

Streaked Horned Lark (*Eremophila alpestris strigata*) Fecundity, Survival, Population Growth and Site Fidelity

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**Streaked Horned Lark (*Eremophila alpestris strigata*)
Fecundity, Survival, Population Growth and Site Fidelity:
Research Progress Report**

For

Washington Department of Transportation and The Nature Conservancy

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The 2006 Streaked Horned Lark surveys included in this report were funded by Washington Department of Transportation and by The Nature Conservancy (See Appendix I for a summary of the sites surveyed during the 2006 field season). The research conducted in previous seasons and in Canada was funded largely by other sources (See Acknowledgments). The purpose of this report is to present our estimates of Streaked Horned Lark survival, fecundity and population growth rate and examine patterns of site fidelity. Table 1 and Figure 1 are copied in whole or in part from our manuscript that compares demographic values between the Streaked and Pallid Horned Larks and was submitted to the journal Ecology for review.

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Abstract

Estimates of population growth rate (lambda, $\lambda = 0.61 \pm 0.10$ SD) indicate that the streaked horned lark (*Eremophila alpestris strigata*) population is declining rapidly (40% per year). This estimate includes only vital rates from populations in the Puget lowlands, lower Columbia River and the Washington coast and does not include rates from populations in the Willamette Valley of Oregon. Estimates of immigration are not built into our estimates of lambda and as a result, the decline in absolute population size could be less than 40% per year if the population is being rescued by immigration. This rapid population decline is apparently the result of both low fecundity and low survival. The low fecundity (0.91 female fledglings/female/year) was the result of low egg hatchability, fledging success, high clutch depredation, and long intervals between initial nests that failed and re-nests. Adult survival (0.51 ± 0.06 , $n = 58$) was also quite low, while juvenile survival (0.16 ± 0.04 , $n = 88$) was relatively high. We compared survival, fecundity and population growth rate between *E. a. strigata* and another subspecies of horned lark, the pallid horned lark (*E. a. articola*), located in a relatively healthy ecosystem near Smithers, B.C. Canada. Although the breeding season was more than twice as long for *E. a. strigata* in Washington, *E. a. articola* in British Columbia produced 35% more fledglings per egg laid and the net result was higher annual fecundity for *E. a. articola*. Adult survival was 18% higher and juvenile survival was 13% higher (without dispersal – see below) for *E. a. articola*. This contemporaneous comparison using nearly identical methods between closely related subspecies lends further support to our estimate of a declining streaked horned lark population throughout a large proportion of its geographic range. Adult survival had the greatest influence on population growth rate for *E. a. strigata* suggesting that conservation actions that improve adult survival are likely to have the greatest benefit to *E. a. strigata*. Adult *E. a. strigata* exhibited extremely high site fidelity (no breeding dispersal observed among regions). We observed examples of *E. a. strigata* natal dispersal with juveniles moving from the Puget lowlands to the Washington coast and lower Columbia River to breed. Because we did not observe examples of natal or breeding dispersal into the Puget lowlands and because this population is apparently declining and continuing to experience threats, there appears to be a high probability that *E. a. strigata* populations will be extirpated in this region in the near future unless this trend is reversed.

Introduction

The streaked horned lark (*Eremophila alpestris strigata*) is a rare migratory sub-species that is classified as a federal candidate for listing under the Endangered Species Act and is listed as endangered by the state of Washington and by the Species at Risk Act in Canada (Canadian Species at Risk Act 2002, c.29). Genetic data indicate that *E. a. strigata* is unique, isolated, and has little genetic diversity (Drovetski et al. 2005). The breeding range of *E. a. strigata* has contracted over time with local extirpation from former breeding sites across the range (northern Puget trough, southern British Columbia, the Washington Coast north of Grays Harbor, and the Rogue River Valley of Oregon) (Rogers 2000, Beauchesne and Cooper 2003, Stinson 2005). When attempting to recover rare species, it is important to target conservation actions toward improving the vital rates and habitat conditions that limit populations. *E. a. strigata* research to date has focused on reproductive success and identifying habitat features important to successful reproduction (Pearson 2003, Pearson and Hopey 2004, 2005, Pearson et al. 2005a). However, *E. a. strigata* populations may be regulated by several factors including suitable breeding and overwintering habitat, reproductive rates, juvenile survival, and/or adult survival.

In this study we estimated *E. a. strigata* juvenile and adult survivorship using mark - resight methods (similar to mark - recapture) and fecundity using data gathered in our previous studies (Pearson 2003, Pearson and Hopey 2004, Pearson et al. 2005a, Pearson and Hopey 2005). We use these vital rates to estimate overall population growth rate (λ) and assess the relative contribution of survival and fecundity to population growth. Determining which vital rates contribute most to overall population growth helps us identify where we should focus conservation actions in order to have the greatest impact on population growth rate.

