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Research Article

Detection Probability of Least Tern and Piping Plover Chicks in a Large River System

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ABSTRACT Monitoring the abundance and stability of populations of conservation concern is often complicated by an inability to perfectly detect all members of the population. Mark-recapture offers a flexible framework in which one may identify factors contributing to imperfect detection, while at the same time estimating demographic parameters such as abundance or survival. We individually color-marked, recaptured, and re-sighted 1,635 federally listed interior least tern (*Sternula antillarum*; endangered) chicks and 1,318 piping plover (*Charadrius melodus*; threatened) chicks from 2006 to 2009 at 4 study areas along the Missouri River and investigated effects of observer-, subject-, and site-level covariates suspected of influencing detection. Increasing the time spent searching and crew size increased the probability of detecting both species regardless of study area and detection methods were not associated with decreased survival. However, associations between detection probability and the investigated covariates were highly variable by study area and species combinations, indicating that a universal mark-recapture design may not be appropriate. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Charadrius melodus*, detection probability, endangered species, interior least tern, mark-recapture, Missouri River, piping plover, *Sternula antillarum*.

Failure to account for imperfect detection can result in biased abundance estimates and ultimately a failure to discern real changes in demographic parameters (MacKenzie et al. 2002, Pollock et al. 2002, Gimenez et al. 2008). For example, if detection probabilities are <1, then estimates of abundance and survival will be biased low, and if detection probability varies from survey to survey then abundance estimates may not be correlated with actual population sizes. Similarly, unaccounted for heterogeneity in detection probability can lead to increasing bias in demographic estimates including apparent survival (Nichols et al. 1984, Devineau et al. 2006, Cubaynes et al. 2010, Fletcher et al. 2012). Consequently, extensive attention has been directed at the development of methods to account for detection probability and thus correct abundance and survival estimates for imperfect detection.

Detection is typically imperfect either because an animal present is not detected (hereafter perception sensu Marsh and Sinclair 1989; e.g., an observer does not hear a bird singing during a point count) or an animal is unavailable for detection (hereafter unavailability; e.g., a bird incubating in a nest cavity or not singing during a point count; Thompson 2002, Diefenbach et al. 2007). In either case, a myriad of study- and species-specific factors can influence detection probability (see Roche et al. 2013), including territory size (Calder 1990), time of day (Skirvin 1981, Conway et al. 2004), season (Best 1981, Skirvin 1981), singing frequency (Farnsworth et al. 2002), and observer skill (Sauer et al. 1994, Conway and Simon 2003, Diefenbach et al. 2003).

Mark-recapture methodologies offer a flexible framework with which to account for imperfect detection while at the same time estimating demographic parameters such as abundance or survival. Arguably, these methods are most informative when used consistently over years to estimate long-term and large-scale changes in population demography, while tying observed trends to specific environmental factors (e.g., Barbraud and Weimerskirch 2001, Peach et al. 2003, Baker et al. 2004). However, even if the long-term use of mark-recapture methodologies is not possible, a 1-time assessment can provide managers with a benchmark for evaluating the accuracy of their current monitoring regimes (e.g. McCorquodale et al. 2013, Shaffer et al. 2013).

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For actively managed species of conservation concern, revealing true patterns of population change is imperative. For example, the federally listed interior least tern (*Sternula antillarum*; endangered) and piping plover (*Charadrius melodus*; threatened) populations nesting along the upper Missouri River both currently face challenges from the increased vegetation and erosion (United States Fish and Wildlife Service [USFWS] 2003) of their sandbar and lakeshore nesting habitat (Carreker 1985, Prindiville Gaines and Ryan 1988, Espie et al. 1996, Kirsch 1996, Schweitzer and Leslie 1999), dynamic changes in water levels to which they may not be well adapted (Anteau et al. 2012*a*), and predation of nests and chicks (Kruse et al. 2001, USFWS 2003, Catlin et al. 2011*a*). Prior to the age at which chicks of either species can fly (hereafter fledge), they are typically confined to the sandbars and shorelines on which they hatched (Elliottt-Smith and Haig 2004, Thompson et al. 1997) and, though mobile, are relatively easy to catch.

By individually marking and recapturing or resighting tern and plover chicks between hatching and fledging, researchers have been able to estimate changes in survival relative to environmental factors under management control such as predator removal (Catlin et al. 2011*a*), river flow (Catlin et al. 2013), and habitat creation efforts (Catlin et al. 2011*b*, Stucker 2013). Although mark-recapture analyses may reveal the factors influencing population dynamics in the face of imperfect detection, it remains important to maximize detection to minimize variance in estimates and reduce the potential for bias (Gimenez et al. 2008, Fletcher et al. 2012). An understanding of factors that increase detection of least terns and piping plovers would direct researchers on how best to design their studies as well as lead to more parsimonious modeling (Pollock et al. 2002, Lindberg 2012).

We investigated the influence of multiple observer-, subject-, and site-level factors on detection of individually color-marked pre-fledge interior least tern and piping plover chicks raised on upper Missouri River sandbars or shorelines. We hypothesized that detection probability would be influenced by chick age, time of day, the level of effort put into detection activities and the amount of habitat researchers would have to search. Our aim was to identify a mark-recapture strategy that would maximize detection probability for these species and ultimately allow us to implement a long-term mark-recapture program for detecting fledging-aged chicks as measures of productivity of both species.

STUDY AREA

We collected data in 4 study areas along a stretch of the Missouri River extending southward from Lake Sakakawea in North Dakota to the Gavins Point Reach in northeast Nebraska (Fig. 1). The Lake Sakakawea study area (SAK; from Garrison Dam near Riverdale, ND to White Tail Bay, ND; see Anteau et al. 2012*b*) was located at the northernmost point of this stretch, approximately 80 km from Bismarck, North Dakota. Habitat at SAK occurred on shoreline beaches or islands. The shoreline at SAK was irregular, dissected, and consisted of numerous substrates, slopes, and aspects (Anteau et al. 2012*b*). The Garrison River Reach study area (GRR) extended from the Garrison Dam to the headwaters of Lake Oahe, approximately 10 km south of Bismarck, North Dakota. Habitat at GRR occurred primarily on mid-channel low- to mid-elevation sandbars with some established woody vegetation. Sandbar size varied temporally due to erosion, accretion, and variation in river stage, but ranged from 0.125 ha to 109 ha as determined from satellite imagery (Quickbird; 0.6-m pixels; DigitalGlobe, Longmont, CO) collected between May and September (L. L. Strong, U.S. Geological Survey, unpublished data). The Lewis and Clark Lake study area (LCL) consisted of a complex of 2–4 constructed sandbars located approximately 24 km upstream from the Gavins Point Dam near Yankton, South Dakota (Catlin et al. 2011*a*, *b*; Sherfy et al. 2012). Individual sandbars ranged in size from 10 ha to 24 ha. The Gavins Point study area (GVP), the southernmost area in the Upper Missouri River, extended downstream from the Gavins Point Dam, approximately 95 km to Ponca State Park, Nebraska (Catlin et al. 2011*a*, *b*; Sherfy et al. 2012). Habitat at this study area was characterized by natural and constructed sandbars of size <0.1 ha through 171 ha.

