and: (1) population size, (2) the proportion of naïve birds in the

population, and (3) use of a high quality breeding site as evidenced by high reproductive success (Colwell *et al.* 2010, 2011, Herman & Colwell 2015). These three covariates represent the influence of population-level phenomena and individual decisions in establishing a spatial pattern. Specifically, we predicted that nests would be more clustered in years of higher population size, when more naïve birds are searching for a first breeding site, or when a higher proportion of the population is breeding in a high quality gravel bar habitat.

METHODS

Study area

We studied plovers in Humboldt County, California for 12 years on ~80 km of ocean-fronting beaches and ~15 km of gravel bars along the lower Eel River (Fig. 1; Colwell *et al.* 2017). On beaches, plovers bred amidst relatively homogeneous sandy substrates vegetated with sparse native (e.g., *Calystegia soldanella*, *Cakile maritima*, *Leymus mollis*, *Abronia umbellata*, *Abronia latifolia*) and invasive species (e.g., *Ammophila arenaria*, *Carpobrotus chilensis*), amidst scattered driftwood, shells, crab carapaces, and garbage. On gravel bars, plovers bred in heterogeneous substrates sparsely vegetated by white sweet clover *Melilotus alba* and willow *Salix* spp. (Colwell *et al.* 2010). Area of suitable habitat remained relatively constant across years (Patrick & Colwell 2014), although dynamic under the influence of river flows and ocean conditions. Active restoration projects also created open foredune habitat, sparsely vegetated with native flora, at some sites (Leja 2015).

Field methods

We monitored a color-marked population of plovers (94.3 ± 3.8% color-marked each year) during the breeding season (early March to mid-September) for 12 years (2001–2012). We determined the sex of birds based on plumage, confirmed by behaviors (e.g., roles in courtship, copulation, and incubation or brooding; Page *et al.* 2009). We determined population size, number of naïve (i.e., locally-marked yearlings, marked immigrants, and unmarked individuals; Nelson 2007) and experienced breeders, and number of birds breeding on the gravel bars and beaches based on individual records of color-marked birds (Herman & Colwell 2015).

Observers surveyed suitable habitat for plovers at least once a month, and more frequently (i.e., every 2–7 days) if they detected plovers. Upon finding a nest, researchers recorded its location with a personal digital assistant equipped with a global positioning system (Dell Axim X50/Holux CF GPS GR-271), and identified nest owners based on colored leg bands. Nest locations provided the distance (m) between nearest conspecific nests that is the basis for analyses. We monitored nests during regular surveys and recorded timing of egg laying (or infrequently floated eggs when we found completed clutches), incubation, and clutch fate (i.e., successfully hatched at least one egg or failed). Observers monitored broods in a similar