For all vital rate analyses, we compare those of *E. a. strigata* in Washington to a population of the pallid horned lark (*E. a. articola*) located at a single site in alpine habitat on Hudson Bay Mountain near Smithers, British Columbia. We make this comparison between these closely related subspecies (Drovetski et al. 2006) because the *E. a. articola* population is located within

a relatively healthy landscape with little human development in the surrounding landscape while *E. a. strigata* is found in relatively degraded, isolated habitats surrounded by considerable human development. Assuming tradeoffs in investment between somatic maintenance and reproduction (Stearns 1989) we predicted that *E. a. articola* at high elevation and latitude in British Columbia would exhibit a “survivor” life history strategy (low fecundity and high survival) due to the relatively short breeding season as a result of persistent spring snow cover and early onset of fall and *E. a. strigata* would exhibit a “high-reproductive” strategy (high fecundity and low survival; Saether et al. 1996, Saether and Bakke 2000). Thus, *E. a. strigata* would have higher fecundity (more reproductive attempts per season) and lower survival than *E. a. articola*. We predicted that our estimates of population growth (λ) would be equal to or to be close to one if *E. a. strigata* and *E. a. articola* populations are not declining.

The final objective of this study is to use our mark – resight data to determine if *E. a. strigata* exhibits site fidelity. Information on site fidelity is critical for developing effective conservation strategies especially when attempting to establish new nesting populations and to assess genetic exchange among nesting populations.

Methods

Study Sites

We used information collected at seven sites in Washington State from 2002-2005 to assess fecundity and survival. In Washington, *E. a. strigata* nests in grass and forb dominated habitats located in south Puget Sound prairies and airports, coastal Washington dune habitats and on islands in the lower Columbia River. Study sites included: Olympia Airport (46° 58' N, 122° 53'W), 13th Division Prairie on Ft. Lewis (47° 01' N 122° 26'W), Gray Army Airfield on Ft. Lewis (47° 05' N 122° 34'W), McChord Air Force Base (47° 08' N 122° 28'W), Damon Point (46° 56'N, 124° 06' W), Midway Beach (46° 46'N, 124° 05' W) and Whites Island on the lower Columbia River (46° 08'N, 123° 18' W). We used information collected at a single site in alpine habitat on Hudson Bay Mountain near Smithers, British Columbia, Canada (52° N, 127° W)

from 2003-2006 to assess *E. a. articola* fecundity and survival.

Banding

Chicks were banded with unique color band combinations on the nest on or around day 7 post-hatching or, on several occasions, shortly after fledging if the young could be captured. For *E. a. strigata*, we banded 26 juvenile birds with unique color bands in 2002 and we did not band any birds or attempt to resight banded birds in 2003. In 2004, we banded 81 birds (24 adult, 57 juvenile) and in 2005, we banded 73 birds (27 adults, 46 juvenile). We conducted complete surveys of the study areas each year to determine which individuals returned. At the Smithers, B.C. study site, we banded 117 adult and 175 juvenile birds between 2003 and 2006 (Camfield Ph.D. dissertation in preparation).

Reproductive success

Throughout the breeding seasons (April through mid-August) of 2002-2006, we searched for nests on horned lark territories. Nests were located by observing adults leaving or approaching nests with and without nesting materials or carrying food, by flushing incubating or brooding adults and by searching appropriate habitat. Nests were found during nest building, incubation and nestling stage. The status of each nest (presence of parents, eggs, nestlings) was recorded approximately every 3-5 days, more frequently near the expected hatch and fledging dates. Reproductive success results for *E. a. strigata* are published in Pearson 2003, Pearson and Hopey 2004, Pearson et al. 2005, and Pearson and Hopey 2005.

Surveys

The funding from Washington Department of Transportation and The Nature Conservancy was used to conduct our 2006 surveys. During the 2006 nesting season, we completed 59 surveys on 21 sites in southwestern Washington (Appendix I). In 2006, each site was visited 1 to 6 times between 19 April and 2 August and nearly all localities where birds were previously banded were visited at least 3 times. We surveyed two previously un-surveyed islands on the lower Columbia River, Hump and Lord islands one time each to assess occupancy. Some of the other Columbia

River island sites and the Artillery Impact Area on Ft. Lewis were also only visited once because of the difficulty gaining access. Previous surveys are described in Pearson and Hopey 2004, Pearson et al. 2005, and Pearson and Hopey 2005. At the Smithers, B.C. study site, *E. a. articola* birds were surveyed throughout the breeding seasons from 2003-2006 (A.F. Camfield Ph.D. dissertation in prep).