Figure 1. Least tern and piping plover nesting areas along the Missouri River included in a mark-recapture project conducted 2006–2009.

METHODS

Field Methods

We used stratified random sampling to choose study units within each study area (hereafter referred to as sites) other than LCL. Study sites consisted of 2-km shoreline or island segments at SAK, 4.8-km river segments at GVP, and 6.4-km river segments at GRR. At LCL, all study units consisted of a single complex of constructed sandbars (2007: 0.55 ha and 4.2 ha, 2008: 17 ha and 38.6 ha). We visited all sandbar and shoreline habitat every 2–3 days from mid-April through end of July to locate nests and mark and recapture all tern and plover chicks.

We captured chicks by hand at the nest site, typically within a day of hatch. We marked chicks of both species using a metal band and a unique combination of color bands. Least tern chicks received 3 celluloid color bands (2 bands placed below the tibiotarsal joint and 1 above) and a size 1A stainless steel United States Geological Survey (USGS) metal band placed below the tibiotarsal joint. Piping plover chicks received up to 2 Darvic color bands placed below the tibiotarsal joint on each leg and a size 1A USGS aluminum band or colored Darvic flag above the tibiotarsal joint on the opposite leg. In >85% of cases, we captured chicks from the same brood and marked them at the same time. We conducted mark-recapture of piping plovers at SAK in 2006–2009, at 37 sandbars at GRR in 2007, and at 31 sandbars at GVP in 2008–2009. Mark-recapture of least terns occurred at 37 sandbars at GRR in 2006–2007, at 31 sandbars at GVP in 2006–2009, and at 4 sandbars at LCL in 2007–2008.

Following chick banding, we revisited each sandbar or shoreline site every 2–3 days and resighted or recaptured chicks. During searches, teams systematically worked through all areas in a grid formation, moving against the river flow and in parallel, recorded information on nest initiation and survival as well as chick recapture information. Teams typically resighted piping plovers with spotting scopes based on color band with physical recapture rare unless required for other concurrent studies (e.g., SAK and GVP). Least tern chicks often lie flat over their leg bands or hide under objects limiting opportunity to observe bands remotely. Accordingly, we recaptured the majority of least terns by hand to allow identification and maintenance of individual color marks. Examples of such maintenance included movement of color bands from tarsus to tibia as tern chicks grew (and thus had more room on the tibia for color bands) and replacement of lost bands. Following capture, we directed terns away from field technicians and toward the center of the site. Once teams had systematically searched a sandbar or shoreline, they walked the edge of the sandbar or shoreline to return to the entry point. Typical site visits took approximately 2 hours and occurred within 4–5 hours of sunrise. Our field protocols were approved by the USGS Northern Prairie Wildlife Research Center Animal Care and Use Committee.

Covariates Associated With Detection Probability

We evaluated detection probability of marked least tern and piping plover chicks in relation to time of day, chick age, year, observation effort, and environmental covariates, including area (ha) of suitable habitat for searching, and area (ha) of unsearched hiding cover. We included site-level covariates in our analysis (i.e., covariate values particular to a least tern or piping plover chick depending on where it hatched) that we believed could be associated with detection probability. Some covariates varied by encounter occasion (i.e., were time varying), whereas others were time invariant and remained constant from hatch day until the cessation of observation. We truncated encounter histories at 18 days for least terns and 25 days for piping plovers. If we did not obtain a covariate value, we used the mean study-area-specific covariate value.

Because we hypothesized that detection of chicks increased with age because of mobility (Whittier and Leslie 2009), we directly coded chick age into our mark-recapture analysis by creating age-structured encounter histories such that each occasion represented a single day-of-age. We then built linear trend models on the logit scale, hereafter denoted as age (in contrast to agecat, which denotes age as a category). We quantified observation effort as the number of hours all observers devoted to searching for chicks (hours searched) and the number of persons searching for chicks (crew size). Finally, we included the number of hours since sunrise or to sunset (time of day) from the midpoint of the survey period as light conditions in mornings and evenings could be more conducive to distinguishing color bands through scopes than in midday. Constructing the covariate in this way allowed for a single covariate that reflected time since midday.

We considered the year that we marked a chick as an additive effect in all mark-recapture models. Additionally, we enumerated the amount (ha) of non-vegetated and sparsely vegetated habitat suitable for searching for least terns and piping plovers (suitable habitat; Fig. 2a) and vegetated hiding cover unsuitable for searching (hiding cover; Fig. 2b) for each sandbar, island, or shoreline segment from land-cover maps derived from annually acquired satellite imagery (M. J. Anteau and L. L. Strong, U.S. Geological Survey, unpublished data). We constructed land-cover maps for GRR, GVP, and LCL study areas using an object-based classification procedure for the above habitat classes. We used satellite imagery for this procedure, which was typically collected between May and September. At the river study areas (i.e., GRR and GVP), we deemed the area (ha) of a sandbar (or shoreline) consisting of bare-substrate (<5% vegetation) or sparse vegetation (5–30% vegetation) to be suitable habitat for chick-searching, whereas we considered the amount of a sandbar (or shoreline) consisting of moderate to dense vegetation, to be habitat unsuitable for searching but ideal hiding cover for chicks. We constructed land-cover maps for SAK using habitat data collected in the field to develop and evaluate a raster-based model to predict the percent cover of vegetation. For this procedure, we used the satellite imagery Probationary System of Earth Observation satellite 5 (SPOT-5; Satellite Imaging Corporation; Magnolia, TX), which was collected between June and August in 2007 and 2008. On SAK, we evaluated available suitable habitat and hiding cover within a 500-m radius circle around a central location for each observation of a brood. We deemed the area (ha) of shorelines and islands with ≤15% predicted vegetation to be suitable habitat for searching and the remaining area as hiding cover. Despite the fact that these covariates were at times correlated, we included both

