



Life history variation between high and low elevation subspecies of horned larks *Eremophila* spp.

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Environmental variation along elevational gradients can strongly influence life history strategies in vertebrates. We investigated variation in life history patterns between a horned lark subspecies nesting in high elevation alpine habitat *Eremophila alpestris articola* and a second subspecies in lower elevation grassland and sandy shoreline habitats *E. a. strigata*. Given the shorter breeding season and colder climate at the northern alpine site we expected *E. a. articola* to be larger, have lower fecundity and higher apparent survival than *E. a. strigata*. As predicted, *E. a. articola* was larger and the trend was toward higher apparent adult survival for *E. a. articola* than *E. a. strigata* (0.69 vs 0.51). Contrary to our predictions, however, there was a trend toward higher fecundity for *E. a. articola* (1.75 female fledglings/female/year vs 0.91). The larger clutch sizes, higher nest survival, and shorter re-nesting intervals have apparently allowed *E. a. articola* to compensate for the short breeding season. Estimates of population growth rate (λ) predicted a stable population for *E. a. articola* ($\lambda = 1.00$) and a rapidly declining population for *E. a. strigata* ($\lambda = 0.62$) this may provide an explanation for the deviations from our expectation of higher reproduction in *E. a. strigata*. We suggest that anthropogenic influences (e.g. habitat loss and degradation and increased nest predator abundance) to *E. a. strigata* nesting sites may be responsible for reducing annual fecundity to the point where it is almost half that of *E. a. articola*. This result suggests that human influenced habitat changes that, in turn, change demographic rates may result in vital rates that do not accurately reflect historically divergent life histories between the two groups. Our results underscore the importance of including estimates of multiple traits in life history studies to provide insight into compensatory interactions among components of demographic rates and to identify recent changes to demographic rates that might result in a mismatch between observed and predicted life history strategies.

Life histories vary greatly among species occupying different environments with most iteroparous species falling along a continuum from 'high-reproductive' species (high fecundity and low survival) to 'survivor' species (low fecundity and high survival; Saether et al. 1996, Saether and Bakke 2000). It is generally assumed that the variation in survival and fecundity is due to tradeoffs in investment between somatic maintenance and reproduction (Williams 1966, Stearns 1989), and that the mechanisms driving these tradeoffs can be influenced by different environmental factors such as predation, climate, food and breeding season length (Krementz and Handford 1984, Jönsson et al. 1991, Martin 1995, Badyaev 1997, Conway and Martin 2000, Sandercock et al. 2005).

As elevation increases, breeding seasons are shorter, mean temperatures lower and the proportion of birds raising multiple broods decreases (Sanz 1998, Martin and Wiebe 2004). For songbirds that have multiple broods, differences in breeding season length can have dramatic effects on fecundity (Grzybowski and Pease 2005), and therefore may influence where a species falls along the life

history continuum. For example, dark-eyed juncos *Junco hyemalis* breeding at two elevations showed a more than two-fold difference in the number of hatchlings produced each year (Bears et al. 2009). This difference may be attributable to differences in the length of the breeding season with high elevation birds experiencing a shorter season. Overall, individuals that live at high elevations have lower reproductive rates but higher survival than those at low elevations (Bears et al. 2009). Similar shifts toward a 'survivor' life history have been shown for other high elevation vertebrate species including ground squirrels, ptarmigan and sparrows (Dobson 1992, Sandercock et al. 2005, Martin et al. 2009).

In addition to differences in demographic parameters, differences in body size are also found among species at different elevations. The general trend, known as Bergmann's rule, is toward increasing body size as latitude and elevation increase (Landmann and Winding 1995, Blackburn and Gaston 1996, Ashton et al. 2000, Ashton 2002, Bears et al. 2008). Differences in body size can correlate with differences in fecundity and survival; large-bodied species

generally have higher survival and lower fecundity than small-bodied species (Western and Ssemakula 1982, Saether 1988, 1989).

