Comparing endangered Streaked Horned Lark *(Eremophila alpestris strigata)* fecundity to other grassland birds

by
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ABSTRACT

Comparing endangered Streaked Horned Lark
(Eremophila alpestris strigata) fecundity to other grassland birds

Jeffrey K. Anderson

The Streaked Horned Lark (*Eremophila alpestris strigata)* is a critically endangered subspecies which breeds on prairie remnants in Washington and Oregon. Dramatic losses in grassland habitat have pushed the lowland Puget populations to the brink of extinction, with projected population losses at 40% a year. In order to investigate potential mechanisms driving this decline, I conducted a case study of Streaked Horned Larks at 13th Division Prairie, Fort Lewis, Washington over a two year period, 2007 and 2009. I analyzed nesting data of all species comprising the grassland ground nesting guild, and compared Streaked Horned Lark fecundity with those of the larger guild to determine if the breeding site itself is a sink, or if low fecundity is specific to Larks. I compared fecundity in two separate groups: (1) Larks vs. the ground nesting guild and (2) Larks vs. Savannah Sparrows (*Passerculus sandwichensis)*. In these comparisons, Streaked Horned Larks had significantly lower values in all measures of reproductive success when compared to both the guild and Savannah Sparrows. Furthermore, the Streaked Horned Lark's low egg hatching rate of 44% suggests that inbreeding depression may be playing a role in the decline of Larks at 13th Division Prairie. Although analyses of nest site habitat variables confirmed that Streaked Horned Larks have unique nesting preferences, cross-year, interspecific comparisons of vital rates and nest site characteristics did not indicate site-wide environmental causes driving Streaked Horned Lark declines. Since these findings are based on a case study of a single breeding site, I recommend further monitoring of this site and other remaining breeding sites, with emphasis on potential inbreeding depression.

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INTRODUCTION

Grassland ecosystems are among the most imperiled in the United States and have been altered to a greater degree than any other biome in North America (Samson and Knopf 1994). Accompanying this loss of habitat is a widespread decline in North American grassland bird populations (Robbins et al. 1989, Knopf 1994, Vickery et al. 1994). This precipitous decrease is not only widespread, but is progressing at a faster and less variable rate than in any other guild of North American birds (Peterjohn and Sauer 1993, Knopf 1994).

Although primarily known for its forested ecosystems, Washington State is also home to native prairie habitats that are disappearing at a rapid rate (Kruckeberg 1995, Stinson 2005). As the remaining prairies of the Pacific Northwest face persisting threats from human development, we continue to lose flora and fauna that have evolved along with these rare, treeless, flat open-spaces (Crawford and Hall 1997, Pearson and Altman 2005). One rapidly disappearing subspecies associated with prairies is the Streaked Horned Lark (*Eremophila alpestris strigata)*.

The Streaked Horned Lark (referred to as “Lark” throughout this thesis) is a rare subspecies of ground-nesting bird that inhabits open grassland habitats of Washington, Oregon, and (previously) British Columbia. In Canada, where they are believed to be extirpated, Larks are listed as endangered by the Species at Risk Act, and in the United States, Streaked Horned Larks are a federal candidate for listing under the Endangered Species Act (Beauchesne and Cooper 2003). At the state level, they are listed in Washington as endangered and in Oregon as a sensitive species, critical category (ODFW

2006, Pearson et al. 2008). Genetic data confirm that this subspecies is unique, isolated and possesses very little genetic diversity (Drovetski et al. 2005). In addition, recent research estimates that Streaked Horned Lark populations are declining at a rate of 40% per year (Pearson et al. 2008, Schapaugh 2009, Camfield et al. 2010).

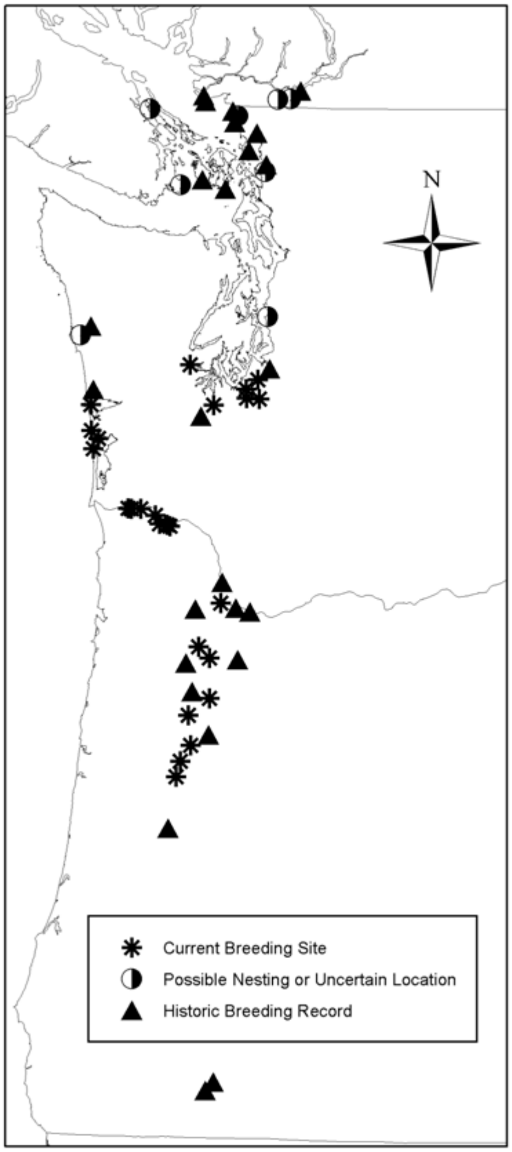

Figure 3. Current and historic Streaked Horned Lark breeding sites and possible historic nesting or uncertain breeding season locations. Figure reproduced from (Pearson and Altman 2005).

There are historical records of Streaked Horned Larks breeding at the northern end of their range in southern British Columbia, the San Juan Islands and additional coastal areas north of Tacoma, but these sites appear to currently be devoid of any Lark populations (Fig 1.) Mirroring the loss of breeding sites to the north, the southern end of the Streaked Horned Lark's range has shrunk towards the north and Larks are no longer found in the Rogue River Valley of southern Oregon (Rogers 2000, Beauchesne and Cooper 2003, Stinson 2005). It appears that the Lark range is retracting towards its core- the wintering habitat of the Willamette Valley and lower Columbia River islands of Oregon and Washington.

Each remaining population of Streaked Horned Larks is estimated to be below 500 individuals: Puget lowlands (222 birds), Washington coast (86 birds), lower Columbia River (68 birds) and the Willamette Valley (398 birds) (Pearson and Altman 2005, Stinson 2005).

