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RESEARCH ARTICLE

Hatch-year Piping Plover (*Charadrius melodus*) prospecting and habitat quality influence second-year nest site selection

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ABSTRACT

Juvenile prospecting, or exploratory behavior for gleaning information about areas or events, can have profound effects on the selection of future breeding habitat, particularly for birds with high site fidelity whose initial choice of breeding habitat could represent a lifetime investment in fitness. We present data from a 10-yr study of Piping Plovers (*Charadrius melodus*) on the Missouri River, USA, to determine whether postfledging, hatch-year (HY) prospecting movements inform second-year (SY) nest site choices. First, we compared the home ranges of HY and adult (after-hatch-year; AHY) plovers to investigate whether differences in habitat use existed between HY and AHY plovers. Second, we evaluated the effects of prospecting, nest density, reproductive success, and nesting and foraging habitat availability on SY plover nest site selection. Lastly, we evaluated the potential reproductive benefits of nesting in prospected areas by comparing the nest success and fledging success of SY plovers that nested within their HY prospecting range with the success of those that nested in presumably unexplored areas. Plover home ranges varied across ages and among years. Both HY and AHY plover home ranges were smaller when the proportion of foraging habitat in the home range was relatively high, compared with nonforaging habitat. Second-year plovers selected sandbars that they had prospected as HY birds more often than would have been expected if nest site selection were random. Second-year plovers also selected sandbars on which other plovers experienced higher average nesting success than on random nesting locations, but we found no evidence that individual SY birds that nested on prospected sandbars had higher reproductive success than individuals that nested in unexplored areas. Coupled with high adult site fidelity, affinity of plovers for sandbars where they experience relatively high average reproductive success could lead to long-term gains in fitness.

Keywords: Charadrius melodus, Piping Plover, prospecting, natal dispersal, home range, habitat selection

La exploración y la calidad del hábitat en el año de eclosión afectan la selección del sitio de anidación en el segundo año en *Charadrius melodus*

RESUMEN

El comportamiento de exploración en los jóvenes para recolectar información sobre áreas o eventos puede tener efectos profundos en la selección de futuros hábitats de reproducción, particularmente en aves con alta fidelidad al sitio para las cuales la selección inicial de un hábitat reproductivo puede afectar su aptitud durante toda la vida. Presentamos datos de un estudio de 10 años sobre *Charadrius melodus* en el río Missouri para determinar si los movimientos de exploración del primer año (PA) proveen información sobre los sitios de anidación del segundo año (SA). Primero, comparamos las áreas de hogar de aves de PA y adultas (de más de un año, MUA) para investigar si existían diferencias en el uso del hábitat entre aves de PA y de MUA. Segundo, evaluamos los efectos del comportamiento de exploración, la densidad de nidos, el éxito reproductivo y la disponibilidad de hábitat para forrajeo y reproducción en la selección de sitios de anidación por parte de aves de SA. Finalmente, evaluamos los beneficios reproductivos potenciales de anidar en áreas exploradas comparando el éxito de los nidos y de emplumamiento entre aves SA que anidaron en su área de exploración de PA y aves que anidaron en áreas presuntamente no exploradas. El área de hogar de *C. melodus* varió entre clases de edad y año de seguimiento. Las áreas de hogar de aves de PA y de MUA fueron más pequeñas cuando la proporción de hábitat de forrajeo en ellas mismo fue relativamente alta, comparado con hábitat de no forrajeo. Las aves de segundo año seleccionaron más frecuentemente bancos de arena que exploraron cuando eran de PA de lo que se esperaría si la selección del sitio de anidación fuera al azar. *C. melodus* seleccionó bancos de arena con mayor éxito de anidación promedio que los sitios de anidación al azar, pero no encontramos evidencia de que las aves de SA que anidaron en bancos de arena previamente explorados tuvieran mayor éxito reproductivo que los individuos que anidaron en áreas no exploradas.

Considerada junto con la alta fidelidad al sitio de los adultos, la afinidad de las aves de SA por bancos de arena con éxito reproductivo relativamente alto podría conducir a ganancias en la aptitud a largo plazo.

Palabras clave: áreas de hogar, *Charadrius melodus*, comportamiento de exploración, dispersión natal, selección de hábitat

INTRODUCTION

Breeding habitat selection is a critically important life history choice that affects individual fitness, community and population dynamics, and gene flow (Clobert et al. 2001). Important components of habitat selection include home range (Choi et al. 2014), site fidelity (Warnock and Takekawa 1996), and space use within a home range (Plissner et al. 2000, Gabbard et al. 2001), which are metrics that may be static in the short term, but can be dynamic across seasons or years, and may vary among individuals and by sex and age (Burt 1943).

In many species, juveniles engage in prospecting behavior, whereby they gather information about areas or events that they may use to inform habitat selection (Reed et al. 1999). This exploratory behavior allows individuals to find, assess, and settle in high-quality habitat, which may yield fitness benefits, including increased survival and fecundity (Ponchon et al. 2012, Saunders et al. 2012, Burkhalter et al. 2015). For birds with relatively high breeding site fidelity, information gained during a juvenile prospecting period could have lasting effects on breeding site selection and lifetime fitness. Indeed, theoretical prospecting models have shown that informed dispersal, or breeding in previously explored habitat patches, is a more adaptive strategy than random settlement (Boulinier and Danchin 1997).

When spatial variation in habitat quality exists, birds may use predictive cues detected during prospecting to assess habitat and choose optimal breeding sites (Cody 1985). Recent work suggests that nonbreeding birds use public information (Danchin et al. 2004), including the presence and density of conspecifics (Doligez et al. 2004a, 2004b) and conspecific reproductive success at explored sites, to assess habitat quality and inform nest site selection (Schjorring et al. 1999, Boulinier et al. 2002, Pärt and Doligez 2003, Doligez et al. 2004a, 2004b, Calabuig et al. 2010, Rioux et al. 2011). For juvenile birds, the postfledging period may be an effective time to explore potential territories and maximize the information gained, because public information from conspecifics is likely to be readily available during this time (Danchin et al. 2004). Despite the costs of decreased survival and increased competition for resources at prospecting locations (Furness and Birkhead 1984, Johnson 1989, Reed et al. 1999, Ponchon et al. 2012, Bosman et al. 2013), juveniles can increase their exposure to important habitat quality and conspecific public information by expanding their home ranges to prospect potential breeding habitat patches, and thus inform their future breeding habitat selection, possibly increasing fitness (Furness and Birkhead 1984). However, few studies have investigated whether juvenile prospecting behavior is related to juvenile home range size, or whether it accurately predicts their subsequent nest site selection and reproductive success as first-time breeders (Pärt et al. 2011).

