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Nest exclosures do not improve Streaked Horned Lark nest success

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ABSTRACT. Improving the conservation status of rare and declining species often requires multiple strategies targeted at several vital rates. We report on one of several ongoing management actions intended to benefit the declining population of Streaked Horned Larks (*Eremophila alpestris strigata*). To improve Streaked Horned Lark fecundity, we employed predator exclosures (wire cages) around nests ($N = 33$ exclosed and 32 not exclosed) in 2009 and 2010 at two sites in Oregon and two in Washington with the goal of excluding larger birds, the primary lark nest predators. We found no statistically significant effect of exclosures on nest success. For exclosed nests, lower rates of nest predation (exclosed = 12%, unexclosed = 48%) were offset by higher rates of nest abandonment (exclosed = 27%, unexclosed = 0%). Nest abandonment was likely caused by a variety of factors including American Kestrels (*Falco sparverius*) perching on exclosures, and predation of adults associated with exclosed nests. Our results suggest that the current exclosure design does not improve Streaked Horned Lark fecundity and may negatively affect adult survival. To improve exclosure effectiveness, we recommend modifications that prevent kestrels from perching on exclosures and deny their access to the nest. We also recommend that modifications be applied in an adaptive management framework that includes close monitoring to assess their effectiveness, and subsequent adaptation that might include continued structural modification of exclosures or discontinued use on some or all sites.

RESUMEN. **Exclusiones de nidos no mejoran el éxito reproductivo de *Eremophila alpestris strigata***

Mejorar el estado de conservación de especies raras y en disminución usualmente requiere de múltiples estrategias dirigidas a muchos aspectos vitales. En este estudio reportamos sobre una de las múltiples acciones de manejo existentes dirigidas a disminuir la reducción de las poblaciones de *Eremophila alpestris strigata*. Para mejorar la fecundidad de *E. alpestris strigata*, pusimos exclusiones de depredadores (jaulas de alambre) alrededor del nido ($N = 33$ con exclusión y 32 sin exclusión) en 2009 y 2010 en dos lugares en Oregón y dos en Washington con el objetivo de excluir aves grandes, principales depredadores de los nidos de *E. alpestris strigata*. No encontramos diferencias estadísticas significativas en el efectos de las exclusiones sobre el éxito reproductivo. Para los nidos excluidos, las menores tasa de depredación (excluidos = 12%, no excluidos = 48%) fueron contrarrestadas con las altas tasa de abandono (excluidos = 27%, no excluidos = 0%). El abandono de los nidos posiblemente fue causado por una variedad de factores que incluyeron *Falco sparverius* perchándose en la jaulas y depredación de adultos asociados a las exclusiones de nidos. Nuestros resultados sugieren que los actuales diseños de exclusión no mejoran la fecundidad de *E. alpestris strigata* y posiblemente afecta negativamente la supervivencia de los adultos. Para mejorar la efectividad de las exclusiones, recomendamos modificaciones que prevengan a *F. sparverius* percharse sobre la jaula y prevengan su acceso a los nidos. También recomendamos que se apliquen modificaciones en un marco de manejo adaptativo que incluya un monitoreo cercano el cual evalué su efectividad y subsecuente adaptación, además que incluya continuas modificaciones estructurales de las exclusiones o descontinuar su uso en algunos o todo los lugares.

Key words: *Eremophila alpestris strigata*, nest predation, predator exclusion, species recovery

Streaked Horned Larks (*Eremophila alpestris strigata*) are a partially migratory subspecies associated with sparsely vegetated grassland habitats (Beason 1995, Rogers 2000, Stinson 2005) and are a federal candidate for listing under the Endangered Species Act. These larks are listed as endangered by the state of Washington and in Canada (Canadian Species at Risk Act 2002). The breeding range of Streaked Horned Larks has contracted over time, with local extirpation from the northern (Puget trough, southern British Columbia, and the Washington Coast north of Grays Harbor) and southern (Rogue River Valley of Oregon) extremes of their range (Rogers 2000, Beauchesne and Cooper 2003, Stinson 2005). The current breeding range

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includes agricultural habitats and grasslands of the Willamette Valley of Oregon, dredge deposition islands along the lower Columbia River, southern Washington coastal dune habitats, and grasslands in the Puget lowlands near Olympia and Tacoma, Washington.