As the amount of suitable Streaked Horned Lark nesting habitat continues to shrink and historic breeding locations cease to be used, it has become critical to assess Lark reproductive output on a site-by-site basis in order to allocate recovery efforts and funds to the places where Larks are successfully reproducing. The intent of this paper is to compare the annual fecundity of Streaked Horned Larks to other ground nesting grassland species at a single breeding site, to determine if low fecundity is unique to streaked horned larks and to identify the factors contributing to low fecundity. I have employed three separate approaches to help answer this question:

1. *Compare fecundity of Streaked Horned Larks with all other ground nesting species that nest at the site; with an additional emphasis on Savannah Sparrows.* Through these comparisons, it may be determined if all species at the site are experiencing low fecundity, or if it is only Streaked Horned Lark productivity that is low.

2. *Compare nest site habitat characteristics of Streaked Horned Larks with those of all other ground nesting species at 13th Division Prairie.* Through these comparisons it can be established which nest site characteristics are most closely related to each species, and to what extent these characteristics are found in nest site plots of both successful and failed nests.

3. *Discuss the possible impacts of environmental factors vs. endogenous factors on fecundity.* A look at annual trends among nesting species can provide insights into the mechanisms driving nesting success or failure.

METHODS

Study Site

Research was conducted on a 202.6 hectare section of 13th Division Prairie (47° 01'N 122° 26'W) (Anderson 2005)) located on the U.S. Army's Fort Lewis in Washington State (Fig. 2). Fort Lewis was established in 1917, with active military training taking place on the surrounding prairies starting in the late 1930s (Dunwiddie et al. 2006). A glacial outwash prairie, 13th Division Prairie is among a handful of south Puget Sound

Figure 4. Western Washington State with star designating the study site location (13th Division Prairie) for both years of the field study.

prairies that have remained undeveloped and retain at least a portion of native Puget prairie flora and fauna (Kruckeberg 1995, Dunwiddie et al. 2006). Although it is merely a remnant of the once extensive Northwest prairie expanse, 13th Division Prairie is among the largest patches of undeveloped, native prairie left in Washington's south Sound region (Kruckeberg 1995, Dunwiddie et al. 2006).

Data Collection

Vital rates and habitat data were collected from April to August for the breeding seasons of 2007 and 2009. Although identical methods of data collection were used for both seasons, I only collected data for the 2009 season. All data from the 2007 season was collected by Mark Hopey, working under the guidance of Dr. Scott Pearson from Washington Department of Fish and Wildlife. The data from 2007 was collected as part of a study that attempted to identify Streaked Horned Lark predators by setting up video cameras at nest locations. In Pearson and Hopey's (2008) study, nests of other species that share a similar nesting ecology to the Streaked Horned Lark were also located and outfitted with cameras in order to ascertain the suite of predators.

The data collected for the 2009 breeding season was part of a larger project under the auspices of Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, and The Nature Conservancy. This project, designed to test predator exclusion nest-cages, enclosed nests in chicken wire cages that were approximately 1m x 1m x1m. These exclosures have openings large enough for Larks to come and go, but restrict nest access by larger predators (mammals, corvids, raptors, etc.). To randomize the experiment, roughly every other Lark nest discovered was outfitted with an exclosure. The potential impacts of the nest exclosure experiment on the results of my study will be discussed further in the 'Results' section of the paper.

Nest Discovery and Monitoring

The standardized methodology for grassland nest searches (Martin and Geupel 1993) was used to locate and monitor nests throughout the 2007 and 2009 breeding seasons. Nests were located by one of four methods: observation of adults carrying food or nesting material back to the site, flush of an incubating or brooding adult, systematic search of areas where adults were routinely observed, and the rope-dragging technique (Martin and Geupel 1993). Nearly all nests were located using search effort and observation centered on Streaked Horned Lark nests. The nests of all other species were found opportunistically through their close proximity to Streaked Horned Lark nests or by through systematic walking transects. Every week (from the end of April to the beginning of August) we walked a site-wide grid transect of 150m intervals in alternating directions (north to south, east to west; northeast to southwest; and northwest to southeast). In addition, we divided the study site into a grid of 7 approximately equal sized polygons which were systematically searched by walking transects spaced at 50m intervals at a typical rate of 1 (of the 7) polygon searched per day.

Once nests were discovered, we monitored them once every 3-5 days, or more frequently if the nest was close to hatching or fledging. Nest observations were made as quickly as possible with efforts being made to visit the nests while the adults were away foraging. The date of the nest check, number of eggs, nestlings and approximate ages were recorded for each nest visit. During nest checks, we also recorded observations of adults that included their sex, locations and behaviors. The information from adult observations was used in determining if nests were abandoned, or still being tended after a disturbance.

A nest was considered successful if evidence indicated successful fledging of at least one chick. Such evidence included observation of the parents making food deliveries near the nest area, nestlings observed outside the nest, or if the nest rim was flattened with droppings located on top of it or outside the nest area, along with no signs of predation.

Nest Site Habitat Sampling

Habitat variables were measured using the methods of Pearson and Hopey (2005) that were derived from Barbour et al. (1980). Vegetation and substrate were measured using a 1m long wooden pin-drop frame that was broken into gradations of 10 cm. At each interval a metal pin was dropped through a hole in the wooden frame and the number of vegetative hits on that pin were counted and keyed out to species. Additionally, the underlying substrate of the pin was recorded, along with the maximum vegetation height at each hit. The pin-drop frame was placed with the midpoint of the meter span directly over the nest and in a north –south orientation. Once vegetation variables were measured, the frame was re-positioned in an east-west orientation and a second round of data was collected.

Substrate results are reported in mean percent cover of the nest area plot and were averaged from pin drops for each nest, resulting in 100% of the nest area falling into one of four categories: thatch, bare ground, rock, or moss/lichen.

For the functional groups, pin drop hits were categorized into individual plant species and then placed into the categories of native annual forbs (NAF), non-native annual forbs (NNAF), native perennial forbs (NPF), non-native perennial forbs (NNPF) native annual grasses (NAG), non-native annual grasses (NNAG), native perennial grasses (NPG), and non-native perennial grasses (NNPG) for analysis. Results should be interpreted as percent coverage of the nest area, but unlike substrate variables, functional group coverage can exceed 100% due to pins contacting multiple species within more than one group on some of the drops. Another variable accompanies the analysis for functional groups: Vegetation height (cm) was calculated by taking the highest point of plant/pin intersection for each pin, adding all the heights and dividing by the number of pins for each nest. This gives an average maximum vegetation height for the overall nest site area

In addition to the above habitat variables, total non-vegetated hits were calculated by adding the number of pins that did not touch any plant and then dividing by the number of pins. This measure gives an approximation of the percent non-vegetated cover.

Vital Rates and Annual Fecundity

We measured 6 vital rates for all bird species:

1) *Clutch size* (C) was determined from nests that were observed with eggs prior to hatching, or, if nests were discovered during the nestling phase, nestlings were counted and added to any unhatched eggs that were also inside the nest. Although counting nestlings may have resulted in artificially low clutch size estimates (i.e., eggs could have

been removed from the nest during the nestling phase) it was necessary to include nests discovered during the nestling phase (n=5, 17%) in order to achieve a sufficient sample size to calculate proportion of eggs hatched. I removed one clutch size record from analysis as an extreme outlier: A Streaked Horned Lark nest was found in 2007 with 11 eggs, which were probably multiple broods laid by the same female, none of which hatched. This nest (with over 3.5 times the mean egg counts of Lark nests) affected the data considerably due to the small sample size of Lark nests. Because the 11 egg nest was more than three standard deviations from the mean, (Osborne and Overbay 2004) it was eliminated from all calculations specific to eggs and their hatching. When this nest was removed from the data set, the standard deviation changed from 1.61 to 0.60 and the mean clutch size decreased from 3.30 to 3.03, which is closer to numbers reported in the literature [3.05±0.07 n=135 nests (Pearson et al. 2008, Camfield et al. 2010)}.