Here, we present data from a 10-yr study of Piping Plovers (*Charadrius melodus*) on the Missouri River, USA, to determine whether second-year (SY) Piping Plovers nest more frequently in areas that they prospect as hatch-year (HY) birds than would be expected if selection were random. Because of the potential importance of HY prospecting, we hypothesized that HY Piping Plovers would explore a longer stretch of river than adult (after-hatch-year; AHY) plovers. Important habitat features, including nesting and foraging areas, are also likely to influence the selection of prospecting locations, as well as eventual nesting sites. In addition, locations visited during the HY prospecting period, and subsequently selected as nest sites, might be influenced by public information, such as conspecific presence, density, and reproductive success. Therefore, we hypothesized that habitat features and public information would influence home range length (length of river explored) and selection of nest sites. Lastly, if HY prospecting were to be an adaptive strategy, then SY plovers ought to nest in prospected areas, and this behavior should confer some benefit on prospectors vs. nonprospectors, such as increased reproductive fitness (i.e. survival, fecundity, lifetime reproductive success, and survival of offspring). Therefore, we hypothesized that SY breeders would nest in prospected locations more often than in random locations, and that birds that nested within their prospecting range would have increased reproductive success.

Due to the difficulty of distinguishing prospecting behaviors from other postfledging behaviors, we defined potential prospecting generally. Any occasion during which a plover was seen as a HY bird (25+ days posthatching; Catlin et al. 2013) was classified as a potential prospecting event, regardless of whether it occurred on a natal or other sandbar. We assumed that if prospecting occurred, then individuals gathered information about their surroundings at all times, and that any of this information could contribute to a site being "accepted" or "rejected" as a future nest site (Reed et al. 1999, Piper 2011).

Our study addressed the following 4 objectives: (1) to identify whether HY prospecting sites (sandbars) are selected as SY nesting sites; (2) to determine whether potential HY prospecting drives variation in habitat use (home range length and composition) between HY and AHY birds; (3) to investigate the effects of habitat type and availability and public information on SY nest site selection; and (4) to assess whether prospectors have higher reproductive success than nonprospectors.

METHODS

Study Species

On the Great Plains, USA, Piping Plovers nest on sparsely vegetated sandbars and lakeshores (Gaines and Ryan 1988, Espie et al. 1996). In our system, plovers nest only on sandbars in the river, due to heavy vegetation along the shoreline and riverbank. Among shorebirds, which typically exhibit nest site fidelity, plovers show a particularly high degree of nest site fidelity (>90% in our system; LeDee et al. 2010, Cohen and Gratto-Trevor 2011, Catlin et al. 2015, Friedrich et al. 2015). In addition, their reproductive output and survival are positively related to foraging and nesting habitat quality (Catlin et al. 2014, 2015).

Study Area

We studied plovers on the Missouri River below the Gavins Point Dam (42.861943°, –97.485341°) and on Lewis and Clark Lake (42.847449°, –97.708539°). The Gavins Point Reach of the Missouri River (hereafter "GVP") is a 95-km stretch downstream of the Gavins Point Dam and is one of the last free-flowing, unchannelized portions of the river. The Lewis and Clark Lake (hereafter "LACL") study area is a network of sandbars that extends ~27 km upriver of the reservoir impounded by the Gavins Point Dam. Approximately 30 km of open water with unsuitable plover habitat separates the LACL and GVP breeding areas. At both locations, plovers nest on sparsely vegetated and/or unvegetated midchannel sandbars. On GVP, there were 13–45 sandbars on which plovers nested between 2006 and 2013, and during the same study period there were 0–12 sandbars on which plovers nested on LACL. Sandbars varied in size (<1 ha to >140 ha), habitat composition (e.g., dry sand, wet sand, vegetation cover), and habitat quality (Catlin et al. 2011, 2015).

Field Methods

During the nesting seasons (late April–late July) of 2006–2013, we searched sandbars for Piping Plover nests by walking transects through potential nesting habitat (unvegetated and sparsely vegetated wet and dry sand habitat) and by observing AHY plover behavior. We recorded nest locations using a handheld Trimble GPS unit (Trimble Navigation, Sunnyvale, California, USA), and estimated incubation stage and nest initiation date by floating at least 1 egg from each nest (Westerskov 1950, Catlin et al. 2011). We checked nests every 2–3 days until hatching or failure. We attempted to identify the AHY plovers associated with each nest by recording the band combination of each AHY that was trapped on the nest or observed incubating eggs or brooding chicks (Catlin et al. 2015).

We captured chicks 0–20 days posthatching and individually marked each one ($n = 2{,}053$) with color bands and a uniquely coded green flag. In most cases, initial capture occurred in or near the nest bowl, but in cases in which the chicks had left the nest area, we determined nest association by the presence of banded parents (Catlin et al. 2011). We attempted to recapture or resight broods every 2–3 days until fledging (~25 days posthatching; Hunt et al. 2013).

We surveyed GVP and LACL sandbars throughout the breeding seasons (April–August) of all years except 2010 and 2011 to locate and identify uniquely marked plovers. In 2010 and 2011, high releases from Gavins Point Dam inundated all of the downriver nesting and foraging habitat by May (2011) and June (2010) through to the end of the season, and thus no chicks were produced on GVP, but chicks were produced on LACL (Catlin et al. 2015). We surveyed sandbars every 2–3 days throughout the breeding season by walking transects across the length of the sandbar, and we recorded location (sandbar), band combination, and age (AHY, HY, or chick) for all plovers that we observed.

