

Short communication

Using remote cameras to validate estimates of nest fate in shorebirds

KRISTEN S. ELLIS,^{1,2*}  JOHN F. CAVITT³
 RANDY T. LARSEN^{2,4} & DAVID N. KOONS¹

¹Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA

²Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT, USA

³Department of Zoology, Weber State University, Ogden, UT, USA

⁴Monte L. Bean Life Sciences Museum, Brigham Young University, Provo, UT, USA

Nest survival is a key demographic parameter, yet little effort has been made to improve the accuracy of field-based methods for assigning nest fates to shorebird nests. We used remote cameras to validate estimates of nest fate from field methods and to assess variation in accuracy of nest-fate assignment for Snowy Plover *Charadrius nivosus* in Utah, USA. We correctly identified the fates of 84% of nests in the field, and photos from camera monitoring revealed incorrect assignments for 22% of successful nests and 7% of depredated nests. Traditional field methods could be improved by checking nests more frequently when hatching date nears and spending additional time searching for eggshell evidence, especially when nests are in areas susceptible to weather disturbance.

Keywords: ground-nesting birds, nest survival, remote cameras, Snowy Plover.

Nest survival is a key demographic parameter for understanding avian productivity and population dynamics. Incorrect assignments of nest fate may have implications for population modelling (Ball & Bayne 2012) and diminish the efficacy of management strategies based on demographic data. Estimation and modelling of nest survival have received considerable attention (Jones & Geupel 2007); however, only limited efforts have been

made to validate assignments of nest fate based on field observations. Correct assignment of nest fates is important because nest survival estimators constitute a special class of 'known-fate' survival estimators where the fates of uncensored nests are treated as 'known' but the timing of failure is not necessarily known (failure often occurs between nest visits; Rotella *et al.* 2004). Many species of shorebirds remove eggshells from nest cups and chicks leave nests shortly after hatching (Mabee *et al.* 2006). Current methods using evidence at nests to determine shorebird nest fate may be incorrect because the final nest visit is often to an empty nest with no sign of adults or young in the area. In these cases, nest fate is generally determined by eggshell evidence at the nest and nest age (Page *et al.* 1985, Paton 1995, Mabee 1997, Mabee *et al.* 2006, Smith *et al.* 2007).

Remote cameras provide a reliable method for monitoring nests (Cutler & Swann 1999, Bolton *et al.* 2007). Remote cameras have been used to monitor shorebird nests, examine incubation behaviours (Smith *et al.* 2012, Burns *et al.* 2013) and identify nest predators (Bolton *et al.* 2007, Liebezeit & Zack 2008, Demers & Robinson-Nilsen 2012). Although remote cameras can help monitor shorebird nests, the effects of camera presence on nest survival could be negative if predators are attracted to a novel stimulus. Alternatively, camera-monitoring may result in higher rates of nest survival if researcher disturbance is minimized or predators avoid unfamiliar features.

To better understand factors influencing the correct assignment of nest-fate in the field, we monitored Snowy Plover *Charadrius nivosus* nests using infrared-triggered cameras and independently assigned nest fates using traditional field observations. Snowy Plovers are a species of conservation concern throughout much of their range (e.g. the Pacific population is listed as threatened under the U.S. Endangered Species Act; USFWS 2012). Because of their conservation status, many populations of Snowy Plover are heavily monitored, making the validation of field methods particularly important. Our objectives were: (1) to assess the accuracy of nest-fate assignment from field methods and identify factors influencing error and (2) to determine whether camera monitoring influenced daily survival rate. We predicted that the fate of successful nests would be more ambiguous than that of unsuccessful nests because chicks are precocial and do not remain in the nest, and adults will remove eggshells after hatching.

METHODS

Study areas

We monitored nests of Snowy Plover in two regions of Utah, USA, between 2011 and 2016. These regions included: (1) Great Salt Lake (Saltair (40°46'00"N,

*Corresponding author.