2) *Proportion of eggs hatched* is the number of eggs in a nest that hatched relative to the number present at hatching (Briskie and Mackintosh 2004). Calculation of this rate precludes eggs from nests that were depredated or abandoned before a full incubation period. Again, this may have resulted in an overestimation of the actual proportion of hatched eggs thus an overestimation of hatch rates.

3) *Fledglings per nest* is the total number of fledglings produced by each nest and includes all nests that had a known outcome.

4) *Nest survival* was determined with Mayfield (1975) estimators and measures the probability of a nest to fledge at least one nestling.

5) *Proportion depredated* represents the proportion of all discovered nests that appeared to be destroyed by a predator. This includes nests where young or eggs went missing from the nest before a probable fledge time could be attributed for their absence. If only a portion of the eggs or chicks in a nest were depredated, the nest was monitored for adult presence. In all of these instances, the nests were abandoned resulting in no fledglings.

6) *Proportion abandoned* is the proportion of all nests that were abandoned throughout any phase of the nesting process.

7) *Annual* fecundity was estimated using an equation from Ricklefs and Bloom (1977) designed to calculate annual production of total fledglings per pair (P). As annual fecundity is the number of female fledglings (Pearson et al. 2008, Camfield et al. 2010), P was divided by two assuming an equal distribution of the two sexes between fledging. The formula for annual production of fledglings (P) is:

$$(P = F \times B)$$

B is the number of days in the breeding season and is corrected for the variance in breeding effort across the months of the breeding season with the formula:

$$B = 30 \exp\ (-\Sigma p_i\ log_e\ p_i)$$

Where p_i is the proportion of clutches that were laid in each month i, and e is the base of natural logarithms.

F is the number of young fledged/pair/day and is calculated as:

$$F = C \times S \times I$$

Where C is clutch size, S is breeding success (measured in fledglings per egg laid) and I is the rate of nest initiation (clutches/pair/day) and is calculated as:

$$I = \frac{m}{p_f + m(p_s r_s + p_f r_f)}$$

Nest mortality rate (m) is the proportion of nests failing per day and was calculated using the midpoint method for the Mayfield (1975) estimator. After the fledging of a successful clutch, r_s represents the time before the next clutch is initiated, and r_f is the time interval between a failed clutch and a new one. Probability of a nest failing before fledging is designated as p_f and calculated:

$$p_f = 1\text{-}p_s$$

Where p_s is the probability that a nest will successfully fledge at least one young and is calculated:

$$p_{s=e^{-mT}}$$

Where T = the length of the nest cycle from clutch initiation to fledging in days. T was calculated for Streaked Horned Larks as 12 days of incubation + 9 days until fledging + a laying day for each egg in the clutch (C) (Beason 1995). T was calculated similarly for Savannah Sparrows, with the exception of an 11-day fledging period (Wheelwright 2008).

Data Analysis

In order to compare the nesting data of Streaked Horned Larks with that of the other species at 13th Division Prairie, two different comparisons of this data set were performed. In the first comparison, Streaked Horned Lark vital rates from 2007 and 2009 were compared to those of a nesting guild comprised of all other ground nesting grassland species at 13th Davison Prairie from the same breeding seasons. This was done by treating nests of all species as a single species (the guild) as described below. The second comparison matches Streaked Horned Larks with Savannah Sparrows.

The purpose of this case study is to more finely assess potential mechanisms driving the decline of a Streaked Horned Lark population, by comparing Lark breeding success with that of the guild. Root (Root 1967) defines a guild as “a group of similar species that exploit a resource in a similar fashion”. Guilds can group animal species on the basis of habitat use or behavioral characteristics (Severinghaus 1981, Brooks and Croonquist 1990). For the purpose of this study, the guild was based on nesting habitat. Although there is an inference of differences in microhabitat use between members of the guild, overall, it has been found that the guild concept can be particularly effective in increasing samples sizes in studies like mine and decreasing statistical variability by virtue of larger sample sizes (Verner 1983, 1984, Block et al. 1986). In addition, use of the guild comparison allows us to explore the idea that Streaked Horned Lark declines are a function of environmental change that would affect all species in the guild (Block et al. 1986). Guild-based studies can also reflect the biological integrity of an area in a more complete way than a look at a single species (Angermeier and Karr 1994, Bishop and Myers 2005). Biological integrity can be defined as, "the ability of an environment to support and maintain a biota (both structural and functional performance) comparable to the natural habitats of the region." (Angermeier and Karr 1994)

The species that comprised the ground nesting grassland guild were Savannah Sparrow, Western Meadowlark (*Sturnella neglecta*), Vesper Sparrow *(Pooecetes gramineus*), Common Nighthawk (*Chordeiles minor*), and Killdeer (*Charadrius vociferous*). This guild represents the entirety of species that nest on the ground at this particular prairie. It is possible that Northern Harrier (*Circus cyaneus*) and Short-eared Owl (*Asio flammeus*) could also be included in this group, but no nests of these species were discovered. The pooled vital rates of these species were then compared to those of Streaked Horned Larks.

In addition to comparisons between Larks and the guild, statistical comparisons were also calculated between Larks and Savannah Sparrows. Savannah Sparrows made for strong pair-wise comparisons because they made up 29 of the 46 guild nests and share a very similar ecology to Streaked Horned Larks. Both Larks and Savannah Sparrows inhabit open country and share a similar diet and foraging behaviors (Beason 1995, Wheelwright 2008). In addition, both species have similar incubation and fledgling times (Martin 1951, Maher 1979, Meunier and Bedard 1984, Beason 1995). Savannah Sparrows and Streaked Horned Larks differ in some aspects of their breeding ecology: Savannah Sparrows select more densely vegetated sites for their nests (Beason 1995, Wheelwright 2008), have slightly longer nestling periods (Wheelwright 2008), and have larger clutch sizes. Clutch size varies geographically, but Horned Larks typically lay 2 to 5 eggs with a mean of 2.5 in Washington and British Columbia (Beason 1995) whereas Savannah Sparrows lay between 2 and 6 eggs with a mean of 4 eggs across North America. Although the two species have some ecological differences, comparing them with one another eliminates some of the confounding variables inherent with the guild approach.

All 6 vital rates (clutch size, proportion hatched, fledglings per nest, nest survival, proportion nests depredated, and proportion nests abandoned) were compared between 2007 and 2009, between Larks and the guild, and between Larks and Savannah Sparrows.