Analytical Methods

Home range. Due to the largely linear nature of habitat on the Missouri River and of plover habitat (e.g., shorelines), we expressed plover home ranges as a linear distance to control for differences in home range area produced by river bends and variable river widths (Stumpf and Mohr 1962, Melquist and Hornocker 1983, Catry et al. 2003, Riedle et al. 2006). We compared home range length (length of river used) and habitat composition of HY and AHY plover home ranges to investigate differences between age classes as it related to HY prospecting behavior. We also evaluated the proportional habitat type composition of HY vs. AHY plover home ranges to understand which habitat types were correlated with the home ranges of HY and AHY plovers and nest site selection by SY plovers.

Because straight-line distance lacks an area component, linear distance here corresponds to the length of river used and includes all habitats within the riverbanks. We report the area of different habitat types within the riverbanks of each linear home range. For home range analyses, we used only sightings of birds on GVP and not LACL because a large gap of unsuitable habitat (~30 km of open water) exists between the 2 sites.

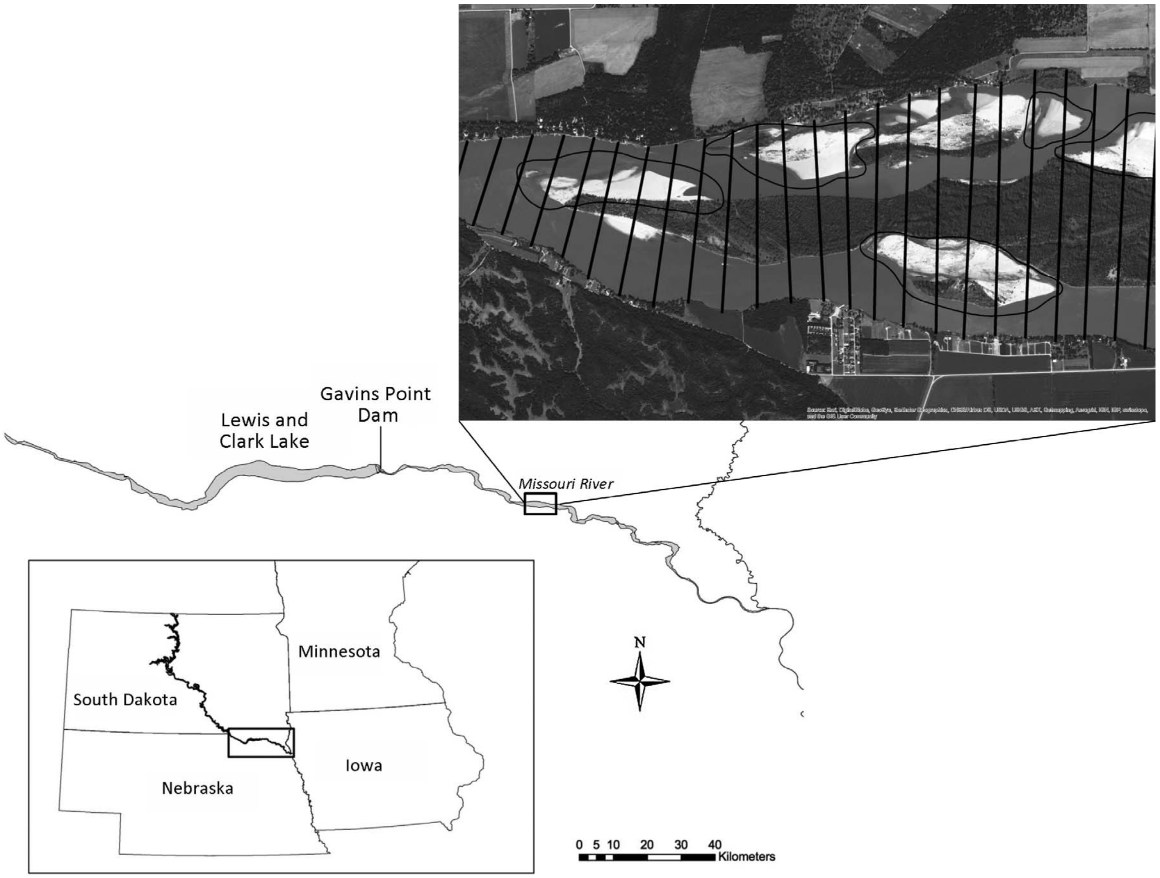

FIGURE 1. Map of the Missouri River, USA (lower left), including the Lewis and Clark Lake (LACL) and Gavins Point Reach (GVP) study areas, where we examined prospecting behavior of hatch-year Piping Plovers in 2006–2013. The satellite image (inset) shows a portion of the GVP study area on the Missouri River. The main river channel was divided into 0.2-km cross-sectional segments, as shown by the black bars. Sandbars are outlined with black polygons.

We traced the riverbanks of the main channel by hand from 2013 satellite imagery of the GVP study area of the river. This created a single polygon that encompassed all of the area within the riverbanks. We divided this polygon into 450 cross-sectional segments, which intersected the main river channel perpendicularly every 0.2 km (Figure 1). We defined a plover's home range length as the distance between the farthest upriver segment and farthest downriver segment used. Plovers observed on only 1 sandbar had a home range length equal to the length of the sandbar. We did not retrace the riverbanks for each year because bank extent in 2013 was representative of other years.

We used land classification coverage maps for the 2006–2013 breeding seasons (between April and October) derived from satellite imagery ('QuickBird' and 'Landsat' [images taken in 2011]) and classified them into different habitat types using Definens Developer Software (L. Strong personal communication). We classified habitat into the following categories: nesting habitat (open and sparsely vegetated [<30%] dry sand), foraging habitat (open and sparsely vegetated wet sand), shrub and scrub (>30% cover, low canopy), tall vegetation (>30% cover, presence of large trees, high canopy), and open water. We divided the total area of each habitat type within each home range by the total area of all habitats in the home range to calculate proportional habitat composition within a plover's home range (farthest downriver to upriver segments) for each year. We used proportions of habitat because home range lengths and cross-section lengths varied among individuals.