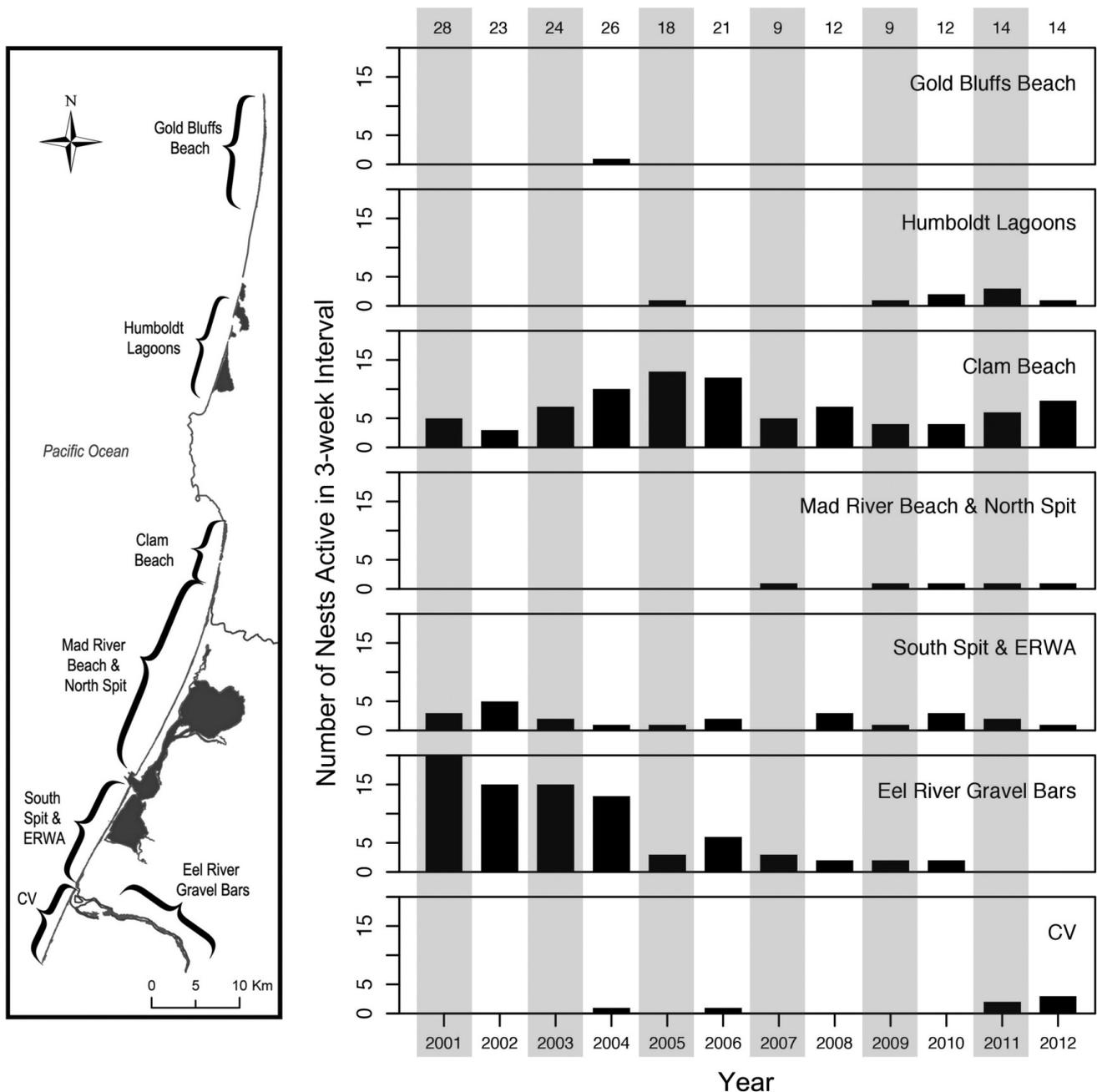


Fig. 1. Annual variation in the number of Snowy Plover nests at 7 sites in Humboldt County, CA. Histograms show active nests during the 3-week interval (21 May–10 June), 2001–2012. Sample sizes shown at top.

manner by relocating broods tended by adults until we determined that young had either fledged or failed to survive to 28 days. Colwell *et al.* (2010, 2017) provide details on field methods. We conducted research under permits (USFWS permit TE-823807-3, USFWS Federal banding permit #22971, California Department of Fish and Wildlife collecting permit #801059-03, State Parks collecting permit #09-635-002, Humboldt State University IACUC #11/12.W.12-A).

Data summary and analysis

We analyzed data for nest locations based on males. We focused on males only because: (1) pairs share a nest and,

therefore, data from females are not independent of the sample for males; and (2) males are thought to choose the coarse-scale nest site, whereas females choose the actual nest when they lay their first egg (Colwell 2010). Additionally, males are easier to monitor because they are responsible for most care of chicks (Page *et al.* 2009).

Given the 4-month egg-laying season and frequent re-nesting by individuals, we analyzed a subset of nests, from a 3-week interval (21 May–10 June). We chose these dates *a priori*, based on the peak of breeding, which coincides with the annual region-wide population survey (USFWS 2007). For each year, we limited the sample of nest locations to one per individually marked male; if a

male had multiple breeding attempts during this 3-week interval, we selected the nest initiated nearest the interval midpoint. We summarized breeding activity over this 3-week period to maximize our sample size while maintaining a single nest (observation) for each breeding male in the population. Additionally, this interval ensured that our sample included virtually all breeding males in the study area ($76 \pm 14\%$ of males), while not double-counting any males (see below). We defined a nest as a scraped depression containing egg(s) or, in a few instances (4.8%; 10/210 attempts), newly hatched chicks. Each observation (nest) had unique UTM coordinates that we used to measure distance (m) to nearest conspecific nest in a geographic information system.