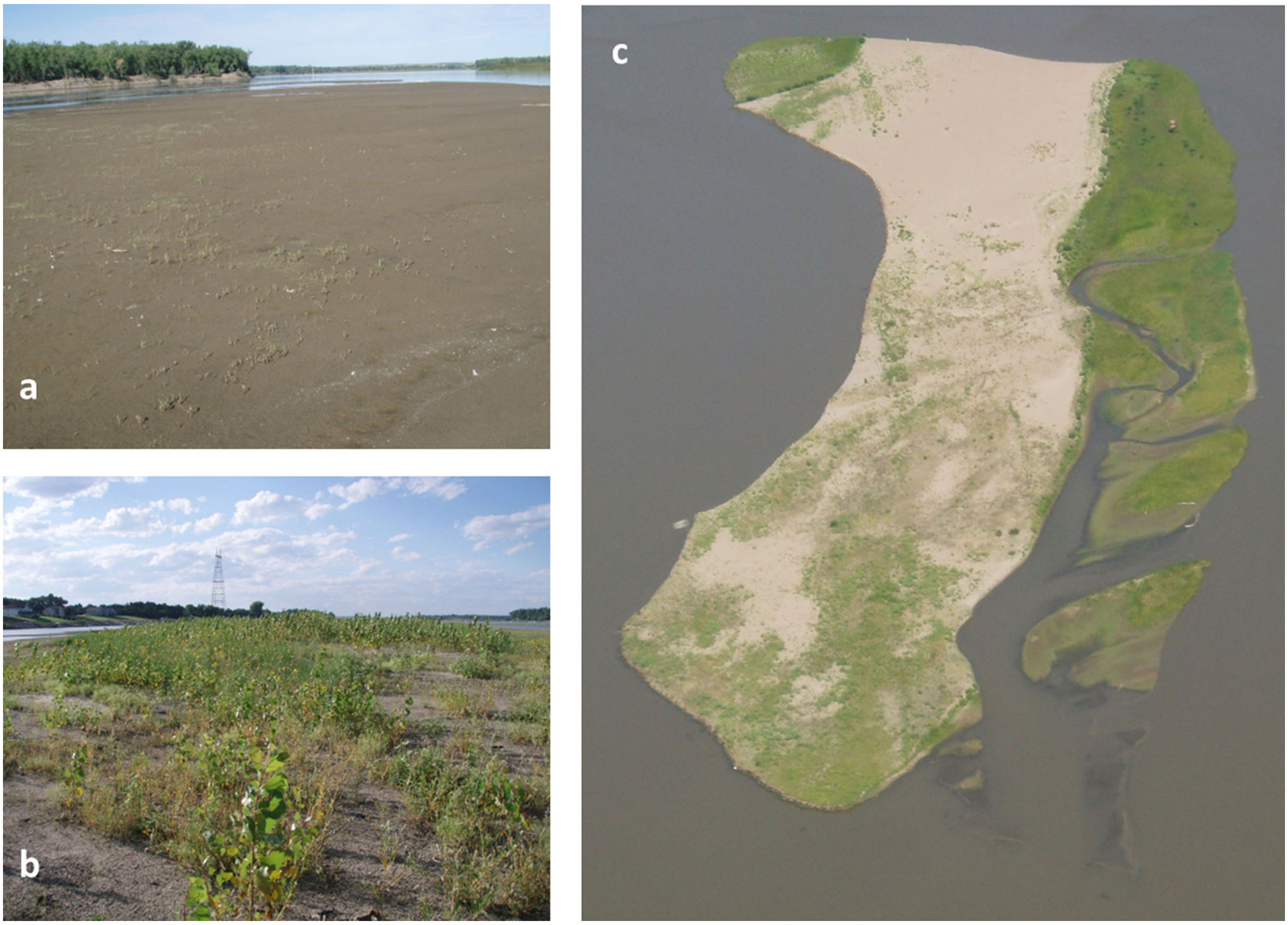

Figure 2. Examples of (a) habitat suitable for searching for least terns and piping plovers (Garrison Reach), (b) vegetated hiding cover unsuitable for searching (Garrison Reach), and (c) one of the many ways vegetation might be distributed on a sandbar that could make chick recapture and resighting challenging (Gavins Point Reach).

hiding cover and suitable habitat as covariates in our models so as to separately test study area- and species-specific effects for both.

Mark-Recapture Analysis

We built Cormack-Jolly-Seber (CJS) recaptures-only models in program RMark 2.0.1 and MARK (White and Burnham 1999, Laake and Rexstad 2011) to estimate the detection probability (p) from a combined dataset of least tern ($n = 1{,}635$) and piping plover ($n = 1{,}318$) chicks from hatching through 18 and 25 days of age, respectively, an approximate point at which fledging occurs in these species (Prindiville Gaines and Ryan 1988, Thompson et al. 1997). We organized data into capture histories consisting of 25 occasions, where an occasion represented a single day of age. For each occasion, a chick received a 1 if we visited its site and resighted or recaptured the chick, received a 0 if we visited its site but did not see the chick, and was censored (.) if we did not visit its site or had not yet banded the chick. We estimated detection probabilities for 6 groups, representing the 6 possible combinations of species by study area: piping plovers at Garrison (PIPL-GRR; $n = 354$), piping plovers at Gavins Point (PIPL-GVP; $n = 713$), piping plovers at Lake Sakakawea (PIPL-SAK; $n = 251$), least terns at Garrison (LETE-GRR; $n = 335$), least terns at Gavins Point (LETE-GVP; $n = 986$), and least terns at Lewis and Clark (LETE-LCL; $n = 314$).

Cormack-Jolly-Seber models concurrently estimate detection probability and apparent survival (φ), the probability an individual survives between sampling occasions and remains on the monitored study area (Sandercock 2006). Because our interest was in estimating the detection probability, we chose a biologically reasonable a priori parameterization for apparent survival, which we then used in all subsequent models to determine the best parameterization for detection probability. We assumed an apparent survival that varied according to a linear trend with age on the logit scale (age) for both least tern and piping plover chicks, φ(species × study area × age), where × indicates a multiplicative relationship among model parameters. Although more highly parameterized models are possible, this model is well supported for daily apparent survival in plover chicks (Colwell et al. 2007, Dinsmore 2008, Roche et al. 2008).

The full model [φ(species × study area × age), p(species × study area × agecat)] included 150 detection parameters and 12 apparent survival parameters. We used the full model to estimate overdispersion ($\hat{c}$) by conducting a within-brood bootstrapping analysis on a sample of our data for which brood membership was known ($n = 2{,}216$ out of 2,953 individuals), following Bishop et al. (2008). We iterated this bootstrap simulation 1,000 times. We then calculated the mean standard deviation (SD) for each estimate of detection. To estimate $\hat{c}$, we divided the squared standard deviation (SD^2) of each age-specific detection estimate by the squared standard error (SE^2) of the corresponding detection estimate from the non-bootstrapped dataset. We then averaged the $\hat{c}$ values for each age-specific detection parameter to calculate our overall $\hat{c}$ value ($\hat{c} = 1.69$). We used this $\hat{c}$ value to correct the Akaike's Information Criterion (AIC_c) rankings generated for each model for overdispersion. We used the resulting QAIC_c values to rank each model; lower QAIC_c values indicated better model fit and, along with relative model weight (w_i), indicated the importance of each covariate tested (Burnham and Anderson 2002). Following Arnold (2010), we report 85% confidence intervals and used these intervals to assess the degree of statistical support for the regression coefficients.

We built models sequentially according to our a priori expectations by adding to a null model the following covariates: 1) year, 2) chick age, 3) observer effort, and 4) environmental effects including time of day, and type of search habitat (e.g., suitable habitat or hiding cover). Parameters in our null model for chick detection varied by species and study area combination but not by chick age [φ (species × study area × age), p(species × study area)]. For each covariate, we built models in which covariate effects were: 1) constant across all species and study area combinations, 2) variable by species, 3) variable by study area, and 4) variable for each species by study area combination. At each step, we selected the parameterization for detection probability with the lowest QAIC_c and used this parameterization as a starting point when modeling the effects of the next covariate on detection probability.