Email: kristensue.ellis@gmail.com

Twitter: @kgurrellis

112°09'50"W) and Antelope Island State Park (41°05'08"N, 112°08'08"W) (2014–2016)) and (2) western Utah (Fish Springs National Wildlife Refuge and the southwest corner of the United States Army Dugway Proving Ground (39°55'40"N, 113°24'50"W) (2011–2016) and Blue Lake (40°32'00"N, 114°01'08"W) (2016)).

Great Salt Lake hosts the largest breeding population of Snowy Plovers in North America (23% of approximately 26 000; Thomas *et al.* 2012) whereas populations in western Utah are relatively small and tied to limited water sources (Ellis *et al.* 2014).

Field procedures

We conducted nest surveys at least once per week to locate new nests and monitor extant nests at each site. Once located, we floated eggs to estimate nest age and initiation date, assuming an egg-laying period of 3 days and a 27-day incubation period (Paton 1995, Page *et al.* 2009). We recorded nest substrate by noting the location of the nest in vegetation, bare ground, or on or next to debris. We chose nests for camera monitoring based on age of nests (≥ 4 days after the onset of incubation to minimize risk of abandonment) and camera availability. We used Reconyx PC900 infrared-triggered cameras (Reconyx, Inc., Holmen, WI, USA) to monitor nests. We mounted each camera on a stake and positioned it 15 cm above the ground and approximately 2 m from the nest. Cameras were set to record two images per second when triggered by a rapid change in temperature within the zone of detection, with no quiet period between triggers.

Once nests had finished, we recorded descriptions of remains including condition of nest cup and surrounding area, eggshell fragments and condition of eggshell membranes (missing or intact). We sorted through the nesting substrate in the field to identify small eggshell fragments. Signs of successful nests included small eggshell fragments (1–5 mm; produced during pipping) inside the nest cup, eggshell membrane partially or completely separated from eggshell, eggshell tops or bottoms, and chicks in the nest cup (Mabee 1997, Mabee & Estelle 2000, Mabee *et al.* 2006). We considered a nest successful if at least one chick hatched and survived to leave the nest. Evidence of depredated nests included eggs disappearing prior to the expected date of hatching or presence of yolk or large eggshell fragments (≥ 6 mm). We analysed images from cameras to determine nest fate after descriptions of nest remains had been recorded in the field and nest fate had been assigned based on these descriptions.

Data analyses

We assessed the accuracy of nest fate assignment by comparing the proportion of successful and depredated nests assigned in the field to those quantified from

photos using two-tailed Fisher exact tests. To determine factors influencing the correct assignment of nest fate, we used logistic regression with the correct assignment of fate based on comparison of camera photos with field assignment as the response variable (1 was correct, 0 was incorrect). We examined whether incorrect assignments were influenced by the individual observer, attributes of the nest (nest age and nesting substrate) and nest predator. Specific covariates included: predator, nest age, observer ($n = 5$), nesting substrate and number of days between actual finish date and date checked by observers. We standardized nest age (z-score) to allow for comparison across studies. We identified five groups of predators from photos: (1) gulls *Larus* spp. ($n = 49$), (2) Common Raven *Corvus corax* ($n = 39$), (3) Coyotes *Canis latrans* ($n = 21$), (4) foxes (Red Fox *Vulpes vulpes* at Great Salt Lake sites and Kit Fox *Vulpes macrotis* at western Utah sites; $n = 31$) and (5) small mammals (White-tailed Antelope Ground Squirrel *Ammospermophilus leucurus* and unidentified mice; $n = 9$). Thus, the covariate for predator represented five predator types with successful nests as a reference. We assigned nests as abandoned when adults discontinued incubation of complete clutches. We assigned nests as weather-related failures if there was evidence of flooding in the nest cup or if eggs were intact but outside of the nest cup following a weather event. We did not incorporate nests that were abandoned ($n = 6$) or failed due to weather ($n = 7$) into the analysis because our accuracy in assignment of these fates was 100%.