Streaked Horned Lark populations in Washington are declining rapidly (Camfield et al. 2011) and conservation efforts are needed that target both survival and fecundity (Camfield et al. 2011). Because low Streaked Horned Lark fecundity (number of young fledged per female) is driven primarily by high rates of nest predation (Camfield 2010), we examined the effectiveness of placing wire-mesh cages (exclosures) around nests to exclude nest predators and increase nest survival. For some species and under some ecological conditions, nest exclosures can increase reproductive success without increasing adult mortality (e.g., Pauliny et al. 2008) and can have positive population effects (e.g., Larson et al. 2002, Smith et al. 2010). For other species, exclosures either have no effect on nest success (e.g., Nol and Brooks 1982, Mabee and Estelle 2000) or have detrimental effects on adult survival (e.g., Murphy et al. 2003). Generally, exclosures significantly increase hatching success and the heterogeneity in this effect is not explained by characteristics of the prey, predator species, location, or by study methods (Smith 2010).

We predicted that exclosures would improve Streaked Horned Lark nest success because we previously placed exclosures around one nest in 2005 and two nests in 2008 and, in all cases, adults returned to nests within 30 min of exclosure placement, resumed incubating, and ultimately fledged young (Pearson and Hopey 2008). In addition, exclosures are particularly effective at excluding large mammalian and avian predators (Mabee and Estelle 2000), the latter being the primary predators of Streaked Horned Lark nests throughout their range (Pearson and Hopey 2008, S. F. Pearson and R. Moore, unpubl. data). In most previous exclosure studies, correlative approaches were used to assess their effectiveness, and exclosures have only been placed around nests of species with precocial young (shorebirds and ducks; Smith et al. 2010). In contrast, we placed exclosures around nests of a ground-nesting passerine with altricial young and used an experimental approach that addressed concerns about study design raised by Mabee and Estelle (2000) and Johnson and Oring (2002). Finally, we employed exclosures in an adaptive management framework (Allan and Stankey 2009), where use of exclosures is viewed primarily as a conservation technique, but is closely monitored to evaluate its effectiveness and to inform potential modifications that might increase their future effectiveness.

METHODS

Study sites. We conducted our study at four sites in Oregon and Washington. The municipal airport in Corvallis, Oregon (44°50′N, 123°29′W), is about 603 ha in size and consists of grass- and forb-dominated infield areas, runways, and taxiways, and adjacent fields planted in annual and perennial grasses. About 80 pairs of Streaked Horned Larks nest in the sparse vegetation adjacent to runways, taxiways, and adjacent fields. William L. Finley National Wildlife Refuge (44°39′N, 123°31′W) is ~16 km south of Corvallis and consists of ~2156 ha of wildlife food crop fields, native prairie, and forests dominated by Oregon white oak (*Quercus garryana*) savannah, bottomland Oregon ash (*Fraxinus latifolia*) forest, big-leaf maple (*Acer macrophyllum*), and Douglas-fir (*Pseudotsuga menziesii*). The site is occupied by up to 40 pairs of larks that nest in crop fields heavily grazed by overwintering geese. Olympia Airport (46°58′N, 122°53′W) in Olympia, Washington, includes ~248 ha of grasslands, taxiways, and runways. The site is dominated by non-native grasses and forbs, and hosts ~17 pairs of larks that nest in sparse vegetation adjacent to runways and taxiways and in areas treated with herbicide to remove invasive yellow nutsedge (*Cyperus esculentus*). Thirteenth Division Prairie (47°01′N, 122°26′W) is located in Pierce County, Washington, and is a 1114-ha prairie dominated by grasses and forbs with a mixture of native and non-native species (Dunwiddie et al. 2006). There are 7–8 nesting pairs on ~390 ha of suitable habitat.