In addition to detection probabilities, we included an observer impact covariate to determine if frequent observer activities associated with our detection effort influenced apparent survival. We created an occasion-specific covariate unique to each individual capture history that posited an attenuation effect of observer impact (OI) on daily survival rates. On a day during which a site was the subject of a targeted search (i.e., a chick had an encounter history value of either 1 or 0), the OI value was equal to 3, a 2 on the day following a search if the site was not visited (i.e., a chick had an encounter history value of "."), and a 1 on the second day following a search (Rotella et al. 2004, Roche et al. 2010). We reset this attenuation pattern at each site visit (i.e., for a capture history of 11…, then the occasion-specific covariate would be 3321) and assigned a 0 after 3 days had passed since the last visit. We considered models in which the impact of observer presence was 1) the same for both species and 2) variable depending on species. We considered a reduction in QAIC_c relative to our best model without this covariate as evidence in support of the observer impact covariate.

We used our top-supported model to project daily detection probabilities over the covariate values observed at a study area for a given species while multiplying all non-focal study area parameters at their site-specific mean values (Table 1). We used the delta method (R package msm; Jackson 2011) to obtain the mean probability and associated confidence intervals among years. To estimate the cumulative probability of detecting a chick at least once in 2–4 site visits just prior to fledging, we used age-specific estimates from our top-supported model and assumed we made site visits on back-to-back days (e.g., probability of detecting a least tern sampled at age 15 and 16 and a piping plover at 22 and 23 days if we completed 2 site visits). We used the delta method to estimate the cumulative probability of detecting a least tern or piping plover chick at search time lengths varying from 2 to 4 hours and following 2–4 site visits.

RESULTS

Out of 2,953 chicks, we banded 94% of all piping plovers ($n = 1{,}238$ of 1,318) and 93% of all least terns ($n = 1{,}523$ of 1,635) within 5 days of hatch; we banded 87% ($n = 1{,}073$) of all piping plovers and 92% ($n = 1{,}396$) of all least terns within a day of hatching. Daily detection probabilities varied by species as well as study area (Table 2, Fig. 3). Although

Table 1. Sample means ($\bar{x}$) and standard deviations (SD) of observation effort and environmental covariates believed to influence detection probability by species (least tern, piping plover) and study area (GRR, Garrison Reach; GVP, Gavins Point Reach; LCL, Lewis and Clark Lake; and SAK, Lake Sakakawea) along the Missouri River in 2006–2009. The covariates representing observation effort included: 1) hours searched, the number of hours spent chick searching; and 2) crew size, the number workers searching for chicks. The covariates representing environmental effects included: 1) suitable habitat, the area (ha) of a sandbar (or shoreline) consisting of bare-substrate (<5% vegetation) or sparse vegetation (5–30% vegetation); 2) hiding cover, the area of a sandbar (or shoreline) consisting of moderate to dense vegetation which could offer hiding cover for least terns or piping plover chicks; and 3) time of day, the time of day at which chick searching occurred measured as the number of hours from sunrise or sunset to the median time at which surveying occurred.

	Suitable habitat (ha)		Hiding cover (ha)		Hours searched		Crew size		Time of day	
Species and study area	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Least tern										
GRR ($n = 335$)	12.74	9.81	17.15	34.69	2.07	1.22	3.70	0.74	4.29	0.85
GVP ($n = 986$)	12.90	10.50	1.66	4.37	1.85	0.85	4.67	0.92	4.67	0.77
LCL ($n = 314$)	19.30	4.84	4.50	10.19	2.02	0.57	5.47	0.66	4.42	0.48
Piping plover										
GRR ($n = 354$)	14.75	9.42	7.90	10.16	2.04	0.91	3.90	0.63	4.40	0.90
GVP ($n = 713$)	17.55	12.98	9.79	22.13	1.53	0.56	4.91	0.77	4.70	0.59
SAK ($n = 251$)	6.26	6.03	17.79	13.41	1.47	0.85	2.75	0.45	4.57	0.87

Table 2. Set of models used to estimate apparent survival (φ) and detection (p) of 1,635 least tern and 1,318 piping plover chicks marked and recaptured or resighted along the Missouri River during 2006–2009. Parameters having independent (i.e., factorial) relationships are joined by $\times$; whereas, parameters having additive relationships are joined by $+$; age specifies a linear trend in apparent survival or detection probabilities based on age and a dot (.) indicates a model in which detection is constant across chick age. The designation species represents grouping by species (i.e., least tern or piping plover), study area designates grouping by study area (i.e., Gavins Point Reach, Garrison Reach, Lewis and Clark Lake, or Lake Sakakawea), hours searched represents the number of hours of chick-searching, crew size represents the crew size searching for chicks, suitable habitat designates the area (ha) of non-vegetated habitat suitable for searching, hiding cover represents the area (ha) of vegetated hiding cover, and time of day represents the time of day at which searching occurs. Akaike's Information Criterion values were corrected for small sample size and overdispersion ($\hat{c} = 1.69$), yielding quasi-AIC ($QAIC_c$) values. We used $\Delta QAIC_c$ values, model weights (w_i), number of parameters (K), and quasi-deviance values (QDev) to rank best-supported models. In all models, apparent survival was parameterized φ(species $\times$ study area $\times$ age).

Rank	p	K	$\Delta QAIC_c$	w_i	QDev
1[a]	(species × study area) + (year × species) + (age × species × study area) + (crew size × species × study area) + (hours searched × species × study area) + (suitable habitat × species × study area) + (hiding cover × species × study area) + (time of day × species × study area)	60	0	0.99	128,374.9
2	(species × study area) + (year × species) + (age × species × study area) + (crew size × species × study area) + (hours searched × species × study area) + (suitable habitat × species × study area) + (hiding cover × species × study area)	54	24.81	0.00	128,411.8
3	(species × study area) + (year × species) + (age × species × study area) + (crew size × species × study area) + (hours searched × species × study area)	42	394.22	0.00	128,805.5
4	(species × study area) + (year × species) + (age × species × study area)	30	1,163.61	0.00	115,487.3
5	(species ×study area) + (year × species)	24	1,173.73	0.00	115,509.4
6	(species × study area)	18	1,331.67	0.00	115,679.4

[a] $QAIC_c = 128{,}495.6$.