We used linear mixed regression to predict the log of the home range length based on age (HY vs. AHY) and habitat composition, with year as a random factor, using PROC NLMIXED in SAS 9.3 (SAS Institute, Cary, North Carolina, USA). We used the log-transformation of home range length as the dependent variable in the regression to improve model fit. All models included a random effect for individual to control for potential nonindependence among home range data for a single individual in multiple years.

We considered the full model, with all variables, as our a priori hypothesis about factors affecting home range length. Therefore, we modeled all predictors and subtracted the factors that had the least effect on home range length. We began modeling with a global model that included year, plover age, proportion of nesting habitat, foraging habitat, short vegetation, and tall vegetation (proportion of water was excluded because it was a linear combination of preceding habitats), and 2 interaction terms: age by habitat class, and age by year. We then repeatedly refit the model after removing the variable with the lowest *F*-value. We continued this process until the Akaike's Information Criterion corrected for small sample bias ($\mathrm{AIC_c}$) value increased (indicating a decrease in model fit); we selected the model prior to this final step as our best model.

Prospecting. We compared sandbars selected by SY plovers for nesting and random sandbars to determine the probability that a sandbar used for nesting had been prospected by a HY plover in the previous year. We looked at the effects of conspecific nest density, conspecific reproductive success (hatching or fledging at least 1 chick), nesting habitat availability (dry sand habitat), and foraging habitat cover (wet sand habitat) to determine the effects of public information on the selection of a first breeding location. Additionally, we examined the reproductive success of individuals that nested within their prospecting ranges vs. the success of those that nested in presumably unexplored areas to determine whether prospectors had higher reproductive success than non-prospectors.

We analyzed plover prospecting behavior using plovers that were seen as a HY bird (t) and subsequently returned to nest as a SY bird ($t+1$) because their nest site selection was unaffected by a prior mate, nest success, or other factors from a previous breeding season. Each individual had at least 1 prospecting sandbar (all sandbars on which it was observed as a HY bird in year t), a nesting sandbar (the sandbar on which the plover nested as a SY bird in year $t+1$), and a randomly selected, paired sandbar from the sandbars available for nesting in year $t+1$. We constrained random sandbar selection to include only sandbars on which plovers nested (at least 1 nest in years t and $t+1$) to ensure that only known suitable nesting locations were sampled and that sandbars were observable in both years t and $t+1$.

We used the area (ha) of wet sand and dry sand on each sandbar to estimate wet sand (foraging habitat) nest density and dry sand (nesting habitat) nest density, respectively. We calculated nest density (nests per ha) for each of the habitat types on sandbars selected for nesting and randomly selected sandbars. We included habitat area and nest density in each individual's prospecting year (t) and breeding year ($t+1$) to predict the effects of these factors on the individual's habitat selection in year $t+1$.

We used logistic regression to estimate the probability that the sandbar selected as the SY nesting location had been prospected during the HY prospecting period vs. had been randomly selected. We modeled the effects of the following variables on plover nest site selection: (1) reproductive success of conspecifics, including nest success (success defined as nests that hatched at least 1 chick) and fledging success (success defined as at least 1 chick surviving to fledging [25 days]), at sandbars used for nesting and random sandbars in the prospecting year (t) and nesting year ($t+1$); (2) nest density of conspecifics at sandbars used for nesting and random sandbars in years t and $t+1$; and (3) nesting and foraging habitat availability at sandbars used for nesting and random sandbars in years t and $t+1$. To control for any effects of natal philopatry or avoidance and nesting year, we included the following variables in all models: (1) natal sandbar ("1" if the sandbar used for nesting or randomly selected sandbar was an individual's hatching location and "0" otherwise); and (2) nesting year ($t+1$; 2007–2013). We compared 8 models, including a global and a null (intercept-only) model, each of which represented an a priori hypothesis regarding the influences on plover nest site selection (Table 1).

Natal dispersal in plovers is distance-dependent, meaning that a negative correlation exists between dispersal probability and distance; thus, exploratory forays and subsequent nest site selection are usually limited to areas surrounding a plover's natal sandbar (Catlin et al. 2015, 2016). Comparing nest site selection using a paired, randomly selected sandbar from the entire study area could erroneously inflate an effect of prospecting if plovers do not explore the entire length of the study area. To address this issue, we used logistic regression to model the probability that a sandbar used for nesting had been prospected using a subset of plovers that nested within their prospecting range (i.e. between the farthest upriver and downriver sandbars at which the plover was observed during the HY prospecting period in year t). For each of these individuals ($n = 29$), we compared the nesting location with randomly selected sandbars that were available for nesting within the range that an individual explored as a HY bird. This was a more conservative analysis than the analysis of the full dataset, because HY prospectors likely were aware of most, if not all, sandbars within their prospecting range, but we may not have observed all of these prospecting movements.

Because plover dispersal is usually limited to areas surrounding natal sandbars, and we defined HY plovers observed on natal sandbars as prospectors, we included an additional analysis to ensure that plovers that nested on their natal sandbars ("natal nesters") did not drive any effects of prospecting. We used our best-supported model from the analysis of the full dataset to examine whether the

TABLE 1. A priori hypotheses and variables predicting nest site selection of Piping Plovers on Lewis and Clark Lake (LACL) and the Gavins Point Reach (GVP) of the Missouri River, USA, 2007–2013.