Nest searching and monitoring. We searched for nests from early April to mid-August in 2009 (Corvallis Airport, Finley, and Thirteenth Division) and 2010 (Olympia Airport). Nests were located by observing adults, flushing incubating or brooding adults, and searching appropriate habitat. Nests were found during the nest building, incubation, and nestling stages. Nest stage (nest building, pre-laying but post-building, incubation, and nestling) was recorded every 1–3 days, and every day or every other day near expected hatch and fledging dates. Expected hatch and fledging dates were estimated using known hatch or egg-laying dates and the following intervals: 1 egg laid per day (thus, the number of eggs in a clutch equals the length of the laying period), an incubation period of 12 days, and nestling period of 9 days (Beason 1995). For nests found during the nestling period or with unknown hatching dates, hatching and fledging dates were estimated using photographic reference images of known-aged chicks that depicted daily changes in down and contour/flight feathering and, because feathering changes so rapidly over the 9-day nestling period, we could estimate chick age ± 1 day. Nests were considered successful if adults were observed with fledglings in their territory (territories were mapped) within 3–4 days of fledging (chicks are unable to fly during this period) or nests were found empty with signs of fledging (flattening of nest cup and fecal droppings in or near nests) on or after the expected fledging date. Nests with signs of predation were counted as unsuccessful. Signs of predation included damaged eggs, blood or feathers in or near a nest, and nests found empty during incubation or during the nestling period when nestlings were too young to have fledged ($<$8 days post-hatching). Nests were considered abandoned if a nest and contents were intact and no adults were observed after 2–3 visits and $>$7 days had passed after the estimated fledge date. Nests that were abandoned and later predated were considered abandoned. Two exclosed nests were lost to flooding during rain events and were considered to have failed due to weather.

Study design and exclosures. Wire-mesh cages were placed around nests to exclose the nest from potential nest predators. Our experimental design addressed concerns associated with similar exclosure studies (e.g., Mabee and Estelle 2000). Specifically, we: (1) had similar numbers of exclosed and unexclosed nests, (2) exclosed similar numbers of nests in May, June, and July, (3) randomly assigned exclosure treatments within study sites to avoid spatial bias, and (4) used statistical analyses that accounted for left-truncation, right-censoring, and interval-censoring. In addition, we used a variety of sites in a variety of habitats that presumably varied in predator assemblages. Ideally, our study would have been repeated for multiple years to determine possible year effects, but given the results reported here, we thought it prudent to discontinue use of nest exclosures, at least with the current design (see Results).

When our study was initiated, we had completed one independent study of nest predators using video cameras in Washington, were initiating a second study in Oregon, and had opportunistically observed predation events in Oregon and Washington by American Crow (*Corvus brachyrhynchos*; $N = 2$), Northern Harrier (*Circus cyaneus*; $N = 1$), and an unidentified garter snake species (*Thamnophis spp*; $N = 1$). Based on these studies and observations, we concluded that we should use exclosures that would exclude larger bird predators. We used the mini-exclosure design previously used for Snowy Plovers (*Charadrius nivosus*; Lauten et al. 2004, Hardy and Colwell 2008) because the wire mesh size (5 × 10-cm) would exclude most bird predators and because nest cages have a greater effect on hatching success than exclusion fences (Smith et al. 2010). Our exclosures were portable and could be set up rapidly (10–15 min) with minimal disturbance to the birds, allowed adult birds quick ingress and egress, and were designed to minimize risk of injury to adult birds. Exclosures were constructed of 5 × 10-cm wire mesh, and were rectangular in shape with a base 1.2 m × 1.2 m and 0.9 m high. Domed wire fencing was fastened to the top of the square frame under which we secured a taut layer of 2-cm polypropylene black mesh netting. This soft layer was used to prevent startled adults from flushing from nests and striking the hard wire top. A door was cut in one side of the exclosure so eggs and chicks could be accessed if necessary; doors were fastened closed with pliable, heavy-gauge wire. Stakes ($\sim$17 cm in length) were placed at each corner and at the margins of exclosures to hold them in place. All nests were exclosed during incubation (average = day 7 of incubation; range = day 2–12).