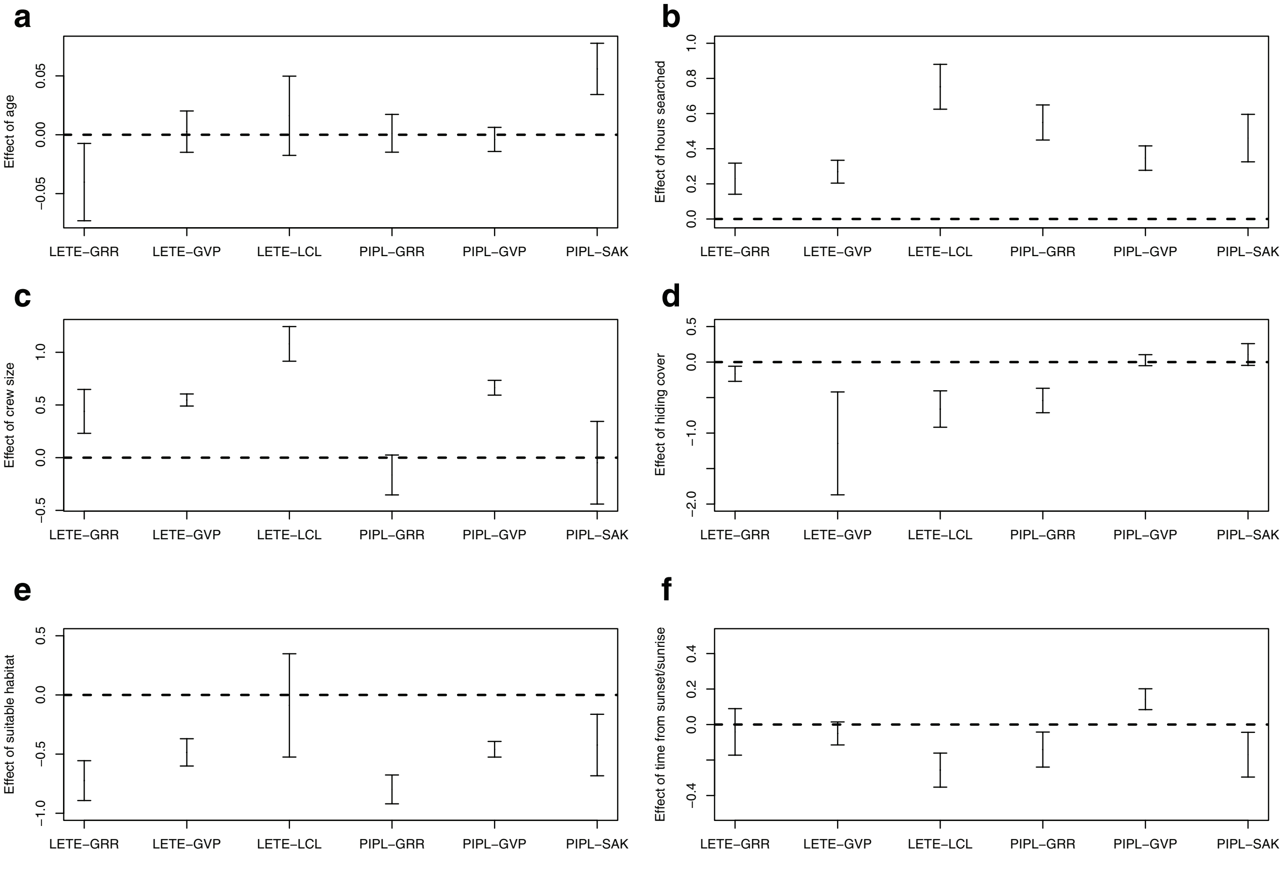

Figure 3. Regression coefficient estimates for covariates included in our top-supported model for detection probabilities of piping plovers (PIPL) and least terns (LETE) at Missouri River study areas in 2006–2009 (GRR, Garrison Reach; GVP, Gavins Point Reach; LCL, Lewis and Clark Lake; and SAK, Lake Sakakawea). These values represent the effect of (a) age, (b) hours searched (mean = 1.88 hrs, SD = 1.22 hrs), (c) crew size (mean = 4.56 people, SD = 2.40 people), (d) hiding cover (mean = 7.81 ha, SD = 18.24 ha), (e) suitable habitat (mean = 14.35 ha, SD = 10.78 ha), and (f) time from sunset or sunrise (mean = 4.56 hrs from sunrise or sunset, SD = 1.68 hrs from sunrise or sunset) on detection probability. Vertical bars are 85% confidence intervals; the effect of a covariate would be supported if 85% confidence intervals do not overlap 0 (the horizontal dashed line). All covariates other than age (which was modeled as a linear trend in the logit scale) were standardized to a mean of 0 and a standard deviation of 1.

detection probabilities were generally unrelated to age (Fig. 3a), detection of least terns at GRR decreased with age (Fig. 3a, $\hat{\beta}_{\text{age}} = -0.03$; 85% CI: −0.06 to −0.01) and detection of piping plovers at SAK increased with age (Fig. 3a, $\hat{\beta}_{\text{age}} = 0.06$; 85% CI: 0.03–0.08).

We found a positive association between hours spent searching and detection probability for both species (Figs. 3b and 4). For example, increasing search time by 0.5 SD (approx. 40 min) was associated with increases in daily detection probabilities of 0.03 (85% CI: 0.02–0.04), 0.03 (85% CI: 0.03–0.04), and 0.09 (85% CI: 0.08–0.11) for least terns at GRR, GVP, and LCL (Fig. 4b). An equivalent increase in search time for piping plovers was associated with increases in daily detection probabilities of 0.07 (85% CI: 0.06–0.08), 0.04 (85% CI: 0.04–0.05), and 0.06 (85% CI: 0.04–0.07) at GRR, GVP, and SAK (Fig. 4a).

The positive effect of crew size was most pronounced for least terns at LCL and for piping plovers at GVP (Figs. 3c and 5a), where an increase in 0.5 SD (approx. 1 person) resulted in daily detection probabilities that increased by 0.13 (85% CI: 0.11–0.15) and 0.08 (85% CI: 0.07–0.09), respectively. Daily detection probabilities increased with increasing crew size for least terns at GRR (an increase of 0.06, 85% CI: 0.03–0.08, with 1 additional crew member) and least terns at GVP (an increase of 0.07, 85% CI: 0.06–0.08, with 1 additional crew member; Fig. 5b).

Increases in the amount of hiding cover (i.e., the habitat unsuitable for searching) were associated with decreases in daily detection probabilities for both species (Fig. 3d). However, although this effect was supported for least terns across all study areas (i.e., 85% CI did not overlap 0), it was supported only for piping plovers at GRR, where an increase in hiding cover of 0.5 SD (approx. 9 ha) resulted in daily detection probabilities that decreased by 0.07 (85% CI: 0.05–0.09; Fig. 3d). For least terns, an increase in hiding cover of 0.5 SD resulted in decreases in daily detection probability of 0.02 (85% CI: 0.01–0.03), 0.14 (85% CI: 0.05–0.22), and 0.08 (85% CI: 0.05–0.11) at GRR, LCL, and GVP.

Increases in the amount of non-vegetated habitat suitable for chick searching (i.e., suitable habitat) were also associated with decreasing detection probabilities for the study area and species areas for which it was supported (Fig. 3e). An increase