Many comparative life history studies have focused on one or a few easily measured traits such as clutch size and the result is a limited or misleading understanding of life history evolution. Examining alternative explanations for variation in life histories and the correlations among multiple life history traits may aid in the continued development of life history theory (Ricklefs 2000, Martin 2004, Sandercock et al. 2005). Most commonly, inter-specific comparative studies are conducted to investigate the mechanisms underlying the reproduction–survival continuum (Reznick et al. 1990, Badyaev 1997, Bielby et al. 2007). However, populations of the same species living in different environments can also show large variations along the continuum. Recent studies have focused on life history variation within single species (Gillis et al. 2005, Ozgul et al. 2006, Bears et al. 2009), thus controlling for potentially confounding influences of phylogenetic relationships among species (Martin 1995, Cardillo 2002, Sandercock and Jaramillo 2002).

We investigate variation in life history patterns between two closely related subspecies of horned larks (Drovetski et al. 2005), one nesting at higher elevation in alpine habitat in British Columbia, Canada *Eremophila alpestris articola*, pallid horned lark, and the other in grasslands and sandy shorelines at lower elevation in the Puget lowlands, coast and lower Columbia River of Washington, USA *E. a. strigata*, streaked horned lark. Ecological factors that differ between the habitats of the two populations allow for specific predictions about the potential trade-offs between vital rates and the life history strategies employed by each subspecies.

We predicted that *E. a. articola* at high elevation in British Columbia would exhibit a survivor life history due to the relatively short breeding season as a result of persistent spring snow cover and early onset of fall. We predicted that *E. a. strigata* at lower elevation in Washington would exhibit a high-reproductive life history where the potential breeding season is fairly long due to the maritime coastal climate and lack of persistent snow. Specifically, we predicted annual fecundity would be lower in *E. a. articola* than *E. a. strigata* because opportunities for multiple broods are likely limited by the shorter breeding season. We also expected adult survival of *E. a. articola* to be higher than *E. a. strigata* to compensate for reduced annual fecundity. We expected that the high elevation *E. a. articola* would be larger in body size than *E. a. strigata* and that the differences in body size would result in higher survival for *E. a. articola* and higher fecundity for *E. a. strigata*.

Methods

Study area and species

We studied *E. a. articola* (pallid horned lark) at a single site in alpine habitat on Hudson Bay Mountain near Smithers, British Columbia, Canada (52°N, 127°W) from 2003–2006. The study area was approximately 4 km² and elevation ranged from 1500–1850 m a.s.l. We studied

E. a. strigata (streaked horned lark) at seven sites in Washington State, USA 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 from 2002–2005. 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 (46° 08'N, 123° 18'W). Study areas ranged in size from 0.07 to 2.49 km² and elevation ranged from 3 to 122 m a.s.l.

Data collection

Field techniques were similar for both *E. a. articola* and *E. a. strigata*. Throughout the breeding season (early May to early August in British Columbia, April to mid-August in Washington), we searched for nests on horned lark territories. Nests were located by observing adults leaving or approaching nests sometimes carrying nesting material or food, by flushing incubating or brooding adults and by searching appropriate habitat. Nests were found during nest building, incubation and nestling stages. 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.

Adult birds were captured using mist nets or bow traps; morphological measurements were taken (wing chord, tarsus and weight) and birds were individually color marked. Nestlings were banded in the nest and individually color marked between days 7–9 post-hatching or occasionally shortly after fledging. Complete surveys of the study areas were conducted each year to determine which individuals from the previous years returned to the study areas. Resighting probabilities of *E. a. articola* and *E. a. strigata* were high and were similar for both studies indicating that the ability to detect returned birds was not biased toward one subspecies.