Statistical analysis. To determine if there was a difference in nest survival between nests with and without exclosures, we used two statistical paradigms: (1) AIC-based model selection and (2) traditional hypothesis testing. For the AIC-based approach, we first assessed pairs of models with and without the variable exclosure. We then examined the effect size and associated confidence interval of the variable exclosure for all models that included this variable. We evaluated competing models of daily survival rate of nests using the logistic exposure method (Stephens 2003, Schaffer 2004, Rotella et al. 2004, Stephens et al. 2005). To build our models, we chose PROC NLMIXED in SAS because it allowed us to model our binomially distributed data while simultaneously considering fixed effects of exclosure (exclosed, unexclosed), nest age in days (day $1 =$ day first egg was laid), nest stage (laying, incubation, nestling), and date (day $1 =$ May first) and random effects of study site (Corvallis Airport, Finley National Wildlife Refuge, Olympia Airport, and Thirteenth Division Prairie) on nest survival (fledged one or more young or failed) (PROC NLMIXED; SAS Institute 2007). Nest age was either measured directly when under observation prior to egg laying or estimated using known dates (egg laying, hatching, fledging) and the egg laying, incubation, and nestling periods above. The SAS code used for this analysis follows Rotella et al. (2004, appendix 4).

We treated exclosure as a time varying covariate for which we assigned 0 to intervals without an exclosure and 1 to intervals with exclosures. We did not include date, age, and stage together in a model because they are functionally related. We include stage to allow for effects of age (or date) that might not be linear and therefore masked by just using age (or date) linearly in models. Pairs of candidate models (with and without exclosure) are presented in Table 1. We evaluated candidate models with Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 2002). We used the effective sample size ("n-ess"; Rotella et al. 2004) when computing AIC_c (n equals the sum, over all nests, of the number of days each nest was under observation and survived, plus the number of observed failures). To assess the effect of the variable exclosure, we used the parameter estimate and associate confidence intervals. If the 95% confidence overlapped with zero, then there was no statistically significant effect of exclosure on survival (alpha $= 0.05$). Prior to starting the experiment, our hope was that exclosures would decrease nest predation rates without increasing abandonment rates. To test for this possibility, we used Fisher's Exact Text comparing the abandonment and depredation rates of exclosed and unexclosed nests.

RESULTS

We exclosed 33 nests (14 at Corvalis Airport, six at Finley National Wildlife Refuge, seven at Olympia Airport, and six at 13th Division Prairie) in 2009 and 2010. Thirty-two nests were not exclosed, with equal sample sizes of non-exclosed nests at all sites except 13th Division Prairie where five were not exclosed. Of the 65 nests, 32 fledged young, 32 failed, and the outcome of one nest was unknown. For the 33 exclosed nests, 16 fledged young and 17 failed (nine abandoned, four predated, two failed due to flooding, and two failed for unknown reasons). Of 31 non-exclosed nests where outcome was determined, 16 fledged young and 15 failed and all failures were due to predation.

We analyzed nest survival for 65 nests (33 exclosed, 32 not exclosed) representing an effective sample size of 655. The best nest survival model included date only (Table 1; $AIC_c = 245.5$; the effect of date was positive, but not statistically significant: $\hat{\beta}_{date} = 0.015$, $P = 0.086$). The second best model included date and exclosure (Table 1; $\Delta AIC_c = 1.929$). However, the inclusion of exclosure did not explain enough variation to justify inclusion in the model and, therefore, should not be interpreted as having any ecological effect (Arnold 2010). As a result, the date-exclosure model should not be considered competitive. In fact, comparing all pairs of models with and without exclosure (Table 1), the AIC_c for the model with exclosure was always 2 greater than the paired model without exclosure, indicating no effect of exclosure (Arnold 2010). For all models including exclosure, the 95% CIs for the exclosure effect overlaps zero, indicating no statistically significant effect of exclosure on overall nest survival (Table 1). In addition, daily survival estimates for exclosed nests were almost identical to those of non-exclosed nests (Fig. 1).

Two exclosed nests failed due to flooding, a random event with nothing to do with the exclosures per se. However, even when we censored these two exclosed nests, we still found no evidence of an effect of exclosures on overall nest survival. The best AIC_c-ranked model only included date and was again followed by the model with date + exclosure ($\Delta AIC_c = 1.614$) and, in the date + exclosure model, the effect of exclosure was not significant ($P = 0.53$).