When multiple unmarked males bred in an area, we determined that there were two different males if their nests were active at the same time or if less than 5 days had elapsed between the failure (or fledging) of one nest and initiation of the other (following Stenzel *et al.* 2011). When we could not determine the male tending a nest ($n = 18$ nests; 0–7 nests per year), we removed the datum from the analysis, which ensured one nest per individual. Removing those males had minimal effect on results (Patrick 2013).

We assessed the extent to which plovers nested in an aggregated pattern by comparing nearest neighbor distances (m) of nests with those of random points placed within suitable habitat. We defined suitable habitat as any linear stretch of ocean-fronting beach or riverine gravel bar that was sparsely vegetated (Patrick & Colwell 2014). We delineated suitable habitat from National Agriculture Imagery Program (NAIP) images of the study areas taken in 2005, 2009, and 2010, using a supervised classification in ERDAS IMAGINE 11 (ERDAS Inc, Norcross, GA). See Patrick (2013) and Leja (2015) for details on supervised classification of substrates and vegetation in the study area.

We used ArcMap 9.3 (ESRI, Redlands, CA) to plot nests and random locations for each of the 12 years separately. We converted suitable habitat to a multi-part polygon, which we populated with random points, equal to the number of nests. Random points were always >20 m from their nearest neighbor (i.e., the minimum distance observed) to mimic the natural spacing of plover nests in our study area (Patrick 2013). We generated random points for 2001–2007, 2008–2009, and 2010–2012 from an image taken coincident with data collection (images from 2005, 2009, and 2010, respectively).

Using nest and random locations, we derived an index of aggregation based on a statistical argument derived from a Kolmogorov-Smirnov test (R Development Core Team 2011). For each year, we ran 2,000 iterations in which we plotted random points equal in number to the sample of nests, and then compared the distribution of these distances with those of nests. The index of aggregation was the number of times (out of 2,000 comparisons) in which the distance between real nests fell outside the upper 95% confidence interval of the distribution of distances between random points.

To evaluate annual variation in the index of nest aggregation, we used an information-theoretic approach (Burnham & Anderson 2002) to examine the relationship between four predictor variables and the index of aggregation (i.e., K-S test result described above). Predictor variables were: (1) population size (i.e., number of breeding adults), (2) percent naïve individuals (i.e., breeding for the first time; Nelson 2007), (3) percent of population breeding on gravel bars of the Eel River, and (4) a null case (intercept only). We excluded models containing both population size and percent gravel bar, as those variables were highly correlated ($r = 0.72$). We used Akaike's Information Criterion for small sample sizes (AIC_c) to rank candidate models. The full model was over-dispersed ($\hat{c} = 161.12$), so we calculated quasi-binomial models and quasi- AIC_c (QAIC_c). We evaluated the strength of the top model using model weight (w_i), confidence intervals of parameters, and percent deviance explained (i.e., $100 \times (\text{null dev} - \text{model dev}) / \text{null dev}$). To further evaluate the influence of population size, we conducted a *post hoc* analysis and excluded from analysis one year (2009) with low population size ($n = 19$ breeding adults).

Finally, we examined whether individual males were consistent in their tendency to nest near conspecifics over multiple years, as indexed by a repeatable distance to nearest nest. We calculated repeatability (intraclass correlation coefficient; Lessells & Boag 1987) for \ln -transformed nearest neighbor distance of males ($n = 43$) that bred in the study area during the 3-week interval for two or more years. We conducted statistical analyses using Program R (R Development Core Team 2011).