Model	Variables included [a]	A priori hypotheses
Global	Prospected + Nest success$_{t,\ t+1}$ + Nesting density$_{t,\ t+1}$ [b] + Foraging density$_{t,\ t+1}$ [c]	Second-year (SY) plovers used public information, including nest density and nest success of conspecifics, from prospecting and nesting years to inform nest site selection.
Prospecting for public information	Prospected + Nest success$_t$ + Nesting density$_t$ + Foraging density$_t$	Public information gained during the hatch-year (HY) prospecting period influenced SY nest site selection.
Prospecting site familiarity and after-hatch-year (AHY) public information	Prospected + Nest success$_{t+1}$ + Nesting density$_{t+1}$ + Foraging density$_{t+1}$	Prospecting was important for SY nest site selection, but SY plovers also used public information available during their first nesting year to inform nest site selection.
No prospecting information	Nest success$_{t+1}$ + Nesting density$_{t+1}$ + Foraging density$_{t+1}$	SY plovers did not use information gained during the HY prospecting period for nest site selection; only public information from the first nesting year was important.
Prospecting for foraging	Prospected + Foraging density$_{t,\ t+1}$	HY plovers prospected for and subsequently selected sandbars with more foraging area (lower wet sand nest density).
Prospecting for nesting	Prospected + Nesting density$_{t,\ t+1}$	HY plovers prospected for and subsequently selected sandbars with more nesting area (lower dry sand nest density).
Prospecting for reproductive success	Prospected + Nest success$_{t,\ t+1}$	HY plovers prospected for and subsequently selected sandbars with higher rates of reproductive success.
Null	Intercept only	None of the variables modeled were important for SY plover nest site selection.

[a] Nest year (2007–2013) and natal sandbar ("0" if nest sandbar was not natal sandbar; "1" if nest sandbar was same as natal sandbar) variables were included in all models.
[b] Dry sand substrate nest density.
[c] Wet sand substrate nest density.

effect of prospecting changed after removal of natal nesters from the dataset.

We used logistic regression to compare reproductive success, including nest success and fledging success, for SY plovers that nested within vs. outside their HY prospecting range. We controlled for the effects of study area (GVP or LACL) and nest year (2007–2013), and we tested the effect of nesting within a HY prospecting range on the probability of nest success. We included the same predictors in the fledging success analysis and included an additional random effect term to control for nonindependence among brood mates. We tested the fit of each global logistic model with a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989). We used AIC$_c$ and model weights to rank our models (Burnham and Anderson 2002). We used the best single model to produce parameter estimates (β) and to investigate relative effect sizes (β/SE). All analyses were performed in SAS 9.3 with PROC NLMIXED (SAS Institute, Cary, North Carolina, USA). We present means ± 1 SE unless otherwise noted.

RESULTS

Home Range

We calculated home range lengths for 1,034 plovers over 6 yr ($n = 1{,}630$ annual home ranges). Before testing, we calculated raw values of average home range lengths that did not control for differences among years. Average home range was 10.0 ± 0.5 km for AHY individuals ($n = 1{,}252$) and 7.7 ± 0.6 km for HY individuals ($n = 378$). The average proportions of all measured land cover types were the same between HY vs. AHY home ranges: 0.1 ± 0.0 for nesting (dry sand) habitat, 0.1 ± 0.0 for foraging (wet

TABLE 2. Results of model selection of generalized linear mixed regression of log(home range length) of hatch-year (HY) and adult (AHY) Piping Plovers on the Gavins Point Reach of the Missouri River, USA, 2006–2009 and 2012–2013. Selection began with the fully parameterized model; we removed the variable with the lowest *F*-value and reran the analysis until the Akaike's Information Criterion corrected for small sample bias (AIC_c) value increased. We selected the last model with a lower AIC_c value. All models included a random effect for individual to account for individuals sampled over multiple years. *K* is the number of model parameters, and ΔAIC_c is the difference in AIC_c from the top model.

Model [a]	Step	*K*	Variable removed	ΔAIC_c [b]
Age × (Dry + Wet + Low canopy + High canopy + Year)	1	21	None	0.9
Age × (Dry + Low canopy + High canopy + Year) + Wet [c]	2	20	Age × Wet	0.0
Age × (Dry + Low canopy + Year) + Wet + High canopy	3	19	Age × High Canopy	0.5
Intercept only	4	1	All	387.6

[a] Parameters in the model included age of individual (Age, AHY vs. HY, estimates for AHY individuals) and the proportion of each home range that was dry sand (Dry), wet sand (Wet), low canopy vegetation (Low canopy), and high canopy vegetation (High canopy). The "×" indicates a multiplicative interaction with the variables in the parentheses in addition to the main effects.

[b] The lowest AIC_c value was 5,511.4.

[c] Pseudo-R^2 (Nakagawa and Schielzeth 2013) = 0.22.

sand) habitat, 0.2 ± 0.0 for low canopy vegetation, and 0.1 ± 0.0 for high canopy vegetation.

The global model, including all factors affecting home range length, performed well against the intercept-only model (Table 2). Only the interaction between age and proportion of foraging habitat was removed from the full model before model fit was reduced; indeed, the selected model was only marginally better than the full model (Table 2). We used the selected model to evaluate factors that affected home range length.

Home range length differed by year ($F_{5,579} = 2.2$, $P = 0.05$), age ($F_{1,579} = 7.0$, $P = 0.01$), and the interaction of year and age (year × age; $F_{5,579} = 5.7$, $P < 0.001$; Figure 2). Home range lengths for HY birds were shorter than for AHY birds in 2006 and 2007, similar in 2008, 2009, and 2012, and longer in 2013 (Figure 2). Across ages, home range lengths were longest in 2006 (13.2 ± 1.1 km) and shortest in 2012 (2.5 ± 0.5 km).

Home range length varied in relation to habitat composition, and effects differed between age classes (Tables 2 and 3). Removal of the interaction between age and proportion of foraging habitat indicated that the age classes did not differ in their responses to foraging habitat in their home ranges. Both age classes had shorter home range lengths as the proportion of foraging habitat within a home range increased (β_{Wet}; Table 3). Proportion of nesting habitat within a home range had no relationship with HY home range length (β_{Dry}; Table 3), but AHY home

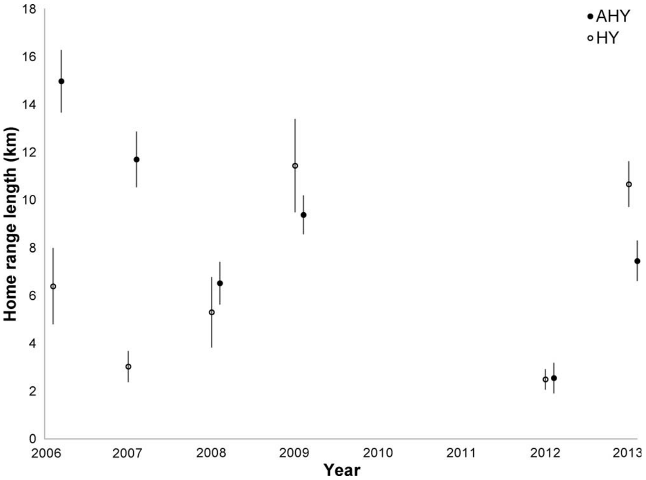

FIGURE 2. Raw values of average home range length of hatch-year (HY, $n = 378$; open circles) and adult (AHY, $n = 1{,}252$; closed circles) Piping Plovers on the Gavins Point Reach of the Missouri River, 2006–2009 and 2012–2013. Error bars represent ±1 SE.