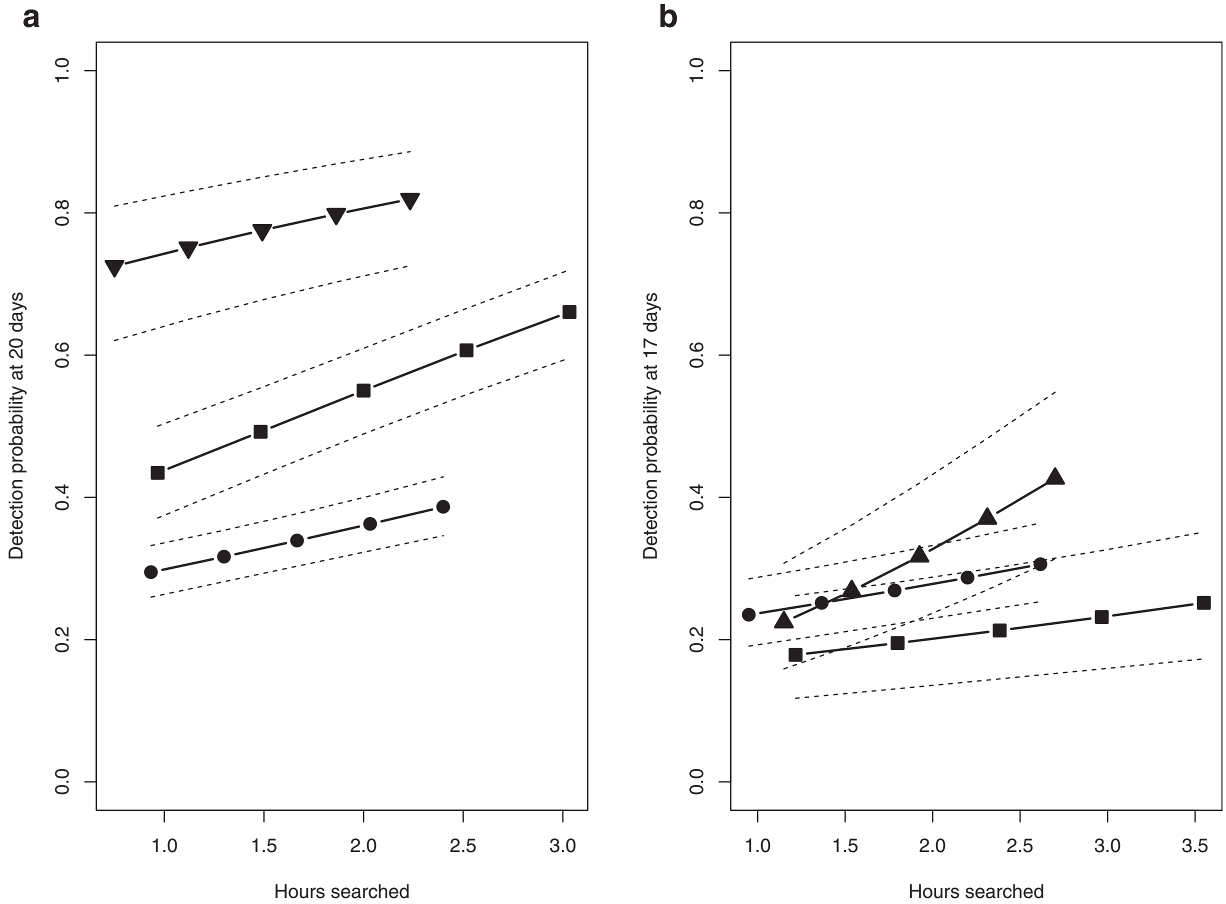

Figure 4. Daily detection probabilities for (a) piping plovers and (b) least terns by number of hours spent searching (hours searched) at each study area (GRR, Garrison Reach; GVP, Gavins Point Reach; LCL, Lewis and Clark Lake; and SAK, Lake Sakakawea) along the Missouri River in 2006–2009. Daily detection probabilities at GRR are represented by squares, at SAK by inverted triangles, at GVP by circles, and at LCL by triangles. Solid fill indicates that the 85% confidence intervals of the regression parameters for an effect did not overlap 0. Dashed lines represent the 85% confidence intervals for the daily detection probabilities. All estimates were generated from the top-supported model while holding all covariates at site-specific mean values and solved only over the values for hours searched observed at the site-specific mean values. We calculated mean values and variances across years using the delta method.

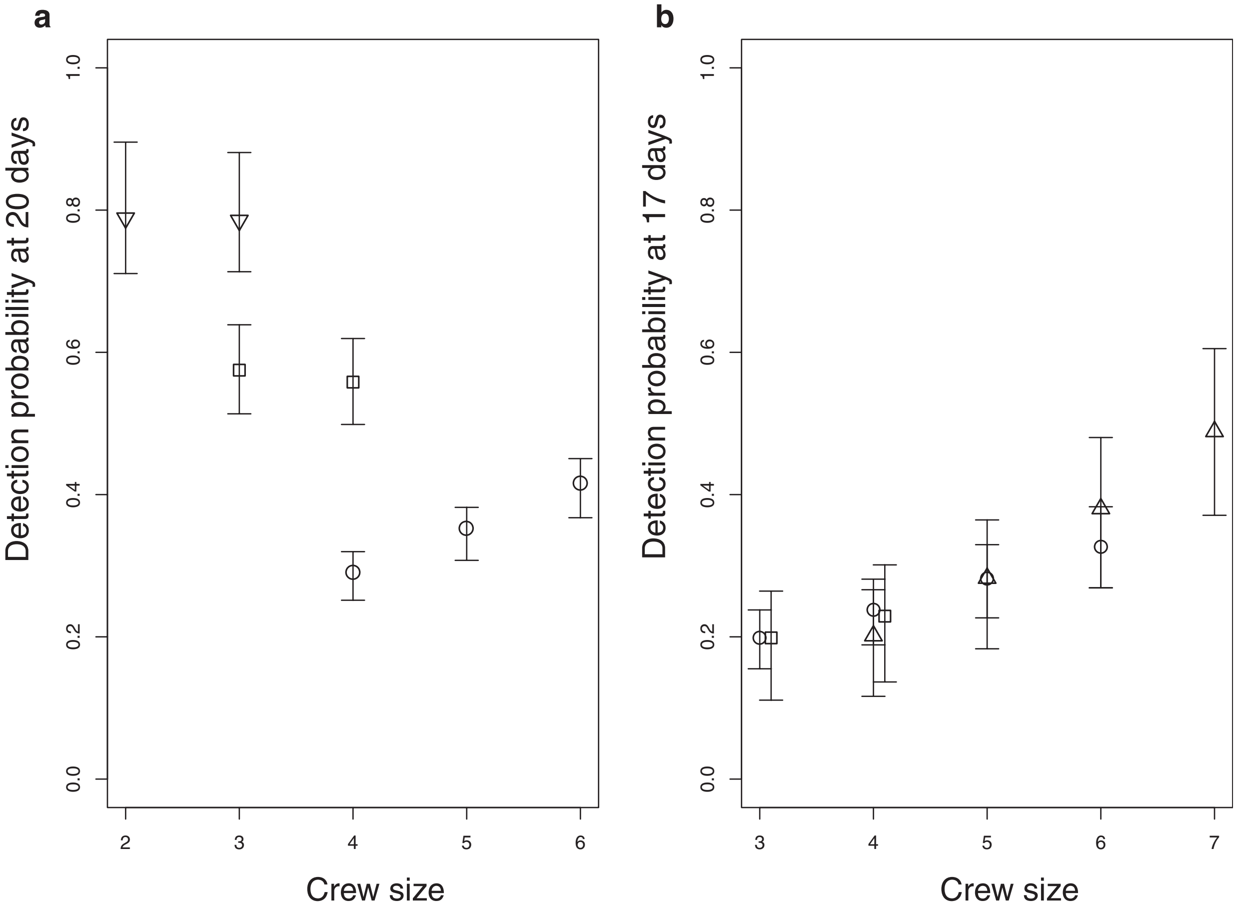

Figure 5. Daily detection probabilities for (a) piping plovers and (b) least terns by crew size at each study area (GRR, Garrison Reach; GVP, Gavins Point Reach; LCL, Lewis and Clark Lake; and SAK, Lake Sakakawea) along the Missouri River in 2006–2009. Daily detection probabilities at GRR are represented by squares, at SAK by inverted triangles, at GVP by circles, and at LCL by triangles. Solid fill indicates that the 85% confidence intervals of the regression parameters for an effect did not overlap 0. Vertical lines represent the 85% confidence intervals for the daily detection probabilities. All estimates were generated from the top-supported model while holding all covariates at site-specific mean values and solved only over the values for crew size observed at the site-specific mean values. We calculated mean values and variances across years using the delta method.