Site fidelity

When examining site fidelity, we measured both natal and breeding dispersal. Natal dispersal is a permanent movement of an individual from its birth site to the place where it reproduces. Breeding dispersal is the inter-annual movement between nesting sites by adults. When examining site fidelity and dispersal, we grouped Olympia Airport, 13th Division Prairie, Gray Army Airfield and McChord Air Force Base in the Puget lowlands region, and Damon Point and Midway beach in the Washington coast region and Whites Island in the lower Columbia River region.

Analysis - Estimation of demographic variables

We estimated 14 demographic variables for each subspecies: 1) Clutch initiation date is the date the first egg in a clutch was laid and, unless observed directly, was calculated by backdating from known dates (hatching dates, estimated age of nestlings, or fledging dates). We used the following time intervals to calculate clutch initiation dates: egg laying = 1 egg laid per day (thus, the number of eggs in a clutch = the length of the egg laying stage), incubation = 12 days, nestling = 9 days (Beason 1995). 2) Breeding season length (*B*) is the interval between the first and last known clutch initiation date. 3) Clutch size (*C*) was calculated from nests that were observed with the same clutch size more than once (at least one day apart) during incubation. 4) Proportion hatched is the proportion of eggs laid that hatched, includes nests that hatched at least one egg with known clutch size and that was observed twice with the same number of nestlings. 5) Proportion fledged is the proportion of nestlings that successfully left the nest and was calculated by subtracting the number of nestlings that disappeared or dead nestlings that remained in the nest after the others had fledged. 6) Fledglings per egg laid (*S*) is the proportion

of eggs laid that produced a fledgling. 7) Nest survival is calculated using Mayfield (1975) estimators and was the probability that a nest fledged at least one nestling. Nests were counted as successful if adults were seen with fledglings or if the nest was found empty with no signs of depredation on or after the expected fledging date. Nests with signs of depredation (blood and/or feathers in or near the nest, damaged nest cup or eggs in or near the nest, nests found empty during incubation or before young could have fledged) were counted as unsuccessful. 8) Proportion nests depredated is the proportion of the total nests found that were destroyed by a predator. 9) Replacement nest interval (r_f) is the number of days between nest failure and the next clutch initiated by the same female. Only nests with banded adults or on territories that were consistently monitored were included. 10) Multiple brood interval (r_s) is the number of days between the successful fledging of a nest and the initiation of an additional brood. Only nests with banded adults or on territories that were consistently monitored were included in the calculation. 11) Annual fecundity (F) is the number of female fledglings per female per year. We estimated annual fecundity using the technique of Ricklefs and Bloom (1977) with the following variables: 1) Length of the breeding season (B) corrected for the fact that breeding effort is not constant across all months; 2) clutch size (C); 3) fledglings per egg laid (S); 4) daily nest mortality rate (m); 5) probability that at least one nestling fledges (p_s); 6) probability that a nest fails (p_f); 7) multiple brood interval (r_s); 8) replacement nest interval (r_f). To estimate the number of female fledglings per female, annual fecundity was divided by two, assuming an equal sex ratio at fledging. 12) Adult survival (ϕ_a) is the probability that an adult bird survived and returned to the study site the following year. Survival rates were estimated for both males and females and corrected for resighting probability. 13) Juvenile survival (ϕ_j) is the probability that a bird banded as a nestling and that successfully fledged returned to the study site the following year. Survival rates were corrected for resighting probability. Because *E. a. strigata* were studied over multiple sites, the survival estimates included juveniles that dispersed from their natal site to one of the other study sites. Estimates of *E. a. articola* juvenile survival are from a single site and hence are likely to be underestimates when compared to *E. a. strigata*. To allow for direct comparisons we provide within site only juvenile survival estimates for *E. a. strigata*. 14) Population growth rate (λ) was estimated using the equation: $\lambda = F\phi_j + \phi_a$, where F is the number of female fledglings produced per female per year, ϕ_j is apparent juvenile survival and ϕ_a is apparent adult female survival (Pulliam 1988). To give the most realistic estimate of

population growth for *E. a. strigata*, we used the juvenile survival estimate including juvenile dispersal among our 7 sites.