RESULTS

Over 12 years, observers found 620 nests in the study area, of which 210 (9–28 per year) were active within the 3-week interval of peak breeding (Fig. 1). Overall, plovers nested an average of 1,284 m (SD = 4,019 m, median = 182 m, range = 20–41,519 m, $n = 210$) from conspecifics; 19% of nests were within 100 m of a conspecific nest (Fig. 2). On beaches, plover nests were spaced farther apart (mean = $1,840 \pm 5,024$ m, $n = 129$) than on gravel bars (mean = 399 ± 721 m, $n = 81$). When we restricted analyses to a smaller study area where most plovers bred (Clam Beach; Fig. 1), average distance was 551 m (SD = 931, median = 180 m, range = 20–4,413 m, $n = 84$); 24% of nests occurred within 100 m of a conspecific nest.

In most years, plovers nested in an aggregated pattern; the one exceptional year was 2009 when population size reached a nadir of 19 and most plovers bred on ocean-fronting beaches (Fig. 3a, b). Although the degree of aggregation varied annually, in most years, the probability arguments derived from the K-S test greatly exceeded the 95% criterion (Fig. 3a, b). Annual variation in aggregation index was best explained by population size, driven by the 2009 datum. In the top model, with 81% of the weight and 85% deviance, population size was the only explanatory variable (Table 1). During years of higher population size, plovers tended to nest nearer

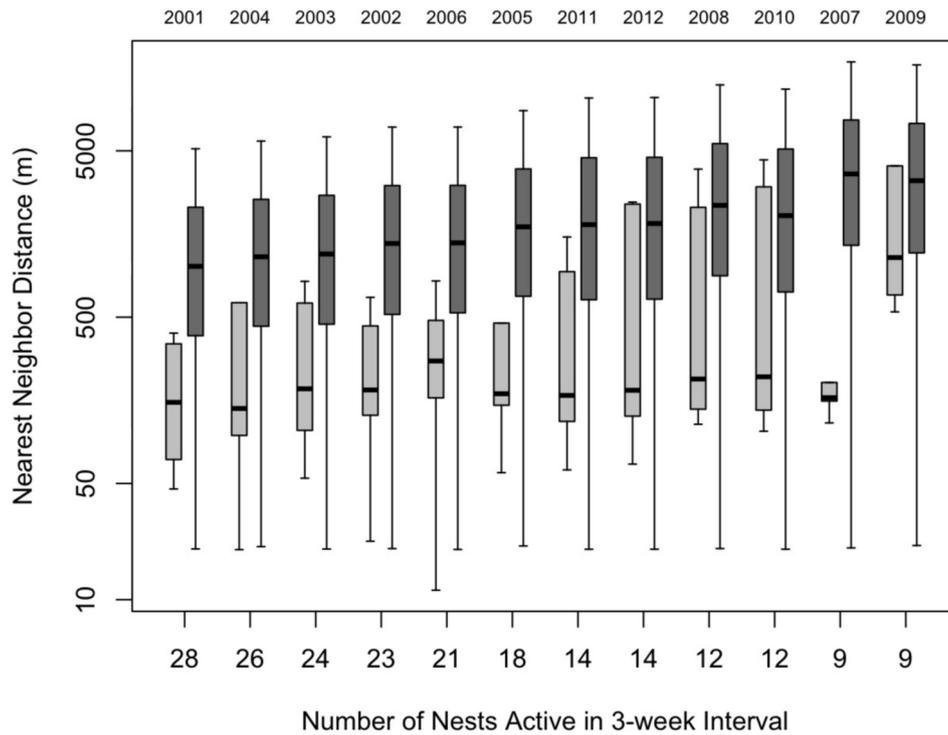


Fig. 2. Boxplots showing distribution of nearest neighbor distances for observed Snowy Plover nests (light grey boxes) and random nests (dark grey boxes) in each year (indicated above figure panel). Years are ordered on x-axis by the number of nests active in the 3-week interval (21 May–10 June). Boxes indicate median and 25th–75th percentiles; whiskers represent maximum and minimum values, not including outliers (not shown).

one another ($\beta = 0.208$, 95% CI = 0.094–0.322). After removing the datum for 2009, the top model, with 95% of the weight and 82% deviance, was percentage of the population breeding on the Eel River gravel bars. The dispersion pattern for nests was more aggregated when a greater proportion of the population bred on gravel

bars ($\beta = 0.061$, 95% CI = 0.037–0.085), which is evident in the closer proximity of nests there (see above).