in suitable habitat of 0.5 SD (approx. 5.5 ha) was associated with daily detection probabilities that decreased by 0.10 (85% CI: 0.08–0.11), 0.06 (85% CI: 0.05–0.07), and 0.05 (85% CI: 0.02–0.09) for piping plovers at GRR, GVP, and SAK, respectively. Although detection probability decreased with increasing non-vegetated habitat for least terns at GVP (a decrease of 0.06, 85% CI: 0.05–0.08, with an increase of 0.5 SD) and GRR (a decrease of 0.09, 85% CI: 0.07–0.11, with an increase of 0.5 SD), we did not find support for this relationship for least terns at LCL (i.e., 85% CI overlaps 0, Fig. 3e).

Daily detection probabilities of piping plovers at GVP increased with the approach of midday, whereas daily detection probabilities of piping plovers at GRR and SAK decreased with hours since sunrise or to sunset (Fig. 3f). With an increase of 0.5 SD (approx. 50 min from sunrise or to sunset), daily detection probabilities increased by 0.02 (85% CI: 0.01–0.03) for piping plovers at GVP, and decreased by 0.02 (85% CI: 0.01–0.03) and 0.02 (85% CI: 0.01–0.04) for piping plovers at GRR and SAK, respectively. The most pronounced effect of time on detection probabilities occurred for least terns at LCL (Fig. 3f); daily detection probabilities decreased by 0.03 (85% CI: 0.02–0.04) with an increase in 0.5 SD from sunrise or to sunset.

The presence of observers was associated with an increase in survival of least tern chicks ($\hat{\beta}_{\text{LETE}}$-OI $= 0.68$, 85% CI: 0.48–0.89), but survival of piping plover chicks ($\hat{\beta}_{\text{PIPL}}$-OI $= -0.09$, 85% CI: -0.30 to 0.11) was unrelated to the presence of observers (addition of the observer impact [OI] covariate led to a 16 point decrease in QAIC_c relative to Table 2, model 1). Daily survival rates of least tern chicks were 0.01–0.02 greater on days during which resighting occurred compared to the day following resighting.

The cumulative probability of detection when we conducted 2 visits of 4 hours was equivalent to 3 visits of 2 hours each, suggesting alternate strategies for increasing detection probability could be pursued. Across all study areas, the cumulative probability of detecting a least tern chick once in 2–4 site visits was 20–40% lower than that for piping plovers. Cumulative probabilities of detecting piping plovers approached or exceeded 80% with 2 visits of 4 hours or with at least 3 visits; for least terns, more than 3 visits of greater than 3 hours would be necessary (Fig. 6).

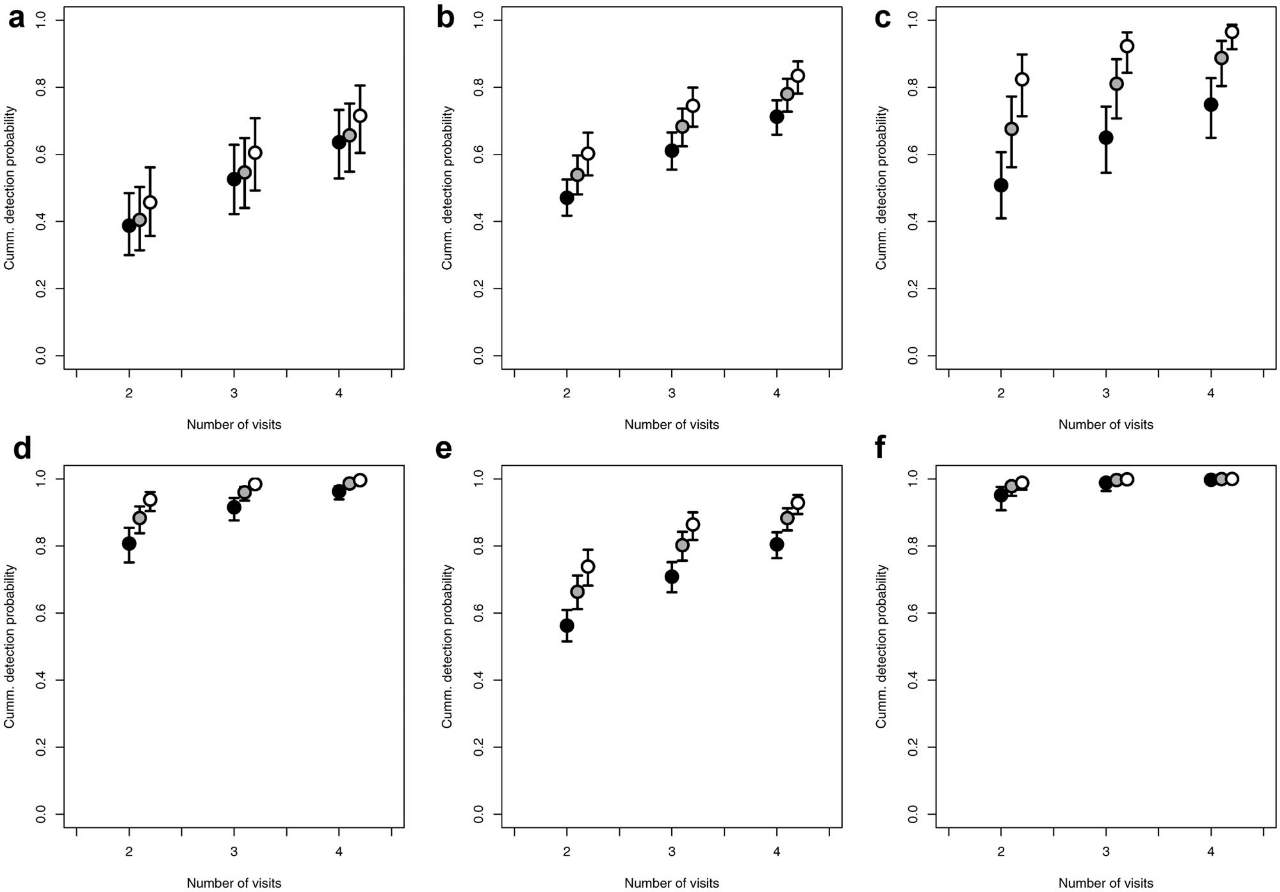

Figure 6. The cumulative (cumm.) probabilities of detecting a fledging-aged chick at least once in 2–4 site visits for 3 different search times (1 hr = white circle, 3 hrs = gray circle, and 4 hrs = black circle) for 17-day-old least terns at (a) Garrison Reach (GRR), (b) Gavins Point Reach (GVP), and (c) Lewis and Clark Lake (LCL) and for 20-day-old piping plovers at (d) GRR, (e) GVP, and (f) SAK along the Missouri River in 2006–2009. Vertical lines represent 85% confidence intervals as calculated by the delta method.