Annual fecundity calculations were calculated using replacement nest interval (r_f) and multiple brood interval (r_s) data from existing literature. Calculations for Savannah Sparrows were done using the interval means of r_s=19 and r_f=5 (Wheelwright 2008)and r_s=22 and r_f=22.25 interval numbers for Streaked Horned Larks (Pearson et al. 2008) No statistical comparisons were done on annual fecundity calculations due to small sample sizes (n=2).

Habitat characteristics around each nest site were compared in two different groupings: substrate (bare ground, rock, moss/lichen, or thatch) and vegetative functional groups (native and non-native, annual and perennial grasses and forbs). Nest site substrate comparisons were performed between successful and failed Lark nests, between successful and failed guild nests, and between all Lark and guild nests. Nest site functional group comparisons were performed between Lark and guild nest sites.

Data from 2007 and 2009 were pooled for all analyses except those regarding annual fecundity and functional group habitat variables. Due to an incomplete data set, the functional group analyses were only performed with the data from 2009, and consequently are based on smaller sample sizes than the data for the substrate and non-vegetated hit analyses.

All comparisons for vital rates and nest site habitat variables were performed with two-sample Wilcoxon Rank Sum tests in the program R (Team 2006). Overall significance for these tests was designated at α=0.05 and all totals are reported as means ±SE, unless otherwise noted. In order to decrease the chance of Type 1 errors from multiple comparisons, Bonferroni corrections (α=0.05/n) were made for vital rate, substrate and functional group calculations (Rice 1989). After these corrections, the overall significance (α=0.05) was adjusted to α=0.008 for vital rates, α=0.0125 for substrate variables, and α=0.008 for functional group variables. Due to the conservative nature of the Bonferroni corrections, the calculated p-values are also included in the results in order to assess which comparisons might be biologically meaningful, albeit not statistically significant (Cabin and Mitchell 2000).

RESULTS

Streaked Horned Lark and Guild Comparison

Vital rates of Lark nests were significantly lower than guild vital rates for 4 of 6 measures of reproductive success (Table 1). The only category where Streaked Horned Larks had significantly higher averages was Proportion of Nests Abandoned, which is equated with nesting failure (Table 1).

In two instances, Lark numbers were more than 50% lower than those of the guild: proportion hatched (Streaked Horned Lark 52% lower than guild), and fledglings per nest (Streaked Horned Lark 64% lower than guild) (Table 1).

Table 7. Vital rates of Streaked Horned Lark and guild nests (2007 & 2009) from 13th Division Prairie, Ft. Lewis, WA. Comparisons that demonstrated significance after Bonferroni corrections (p<0.008) are in bold. Values are means ±SE with number of nests in parentheses. W and p statistics from Wilcoxon Rank Sum tests.

	Streaked Horned Lark *(E. a. strigata)*	Guild	Statistic	P value
Clutch size	3.03±0.12 (29)	3.38±0.15 (39)	W = 699	0.08
Proportion hatched	**0.44±0.09 (17)**	**0.91±0.03 (29)**	**W = 410**	**<0.0001**
Fledglings per nest	**0.66± 0.20 (27)**	**1.82±0.26 (40)**	**W = 738**	**0.003**
Nest survival	**0.27±.03 (30)**	**0.46±0.04 (44)**	**W=1029**	**<0.0001**
Proportion nests depredated	0.33±0.09 (30)	0.32±0.07 (46)	W = 685	0.9531
Proportion nests abandoned	**0.27±0.08 (30)**	**0.00±0 (46)**	**W = 506**	**0.0002**

For four indicators of fecundity (hatch rate, fledglings per nest, clutch size, and fledglings per egg) the annual differences in vital rates between Larks and the guild showed no clear pattern (Fig. 3). In 2007, Streaked Horned Lark nests had lower productivity in hatch rate, fledglings per nest, clutch size and fledglings per egg than they did in 2009. In contrast, guild nests actually had higher productivity in 2007 for hatch rate, fledglings per nest, and fledglings per egg than they did for 2009.

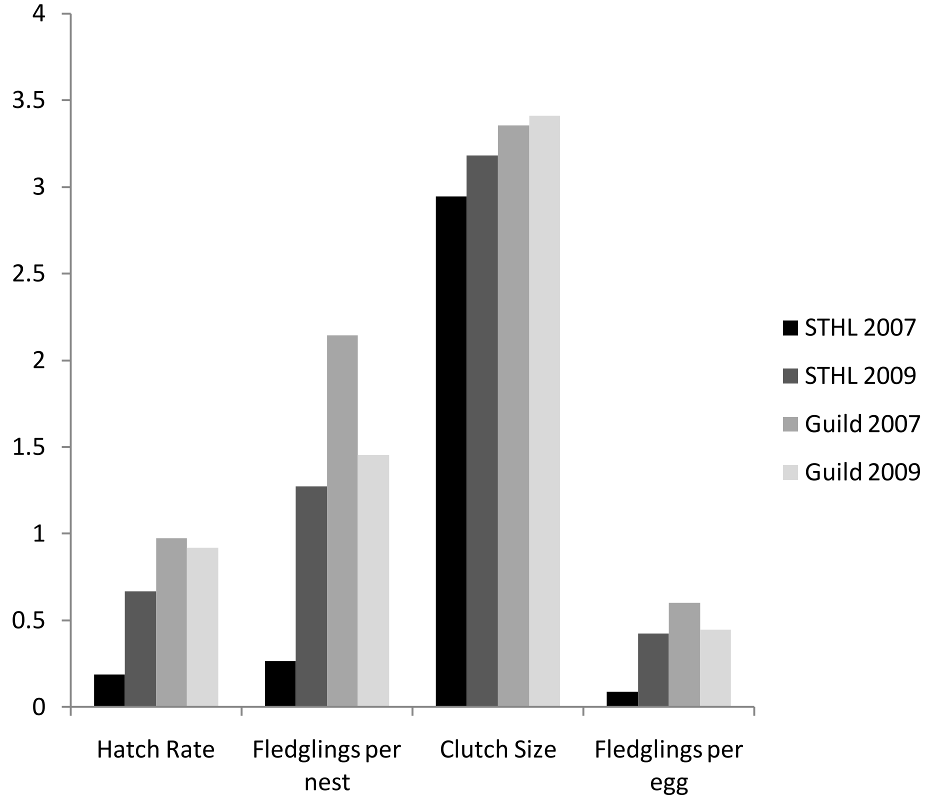

Figure 3. Vital rates by year for Streaked Horned Lark and guild nests.

<u>Streaked Horned Lark and Savannah Sparrow Comparison</u>

In the Lark vs. Savannah Sparrow comparison, these species differed significantly on all but one of the vital rates: proportion of nests that suffered predation (Table 2). As with the guild comparisons, Streaked Horned Lark vital rates were only significantly higher in one category: proportion of nests abandoned (Table 2). As with the guild comparisons, there were two vital rates that differed by a margin of more than 50%: proportion hatched (Streaked Horned Lark 54% lower than Savannah Sparrow), fledglings per nest (Streaked Horned Lark 66% lower than guild). In these two comparisons that differed by more than 50%, Streaked Horned Lark results were lower when compared with Savannah Sparrows than they were against the guild as a whole.