Because we had relatively few instances where nest fate was incorrectly assigned, we limited our models to a maximum of two main effects to avoid overfitting. Considering only two-variable models may have limited our ability to predict inaccuracies in nest-fate assignment, but this approach helps to avoid spurious effects from fitting models with too many parameters relative to the sample size (Burnham & Anderson 2002). To avoid fitting models with collinear predictors, we assessed correlation coefficients between pairs of predictor variables and none exceeded $|0.5|$ (Pearson correlation). We considered all combinations of covariates resulting in 16 *a priori* models including five univariate models, 10 two-variable models and an intercept-only model. We also calculated the variance inflation factor (VIF) for each model considering a threshold value of three (Zurr *et al.* 2010). We used Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson 2002) to compare support among models. All analyses were conducted in R (version 3.3.1; R Development Core Team, 2012). Using Akaike model weights, we averaged models using the MuMIn package (Barton 2016) in R. Because evidence at the nest is dependent on nest fate (i.e. small fragments indicate successful nests and would be correctly assigned in the field but may also lead to an incorrect assignment of successful

when nests were depredated), we used Fisher's exact tests (with Bonferroni correction) to compare evidence at nests between correct and incorrect field assignment.

To test whether camera-monitoring influenced nest predation, we estimated daily survival rates between nests monitored with cameras and an additional set of nests monitored without cameras during the same time and at the same study sites (Table 1). We estimated daily survival rates using the nest survival model in the RMark package (Dinsmore & Dinsmore 2007, Laake & Rexstad 2012) in R. Exposure days began the day the nest was found (for nests monitored without cameras) or the day the camera was placed at the nest (for camera-monitored nests). This method provides a conservative estimate of daily survival rate for nests monitored with cameras (McKinnon & Bêty 2009). Estimates of daily nest survival were derived from a single model that included presence of cameras in addition to effects of site, year and nest age, which have been shown to contribute to variation in daily nest survival (Ellis *et al.* 2015). To evaluate parameter significance, we assessed the degree of overlap in 95% confidence intervals around zero for beta estimates. We calculated estimates of nest success by exponentiation of daily survival rate to 27, consistent with a 27-day incubation period with confidence intervals calculated using the delta method (Seber 1982).

RESULTS

We monitored 358 Snowy Plover nests with infrared-triggered cameras between 2011 and 2016. We removed 17 nests from our sample due to camera error ($n = 3$), unhatched eggs ($n = 1$), abandonment ($n = 6$) and weather-related failure ($n = 7$). The mean number of

Table 1. Number of Snowy Plover nests monitored with cameras, number of correct assignments of nest fate, and total number of nests monitored at Great Salt Lake and in western Utah between 2011 and 2016.

Site	Year	Camera	Correct assignments	Total nests
Western Utah	2011	6	6 (100%)	9
Western Utah	2012	12	10 (83%)	18
Great Salt Lake	2013	2	2 (100%)	2
Western Utah	2013	7	6 (86%)	22
Great Salt Lake	2014	50	39 (78%)	124
Western Utah	2014	42	36 (86%)	52
Great Salt Lake	2015	43	40 (93%)	63
Western Utah	2015	25	23 (92%)	36
Great Salt Lake	2016	54	45 (83%)	74
Western Utah	2016	100	80 (80%)	108
Total		341	287 (84%)	508

days between actual finish date and last date checked was 4.19 (± 0.10 se). We correctly identified the fates of 287 (84%) nests in the field. Photos from camera monitoring revealed incorrect assignment for 44 of 197 (22%) successful nests and 10 of 144 (7%) depredated nests. Overall, the odds of correctly assigning the fate of depredated nests were 3.84 (95% confidence interval (CI) 1.82–8.90; $P < 0.01$) times greater than the odds of correctly assigning the fates of successful nests.