Analysis – Survival and population growth estimates

We used the Program Mark Version 3.1 (White and Burnham 1999) to estimate apparent survival rates from live encounter data using the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). The median \hat{c} approach (Cooch and White 2006) was used in Program Mark to assess goodness-of-fit of the global models (ϕ_{t*s} p_{t*s}) with two groups for males and females (s) and time dependence (t) for apparent survival and probability of encounter for adults and time dependence (t) only for juveniles. Information-theoretic procedures using AICc (Burnham and Anderson 2002) were used for model selection. We used a Monte Carlo simulation approach of 10,000 replicates to generate beta distributions for apparent survival of adult females and juveniles based on the estimated mean and variation. A stretched beta distribution was used to simulate fecundity and these parameter estimates were then used to calculate λ . The stretched beta distribution is a rescaled beta distribution that reflects a biologically realistic range for the simulated vital rate (Morris and Doak 2002). Finally we used Life-Stage Stimulation Analysis (Wisdom and Mills 1997, Wisdom et al. 2000) to assess the effect of changes in F , ϕ_j , and ϕ_a on λ . We performed linear regressions of λ on each vital rate while allowing the other vital rates to vary simultaneously. The coefficient of determination (r^2) shows the proportion of the variation in λ over all simulations that is explained by variation in each vital rate. Monte Carlo simulations and regressions were performed using the program R (R Development Core Team 2006), z -tests were used to compare nest survival and depredation, comparisons of survival rates were done using χ^2 statistics in Program Contrast (Sauer and Williams 1989), t -tests and Mann-Whitney U -tests were used for all other pairwise comparisons and were performed using SPSS version 10.1 (SPSS Inc. 1999), $\alpha=0.05$. Means are reported \pm SE except where noted.

Results

Demographic variables and overall fecundity

The majority of demographic variables measured differed between the two horned lark

populations (Table 1). The mean initiation date for first clutches was 16 days earlier for *E. a. strigata* than *E. a. articola* and the length of the breeding season was less than half as long in British Columbia as in Washington (38.5 and 94 days, respectively). Clutch size was 0.56 eggs smaller for *E. a. strigata* than *E. a. articola*, with no correlation between date of first egg and clutch size for either population (*E. a. strigata*: $r^2_{135} = 0.06$, $p=0.49$, *E. a. articola*: $r^2_{78} = 0.09$, $p=0.45$, Spearman's rank correlation), and no difference between clutch size for initial and replacement clutches (*E. a. strigata*: initial 3.05 ± 0.06 vs. replacement 2.75 ± 0.25 , $Z_{135,8} = -1.30$, $p=0.19$, *E. a. articola*: initial 3.53 ± 0.08 vs. replacement 3.77 ± 0.16 , $Z_{55,22} = -1.45$, $p=0.15$, Mann-Whitney U-test). Hatching success was 9% lower and fledging success 4% lower for *E. a. strigata* than *E. a. articola*. Low hatchability of eggs and fledging success and 10% higher clutch depredation for *E. a. strigata* resulted in 12% more fledglings per egg laid by *E. a. articola* (0.35) than *E. a. strigata* (0.23).

Table 1. Demographic rates of the Pallid (*E. a. articola*) (2003-2006) and Streaked (*E. a. strigata*) (2002-2005) horned larks; dates are Julian dates with day 1 = January 1, values reported are means \pm SE or proportions (with "n" in parentheses). Data abstracted from Camfield et al. 2007b.

	Pallid <i>E. a. articola</i>	Streaked <i>E. a. strigata</i>	Statistic	<i>p</i>
<u>A. Breeding Season</u>				
Clutch initiation date	151 \pm 0.61 (129)	135 \pm 1.25 (143)	$Z_{143,129} = -9.54$	< 0.0001
Season length (days)	38.5 \pm 1.26 (4)	94.0 \pm 10.53(4)	$Z_{4,4} = -2.32$	0.02
<u>B. Fecundity</u>				
Clutch size (C)	3.61 \pm 0.07 (93)	3.05 \pm 0.06 (135)	$Z_{93,135} = -5.51$	< 0.0001
Proportion hatched	0.92 \pm 0.02 (65)	0.83 \pm 0.03 (61)	$Z_{65,61} = -2.37$	0.02
Proportion fledged	0.91 \pm 0.03 (39)	0.87 \pm 0.03 (38)	$Z_{39,38} = -1.11$	0.27
Fledglings per egg laid	0.35 \pm 0.04 (91)	0.23 \pm 0.04 (123)	$Z_{123,91} = -2.12$	0.03
Nest Survival	0.35 (188)	0.23 (257)	$z = 2.78$	0.005
Proportion nests depredated	0.35 (188)	0.45 (249)	$z = 2.11$	0.03
Replacement nest interval days (r_f)	5.97 \pm 0.84 (38)	22.25 \pm 4.25 (8)	$t_{44} = 3.76$	< 0.001
Multiple brood interval (r_s)	6.00 \pm 0.91 (8)	22 (1)		
Annual fecundity	1.75 \pm 0.24 (4)	0.91 \pm 0.17 (4)	$t_6 = 2.82$	0.03
<u>C. Apparent Survival</u>				
Adult (ϕ_a)	0.69 \pm 0.04 (117)	0.51 \pm 0.06 (58)	$\chi^2=6.23$	0.01
Male	0.72 \pm 0.06 (65)	0.55 \pm 0.08 (32)	$\chi^2=2.89$	0.09
Female	0.65 \pm 0.07 (52)	0.47 \pm 0.08 (26)	$\chi^2=2.87$	0.09
Juvenile without dispersal (ϕ_j)	0.20 \pm 0.05 (175)	0.074 \pm 0.03 (80)	$\chi^2=4.67$	0.03
Juvenile with dispersal	n/a	0.16 \pm 0.04 (88)	n/a	n/a