Table 8. Vital rates of Streaked Horned Lark and Savannah Sparrow nests (2007 & 2009) from 13th Division Prairie, Ft. Lewis, WA. Comparisons that demonstrated significance after Bonferroni corrections ($p<0.008$) are in bold. Values are means ±SE with number of nests in parentheses. W and p statistics from Wilcoxon Rank Sum tests.

	Streaked Horned Lark *(E. a. strigata)*	Savannah Sparrow *(P. sandwichensis)*	Statistic	P value
Clutch size	3.03±0.12 (29)	3.61±.18 (23)	W = 460.5	0.01
Proportion hatched	**0.44±0.09** **(17)**	**0.96±0.02** **(17)**	**W = 248.5**	**0.0001**
Fledglings per nest	**0.66± 0.20** **(27)**	**0.96±0.31** **(28)**	**W= 519.5**	**0.004**
Nest survival	**0.27±0.03** **(30)**	**0.39±0.03** **(29)**	**W = 705**	**<0.0001**
Proportion nests depredated	0.33±0.09 (30)	0.34±0.09 (29)	W = 440	0.9337
Proportion nests abandoned	**0.27±0.08** **(30)**	**0.00±0.00** **(29)**	**W = 319**	**0.003**
Annual fecundity	0.99 (2)	3.25 (2)		

Average Streaked Horned Lark annual fecundity for the two breeding seasons was 70% lower than that of Savannah Sparrows (Table 2).

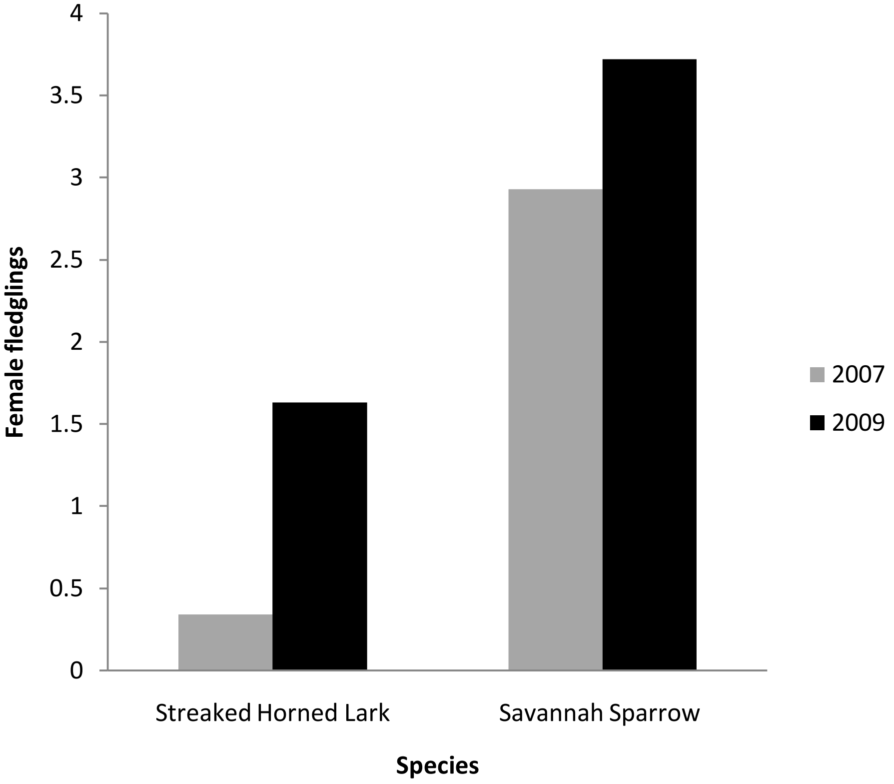

Figure 4. Annual fecundity (mean annual female fledglings per pair) for Streaked Horned Larks and Savannah Sparrows.

Both Larks and Savannah Sparrows had higher annual fecundity in 2009 than in 2007 (Fig. 4). Estimated annual fecundity for Larks was 0.34 in 2007 and 1.63 in 2009. Savannah Sparrow fecundity was 2.93 for 2007 and 3.72 for 2009. Compared to 2007, the 2009 breeding season represented a 79% increase in annual fecundity for Larks and a 21% increase for Savannah Sparrows.

Impact of Nest Exclosures

The predation rates of Streaked Horned Lark nests in this study may be artificially low due to the nest-exclosure experiment that was carried out during the

2009 breeding season. As the exclosure experiment results have not been published (the study is ongoing) the data here can only reflect their effectiveness at 13th Division Prairie during the 2009 breeding season. Out of the six exclosed nests, three failed and three produced fledglings. Therefore, predation rates could conceivably have been as high as 55% for the 2009 season (that is, if all three successful exclosed nests were never exclosed and ended up being depredated). It should also be noted here that three of the nests that were exclosed still failed: two from predation and one from starvation, possibly due to a severely malformed beak on the nest's single nestling.

Nest Site Habitat Comparison

A comparison between successful and failed (depredated or abandoned) Streaked Horned Lark nests revealed that nests that successfully fledged at least one young were built in substrates that contained much higher percentages of moss/lichen than thatch (Table 3). The percentage of ground covered in moss or lichens for successful Lark nests was 34.2% higher than moss and lichen coverage surrounding failed nests, whereas failed nests were situated among a 34.8% higher percentage of thatch covered substrate than successful nests.

Table 9. Comparison of Streaked Horned Lark nest site substrate variables between successful nests (produced at least 1 fledgling) and failed nests (abandoned or depredated) from 2007 and 2009. Comparisons that demonstrated significance after Bonferroni corrections (p<0.0125) are in bold. Values are means ±SE percent cover with number of nests in parentheses. W and p statistics are from Wilcoxon Rank Sum tests.

	Successful Nests (9)	Failed Nests (17)	Statistic	P value
Bare Ground	9.3±2.6	16.7±4.9	W = 80.5	0.84
Moss/Lichen	**50.9±9.0**	**16.7±5.3**	**W = 28.5**	**0.009**
Rock	25.0±7.7	16.2±5.9	W = 53	0.20
Thatch	**15.7±3.2**	**50.5±3.2**	**W = 129.5**	**0.004**

At the guild level, all nests, both failed and successful had a higher percentage of thatched substrate than other substrates, with the other three substrate variables combined filling less than 15% of nest site areas (Table 4). At the guild level, there were no significant differences between substrate variables for failed versus successful nests (Table 4).

Table 10. Comparison of guild nest site substrate variables between successful nests (produced at least 1 fledgling) and failed nests (abandoned or depredated) from 2007 and 2009. Values are means ±SE percent cover with number of nests in parentheses. W and p statistics are from Wilcoxon Rank Sum tests.