Table 1. Logistic exposure models of Streaked Horned Lark nest ($N = 65$) daily survival rates, showing the estimated effect of exclosure (95% CI) as well as AIC_c values for each pair of models (with and without the exclosure parameter). Nests were monitored at two sites in Oregon and two in Washington, 2009–2010. The best nest survival model included date only ($AIC_c = 245.5$). K = number of parameters in the model.

Model	K	AIC_c with exclosure	AIC_c without exclosure	Exclosure effect estimate	95% CI	
Exclosure + Date	3	247.4	245.5	0.11	−0.60	0.82
Exclosure	2	248.5	N/A	0.02	−0.68	0.73
Exclosure + Date + Site	4	249.4	247.5	0.12	−1.04	1.26
Exclosure + Site	3	250.5	248.5	0.02	−1.12	1.16
Exclosure + Age + Site	4	252.0	250.0	−0.02	−1.17	1.14
Exclosure + Stage + Site	4	254.2	252.1	0.01	−1.18	1.19

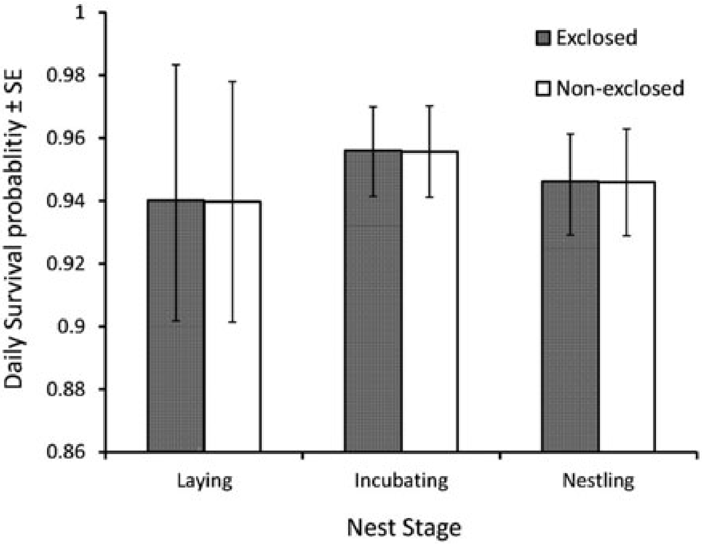

Fig. 1. Daily Streaked Horned Lark nest survival estimates (±SE) did not differ between exclosed ($N = 34$) and non-exclosed ($N = 31$) nests for any nest stage at two sites in Oregon and two in Washington, 2009–2010.

We observed more predation at non-exclosed (15 of 31, or 48.4%) than exclosed (4 of 33, 12.1%) nests (Fisher's exact test, $P = 0.0014$) and more abandonment at exclosed (9 of 33, 27.3%) than non-exclosed nests (0 of 31; $P = 0.0014$). Of nine abandoned nests, one was abandoned within three days of exclosure placement and abandonment may have been caused by exclosure placement. Another nest was abandoned within 3 d of discovery after a lawn mower past over the top. This nest was originally intended as a control (unexclosed), but was not included in the analysis because a clutch was not initiated. The other eight abandoned nests continued to be attended by adults for >9 d, so abandonment was likely not caused by exclosure placement. Two abandoned nests may have had infertile eggs (incubated for >10 d). For two other abandoned exclosed nests, we found evidence that an adult was predated (flight feathers and blood) at one and potentially at a second (contour feathers only). An American Kestrel was observed perching on one of the abandoned nests.

We observed two incidents of nest predation by American Kestrels at the Corvallis Airport, one resulting in the killing of all nestlings in a non-exclosed nest and the other resulting in loss of two of three nestlings in an exclosed nest (the third chick ultimately fledged so this nest is scored as fledged). The identity of predators at the other nests could not be determined.