Although the breeding season was much longer in Washington, the replacement nest and multiple brood intervals for *E. a. strigata* were almost four times longer than *E. a. articola* (Table 1). The extremely long re-nesting intervals for *E. a. strigata* combined with smaller clutch size, low hatchability of eggs and fledging success and high clutch depredation rates resulted in the reverse pattern with higher annual fecundity in *E. a. articola* (1.75 female fledglings/female/year) than in *E. a. strigata* (0.91, Table 1).

Survival

Apparent survival rates for adults and juveniles were calculated using a reduced model with survival and probability of encounter held constant (ϕ , p). This model was the most parsimonious model for juvenile survival and one of the most parsimonious ($\Delta AIC_c < 2$) for adult survival. Since models that included groups for males and females had little support for both *E. a. strigata* and *E. a. articola* ($\Delta AIC_c > 3$), we compared adult survival at both sites with males and females pooled (Table 2). Median \hat{c} estimates showed no lack of fit of the global models for the mark recapture data. Overall, adult and juvenile survival were significantly lower for *E. a. strigata* ($\phi_{adult}=0.51$, $\phi_{juvenile}=0.074$; Table 1) than *E. a. articola* ($\phi_{adult}=0.69$, $\phi_{juvenile}=0.20$; Table 1). For all adult horned larks the probability of encounter was 1. The probabilities of encounter for *E. a. strigata* and *E. a. articola* juveniles were 0.83 ± 0.15 and 0.79 ± 0.18 , respectively. The values used to compare juvenile dispersal between the two sites were calculated using only *E. a. strigata* juveniles that had returned to their natal sites. This is a more valid pairwise comparison than including recruitment across sites for *E. a. strigata* juveniles. For the analyses that follow we used the estimate for *E. a. strigata* juvenile survival including juveniles that had dispersed to other non-natal study sites (0.16 ± 0.04 ; $n=88$) since we wanted the results to reflect as closely as possible the true value of population growth for the *E. a. strigata* subspecies. Our data for resights of hatch-year juveniles indicates that most juvenile mortality occurs during the first few weeks after hatching (Table 2). Of juveniles banded in 2004, greater than half were not resighted within their hatch year suggesting low survival in the first few weeks after fledging (Table 2).

Population growth rate (λ)

To estimate λ we used estimates for female survival only. From our simulation estimates of apparent survival and fecundity, population growth rates predicted a decreasing population for *E. a. strigata* ($\lambda = 0.61 \pm 0.10$ SD; Figure 1A.) and a stable population for *E. a. articola* ($\lambda = 1.00 \pm 0.12$ SD; Figure 1B.).

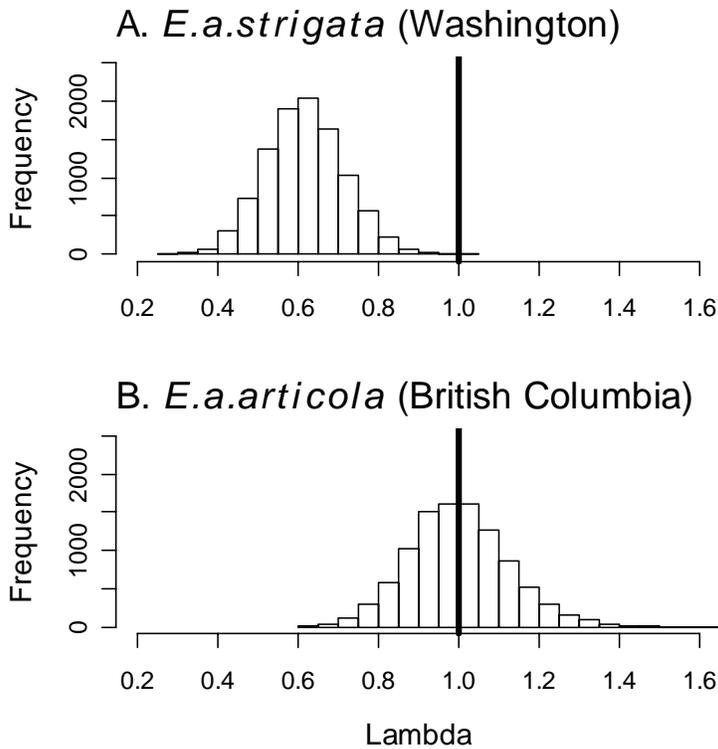


Figure 1. Frequency distribution of estimates of lambda for two horned lark subspecies. The vertical bold line indicates $\lambda = 1$, values to the right of the line show the proportion of simulations that predicted a growing population. None of the simulations predicted a growing population for the Streaked Horned Lark (*E. a. strigata*), while forty seven percent of the simulations predict a growing population for the Pallid Horned Lark (*E. a. articola*). From Camfield et al. 2007b.