There was little evidence that the 43 males with reproductive histories spanning 2–10 years were consistent in their tendency to nest near conspecifics (Fig. 4). The overall repeatability was low (intraclass correlation coefficient =

Table 1. Models predicting degree of aggregated nesting of Snowy Plover 2001–2012, ranked according to QAIC_c value.

Model	K	logL	QAIC _c	ΔQAIC _c	w _i
Population size	3	−4.35	17.71	0	0.81
%Naïve + Population size	4	−3.53	20.78	3.08	0.17
Population size + %Naïve + %Gravel bar	5	−3.28	26.57	8.86	0.01
%Naïve + %Gravel bar	4	−6.60	26.92	9.21	0.01
%Naïve	3	−12.12	33.23	15.53	0
%Gravel bar	3	−24.14	57.28	39.57	0
Null	2	−27.73	60.79	43.08	0

K: number of parameters in the model.

QAIC_c: Akaike's Information Criterion with small sample size correction and quasi fit.

ΔQAIC_c: difference in AIC_c value between each model and the top model.

w_i: QAIC_c weight; the proportion of total weight that can be attributed to an individual model.

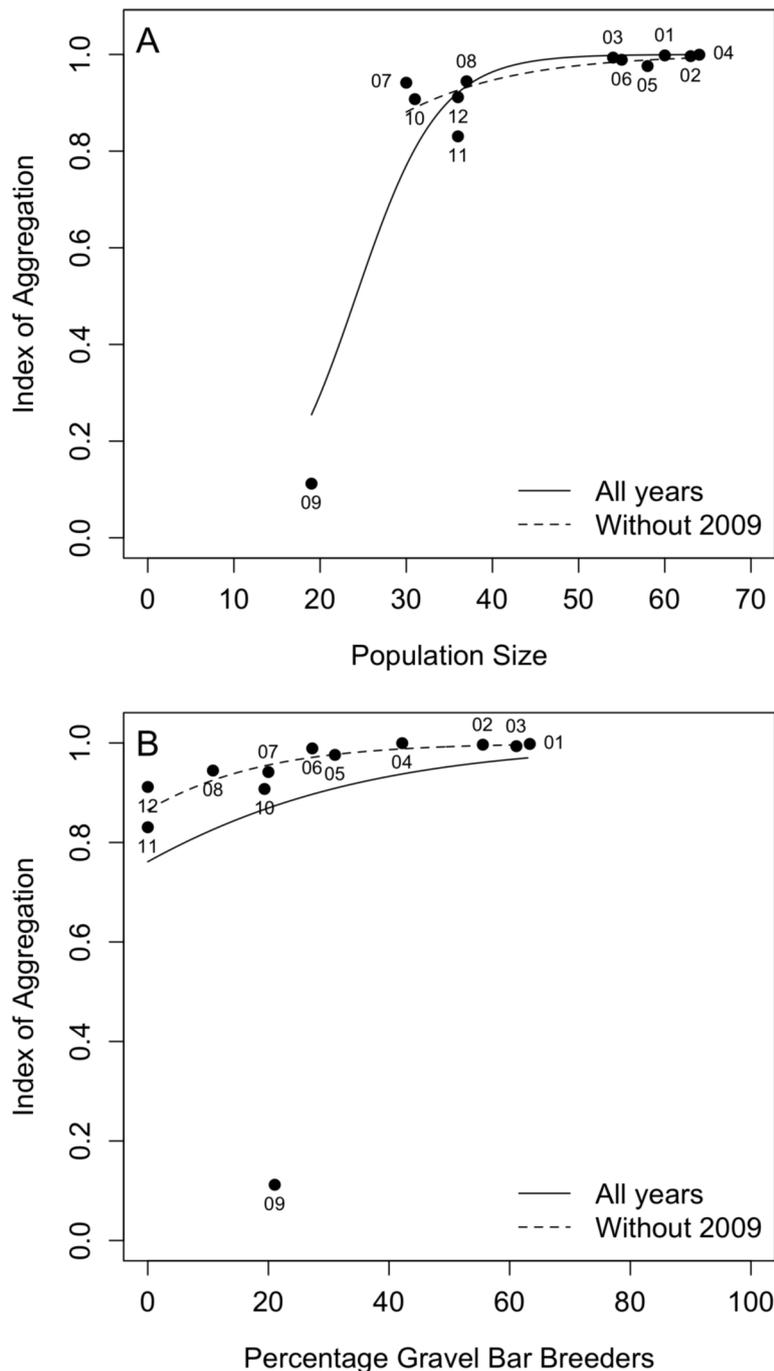


Fig. 3. (A) The index of aggregation (proportion of Kolmogorov-Smirnov tests where nests were more aggregated than by chance) predicted by population size in all years (solid line) and when 2009 was excluded (dashed line). **(B)** The index of aggregation predicted by the percentage of the population that bred on the Eel River gravel bars in all years (solid line) and when 2009 was excluded (dashed line).

0.17; $F_{42,100} = 1.66$, $P = 0.02$). There was no correlation between the number of years an individual bred locally and average nearest neighbor distance (Pearson's correlation, $r = -0.03$, $t = -0.19$, $P = 0.85$, $df = 41$).