Demographic rates of horned larks

We measured 10 demographic variables and estimated 4 population parameters 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 day⁻¹ (thus, the number of eggs in a clutch = the length of the egg laying stage), incubation = 12 d, nestling = 9 d (Beason 1995). 2) Breeding season length (B) is the interval between the first and last known clutch initiation date within one year. 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 and includes nests that hatched at least one egg with a known clutch size. 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 and dividing by the number of eggs that hatched. 6) Fledglings per egg laid (S) is the proportion of eggs laid that produced a fledgling. 7) Nest survival was calculated using the Mayfield (1975) estimator and is 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 (damaged eggs, blood and/or feathers in or near the nest and nests found empty during incubation or during the nestling period when nestlings were too young to 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. 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. For parameters 9 and 10, 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 female⁻¹ year⁻¹ and was estimated using the technique of Ricklefs and Bloom (1977) with the following variables: B , C , S , m , r_s , r_f , p_s (probability that at least one nestling fledges), p_f (probability that a nest fails). To estimate the number of female fledglings per female, annual fecundity was divided by two assuming an equal sex ratio at fledging. 12) Apparent adult survival (ϕ_a) is the probability that an adult bird survived and returned to the study site the following year. 13) Apparent juvenile survival (ϕ_j) is the probability that a bird banded as a nestling and that successfully fledged returns to the study site the following year. Because *E. a. strigata* were studied over multiple sites, the apparent survival estimates included juveniles that returned to their natal site or dispersed from their natal site to one of the other study sites. Estimates of *E. a. articulata* 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 also provide *E. a. strigata* apparent juvenile survival estimates including only individuals that returned to their natal sites. We did not make this correction for adult apparent survival since we found no cases of adult dispersal among the study sites. 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). With the exception of our estimate of juvenile survival for *E. a. strigata* we assumed a closed population. For *E. a. strigata* we used the juvenile survival estimate including juvenile dispersal between sites to give the most realistic estimate of population growth.

Data analysis

We used the Program MARK Version 5.1 (White and Burnham 1999) to estimate apparent survival rates (ϕ) corrected for the probability of resighting (p ; the probability

the bird was seen given that it was alive) from live encounter data using the Cormack–Jolly–Seber model (Cormack 1964, Jolly 1965, Seber 1965). Adult horned larks cannot be reliably aged in the field (Pyle 1997), therefore we estimated apparent survival using a model that included sex (for adults only), but not age. The bootstrapping procedure in Program MARK (Cooch and White 2006) was used 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. The variance inflation factor (\hat{c}) was used to measure over-dispersion in the data and was calculated by dividing the observed model \hat{c} (observed deviance divided by the deviance degrees of freedom) by the mean \hat{c} of 1000 bootstrapped simulations (Cooch and White 2006). This approach was chosen because it gave the most conservative \hat{c} estimates. To correct for over-dispersion, \hat{c} estimates were used to inflate the variance of the apparent survival estimates. Information-theoretic procedures using QAIC_c (Burnham and Anderson 2002) were used for model selection. Given uneven and non-overlapping time intervals for *E. a. articulata* and *E. a. strigata* we evaluated estimated apparent survival for each subspecies separately. We used a 2 age-class model in MARK (Cooch and White 2006) to estimate juvenile survival where juvenile survival was the probability of surviving in the first year after fledging, and adult survival was the probability of surviving in subsequent years. Because of small sample sizes, we were only able to evaluate the simplest model for juvenile survival assuming constant survival without time dependence or sex. We conducted post hoc comparisons of apparent survival using χ^2 statistics in Program Contrast (Sauer and Williams 1989) in addition to providing 95% confidence intervals.

We used a Monte Carlo simulation approach of 10 000 replicates to generate standard deviations for our estimates of λ . We modeled apparent survival of adult females and juveniles using random draws from beta distributions using the variances from the survival estimates. The beta distribution constrains the random variables between 0 and 1 and is therefore appropriate for modeling survival probabilities which must remain within these values (Morris and Doak 2002). To model fecundity, we used a stretched beta distribution which is a re-scaled beta distribution that allows values greater than 1 and therefore reflects a more biologically realistic range for estimates of fecundity (Morris and Doak 2002). We defined the minimum fecundity value as 0 and the maximum value as 6 for *E. a. articulata* and 7.5 for *E. a. strigata*. Maximum values were estimated by multiplying the maximum observed clutch size by the maximum observed number of broods year⁻¹ and divided by 2 to estimate the number of female fledglings. Estimates of the variance of vital rates are conservative because years were pooled, and therefore it was not possible to separate process from sampling error (Gould and Nichols 1998). We treated parameters as independent and after each iteration the randomly drawn parameter estimates were used to calculate λ .

A consistent effort was made to survey sites in Washington for replacement nests and multiple broods, however, because a conservative approach was used when determining pairs to include in the estimates of re-nesting intervals (above), the sample sizes for *E. a. strigata* replacement nest

and multiple brood intervals were small. Also, the sampling regime across multiple sites in Washington may have made it more likely that replacement nests were not detected. To account for the possibility that the estimates of replacement nest and multiple brood intervals were low we re-estimated fecundity and lambda for *E. a. strigata* using the estimates from *E. a. articola* and using the minimum observed replacement nest interval for *E. a. strigata*.