None of the simulations predicted $\lambda > 1$ for *E. a. strigata*, while 47% of the simulations predicted $\lambda > 1$ For *E. a. articola*. Our mean estimate of lambda suggests that the streaked horned lark is declining at a rate of 40% per year. This estimate does not include potential immigration into the population from the Willamette Valley.

To examine the proportion of the variation in λ due to our three key vital rates, we conducted a Life-Stage Stimulation Analysis. Our analyses revealed that Adult survival explained the highest proportion of variation in λ for *E. a. strigata* ($r^2 = 0.75$) followed by juvenile survival ($r^2 = 0.17$) and annual fecundity ($r^2 = 0.08$). In contrast, for *E. a. articola*, juvenile survivorship accounted for the majority of the variation in λ ($r^2 = 0.56$) followed by adult survivorship ($r^2 = 0.29$) and annual fecundity ($r^2 = 0.14$).

Site Fidelity

Table 3 summarizes the resight locations for *E. a. strigata*. Adults birds were only resighted in the region where they were originally banded (Puget lowlands, Washington coast, lower Columbia River) and in most cases at the same site where they were banded (e.g., Olympia Airport, 13th Division Prairie, or Damon Point). Adult *E. a. strigata* are demonstrating extremely strong site fidelity to their nesting sites.

Table 2. Resights of *E. a. strigata* banded on the nest or shortly after fledging (juvenile) and as adults (in their first breeding season or older) on all Puget lowland, coastal Washington, and lower Columbia river sites combined. Only resights during the nesting season (April – August) are included. The table follows the fate of birds banded in a specific year (2002, 2004, and 2005). No attempt was made to resight birds in 2003. Only juveniles known to successfully fledge are included and all adults are included regardless of their fate.

Year Banded	AGE	# BANDED	Resights in 03	Resights in 04	Resights in 05	Resights in 06
2002	Juvenile	23		6 (26%)	2 (8.7%)	2* (8.7%)
2002	Adult male	0				
2002	Adult female	0				
2004	Juvenile	26		12 (46%)	8 (31%)	6 (23%)
2004	Adult male	14		14 (100%)	11 (79%)	2 (14%)
2004	Adult female	10		7 (70%)	7 (70%)	2 (20%)
2005	Juvenile	37			5 (13.5%)	5 (13.5%)
2005	Adult male	17			17 (100%)	11 (65%)
2005	Adult female	10			5 (50%)	3 (30%)

For juveniles, most (79%) were resighted in the region where they were born. Five birds

dispersed from the Puget lowlands to either the Washington coast or lower Columbia River for their first breeding season (examples of natal dispersal; Table 3).

Table 3. Resights of *E. a. strigata* banded as nestlings or recently fledged young (Juveniles) or as adults in the year following banding.

<i>Juvenile</i>				
		Resight location		
Banding location		Puget Lowlands	Washington Coast	Columbia River
	Puget Lowlands	11	4	1
	Washington Coast		4	
	Columbia River			4
<i>Adult</i>				
		Resight location		
Banding location		Puget Lowlands	Washington Coast	Columbia River
	Puget Lowlands	12		
	Washington Coast		8	
	Columbia River			12

Larks leave the Puget lowlands during the winter and over-winter along the coast, lower Columbia River and Willamette Valley (Pearson et al. 2005b). Young of the year may choose to breed at the over-wintering sites rather than return to their natal site, resulting in a movement from the Sound to the coast and Columbia River. This observation is based on a very small sample size and deserves additional study.

Discussion

Our estimates of population growth rate (λ , $\lambda = 0.61 \pm 0.10$ SD) indicate populations of *E. a. strigata* in Washington are declining rapidly (40% per year). This estimate only includes vital rates from birds found at nesting sites in the Puget lowlands (n = 4), lower Columbia River (n = 1) and the Washington coast (n = 2) and does not include rates from sites in the Willamette Valley of Oregon. Some birds that breed in Washington overwinter in the Willamette Valley of

Oregon (Pearson et al. 2005b). We don't know if birds produced in the Willamette Valley will move into Washington to breed. If they do, it is possible that *E. a. strigata* nesting sites in Washington are population sinks and the Oregon Willamette valley sites are population sources for Washington. However, given the low to moderate *E. a. strigata* reproductive success reported by Altman (14%, n = 13 nests; Altman 1999) and by Moore (27%, n = 16 nests in 2007; personal communication) for the Willamette Valley, this rescue effect scenario seems unlikely but is worth exploring further.