All models had VIF values < 3 and we therefore considered each additive, two-variable combination as plausible. Our most supported model ($w_i = 0.51$) included nest outcome separated by predator type (with successful nests as a reference) and nest age (Table 2). Assignment of nest fate (successful or depredated) in the field was less likely to be correct as nest age increased ($\beta = -0.66$, 95% CI: -1.33 to -0.07). Nests depredated by Coyotes ($\beta = 1.11$; 95% CI: -0.59 to 4.03), foxes ($\beta = 1.55$; 95% CI: -0.12 to 4.48), gulls ($\beta = 1.05$; 95% CI: -0.31 to 2.95) and Common Ravens ($\beta = 1.20$; 95% CI: -0.10 to 3.06) were

Table 2. Ranking of 16 *a priori* logistic regression models used to identify variables influencing accuracy of nest-fate assignment for Snowy Plover *Charadrius nivosus*.

Model	ΔAIC_c	w_i	LL	K
Predator + Nest age	0	0.51	-132.84	7
Predator + Substrate	1.91	0.19	-132.75	8
Predator	2.73	0.13	-135.25	6
Nest age	4.38	0.06	-140.18	2
Predator + NDays	4.48	0.05	-135.08	7
Predator + Observer	5.38	0.03	-139.66	7
NDays + Nest age	6.68	0.02	-139.29	3
Observer + Nest age	9.75	0	-137.71	3
Substrate + Nest age	10.71	0	-133.96	4
Intercept-only	19.99	0	-149	1
Observer	21.07	0	-148.52	2
NDays	23.23	0	-148.58	2
Observer + NDays	24.22	0	-145.99	3
Substrate + Observer	24.42	0	-148.16	4
Substrate	25.11	0	-145.39	3
Substrate + NDays	26.73	0	-145.15	4

The predator covariate represented nest predation by Coyote *Canis latrans*, foxes (Kit Fox *Vulpes macrotis* and Red Fox *Vulpes vulpes*), gulls *Larus* spp., Common Raven *Corvus corax* and small mammals (White-tailed Antelope Ground Squirrel *Ammospermophilus leucurus* and unidentified mice); successful nests were used as a reference. Observer ($n = 5$) and nesting substrate (barren ground, vegetation or debris) were also included as categorical independent variables. The number of days between hatch date and last date checked by observers (NDays) and nest age (z-score standardized) were included as continuous independent variables. K denotes the number of parameters in a model, w_i the Akaike model weight and LL the log-likelihood.

positively related to correct assignments of nest fate compared to successful nests, although confidence intervals overlapped zero in each case. However, nests depredated by small mammals were less likely to be correctly assigned than successful nests ($\beta = -1.68$; 95% CI: -1.33 to -0.07) (Fig. 1a). Our second competing model ($w_i = 0.19$) included predator and an effect of nesting substrate. Nests that were located on vegetated substrates were more likely to be assigned a nest fate correctly than were nests located on barren substrates ($\beta = 1.02$, 95% CI: 0.12 – 1.89).

From model-averaged estimates, the probability ($\pm 95\%$ CI) of correctly assigning nest fate depredated by small mammals was 0.55 (0.16 – 0.95) compared with 0.94 (0.82 – 1.00) for Coyotes, 0.95 (0.86 – 1.00) for foxes, 0.94 (0.85 – 1.00) for gulls, 0.94 (0.85 – 1.00)

for Common Ravens and 0.82 (0.74 – 0.90) for successful nests (Fig. 1a). The odds of incorrectly assigning a depredated nest as successful were $210.48:1$ (95% CI: 25.24 – 3556.65 ; $P < 0.01$) when small fragments were present. Alternatively, the odds of incorrectly assigning a successful nest as depredated were $27.63:1$ (95% CI: 5.75 – 264.53 ; $P < 0.01$) when there were egg pieces present and $62.55:1$ (95% CI: 18.77 – 276.72 ; $P < 0.01$) when there was no evidence at the nest (Fig. 1b).