DISCUSSION

Our quantitative assessment of distance to nearest conspecific nest indicates that Snowy Plovers in our study

population bred in an aggregated pattern (Stamps 1988), in which large stretches of suitable habitat remained unoccupied (Patrick & Colwell 2014, Leja 2015). In their assessment of spacing patterns and social organization, Page *et al.* (2009) described Snowy Plovers as defending breeding territories. They acknowledge, however, that it is unlikely that food resources are the cause of this spacing pattern because individuals commonly feed several km from their breeding locations. While we suspect that this

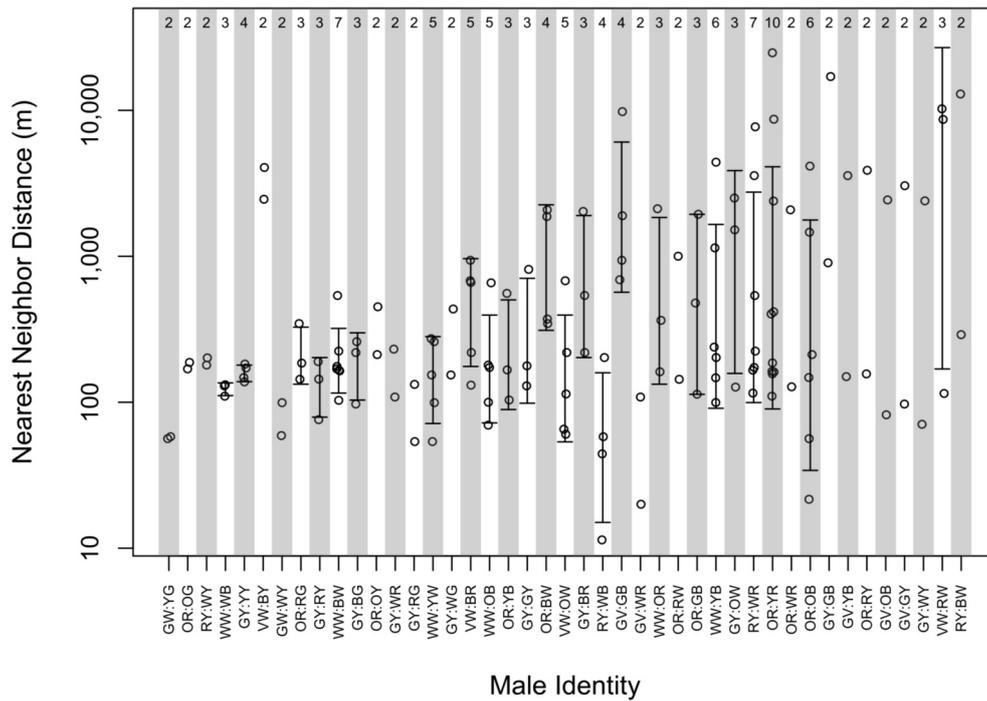


Fig. 4. Individual variation (arranged from smallest to largest) in nearest neighbor distances (open circles) for 42 individually marked male Snowy Plovers that bred for 2–10 years in Humboldt County, CA. Males are identified by their colored leg bands (left top, left bottom: right top, right bottom). Sample sizes of nests for each male are shown at the top. Error bars are ± 1 standard deviation.

description is generally accurate, we think that a better descriptor of the social system is required. Defense of space in the immediate vicinity of the nest is the extent to which plovers are territorial. In dense breeding aggregations, we suspect that agonistic interactions occur frequently between conspecifics, especially at the time of nest site selection (Colwell 2010).