TABLE 3. Beta estimates, standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits for potential factors affecting log(home range length) of hatch-year (HY) and adult (AHY) Piping Plovers along the Gavins Point Reach of the Missouri River, USA, 2006–2009 and 2012–2013. Estimates are from a linear mixed regression. The response variable was log-transformed home range length.

Parameter [a]	Estimate (β)	SE	Effect size [b]	LCL	UCL
Intercept	1.40	0.52	2.71	0.39	2.42
Age	0.71	0.57	1.25	−0.41	1.84
Dry	−1.28	1.68	−0.76	−4.58	2.02
Wet	−7.21	1.06	−6.78	−9.30	−5.12
Low canopy	1.29	0.94	1.38	−0.55	3.13
High canopy	3.43	1.53	2.24	0.42	6.44
Age × Dry	−7.29	1.92	−3.80	−11.06	−3.52
Age × Low canopy	−2.17	1.03	−2.10	−4.20	−0.14
Age × High canopy	2.80	1.73	1.62	−0.60	6.20

[a] Parameters in the model included age of individual (Age, AHY vs. HY, estimates for AHY individuals) and the proportion of each home range that was dry sand (Dry), wet sand (Wet), low canopy vegetation (Low canopy), and high canopy vegetation (High canopy). Year ($F_{5,579} = 2.2$, $P = 0.05$), Age × Year ($F_{5,579} = 5.7$, $P < 0.001$), and a random effect for individual were also included in the model.

[b] Effect size relative to SE: (β)/SE.

ranges were shorter as the proportion of nesting habitat increased within a home range ($\beta_{\text{Age×Dry}}$; Table 3). Presence of low canopy vegetation did not affect HY home range length ($\beta_{\text{Low canopy}}$; Table 3), but AHY home ranges were shorter as the proportion of low canopy vegetation increased ($\beta_{\text{Age×Low canopy}}$; Table 3). As the proportion of high canopy vegetation increased, HY and AHY plovers' home range lengths increased ($\beta_{\text{High canopy}}$; Table 3), though evidence of this trend was stronger for HY plovers ($\beta_{\text{Age×High canopy}}$; Table 3).

TABLE 4. Estimates, standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits for variables affecting nesting on prospected sandbars by Piping Plovers on Lewis and Clark Lake and the Gavins Point Reach of the Missouri River, USA, 2006–2013. Plover-chosen nest sites were modeled as "1" and randomly selected nest sites were modeled as "0". Estimates are from the best model (lowest AIC$_c$) from a set of a priori models.

Parameter [a]	Estimate (β)	SE	Effect size [b]	LCL	UCL
Intercept	0.24	0.53	0.45	−0.80	1.29
Prospected [c]	1.03	0.41	2.51	0.21	1.84
Natal	−0.18	0.51	−0.35	−1.19	0.82
Nest success$_{t+1}$	0.01	0.00	2.00	0.00	0.02
Nesting density$_{t+1}$ [d]	0.00	0.00	1.43	0.00	0.00
Foraging density$_{t+1}$ [e]	−0.08	0.03	−2.67	−0.14	−0.02

[a] Year ($F_{5,202} = 2.2$, $P = 0.96$) was also included in the model. Model pseudo-$R^2 = 0.22$.
[b] Effect size relative to SE: (β)/SE.
[c] Prospected was modeled as a binary variable: "0" if individual did not prospect sandbar and "1" if individual did prospect sandbar. The probability modeled was "1"; individual did prospect sandbar.
[d] Dry sand substrate nest density.
[e] Wet sand substrate nest density.

Prospecting

We observed 101 HY prospectors that returned to nest as SY breeders. Of these 101 birds, 29 nested within the prospecting range that they had explored as HY birds. Second-year plovers were more likely to nest on a sandbar that they had prospected in the previous year than on a randomly selected sandbar ($\beta_{\text{Prospected}}$; Table 4). The prospecting variable appeared in the 3 highest-ranked models predicting nest site selection, which cumulatively received 96% of the total weight in our model set (Table 5). Even when we constrained the sandbars available for selection to those within an individual's prospecting range, birds were still more likely to eventually nest on a sandbar that they had previously prospected than on a randomly selected sandbar ($\beta_{\text{Prospected}} = 0.9 \pm 0.4$). In addition, when we removed plovers that nested on their natal sandbar from the analysis, we found that prospecting was still positively correlated with SY nest site selection ($\beta_{\text{Prospected}} = 0.6 \pm 0.3$).

In addition to prospecting, conspecific nesting density (dry sand nest density), foraging density (wet sand nest density), and reproductive success in year $t + 1$ affected nest site selection (Table 4). Nesting density and nest success in year $t + 1$ were higher at SY plover-chosen sandbars than at randomly selected sandbars, and foraging density ($t + 1$) was lower at SY plover-chosen sandbars than at randomly selected sandbars (Table 4). Foraging density in year $t + 1$ appeared in the top 4 models (cumulative weight = 0.98), and nest success and nesting density in year $t + 1$ appeared in the top 2 models (cumulative weight = 0.85).

There was no significant difference in nest success for plovers that nested within their prospecting ranges vs. those that nested outside their prospecting ranges (Table 6).