We used the program R (R Development Core Team 2006) to perform Monte Carlo simulations, χ^2 statistics in Program Contrast (Sauer and Williams 1989) to compare adult and juvenile survival rates, SPSS ver. 10.1 (SPSS Inc. 1999) to perform z-tests to compare nest survival and depredation and to perform t-tests and Mann–Whitney U-tests for all other pairwise comparisons. Overall significance was designated at $\alpha = 0.05$. To reduce the possibility of type I errors we conducted Bonferroni corrections ($\alpha = 0.05/k$) for each of the four categories in Table 1 (Rice 1989). After Bonferroni corrections, $\alpha = 0.025$ for breeding season, $\alpha = 0.008$ for morphology, $\alpha = 0.006$ for fecundity and $\alpha = 0.01$ for survival. However, because Bonferroni corrections are highly conservative we include the calculated P-values for each test in Table 1 to allow readers to evaluate for themselves which contrasts were biologically meaningful (as per Cabin and Mitchell 2000). Means are reported \pm SE except where noted.

Results

During the course of this study we monitored 188 *E. a. articola* nests and 257 *E. a. strigata* nests. We banded 117

adult and 175 juvenile *E. a. articola* and 58 adult and 88 juvenile *E. a. strigata*.

Breeding season length was significantly longer in Washington than British Columbia (Table 1). The mean initiation date for first clutches was 16 d later for *E. a. articola* than *E. a. strigata*, and the length of the breeding season in alpine habitat in British Columbia was less than half as long as in Washington (38.5 and 94 d, respectively). Consistent with our expectations, male and female *E. a. articola* in British Columbia were considerably larger and heavier than *E. a. strigata* in Washington (Table 1).

Clutch size was 0.56 eggs larger for *E. a. articola* than for *E. a. strigata*, with no correlation between date of first egg and clutch size for either population (*E. a. articola*: $r_{578} = 0.09$, $P = 0.45$, *E. a. strigata*: $r_{5135} = 0.06$, $P = 0.49$, Spearman's rank correlation), and no difference between clutch size for initial and replacement clutches (*E. a. articola*: initial 3.53 ± 0.08 vs replacement 3.77 ± 0.16 , $Z_{55,22} = -1.45$, $P = 0.15$, *E. a. strigata*: initial 3.05 ± 0.06 vs replacement 2.75 ± 0.25 , $Z_{135,8} = -1.30$, $P = 0.19$, Mann–Whitney U-test). The replacement nest and multiple brood intervals for *E. a. strigata* were almost four times longer than for *E. a. articola* (Table 1). The extremely long re-nesting intervals for *E. a. strigata* combined with smaller clutch size, lower hatchability of eggs, lower fledging success and high clutch depredation rates resulted in 12% more fledglings per egg laid by *E. a. articola* (0.35) than *E. a. strigata* (0.23), and thus higher annual fecundity in *E. a. articola* (1.75 female fledglings female⁻¹ year⁻¹) than in *E. a. strigata* (0.91, Table 1). Although the differences in the number of fledglings per egg laid and annual fecundity were not statistically significant

Table 1. Demographic rates of *E. a. articola* (2003–2006) and *E. a. strigata* (2002–2005). Dates are Julian dates with day 1 = 1 January, and data are means \pm SE or proportions (with n in parentheses). Where we were able to make a priori predictions they are included below. P-values are given after Bonferroni correction.