We constructed valid encounter histories for 508 nests over a 109-day monitoring period for nest survival analysis (29 April to 16 August; Table 1). We did not detect a significant effect of camera-monitoring on daily nest survival ($\beta = 0.12$, 95% CI: -0.19 to 0.43) (Fig. 2). Overall nest success for nests monitored with cameras

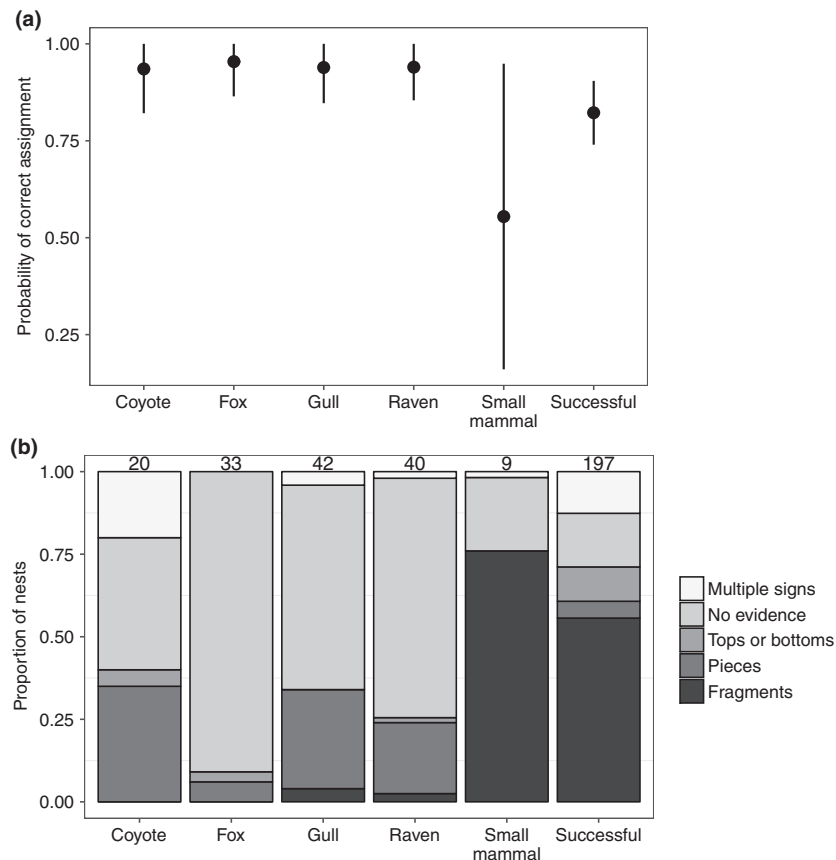


Figure 1. (a) Probability ($\pm 95\%$ confidence interval) of correctly assigning Snowy Plover nest fate for depredated nests according to each predator group (columns 1–5) and successful nests (last column) using the mean for each covariate from our model-averaged set. (b) Proportion of eggshell evidence present at depredated and successful nests. Eggshell fragments were 1–5 mm in size and eggshell pieces were ≥ 6 mm. Multiple signs represent the presence of more than one type of eggshell evidence. The sample size for each group is given above bars. Predator groups include Coyotes *Canis latrans*, foxes (Red Fox *Vulpes vulpes* at Great Salt Lake and Kit Fox *Vulpes macrotis* at western Utah sites), gulls *Larus* spp., Common Ravens *Corvus corax* and small mammals (White-tailed Antelope Ground Squirrels *Ammospermophilus leucurus* and unidentified mice).