	Successful Nests (26)	Failed Nests (12)	Statistic	P value
Bare Ground	1.9±1.1	1.4±0.9	W = 162	0.77
Moss/Lichen	7.4±2.8	8.3±5.3	W = 149.5	0.81
Rock	4.8±2.9	4.2±3.5	W = 157.5	0.96
Thatch	85.9 ±5.3	86.8±8.7	W = 178	0.46

The graph below (Fig.5) combines Tables 3 and 4 for a visual representation of the interplay between nest fate and substrate variables.

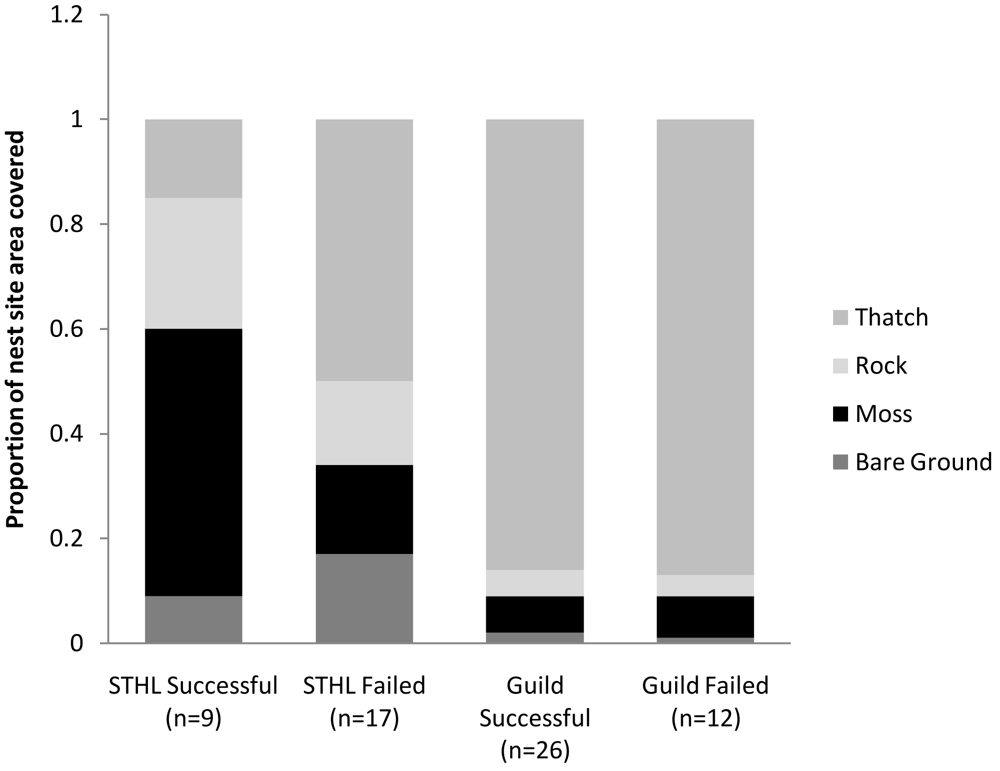

Figure 5. Mean proportion substrate cover of nest area for successful and failed STHL and guild nests. Number of nests is given in parenthesis.

Nest site substrate variables were significantly different between Streaked Horned Lark and guild nests in all four categories. Although a thatched substrate is the highest of the four associated with Streaked Horned Lark nests, it is still 47% lower than thatch coverage associated with guild nests (Table 5).

Table 11. Comparison of Streaked Horned Lark (STHL) and guild nest site substrate variables from 2007 and 2009. Comparisons that demonstrated significance after Bonferroni corrections (p<0.0125) are in bold. Values are means ±SE percent cover with W and p statistics from Wilcoxon Rank Sum tests.

	STHL (n=26)	Guild (n=38)	Statistic	P value
Bare ground	**14.1±3.4**	**1.8±0.8**	**W=226.5**	**<0.00001**
Moss/Lichen	**28.5±5.6**	**7.7±2.5**	**W=249.5**	**0.0003**
Rock	**19.2±4.7**	**4.6±2.3**	**W=280**	**0.0005**
Thatch	**38.5±5.7**	**86.2±4.5**	**W=877**	**<0.00001**

Nest site coverage by functional group showed no significant differences between Streaked Horned Lark nests and those of guild species. While there was only one significant difference between functional group variables (non-vegetated nest area), some of the other differences are also worth noting; in particular, differences in percent cover of native perennial grasses (Larks= 19.4±6% vs. Guild=51.9±8.3%; p=0.03) and differences in vegetation height (Larks=15.9 ±3.4 cm vs. Guild=21.9±2.0 cm; p=0.11) (Table 6).

Table 12. Comparison of Streaked Horned Lark (STHL) and guild nest site vegetative functional group variables from 2009. Comparisons that demonstrated significance after Bonferroni corrections (p<0.008) are in bold. Values are means ±SE percent cover, except for Vegetation Height, which is the mean maximum height of vegetation at the nest site. The data for mean percent cover of non-vegetated nest area is from 2007 and 2009. W and p statistics are from Wilcoxon Rank Sum tests.

	STHL (n=9)	Guild (n=19)	Statistic	P value
Non-native annual grass	11.1±5.0	5.7±2.0	W=74.5	0.57
Non-native perennial forb	12.0±3.4	9.6±3.1	W=68	0.38
Non-native perennial grass	38.9±10.6	43.4±7.3	W=93	0.73
Native perennial forb	7.4±4.0	5.3±1.8	W=83	0.91
Native perennial grass	19.4±6.9	51.9±8.3	W=129	0.03
Vegetation height (cm)	15.9 ±3.4	21.9±2.0	W=118.5	0.11
Non-vegetated nest area	**29.8±4.9**	**14.5±3.6**	**W=289**	**0.004**

Although differences in non-vegetated area between Larks and the guild are significant, there is very little difference in non-vegetated area within each group, regardless of nest outcome (Fig. 6).