	<i>E. a. articola</i>	<i>E. a. strigata</i>	Statistic	P	Predicted	Outcome
A. Breeding season:						
Clutch initiation date	151 \pm 0.61 (129)	135 \pm 1.25 (143)	$Z_{143,129} = -9.54$	<0.001	BC >WA	BC >WA
Season length (d)	38.5 \pm 1.26 (4)	94.0 \pm 10.53 (4)	$Z_{4,4} = -2.32$	0.02	BC <WA	BC <WA
B. Morphology:						
Wing chord (mm; female)	101.58 \pm 0.29 (43)	89.75 \pm 0.52 (20)	$t_{61} = -21.24$	<0.001	BC >WA	BC >WA
Tarsus (mm; female)	21.81 \pm 0.14 (44)	20.63 \pm 0.19 (18)	$t_{60} = -4.83$	<0.001	BC >WA	BC >WA
Weight (g; female)	34.01 \pm 0.34 (44)	26.92 \pm 0.47 (14)	$t_{56} = -10.70$	<0.001	BC >WA	BC >WA
Wing chord (mm; male)	108.85 \pm 0.38 (47)	97.45 \pm 0.36 (31)	$t_{76} = -20.67$	<0.001	BC >WA	BC >WA
Tarsus (mm; male)	22.71 \pm 0.13 (47)	21.18 \pm 0.43 (31)	$t_{76} = -4.05$	<0.001	BC >WA	BC >WA
Weight (g; male)	35.14 \pm 0.40 (47)	28.56 \pm 0.28 (27)	$t_{72} = -11.63$	<0.001	BC >WA	BC >WA
C. Fecundity:						
Clutch size (C)	3.61 \pm 0.07 (93)	3.05 \pm 0.06 (135)	$Z_{93,135} = -5.51$	<0.001		BC >WA
Proportion hatched	0.92 \pm 0.02 (65)	0.83 \pm 0.03 (61)	$Z_{65,61} = -2.37$	0.02		BC >WA
Proportion fledged	0.91 \pm 0.03 (39)	0.87 \pm 0.03 (38)	$Z_{39,38} = -1.11$	0.27		BC >WA
Fledglings per egg laid	0.35 \pm 0.04 (91)	0.23 \pm 0.04 (123)	$Z_{123,91} = -2.12$	0.03		BC >WA
Nest survival	0.35 (188)	0.23 (257)	$z = 2.78$	0.005		BC >WA
Proportion nests depredated	0.35 (188)	0.45 (249)	$z = 2.11$	0.03		BC <WA
Replacement nest interval (r_f)	5.97 \pm 0.84 (38)	22.25 \pm 4.25 (8)	$t_{44} = 3.76$	<0.001		BC <WA
Multiple brood interval (r_s)	6.00 \pm 0.91 (8)	22 (1)				BC >WA
Annual fecundity	1.75 \pm 0.24 (4)	0.91 \pm 0.17 (4)	$t_6 = -2.82$	0.03	BC <WA	BC >WA
D. Apparent survival						
Adult (ϕ_a)	0.69 \pm 0.04 (117)	0.51 \pm 0.07 (58)	$\chi^2 = 4.98$	0.02	BC >WA	BC >WA
Male	0.72 \pm 0.06 (65)	0.55 \pm 0.10 (32)	$\chi^2 = 2.13$	0.14		BC >WA
Female	0.65 \pm 0.07 (52)	0.47 \pm 0.10 (26)	$\chi^2 = 2.17$	0.14		BC >WA
Juvenile without dispersal (ϕ_j)	0.20 \pm 0.05 (175)	0.095 \pm 0.04 (80)	$\chi^2 = 2.95$	0.08	BC >WA	BC >WA
Juvenile with dispersal (ϕ_j)	n/a	0.17 \pm 0.06 (88)	n/a	n/a		

Table 2. Model rankings from program MARK (White and Burnham 1999) to estimate apparent survival (ϕ) and resighting probabilities (p) for *E. a. articola* and *E. a. strigata* adults. Models included groups for apparent survival for adult males and females. The period symbol (.) means that the parameter was held constant in the model. Resighting probabilities were held constant because $p = 1$ for males and females of both species.

Model	QAICc	Δ QAICc	AICc Weights	Parameters	Deviance
A. <i>E. a. articola</i> adults:					
{ ϕ (.)P(.)}	142.17	0	0.69	2	9.66
{ ϕ (sex.)P(.)}	143.73	1.56	0.31	3	9.11
B. <i>E. a. strigata</i> adults:					
{ ϕ (.)P(.)}	70.32	0	0.72	2	7.40
{ ϕ (sex.)P(.)}	72.18	1.86	0.28	3	7.09

after Bonferroni correction, the trend was toward higher fecundity for *E. a. articola* for all components of fecundity (with the exception of breeding season length).