DISCUSSION

Factors Affecting Detection Probability

The diversity of conditions in the Upper Missouri River system leads to a number of logistical challenges to implementing a mark-recapture program. Chief among them is that factors associated with increasing detection probability varied by study area, species behavior, and detection method, a result that is not unique to this system (Pagano and Arnold 2009, Durso et al. 2011, Roche et al. 2013). In general, daily detection probabilities were substantially greater for piping plover chicks than for least terns, indicating that current mark-recapture methodologies are better suited for detecting plovers than terns.

A relationship between age and detection was supported for only 2 groups and could be explained by the unique properties of the shoreline-sandbar habitat. Older chicks are more likely to feed at the water's edge (Elliottt-Smith and Haig 2004, Whittier and Leslie 2009) and along lakeshore habitat, such as the SAK study area, this might make older piping plover chicks more visible at a distance with age. In contrast, GRR consisted largely of sandbar habitat with intermixing patches of suitable habitat and hiding cover (e.g., Fig. 2c), meaning that it was likely observers would flush chicks into hiding cover. The decreasing probability of resighting or recapturing least terns with age likely reflects the fact that they become increasingly mobile and difficult to catch (discouraging reading bands in hand) and more likely to make it to hiding cover where they can avoid being resighted. Although we did not find much support for an association between detection probability (here generated through a combination of resighting and recapture) and age, we caution that the actual probability of physical recapture of piping plover chicks does decrease with age (Catlin et al. 2013).

Detection probabilities for both species increased with search effort (i.e., hours spent searching and crew size), strengthening support for the influence of effort on probability of detection (e.g., Mack et al. 2002, Smith et al. 2009, Vine et al. 2009, Christy et al. 2010, Jeffress et al. 2011). Consistent with the results of Hunt et al. (2013), we found no negative impact of the presence of observers on the survival of terns and plovers. The more pronounced effect of hours spent searching on the detection of plovers relative to terns is most likely explained by the manner in which chicks were detected. Increasing the time spent resighting band combinations leads to the discovery of more (would-be) unseen combinations. However, physical recapture, which is more frequently used on least tern chicks, causes chicks to scatter in the direction of vegetation or other cover that might be too difficult to search safely. Additionally, least terns appear to be particularly adept at hiding, being more likely to crawl into inaccessible locations or even bury themselves in sand (C. Dovichin, U.S. Geological Survey, personal observation).

Although previous studies on shorebirds have found detection increases with the number of observers (Lyons et al. 2012), in our study, only detection probability for least terns increased with crew size in all study areas. Piping plover chicks of all ages are more likely to run from surveyors than least terns, exposing their unique band combinations; however, least tern chicks are far more likely than piping plover chicks to crouch hidden in vegetation, requiring the physical recapture of a chick to read a band combination. Thus, although a single surveyor with a spotting scope could theoretically read multiple piping plover band combinations from a stationary position, a single surveyor searching through vegetation may actually cause least tern chicks to become more scattered, better hidden, and more difficult to find. Thus, a larger team of individuals searching concurrently is likely to have a greater probability of success resighting least tern chicks than is a smaller crew. Following this logic, crew size is less likely to have an influence on the detection of piping plovers if they are being resighted, as was the case at GRR and SAK.

For some species, detection probabilities may vary with time-of-day or lighting conditions because of changing behaviors (Bailey et al. 2009, Pagano and Arnold 2009, Christy et al. 2010, Niemuth et al. 2012). We initially suspected the detection of piping plover chicks might vary with time-of-day because forage availability changes throughout the day with peaks in the morning (Anteau and Sherfy 2010) and evening (Lee 2007) and intently foraging plovers might be easier to observe. However, the lack of a consistent pattern, for both species, offered no compelling evidence for an effect of time of day on detection.

Many studies have demonstrated shorebirds are negatively associated with vegetative cover (Fernández and Lank 2006, Pomeroy 2006, Van den Hout et al. 2008) but most, like Brindock and Colwell (2011) who demonstrated that snowy plovers (*Charadrius alexandrines*) avoid areas of high cover, have explained this negative association as a real avoidance and not due to decreased detection. When we controlled for number of hours searched, crew size, and time of day, both the amount of hiding cover (i.e., areas considered unsuitable for chick searches because of >15% vegetation cover) and non-vegetated suitable habitat (i.e., habitat most easily searched) were consistently associated with decreased daily detection probabilities. We found only 2 exceptions to these patterns, both of which could be explained by unique aspects of a few sites unaccounted for in our analysis. For example, the presence of pipes at 1 of the LCL sites enabled least terns to hide themselves beyond the physical reach of technicians (C. Dovichin, personal observation). At GRR, vegetative cover on the sandbars was consistently patchier than in the other areas (see Fig. 2c for an example of patchy vegetative cover). As a result, piping plover chicks, which were generally more likely to run and crouch rather than hide, were more easily able to flee into hiding cover during recapture events.

Although we limited our analysis to the amount of suitable (largely barren) habitat and hiding cover at a site, the habitat at which piping plover and least tern chicks are found in the Missouri River system is highly diverse. Sandbars ranged in size from 0.125 ha to 171 ha with the degree of vegetation ranging from completely unvegetated to sandbars nearly completely covered by vegetation growing since the last major flood in 1997 (USFWS 2000). At some locations, chicks are found and observed along longitudinal shoreline habitat, bounded on 1 side by water and the other a dune, bluff, or treeline, which minimizes the potential for a chick to move into hiding cover (Anteau et al. 2012*b*). This is not the case on large sandbars where chicks may escape through vegetation to an opposite shoreline and thus more easily evade observation. Additionally, the location of vegetation on a sandbar (or lakeshore) along with the shape of the sandbar itself, can have serious consequences on the ease at which resighting or recapture occurs, with large sandbars punctuated by several discrete vegetated areas offering some of the most logistically difficult conditions, and narrow unvegetated relatively small sandbars some of the easiest (Fig. 2c). Consequently, at each location, observers are faced with different logistical constraints and considerations.

MANAGEMENT IMPLICATIONS

Given that 1) increasing search times is probably more cost-effective than adding additional team members to a crew, and 2) increasing search times increased the probability of detection for both species at all study areas, the most efficient means by which to increase overall daily detection probability would be to increase the length of site visits. To account for the possible influence of heterogeneity in the lower detection probabilities associated with least tern chicks, researchers should use a combination of modern statistical methods designed to account for heterogeneity (Royle 2008, Calvert et al. 2009, Gimenez and Choquet 2010) or include observer-, site-, or individual-specific covariates believed to influence detection (Pollock et al. 2002, Lindberg 2012).

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use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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