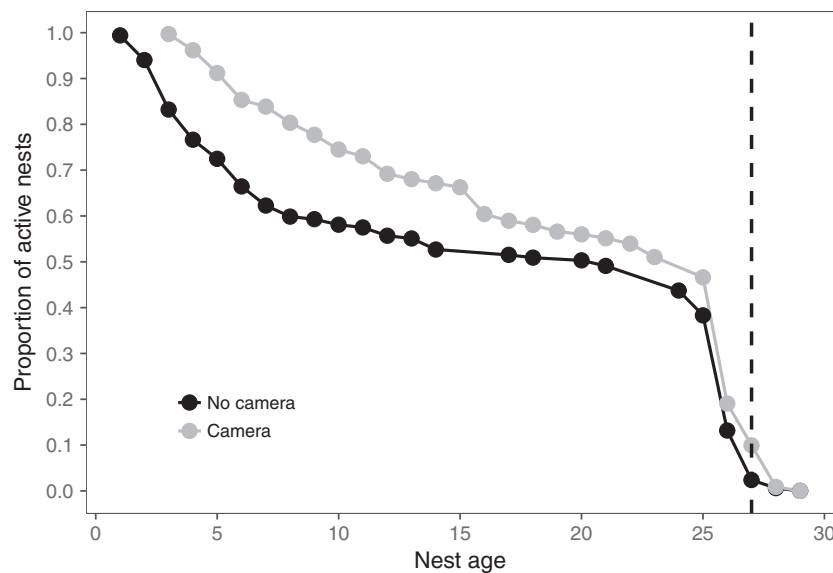


Figure 2. Proportion of active nests across the incubation period for nests monitored with and without cameras. To minimize the risk of abandonment, we did not begin monitoring nests with cameras until 4 days after the onset of incubation. The dashed line corresponds to the mean incubation period in Snowy Plovers *Charadrius nivosus* (27 days).

was 0.46 (95% CI: 0.38–0.53) compared with 0.42 (95% CI: 0.31–0.51) for nests that were not monitored with cameras.

DISCUSSION

We found that field-based methods of determining nest fate in our system were reasonably accurate at 84%. Similar measures of accuracy for estimates of nest fate have previously been reported (Pietz & Granfors 2000, Williams & Wood 2002, Ball & Bayne 2012). Accuracy of nest-fate assignment for passerines varied by nest fate and was lowest when nests were depredated (Ball & Bayne 2012). We found that the probability of correctly assigning nest fate was lowest when small mammals depredated nests, due to the presence of small eggshell fragments, although confidence intervals around this estimate were large due to a small sample size ($n = 9$; Fig. 1a). However, successful nests were less likely to be assigned correctly than were nests that were depredated by Coyotes, foxes, gulls and Common Raven, although confidence intervals did overlap (Fig. 1a). Determining nest fate for many species of shorebirds can be difficult because adults remove eggshell evidence soon after chicks hatch (Mabee *et al.* 2006) and we occasionally observed adults removing eggshells following depredation. Nest location could further alter the probability of correctly assigning nest fate. We documented a decrease in accuracy when nests were located on barren substrates, probably because eggshell evidence was more susceptible to disturbance from wind and precipitation,

which makes it challenging to estimate relations between habitat and nest survival.

Signs and evidence at nests may lead to incorrect assignments of nest fate. Depredated nests that were incorrectly assigned contained small fragments (80% of nests) and eggshell tops (30% of nests), which are both indicators of hatching (Mabee 1997, Mabee *et al.* 2006). Conversely, 64% of successful nests that were incorrectly assigned had no eggshell evidence and 27% had large eggshell pieces in the nest suggesting nest predation. Of our incorrect assignments for successful nests, 52% had incomplete clutches following partial depredation compared with 10% of correctly assigned nest fates. Traditional nest survival analyses consider a nest successful if at least one egg hatches. However, partial nest predation can create conflicting evidence, leading to inconclusive assignments of nest fate (Lariviere 1999). As a result, the prevalence of partial nest predation is poorly understood in most systems (Lariviere 1999, Ackerman *et al.* 2003, Isaksson *et al.* 2007). In our study areas, partial predation was relatively common (19% of all successful nests).

There has been concern that nest predators could be either attracted or deterred by cameras, creating potential bias when used. We did not detect a significant effect of cameras on nest survival rates (Fig. 2). Evidence suggests that rates of predation for shorebird nests are not greater when cameras are present (Liebezeit & Zack 2008, McKinnon & Bêty 2009, Demers & Robinson-Nilsen 2012) similar to evidence for passerines (Pietz & Granfors 2000, Richardson *et al.* 2009).

Predators may identify visual and olfactory cues of observers when observers repeatedly monitor nests that are not associated with cameras (Conover 2007) and thus cameras may represent a method for minimizing disturbance.