Several important findings emerge from our findings. First, the aggregated pattern prevailed in 11 of 12 years across approximately 100 km of suitable habitat near the northern limit of the species' range where population size is low (Eberhart-Phillips *et al.* 2015). Second, large extents of suitable habitat remained unoccupied in most years (Fig. 1; Patrick & Colwell 2014, Leja 2015). Finally, our results offer important insight to guide management and conservation actions for this federally listed species, and other taxa that may form loose breeding aggregations.

Spatial and temporal variation

The aggregated pattern of nests is noteworthy given that we studied plovers near the northern limit of the species' range (Page *et al.* 2009, Eberhart-Phillips *et al.* 2015). Theory predicts that abundance should be lowest near range limits (Sexton *et al.* 2009). Plover abundance along the northern California coast is the lowest observed for various segments of the listed population segment (Eberhart-Phillips *et al.* 2015). Given the strong relationship between aggregation and population density (Table 1), and low abundance in our study area, we predict that

applying the same metrics to plovers breeding near the core of their range (e.g., southern California) would produce even stronger evidence of aggregation. Given that the Pacific coast population of the Snowy Plover is threatened, population sizes may be well below carrying capacity. However, the strength of the relationship between population size, availability of suitable habitat, and degree of aggregation remains unknown, and should be quantified elsewhere in the species' range where populations breed at higher densities.

Our 12-year study showed that plovers nested in an aggregated pattern in most years; the one exception was the year when the population declined to its lowest point (Colwell *et al.* 2017). Model results showed that population size was the strongest predictor of the aggregated pattern. This result emphasizes the importance of long-term studies in detecting ecological patterns; had we not monitored the population at its nadir, we would not have obtained the strong result between population size and aggregation.

Habitat quality, whether measured directly or indirectly (Morrison *et al.* 2006), likely influenced the nesting dispersion pattern in the population each year. Our *post hoc* analysis that eliminated the single influential year (2009) produced a result that suggested that the habitat effect of the gravel bars may have influenced our initial result. Specifically, gravel habitats are consistently higher quality (e.g., per capita fledging success) than ocean-fronting beaches (Colwell *et al.* 2010, Herman & Colwell 2015).

As a result, individual plovers may have opted to nest in denser aggregations on gravel bars because of social attraction and information conveyed by the presence of adults tending eggs or chicks. Earlier, unpublished work (Nelson 2007) suggested that conspecific attraction influenced nearest neighbor distance in this population. If habitat quality was influential, then we would predict that plovers still bred in high densities on gravel bars. In recent years, however, the population ceased breeding in these high quality habitats, subsequent to the population nadir of 19 adults. Since then, the population has increased to the number (72 adults) present early in our study. However, no plovers have bred in these high quality gravel substrates since their local extirpation in 2011 (Colwell *et al.* 2017). Finally, while acknowledging the effect of habitat quality in the dispersion pattern, our analysis was conducted at the level of the population, with each year a datum. Precisely how habitat affects where individuals choose to breed remains an open question. Spatial extent of a study can influence detection of dispersion pattern (Krebs 1999). Over the 17 years that we have conducted research on the local population of plovers, our principal research objective was to monitor population growth (Colwell *et al.* 2010, 2017, Mullin *et al.* 2010); we did this across nearly 100 km of beach and riverine habitats, which was an order of magnitude larger than other studies of Snowy Plovers. Consequently, we detected more 'solitary' individuals, greater average distances between nests, and higher variances in nest proximity ($1,841 \pm 5,024$ m) than reported from elsewhere in the species' range (Page *et al.* 1983, Paton & Bachman 1996, Powell 2001, Saalfeld *et al.* 2012). For a direct comparison, Saalfeld *et al.* (2012) used similar methods (i.e., analysis of nearest nest) to quantify average distances of 144 m (range: 6–1,811; 57% within 100 m of a conspecific) between plover nests along several km of saline lakeshore in Texas. These and other estimates (see Page *et al.* 2009 for details) are considerably smaller than the distances we recorded. We strongly suspect that the larger spatial extent of our study accounted for these differences. Accordingly, we restricted the spatial extent of analysis to an 8-km beach (Clam Beach) where plovers consistently bred at higher densities (Fig. 1). This analysis produced an average nearest neighbor distance of ~550 m (vs. 1,284 m for the entire study area), with a greater percentage (24% vs. 19%) of nests within 100 m of a conspecific. Elsewhere, Nelson (2007) showed that naïve plovers opted to nest nearer experienced individuals along this same stretch of beach, which provides insight into behaviors influencing nesting aggregations.