TABLE 5. Candidate model rankings for logistic regression models used to estimate the likelihood that a Piping Plover nested on a sandbar that it prospected as a hatch-year bird on the Missouri River, USA, 2006–2013. Models were ranked according to differences in Akaike's Information Criterion adjusted for small sample bias (ΔAIC$_c$) and Akaike weights (w_i). K is the number of model parameters, Likelihood is the plausibility of the given model being the actual best model given the data, and −2ln$L$ is the maximized log-likelihood.

Model [a]	K	−2ln$L$	ΔAIC$_c$ [b]	Likelihood	w_i
Prospected + Nest success$_{t+1}$ + Nesting density$_{t+1}$ [c] + Foraging density$_{t+1}$ [d]	12	244.54	0.00	1.00	0.67
Prospected + Nest success$_{t,\ t+1}$ + Nesting density$_{t,\ t+1}$ + Foraging density$_{t,\ t+1}$	15	240.03	2.68	0.26	0.18
Prospected + Foraging density$_{t,\ t+1}$	11	250.46	3.67	0.16	0.11
Nest success$_{t+1}$ + Nesting density$_{t+1}$ + Foraging density$_{t+1}$	11	253.16	6.36	0.04	0.02
Prospected + Nest success$_t$ + Nesting density$_t$ + Foraging density$_t$	12	252.81	8.28	0.02	0.01
Intercept only	1	280.03	11.87	0.00	0.00
Prospected + Nest success$_{t,\ t+1}$	11	260.24	13.44	0.00	0.00
Prospected + Nesting density$_{t,\ t+1}$	11	261.87	15.08	0.00	0.00

[a] Nest year (2007–2013) and natal sandbar ("0" if nest sandbar was not natal sandbar; "1" if nest sandbar was same as natal sandbar) variables were included in all models. Pseudo-R^2 value for the best-supported model was 0.22.
[b] The lowest AIC$_c$ value was 270.2.
[c] Dry sand substrate nest density.
[d] Wet sand substrate nest density.

TABLE 6. Estimates, standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits for variables affecting nest success (the probability of hatching at least 1 chick) and fledging success (the probability of fledging at least 1 chick) for individuals that nested within vs. outside their hatch-year prospecting range (farthest upriver and downriver sandbars visited during their postfledging exploratory periods).

Parameter	Estimate	SE	Effect size [a]	LCL	UCL
Nest success [b]					
Intercept [c]	0.58	36.17	0.02	−70.32	71.47
Study area	0.48	0.26	1.83	−0.03	1.00
Prospected	0.39	0.29	1.35	−0.18	0.95
Fledging success [d]					
Intercept	3.60	1.23	2.93	1.14	6.05
Study area	−2.61	0.96	−2.72	−4.53	−0.69
Prospected	0.31	0.80	0.38	−1.26	1.87
Random effect	3.18	1.58	2.01	0.01	6.35

[a] Effect size relative to SE: (β)/SE.

[b] Parameters in the nest success model included study area ("GVP" for below Gavins Point Dam and "LACL" for Lewis and Clark Lake; the probability of GVP was modeled) and Prospected, which was included as a binary variable: "0" if the nest was not in the parent's prospecting range, "1" if the nest was in the parent's prospecting range, where prospecting range was the farthest upriver and downriver sandbars that parents visited during the postfledging exploratory period. The probability modeled was "1"; nest was in the parent's prospecting range. Year ($F_{5,95} = 2.3$, $P = 0.20$) was also included in the model.

[c] The probability of hatching at least 1 chick for the year 2013 was modeled as the reference group and is thus represented by the intercept for the nest success and fledging success analyses.

[d] Parameters in the fledging success model included study area ("GVP" for below Gavins Point Dam and "LACL" for Lewis and Clark Lake; probability of GVP was modeled) and prospected, which was included as a binary variable: "0" if the nest was not in the parent's prospecting range, "1" if the nest was in the parent's prospecting range, where prospecting range was the farthest upriver and downriver sandbars that parents visited during the postfledging exploratory period. The probability modeled was "1"; nest was in the parent's prospecting range. Year ($F_{5,56} = 2.4$, $P = 0.05$) and a random effect to control for the effects of nonindependence among brood mates on survival to fledging were also included in the model.

Twenty of 29 nests (69%) on prospected sandbars were successful, and 46 of 72 nests (64%) on sandbars that were not prospected were successful ($\chi^2 = 0.2$, $P = 0.63$). Similarly, there was no significant difference in fledging success between birds that nested within their HY prospecting ranges and those that nested outside that range (Table 6); 22 chicks fledged (1.10 chicks per pair) from nests on prospected sandbars, and 63 chicks fledged (1.37 chicks per pair) from nests on sandbars that were not prospected ($\chi^2 = 0.2$, $P = 0.67$). Nest success and fledging success were positively but not significantly correlated with nest site selection within the prospecting range (Table 6).

DISCUSSION

Second-year plovers selected nest sites within their HY prospecting range more often than would have been expected if nest site selection were random. Indeed, SY plovers nested more frequently on sandbars that they had prospected as HY birds vs. randomly selected sandbars, even when random sandbar selection was constrained to include only available sandbars within an individual's HY prospecting range. Our study likely did not capture all sandbar visits made by prospecting individuals, a common issue in many prospecting studies (Piper 2011), thus our estimate of prospecting effects on breeding site selection is likely conservative. However, prospecting was still a significant predictor of nest site selection by SY individuals. Second-year plovers also were more likely to nest on sandbars with higher nesting density relative to nesting habitat, lower nesting density relative to foraging habitat, and higher average nest success relative to randomly selected sandbars in year $t + 1$.

In addition to prospecting, the availability of foraging habitat was correlated with plover home range length and the selection of a first nesting location. As the availability of foraging habitat increased, home range length decreased, and SY breeders nested preferentially on forage-rich sandbars. Several studies of plover ecology, survival, and immigration have highlighted the importance of foraging habitat and nest density, indicating that plover ecology is strongly related to food resources and that their demography is density-dependent (Cohen et al. 2009, Catlin et al. 2013, 2014, 2015). Despite the apparent relationship between HY prospecting and SY nest site selection, we found that HY home ranges were rarely longer than those of AHY plovers (Figure 2). Due to the high site fidelity of AHY plovers to previous nesting sites, we were surprised that AHY plovers sometimes, and perhaps often, explored longer sections of the river than did HY plovers. We did not design our study to address AHY prospecting behavior, but this is an interesting result that warrants further investigation.