When close attention is paid to nest age and evidence at nests, traditional protocols for determining nest fate are effective, particularly given that we did not detect a difference in the probability of correct assignment among individual observers (Mabee 1997, Williams & Wood 2002, Mabee *et al.* 2006, Ball & Bayne 2012). The most conservative method for assigning nests as successful is to locate chicks; however, because shorebirds often leave their nest within hours of hatching, this method can be impractical. Additional time spent in the field describing nest conditions or collecting nest substrate to be sorted in a lab setting may aid in locating small eggshell fragments after hatching. An effort to check nests more often as anticipated hatch date approaches may also increase the accuracy of assigning nest fate (Williams & Wood 2002, Ball & Bayne 2012) but the increased presence at the nest by observers could lead to deleterious effects on rates of predation. Remote cameras provided unambiguous data regarding nest predators and nest fate. If it is not feasible for all nests to be monitored with remote cameras, we suggest using cameras on a subset of nests to identify predators and characterize eggshell evidence in the field that may be specific to each system.

We thank D. Arande, D. Collins, J. Fullmer, C. Russell, K. Spainhower and L. Watkins for assistance in the field. Fish Springs National Wildlife refuge provided use of facilities while we conducted this study. We thank J. Smart, anonymous reviewers and the editors for comments that greatly improved the quality of the manuscript. This project was funded by U.S. Hill Air Force Base, U.S. Army Dugway Proving Ground, Tracy Aviary Conservation Science Program, Tides Foundation, Rio Tinto Kennecott, BirdLife International, U.S. Fish and Wildlife Service Region 6, Denker's Family Foundation, Weber State University and the Utah Chapter of The Wildlife Society.

REFERENCES

- Ackerman, J.T., Eadie, J.M., Loughman, D.L., Yarris, G.S. & McLandress, M.R. 2003. The influence of partial clutch depredation on duckling production. *J. Wildl. Manage.* **67**: 576–587.
- Ball, J.R. & Bayne, E.M. 2012. Using video monitoring to assess the accuracy of nest fate and nest productivity estimates by field observation. *Auk* **129**: 438–448.
- Barton, K. 2016. *MuMIn: Multi-Model Inference. R package version 1.15.6*. Available at <https://CRAN.R-project.org/package=MuMIn> (accessed 10 January 2017).
- Bolton, M., Butcher, N., Sharpe, F., Stevens, D. & Fisher, G. 2007. Remote monitoring of nests using digital camera technology. *J. Field Orn.* **78**: 213–220.
- Burnham, K.P. & Anderson, D. 2002. *Model Selection and Multi-model Inference*. New York, NY: Springer.
- Burns, F., McCulloch, N., Dos Remedios, N., Bolton, M. & Szekely, T. 2013. Sex differences in incubation behaviour but not mortality risk in a threatened shorebird. *Ibis* **155**: 877–880.
- Conover, M.R. 2007. *Predator-prey Dynamics: The Role of Olfaction*. New York, NY: CRC Press.
- Cutler, T.L. & Swann, D.E. 1999. Using remote photography in wildlife ecology: a review. *Wild. Soc. Bull.* **27**: 571–581.
- Demers, S.A. & Robinson-Nilsen, C.W. 2012. Monitoring Western Snowy Plover nests with remote surveillance systems in San Francisco Bay, California. *J. Fish Wildl. Manag.* **3**: 123–132.
- Dinsmore, S.J. & Dinsmore, J.J. 2007. Modeling avian nest survival in Program MARK. *Stud. Avian Biol.* **34**: 73–83.
- Ellis, K.S., Larsen, R.T., Knight, R.N. & Cavitt, J.F. 2014. Occupancy and detectability of Snowy Plovers in western Utah: an application to a low density population. *J. Field Orn.* **85**: 355–363.
- Ellis, K.S., Cavitt, J.F. & Larsen, R.T. 2015. Factors influencing Snowy Plover *Charadrius nivosus* nest survival at Great Salt Lake, Utah. *Waterbirds* **38**: 58–67.
- Isaksson, D., Wallander, J. & Larsson, M. 2007. Managing predation on ground-nesting birds: the effectiveness of nest exclosures. *Biol. Cons.* **136**: 136–142.
- Jones, S.L. & Geupel, G.R. (eds). 2007. *Beyond Mayfield: Measurements of Nest-survival Data*. Stud. Avian Biol., No. 34. Camarillo, CA: Cooper Ornithological Society.
- Laake, J.L. & Rexstad, E.A. 2012. *RMark – An alternative approach to building linear models in MARK*. In Cooch, E. & White, G.C. (eds) *Program MARK: 'A Gentle Introduction'*. C1–C115. <http://www.phidot.org/software/mark/docs/book> (accessed 3 March 2010)
- Lariviere, S. 1999. Reasons why predators cannot be inferred from nest remains. *Condor* **101**: 718–721.
- Liebezeit, J.R. & Zack, S. 2008. Point counts underestimate the importance of Arctic foxes as avian nest predators: evidence from remote video cameras in Arctic Alaskan oil fields. *Arctic* **61**: 153–161.
- Mabee, T.J. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bull.* **109**: 307–313.
- Mabee, T.J. & Estelle, V.B. 2000. Nest fate and vegetation characteristics for Snowy Plover and Killdeer in Colorado, USA. *Wader Study Group Bull.* **93**: 67–72.
- Mabee, T.J., Wildman, A.M. & Johnson, C.B. 2006. Using egg flotation and eggshell evidence to determine age and fate of Arctic shorebird nests. *J. Field Orn.* **77**: 163–172.
- McKinnon, L. & B  ty, J. 2009. Effect of camera monitoring on survival rates of High-Arctic shorebird nests. *J. Field Orn.* **80**: 280–288.
- Page, G.W., Stenzel, L.E. & Ribic, C.A. 1985. Nest site selection and clutch predation in the Snowy Plover. *Auk* **102**: 347–353.
- Page, G.W., Stenzel, L.E., Warriner, J.S., Warriner, J.C. & Paton, P.W. 2009. Snowy Plover (*Charadrius nivosus*). In Poole, A. (ed.) *The Birds of North America*. no. 154. Ithaca, NY: Cornell Lab of Ornithology.
- Paton, P.W. 1995. Breeding biology of Snowy Plovers at Great Salt Lake, Utah. *Wilson Bull.* **107**: 275–288.