DISCUSSION

We found no evidence that nest exclosures increased nest success of Streaked Horned Larks. For exclosed nests, lower rates of nest predation were offset by higher rates of nest abandonment, resulting in no overall effect of exclosures on nest success. In contrast, in a meta-analysis of 16 studies where exclosures were placed around nests of six species of shorebirds and various species of ducks, Smith et al. (2010) found that exclusion fences or nest cages tended to increase hatching success for both declining and increasing bird populations. The reason for our low overall exclosed nest success was high nest abandonment associated with exclosures. Our nest abandonment rate for exclosed nests was higher than reported in all but one study reviewed by Smith et al. (2010) and the high abandonment rate in that study (Engley and Prescott 2005) was described as "unexplained." Anecdotal evidence suggests that our high abandonment rate may have been caused by a combination of adult predation, use of exclosures as perches by raptors, and infertile eggs. Although we found no exclosure effect on nest survival, we caution against concluding that exclosures cannot be effective for Streaked Horned Larks and other ground-nesting songbirds without considering the context and potential causes of high abandonment rates and how the method could be modified to make it more effective.

We found evidence of predation of an adult Streaked Horned Lark at one exclosed nest and potentially at a second. In other studies, the effect of exclosures on nest abandonment and adult mortality appears to vary with local predator assemblages. Some investigators have found that predators appear to use exclosures to locate and kill adults in or near exclosures (Smith et al. 2010; table 1). These events are generally episodic (Murphy et al. 2003, Neuman et al. 2004, Hardy and Colwell 2008), differ among habitats (Murphy et al. 2003), are caused primarily by mustelids and raptors (Murphy et al. 2003, Issakson et al. 2007, Hardy and Colwell 2008, Smith 2010), and depend on how the enclosed species leaves nests in response to the presence of a predator. Early flushing species are less likely to be trapped in exclosures by predators (Smith et al. 2010). Only female Streaked Horned Larks incubate (Pearson and Hopey 2008, R. Moore, unpubl. data) and they generally flush from nests early in response to potential predators (including approaching researchers), suggesting that they should not be particularly vulnerable to exclosure-associated predation.

The reduction in nest predation rates at exclosed nests in our study was offset by higher abandonment rates. Higher abandonment rates may be the result of both adult predation and predators perching on exclosure cages, preventing adults from accessing nests and ultimately causing abandonment. Surveys at our Washington study sites indicate that Northern Harriers (*Circus cyaneus*) and American Kestrels are absent at some sites and occur in low numbers at others (S.F. Pearson, unpubl. data). In contrast, both species are relatively abundant residents at our Oregon study sites in the Willamette Valley. Only at the Oregon sites did we observed American Kestrels: (1) perched on exclosures around nests that were ultimately abandoned and where adults were later observed alive, (2) predating an exclosed and an unexclosed nest, and (3) perching on an exclosure where there was evidence of adult predation. These observations suggest that differences in predator assemblages between our Oregon and Washington sites may help explain the high levels of nest abandonment at the Oregon sites.

Our results and those of other studies where nest exclosures were used suggest that exclosures should not be used at sites with resident or migrating falcons or with other species that may use exclosures to detect and kill adult birds (Murphy et al. 2003, Neuman et al. 2004, Niehaus et al. 2004, Isaakson et al. 2007, Hardy and Colwell 2008). Our results also suggest that exclosures should be used cautiously, with frequent assessment of their effectiveness. Avoiding negative effects on adult survival is particularly important for species like Streaked Horned Larks because of the disproportionate effect on population growth (Camfield et al. 2011). We therefore recommend that use of exclosures should be accompanied by close monitoring to evaluate their effectiveness (Hardy and Colwell 2008) and, if found to be ineffective or detrimental, that their use be discontinued (Pauliny et al. 2008) or managed to address the shortcomings of the equipment design.

To reduce or eliminate nest abandonment and predation of adults and young caused by the use of exclosures as perches by raptors such as American Kestrels, commercially available or hand-constructed perch deterrents could be attached to the exclosure roof and a slightly smaller mesh size could be used for the exclosure walls. If nest exclosures are used in future studies of larks and other species of conservation concern, we also recommend video monitoring to determine if exclosed nests are being targeted by predators. If predation of adults or young occurs or is suspected, use of nest exclosures should be discontinued immediately.

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