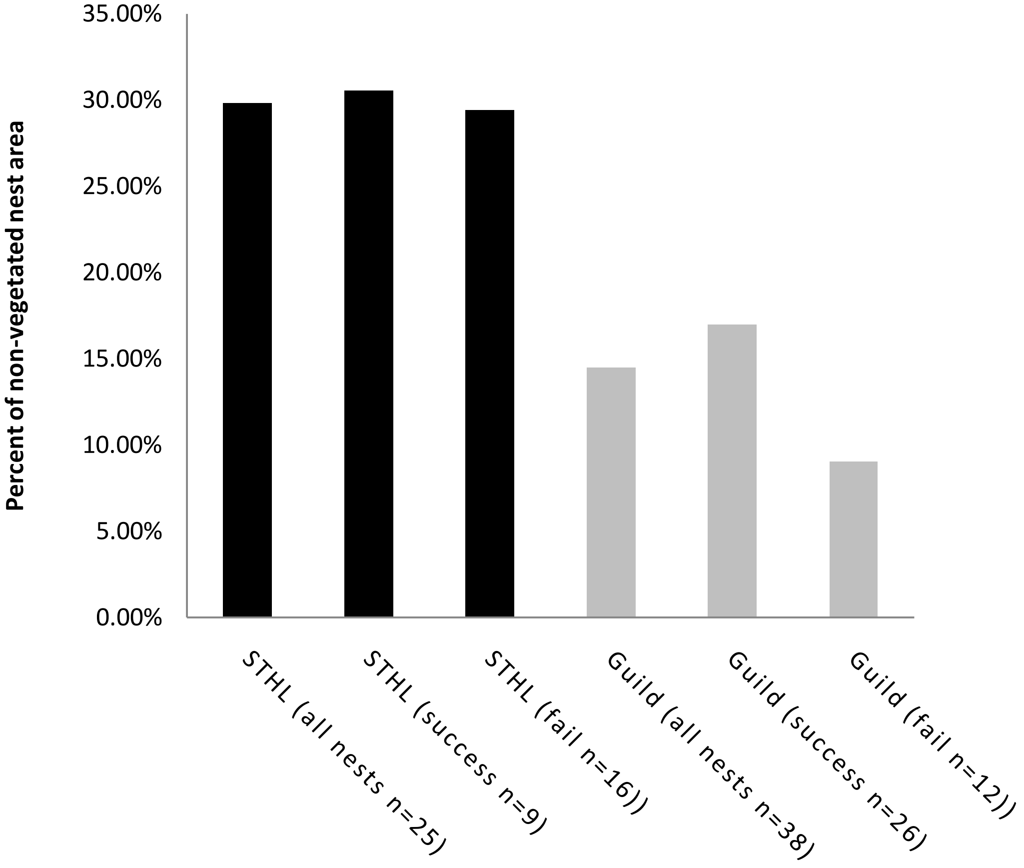

Figure 6. Mean percent of non-vegetated nest area for STHL and guild nests based on total nests and nest success. Number of nests in parenthesis.

DISCUSSION

Streaked Horned Larks at our study site had reduced fecundity when compared with either the ground nesting guild as a whole, or Savannah Sparrows specifically. For both guild and Savannah Sparrow comparisons, Streaked Horned Lark rates were considerably lower in all categories except proportion of depredated nests and clutch size.

Clutch size

In this study, clutch size is not a very informative measure of reproductive success. Clutch size is species specific and not necessarily an indication of relative fitness. For example, Common Nighthawks almost always have a clutch size of two (Poulin et al. 2006). The Streaked Horned Lark clutch size reported in this study (3.03 eggs per nest) is very similar to that found by Pearson et al (2008) in a study of 135 Lark nests (3.05 eggs per nest). Although clutch size may not be the most effective measure of fecundity in cross-species studies, Streaked Horned Lark clutch sizes are lower than other subspecies of Horned Larks (Camfield et al. 2010), and this may indicate a disadvantage.

Proportion hatched

Every egg laid reflects a considerable expenditure in energy for that particular bird (Koenig 1982). For this reason, most passerine species across the world average a high hatch rate of about 90% (Koenig 1982). The results of this study were consistent with this finding for the guild and Savannah Sparrows, whose mean (across two seasons) hatch rates were 91% and 96% respectively. Although Streaked Horned Lark hatch rates were much lower (44%), it should be noted that all subspecies of Horned Larks may have relatively low hatch rates. A sample of three studies of three different Horned Lark subspecies returns three different hatch rates: Pickwell's (1931) study of 82 eggs had a hatch rate of 79%, Beason and Franks (1974) study of 26 eggs had a hatch rate of 50%, and in a study of 65 eggs Camfield et al (2010) had a hatch rate of 92%. In addition, Camfield et al (2010) reported a Streaked Horned Lark hatch rate of 83% for a sample of 61 eggs in Washington State. Although there is a lot of variation in the hatch rates found in these studies, they are all still higher than the 44% hatch rate reported in this study. Low hatch rates do occur in wild populations of other endangered species, and hatch rates of less than 50% have been routinely observed in a suite of endangered bird species in New Zealand (Briskie and Mackintosh 2004, Congdon and Briskie 2010).

Although the mechanisms that explain variation in egg hatching proportions are not fully understood (Knape et al. 2008), low egg hatchability can be a result of environmental effects (such as calcium deficiency), contamination from pollutants (DDT), and environmental changes which force large percentages of the population to alter typical behaviors (Congdon and Briskie 2010). However, if these factors could explain the low hatch rates among Streaked Horned Larks, then I would have expected to see similar low hatch rates in other species at my study site that have similar diets (Beason 1995, Poulin et al. 2006, Wheelwright 2008). Although there is a possibility that hatch rates are affected by influences at the wintering grounds in the Willamette and Columbia River Valleys, the more likely source of low hatch rates seems to be inbreeding depression.

While the source of low hatch rates for Streaked Horned Larks at 13th Division Prairie is unknown, Drovetski et al. (2005) hypothesize that Streaked Horned Lark declines are due to genetic factors resulting from a population bottleneck. As Drovetski et al. (2005) point out, several pieces of evidence point to a bottleneck leading to inbreeding depression including, low genetic diversity, (Drovetski et al. 2005) combined with a well documented contraction in range (Rogers 2000, Beauchesne and Cooper 2003, Pearson and Altman 2005, Stinson 2005), and genetic patterns consistent with a bottleneck (Drovetski et al. 2005). Congdon and Briskie (2010) define population bottlenecks as abrupt and temporary reductions in population size, in which populations can suffer the loss of genetic variation and a subsequent increase in inbreeding. Inbreeding depression can significantly affect the viability of a population through lower birth weights, survival, reproductive success, and resistance to environmental stress, predation and disease (Keller and Waller 2002). Briskie and Mackintosh (2004) found that in 11 species of New Zealand birds that passed through a bottleneck of <150 individuals, there were significantly higher rates of hatching failure. Of the 4 Streaked Horned Lark populations, (see Introduction) all but the Willamette Valley have Lark numbers close to or below Briskie and Mackintosh's (2004) threshold of <150 individuals. The Larks at my study site are part of the Puget lowlands population of approximately 222 birds (Pearson and Altman 2005, Stinson 2005), and of those perhaps 25 breed at 13th Division Prairie. Given the estimated declines of 40% per year for the three Washington populations (Pearson et al. 2008, Camfield et al. 2010) and the infrequent dispersal of individuals between Puget lowland breeding sites (Pearson et al. 2008) it would seem that genetic exchange at 13th Division prairie will only become more limited with each breeding season.

Fledglings per nest

Fledglings per nest is perhaps one of the most important vital rates, and one in which Streaked Horned Larks fall far behind the other breeding species at 13th Division Prairie. In essence, the number of fledglings produced each breeding season might be a more telling metric of reproductive success than Mayfield nest survival, as was the case with Streaked Horned Larks in 2009. In 2009, eight of the 11 nests survived (Mayfield nest survival of 0.465) but they only produced a mean of 1.27±0.33 fledglings per nest.

Compare this to the numbers for Savannah Sparrows in the same year, in which many nests were depredated and they had a Mayfield nest survival of 0.227 (less than half of Streaked Horned Larks') but still had a higher mean number of fledglings per nest with 1.67±0.43.