- Pietz, P.J. & Granfors, D.A. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *J. Wildl. Manage.* **64**: 71–87.
- R Development Core Team 2012. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Richardson, T.W., Gardali, T. & Jenkins, S.H. 2009. Review and meta-analysis of camera effects on avian nest success. *J. Wildl. Manage.* **73**: 287–293.
- Rotella, J., Dinsmore, S. & Shaffer, T. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Anim. Biodivers. Conserv.* **27**: 187–205.
- Seber, G.A. 1982. *The Estimation of Annual Abundance and Related Parameters*, 2nd edn. New York: Macmillan.
- Smith, P.A., Gilchrist, H.G. & Smith, J.N.M. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. *Condor* **109**: 15–31.
- Smith, P.A., Tulp, I., Schekkerman, H., Gilchrist, H.G. & Forbes, M.R. 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. *Animal Behav.* **84**: 835–842.
- Thomas, S.M., Lyons, J.E., Andres, B.A., Elliot-Smith, E., Palacios, E., Cavitt, J.F., Royle, J.A., Fellows, S.D., Maty, K., Howe, W.H., Mellink, E., Melvin, S. & Zimmerman, T. 2012. Population size of Snowy Plovers breeding in North America. *Waterbirds* **35**: 1–14.
- USFWS 2012. Endangered and threatened wildlife and plants; revised designation of critical habitat for the Pacific Coast Population of the Western Snowy Plover. *Fed. Reg.* **77**: 36728–36869.
- Williams, G.E. & Wood, P.B. 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with Wood Thrushes *Hylocichla mustelina* using miniature video cameras. *Auk* **119**: 1126–1132.
- Zurr, A.F., Ieno, E.N. & Elphinstone, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**: 3–14.

Received 28 August 2017;
revision accepted 8 April 2018.
Associate Editor: Niall Burton.