Although the dispersion pattern of the population was nearly always aggregated, individuals varied greatly (i.e., repeatability was low) in their tendency to nest near conspecifics. This result contrasts with evidence for other species (e.g., Barn Swallow *Hirundo rustica*; Møller 2002) showing a heritable nature of 'sociality'. However, our result is similar to that reported for Black Kites *Milvus migrans* (Sergio & Boto 1999), in which individuals occasionally (10%) switched between nesting solitarily or in

loose aggregations. Repeatability may be sensitive to the scale at which proximity is measured (see above), interacting with the nature of the social system (i.e., the degree to which territories are defended). In plovers, the low repeatability of distance to nearest conspecific and strong population-level effects suggest that individuals have little control over this facet of sociality. Perhaps this is not surprising given that proximity (and the resulting pattern of dispersion) arises from the timing of choice of breeding site and complex nest site selection behaviors, which are poorly studied in shorebirds (Colwell 2010). For instance, plover courtship begins with scraping behavior as pairs search within suitable habitat for a nest location where a female lays her first egg. Once a female has laid an egg, however, the pair has little option (other than aggression) to influence a conspecific seeking to nest nearby. The annually variable spatial pattern and evidence of low repeatability for individuals suggest that aggregated nesting is an artifact of population size rather than a product of rigid behavioral differences among individuals.

Conservation implications

Our findings have value in conservation of this federally threatened species. First, estimates of breeding density (derived from areas where a species aggregates) are sometimes used to estimate population size; densities are extrapolated to un-surveyed habitats to produce an estimate. For example, Long *et al.* (2008) used estimates of breeding density for Black-banded Plover *C. thoracicus* coupled with an estimate of suitable habitat to extrapolate a total population size of 3,100. However, Black-banded Plovers may also have a patchy distribution, although the social system is poorly known. For Snowy Plovers, the patchy distribution, highly variable densities, and absence of plovers from suitable breeding habitats (Patrick & Colwell 2014, Leja 2015) suggest caution when extrapolating from local densities to estimate total population size.

Second, an aggregated breeding pattern may have consequences for the effectiveness of management practices. In our study area, management actions have attempted to restore habitat with physical features attractive to Snowy Plovers (Patrick & Colwell 2014, Leja 2015). However, if plovers use conspecifics to prospect for breeding sites (Rioux *et al.* 2011), then restoration of physical habitat features may not attract individuals if conspecifics are not present (Nelson 2007).

Finally, aggregated breeding (i.e., high nest density) may have consequences for vital rates that drive population growth. If predators forage in a density-dependent manner (i.e., develop a search image), then one would predict that reproductive success of plovers may be reduced in areas of high nest density. Page *et al.* (1983) tested this hypothesis experimentally (using artificial nests with eggs of quail *Coturnix coturnix*) at Mono Lake, CA. Snowy Plover nest densities were greater than those we report, based on experimental treatments of 1, 20 and 40 nests per 6 ha; however, nest survival decreased with higher nest density. Consequently, areas of high breeding density

may require special management actions (e.g., lethal predator control, nest exclosures) to maintain high productivity, which is necessary for recovery of threatened or endangered taxa such as the Snowy Plover. Moreover, they illustrate the value of linking ecological patterns (e.g., dispersion) with an understanding of causes of variation in productivity for rare species. This latter relationship deserves further study.

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