The projected rapid *E. a. strigata* population decline is apparently the result of both low fecundity and survival. The low fecundity (0.91 female fledglings/female/year), resulted from low egg hatchability and fledging success, high clutch depredation, and long intervals between initial nests and re-nests. Adult *E. a. strigata* survival (0.51 ± 0.06 , n = 58) was also quite low, while juvenile survival (0.16 ± 0.04 , n = 88) was relatively high but most estimates of juvenile survival don't include emigration which is included in our estimate.

Adult survival had the greatest influence on population growth rates for *E. a. strigata* suggesting that conservation actions that improve adult survival are likely to have the greatest influence on population growth. However, estimates of *E. a. strigata* fecundity are low which may inflate the importance of adult survivorship above what it may have been historically. A similar result was found for Mariana crows (*Corvus kubaryi*) on Guam (Beissinger et al. 2006). Nest predation by introduced brown tree snakes (*Boiga irregularis*) led to severely reduced fecundity in the crows and elasticity analyses showed a tremendous importance of adult survival to overall population growth rate. Because the model was based on fecundity values that were depressed by the snake predation, the importance of adult survival was exaggerated (Beissinger et al. 2006). These results are especially important to consider when designing management plans for *E. a. strigata* because this subspecies also appears to have depressed fecundity rates. While it is clearly important to maintain high levels of adult and juvenile survival, managing for survival alone may ignore an important cause of the decline of *E. a. strigata*.

When comparing vital rates and population growth rates of *E. a. articola* nesting in a relatively healthy ecosystem to those of *E. a. strigata*, we found that *E. a. articola* produced 35% more

fledglings per egg laid and adult survival was 18% higher and juvenile survival was 13% higher (without dispersal). These differences in survival and fecundity resulted in our estimates of a rapidly declining *E. a. strigata* population and a stable *E. a. articola* population. This contemporaneous comparison using nearly identical methods between closely related subspecies lends further support to our estimate of a declining streaked horned lark population throughout a large proportion of its geographic range.

We predicted that the higher elevation and latitude population *E. a. articola* would exhibit a survivor life history strategy and the lower elevation and latitude *E. a. strigata* populations would exhibit a reproductive strategy primarily because of the longer breeding season at lower elevations and latitudes. As predicted the breeding season was longer for *E. a. strigata*, however, counter to our prediction, fecundity was lower in *E. a. strigata*. This appears to be an indication that the ecological conditions that *E. a. strigata* faces today are different from those that it faced historically.

We did not observe examples of natal or breeding dispersal of *E. a. strigata* to the Puget lowlands and this population is apparently declining and continuing to experience threats. Given the net movement of birds out of the Puget lowlands and low estimates of fecundity and adult survival, there is a high probability that we will lose the remaining populations in this region in the near future unless immediate actions are taken to reverse this trend.

Primary threats to *E. a. strigata* nesting sites include loss of habitat and young to development and dredging activities. In recent years, we have observed the loss of nesting and foraging habitat on Gray Army Airfield due to development, temporary loss of nesting habitat and direct loss of chicks and eggs when dredge material was deposited on top of nests on the lower Columbia River, and the loss of the Rivergate nesting site near Portland Oregon. There is an attempt underway to create a replacement nesting site at the capped landfill near the Rivergate site but the area of restored habitat is considerably smaller than the area that was lost and it is unclear if the birds will use the new site for nesting. Other threats have been described in Pearson and Altman 2005 and Stinson 2005.

E. a. strigata has low genetic diversity and has likely gone through a population bottleneck (Drovetski et al. 2006). Low genetic variability coupled with small and apparently rapidly declining nesting populations and extremely high breeding site fidelity is likely to result in continued loss of genetic variability. This scenario is particularly likely for the Puget lowland population because, as mentioned previously, we did not observe any examples of natal or breeding dispersal into the Puget lowlands suggesting no future source of genetic variability from new immigrants. Remaining *E. a. strigata* populations within the Puget lowlands are small (approximately 222 birds; Pearson and Altman 2005, Stinson 2005) and several nesting sites have very few individuals (< 15 individuals; Pearson and Altman 2005, Stinson 2005). Small population sizes coupled with observations of mother - son pairings in horned larks (Camfield et al. 2007a) and in *E. a. strigata* (Pearson unpublished) may explain the relatively low egg hatchability of *E. a. strigata* reported in this paper.