Young birds often experience conspecific aggression when they are in occupied territories (Catlin 2009), and evidence suggests that they remain subordinate to AHY plovers as SY birds (first nesting attempt; Catlin et al. 2015). If territorial aggression deters HY plovers from exploring sandbars, or from remaining there long if they do, then we might expect to see shorter home ranges in young plovers. Indeed, before 2010, when HY home range lengths were shorter than those of AHY plovers, nesting habitat area was relatively limited compared with other years. Plover density on the few available nesting sandbars was high (Catlin et al. 2015), and these high nesting densities likely led to increased aggressive interactions between AHY nesters and HY prospectors, which may have limited the home range lengths of HY plovers.

However, HY and AHY home ranges were shortest in the year with the smallest AHY breeding population and lowest nest densities (2012; Figure 2; Catlin et al. 2015, K. Hunt personal observation). Plover mortality and lack of reproductive success during flood events of 2010 and 2011, coupled with dramatically increased nesting habitat availability postflood, resulted in low nesting densities. This low density likely influenced the home range lengths observed postflood. Adult plovers did not have to travel far to find suitable nesting and foraging habitat, and although HY prospectors likely experienced little conspecific aggression when exploring new territory, they did not have to travel far to find forage-rich sandbars and potential nesting sites. These results suggest that HY home range length is related to more than prospecting or aggressive interactions with AHY birds. Observed differences in individual home-range lengths across years and the importance of foraging habitat to SY nest site selection may suggest quality-mediated habitat selection.

Plover habitat use suggests a requirement for heterogeneous rather than large home ranges (Nicholls and Baldassarre 1990, Cohen et al. 2009). On the Gulf of Mexico wintering grounds, plovers often choose peninsular and island habitats, with both bayside tidal flats for foraging and Gulf-side sandy beaches for roosting, over mainland shore habitats (LeDee et al. 2008). Similarly, heterogeneous foraging habitats are particularly important for European Golden-Plovers (*Pluvialis apricaria*; Pearce-Higgins and Yalden 2004) and Bar-tailed Godwits (*Limosa lapponica*; McCaffery 1998). Indeed, our results are consistent with the idea that foraging habitat is an important factor driving habitat selection and home range size, as the home range lengths of HY and AHY Piping Plovers decreased as the proportion of foraging habitat within their home ranges increased. In addition, foraging habitat area was the most important predictor of nest site selection included in our prospecting models.

Despite the relatively low proportion of prospectors that nested on known prospected sandbars (20%), prospecting was an important predictor of nest site selection. In addition to our inability to detect all HY prospecting movements, one possible explanation for this low percentage could be the relative instability of sandbars between years. River sandbars are highly unstable habitats for nesting birds (McNicholl 1975). From year to year, erosion, vegetation encroachment, and flooding can alter sandbar habitat (Catlin et al. 2011, 2015), leading to variation in availability and quality. When habitat quality variation between years is extreme, plovers may not benefit from prospecting as HY (or as AHY) birds because nesting habitat that is available during the prospecting period may be completely degraded by the following breeding season. Indeed, we found evidence for year-to-year variation in home range length for AHY and HY plovers, possibly mediated by variable habitat characteristics, such as foraging habitat availability, and density-dependent factors among years. Both HY and AHY plover home ranges were shorter when the proportion of foraging habitat in the home range was relatively high, compared with non-foraging habitat.

We did not find a strong positive relationship between an individual's reproductive success and nest-site selection on prospected vs. random sandbars, but we did observe that SY plovers preferentially nested on sandbars on which other plovers experienced higher average nest success compared with randomly selected sandbars. Second-year plovers also selected nesting locations that had higher nest densities within nesting habitats rather than random locations. Some birds use such cues to evaluate and choose habitat themselves (Doligez et al. 2004a, 2004b). Furthermore, numerous studies have suggested that selection of "familiar" habitats may have long-term benefits for survival and reproductive success (Piper 2011, Saunders et al. 2012). Among shorebirds, which typically exhibit nest site fidelity, AHY plovers show a particularly high degree of nest site fidelity (LeDee et al. 2010, Cohen and Gratto-Trevor 2011, Catlin et al. 2015, Friedrich et al. 2015). Greater than 90% of plovers in this population return to the same area for nesting each year (Catlin et al. 2015), and 50% of AHY plovers move <153 m between nests in successive breeding seasons (Friedrich et al. 2015). This high fidelity to nesting areas means that the nest site selected by a plover for its first breeding attempt can be an important nesting location throughout the bird's lifetime. In addition, AHY plovers with unknown nesting status appear to have reduced survival probabilities (Catlin et al. 2015). Thus, territory familiarity gained through prospecting may be an important component of a bird's lifetime site fidelity, annual survival, and long-term fitness (Saunders et al. 2012). Moreover, in addition to familiarity with a site, there was evidence in our study that the conditions of nesting habitat in the nesting year were of greater importance to selection than those same conditions the year before. For instance, the effects of conspecific nest success and conspecific nesting and foraging densities were more important in the nesting year than in the prospecting year. Taken together, the importance of prospecting along with average nest success at selected nesting sites and high site fidelity throughout life suggest that the information gained during prospecting may confer benefits throughout a bird's life during the nesting and chick rearing periods, and that young birds ultimately select habitat that improves nest success on average.

Although familiarity with a site had an effect on selection, SY plovers made choices that were related to current conditions as well, which could have affected the rate at which birds nested on prospected habitat (Burkhalter et al. 2015). Understanding how habitat use influences individual breeding site selection and, more broadly, how it affects population dynamics, may allow us to predict and anticipate colonization and emigration patterns and manage habitats to encourage recruitment or dispersal.

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