Proportion nests depredated

Predation is the leading cause of nest failure among grassland birds (Best 1978, Johnson and Temple 1990) and the leading cause of Streaked Horned Lark nest failures (Pearson and Altman 2005). The results of this study show that although predation was indeed the leading cause of nest failure for all species studied, the rates of predation for Streaked Horned Lark nests were not much different than those of the guild nests (Streaked Horned Larks= 33%; guild nests=32%).

Proportion nests abandoned

Nest abandonment had a large impact on the breeding failures of Streaked Horned Larks, but was confined to the 2007 season when almost a third of Lark nests were abandoned. In fact, no other nests of any species were abandoned throughout the study. This, of course, brings up the question of why so many Lark nests were abandoned that particular year. In 2007 cameras were placed at nests in order to identify the suite of predators at 13th Division Prairie. Although this could have something to do with nest abandonment, it seems unlikely; after cameras were placed at nests, all incubating females were back on the nests within 15-20 minutes (Pearson and Hopey 2008). Although their study did not involve camera surveillance, Beason and Franks (1974) report in their study of Horned Larks in Illinois that although some abandonment occurred, it was never a result of researchers briefly checking a nest or measuring eggs or young. Conversely, in a study of videotaped grassland bird nests in North Dakota, 23% of 69 nests were abandoned within one day of camera installation (Pietz and Granfors 2000), however it should be noted that this was not a study of Horned Lark nests. Although the reason behind such high abandonment rates remains unknown, it is clear that within the scope of this study, it seriously impacted Streaked Horned Lark vital rates.

Annual Fecundity

This study found the two-year mean annual fecundity of Streaked Horned Larks to be far below that of Savannah Sparrows (STHL=0.99 vs. Sav. Sparrow=3.25). The annual fecundity of 0.99 female fledglings per female per year that I estimated is similar to the 0.91 annual fecundity found by Pearson et al. (2008) for Streaked Horned Larks in Washington from 2003-2006. Annual fecundity for Streaked Horned Larks in Washington is much lower compared to the annual fecundity of 3.40 estimated by Ricklefs and Bloom (1977) for a population of Horned Larks in Kansas, and an annual fecundity of 1.75 estimated by Camfield et al (2010) for a population of Horned Larks in British Columbia.

Nest Site Habitat Analysis

Habitat variables at the nest site scale were significantly different between Larks and the guild in regards to substrate, but not significantly different in regards to functional group variables. Additionally, Lark nests were located in less densely vegetated areas than guild nests. Given that Savannah Sparrows (who nest in dense vegetation) made up two-thirds of the guild, these findings seem to agree with the literature (Beason 1995, Wheelwright 2008). In other studies, Streaked Horned Lark nests were typically associated with sparsely vegetated areas (Rogers 2000, Pearson and Hopey 2005), as was the case in my study.

Although functional group variables did not vary significantly between Lark and guild nests, the difference in vegetation height did vary considerably (Lark 15.9cm vs. Guild 21.9cm; p=0.11), as did the difference between Lark nests and guild nests in percentage of non-vegetated hits (Lark 29.8% vs. Guild 14.5%; P=0.004). These findings reinforce the conclusion that Larks tend to prefer nest site habitat that is short and sparsely vegetated (Beason 1995, Rogers 2000, Pearson and Hopey 2005).

Impacts of Environmental Factors on Vital Rates

For each species at a shared breeding site, there are optimal sites, structures, and locations for nests that are the result of the evolutionary importance of nest success in regards to fitness (Cody 1981, Bekoff et al. 1989, Wiebe and Martin 1998). Although this study found significant differences in nest site habitat variables between Lark and guild nests, this difference did not appear to affect rates of predation on Lark nests. Predation rates between the two groups were nearly identical, which suggested that predation had a similar effect on nest success across species, regardless of environmental factors.

Clutch size, though not one of the more informative metrics for an interspecific comparative study, can also be influenced by environmental factors, but only to a very small degree (Haywood and Perrins 1992). One way of assessing if environmental factors are driving clutch size and other vital rates is to look at them in a year by year comparison. If a vital rate shows declines for two or more species in the same year, then environmental factors might be having an influence on that particular measure of nesting success. For example, if a breeding area is hit by a late freeze during incubation, hatch rates might be low for all species breeding in that area during the freeze. Figure 4 (see Results) presents yearly breakdowns of four vital rates that are critical to productivity and shows that, although there were differences in fecundity between 2007 and 2009 for both Larks and the guild, there are no annual trends that matched between Larks and the guild; guild nests were more productive in 2007, while Lark nests were more productive in 2009. This lack of annual trends lends credence to, but does not necessarily prove, the hypothesis that low productivity among Streaked Horned Larks at 13th Division Prairie is primarily due to endogenous and not environmental factors.

Still, exogenous environmental factors such as vegetative cover and thatch should not be underestimated. Past Lark population declines were primarily driven by loss of suitable breeding habitat (Pearson and Altman 2005), combined with changes in vegetation at remaining breeding grounds (Crawford and Hall 1997). However, current declines in key measures of productivity, such as fledglings per nest and hatch rate would suggest that endogenous factors have also come to play an increasingly detrimental role in Streaked Horned Lark declines.

RECOMMENDATIONS FOR FURTHER RESEARCH

If pending analyses of nest exclosure data support a decrease in rates of predation with no increase in rates of abandonment, I recommend that the nest exclosure program be continued. Although rates of predation were not significantly different between Larks and the guild in this study, Lark numbers are so low that any measure that increases nest success can only help. In addition, although predation rates were nearly identical between Streaked Horned Larks and the nesting guild at 13th Division Prairie, a depredated Lark nest has a much greater impact on that species' total population than, say, a depredated Savannah Sparrow nest.

Secondly, given the extremely low numbers of Streaked Horned Larks left at each remaining breeding site, in addition to their strong nest site fidelity, I highly advise further investigation into the possible effects of inbreeding depression in Streaked Horned Larks, as well as research of potential strategies to help alleviate these effects. For example, management might consider pursuing an egg exchange experiment in order to increase genetic diversity among breeding sites. When nests are discovered, egg age could be determined and a portion of those eggs could be swapped with eggs of roughly the same age in other breeding areas. Although this is a relatively drastic measure and the intricacies of such a program lie beyond the scope of this paper, I nevertheless believe it should be investigated and pursued, particularly if the nest exclosure program continues to employ personnel intensively searching for nests each breeding season.

Lastly, given the dramatic loss of grassland habitat in the Pacific Northwest, it is now more important than ever to maintain the quality of what little Streaked Horned Lark habitat remains. In addition to protections being placed on the lands where Streaked Horned Larks nest, management actions might focus on maintaining sparsely vegetated areas in remaining grassland breeding grounds, and perhaps even establishing new breeding sites. There are still lowland Puget grasslands such as 13th Division Prairie that can continue to function as healthy breeding grounds for grassland birds if protected and maintained.

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