Given the high site fidelity of *E. a. strigata* and an apparently rapidly declining population, it may be difficult to lure birds to newly created sites through habitat restoration until the negative population trend is addressed. However, after the negative population trend has been reversed, juvenile birds, not adults are the age class likely to naturally colonize new or restored nesting sites because we only observed examples of natal dispersal among regions.

Management Implications

- Our estimates of lambda indicate that *E. a. strigata* populations in the Puget lowlands, Washington coast and lower Columbia River are declining by 40% per year using the estimates of survival and fecundity during the period of this study. The Puget lowland nesting populations are particularly vulnerable to extirpation in the near future because of low survival and fecundity.
- The Puget lowland nesting populations are also vulnerable to continued loss of genetic diversity because of this apparent one-way movement of individuals out of the population, small population sizes and already low levels of genetic variability (Drovetski et al. 2006).
- Actions that improve adult survival are likely to have the greatest effect on population

growth. However, because this analysis was based on fecundity values that were depressed by other factors, the importance of adult survival may be insufficient to recover and achieve stable populations. As a result we recommend that conservation actions focus on both fecundity and adult and juvenile survival.

- Given the very high *E. a. strigata* site fidelity and an apparently rapidly declining population, it may be difficult to lure birds to newly created sites (assuming that these newly created habitats are indeed suitable) through habitat restoration until the negative population trend is addressed.
- When considering creating new populations in the future, juvenile birds, not adults, is the age class likely to naturally colonize new or restored nesting sites.
- Any additional loss of nesting sites and suitable habitat in the Puget lowlands could have significant impacts on remaining *E. a. strigata* populations.
- Recommend examining methods for reducing nest predation rates (e.g., use of nest exclosures).
- Recommend examining methods to improve post-fledging juvenile survival.
- Recommend developing site-specific management plans that address local threats and non-native and invasive species in particular and also the use of fire to improve nesting conditions (Pearson et al. 2005b).

Future Research Needs

- We have initiated additional analyses to: 1) examine the relative contribution of fecundity and juvenile and adult survival to overall population growth rate (λ); 2) determine which of these three vital rates can most easily be manipulated by conservation actions; and 3) examine how much we would need to adjust these vital rates either independently or in concert to achieve a stable or increasing *E. a. strigata* population growth rate.
- Previous genetic research used haplotypes to examine genetic relatedness and diversity in *E. a. strigata* and in larks from adjacent localities. We recommend additional research using nuclear genes to examine genetic diversity and structuring in *E. a. strigata* throughout its

range. This might also allow identification of which populations support or retain good genetic diversity that might be used as a nucleus to connect to other sites in a metapopulation framework.

- Because both contaminants and inbreeding can result in the pattern of low egg hatchability observed in *E. a. strigata*, we also recommend examining levels of contaminants in eggs and/or lark tissues.
- We recommend initiating a study to examine the feasibility of creating a functioning *E. a. strigata* metapopulation on dredge material islands on the lower Columbia River. Larks currently use these islands for nesting and over-wintering habitat. However, suitable lark habitat on these islands is being lost to succession. In addition, dredge material placed on nest sites during the nesting season has destroyed nests, chicks and eggs (S.F. Pearson unpublished). After deposition, nesting habitat is not suitable for the first year or two until it becomes sparsely vegetated with grasses and forbs. If designed correctly, dredge material could be used to create a functioning metapopulation on the lower Columbia River.
- We recommend developing a comprehensive monitoring scheme to examine range wide population trends that could also be used to evaluate the effectiveness of management actions.

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Appendix I

Number of visits and estimated number of streaked horned lark pairs at each site surveyed during the 2006 nesting season. We used the maximum number of territorial males observed/site and assumed that all males were paired to estimate the number of breeding pairs/site. Note: these surveys are not designed to estimate population size at a given nesting site.

Region	Site	# Visits	# Pairs
Washington Coast	Damon Point	4	4-5
	Leadbetter Point	4	3-5
	Midway Beach	6	8
	Shoalwater Indian Reservation	2	0
Columbia River	Crims Island	1	0
	Hump Island	1	0
	Lord Island	1	0
	Miller Sands	3	6
	North Portland (Rivergate)	4	7
	Pillar Rock Sands	3	6
	Rice Island	3	9
	Sandy Island	1	4
	Tenasilahee Island	1	2
	Wallace Island	1	0
	Whites Island (Browns)	3	13
Puget Sound	13th Division Prairie	5	7
	Artillery Impact Area	1	4
	Grey Army Airfield	6	16
	McChord AFB	3	14
	Olympia Airport	3	17
	Shelton Airport	3	7