Goodness-of-fit tests indicated that there was insufficient data to fit a time dependent model for apparent adult survival ($\hat{c} > 4$), therefore we evaluated only 2 models for adult survival one including differences in sex (s) and one without differences in sex (.). The probability of encounter (p) was 1 for adult males and females of both subspecies therefore we did not allow the probability of resighting to vary by sex. The most parsimonious model for adult survival was a reduced model with survival and probability of encounter held constant (ϕ , p .; Table 2). Because models that included groups for males and females had less support than the reduced models for both subspecies, we present data for apparent adult survival with males and females pooled and with each sex separately (Table 2). Goodness-of-fit tests indicated only minor over-dispersion ($\hat{c} = 1.01$ and 1.06 for adult and juvenile *E. a. articola* and $\hat{c} = 1.55$ and 1.49 for adult and juvenile *E. a. strigata*). As predicted, overall apparent adult survival was higher for *E. a. articola* ($\phi_{\text{adult}} = 0.69$; 95% CI 0.60, 0.77) than *E. a. strigata* ($\phi_{\text{adult}} = 0.51$; 95% CI 0.37, 0.65; Table 1). However, after Bonferroni correction the trend was not significant. There was also a non-significant trend toward higher juvenile survival for *E. a. articola* ($\phi_{\text{juvenile}} = 0.20$; 95% CI 0.12, 0.33) than *E. a. strigata* ($\phi_{\text{juvenile}} = 0.095$; 95% CI 0.04, 0.20; Table 1). The probabilities of encounter for *E. a. articola* and *E. a. strigata* juveniles were 0.79 ± 0.18 and 1, respectively.

To compare apparent juvenile survival between the two subspecies, we used only *E. a. strigata* juveniles that had returned to their natal sites. However, when dispersed *E. a. strigata* juveniles were added, apparent survival was 0.17 ± 0.06 ($n = 88$; 95% CI = 0.08, 0.32), the probability of encounter was 0.78 ± 0.21 and $\hat{c} = 1.45$. To calculate lambda, we used the estimate for *E. a. strigata* apparent juvenile survival including juveniles that had dispersed, because we wanted the results to reflect as closely as possible the true value of population growth for the *E. a. strigata* subspecies.

The estimates of lambda predicted a stable population for *E. a. articola* ($\lambda = 1.00 \pm 0.12$ SD; Fig. 1a), and a decreasing population for *E. a. strigata* ($\lambda = 0.62 \pm 0.12$ SD; Fig. 1b). For *E. a. articola*, 48% of the simulations predicted $\lambda > 1$ while none of the simulations predicted $\lambda > 1$ for *E. a. strigata*.

To examine the impact of the prolonged re-nesting interval for *E. a. strigata* we re-estimated fecundity and

lambda using the replacement nest and multiple brood intervals for *E. a. articola* (5.97 and 6 d) and using the minimum observed replacement nest interval for *E. a. strigata* (10 days). Using these values, estimates of fecundity for *E. a. strigata* increased to 1.67 ± 0.32 and 1.38 ± 0.26 female fledglings female⁻¹ year⁻¹, respectively and estimates of lambda increased to 0.75 ± 0.15 and 0.70 ± 0.14 .

Discussion

Variation in physical and environmental factors such as body size, food availability, predation and climate have all been invoked to explain patterns of life history differences among species (Lack 1966, Saether 1989, Martin 1995, Sandercock et al. 2005). Our detailed demographic data for two subspecies of horned larks demonstrates that large variation in the mean values of vital rates can be found even among closely related groups. Consistent with our predictions, we found that the high elevation subspecies, *E. a. articola*, had a larger body size and showed trends toward higher apparent adult and juvenile survival than the low elevation subspecies *E. a. strigata*. However, contrary to our predictions, we also found a trend towards higher annual fecundity for *E. a. articola* than for *E. a. strigata*. Below we discuss possible strategies that allowed *E. a. articola* to compensate for reductions in breeding season length and the implications of anthropogenic disturbance on vital rates that may have resulted in mismatched life history predictions for *E. a. strigata*.

Birds in the lark family (Alaudidae) inhabit a wide range of environments from arid deserts to arctic tundra and have been the subject of a number of studies that investigate physiology, behavior and life history across environmental gradients (Tielemans and Williams 2002, Tielemans et al. 2004, Tielemans 2005). Differences in fecundity were found in larks along an aridity gradient from moist grasslands to hot, arid deserts with reduced fecundity in more arid environments. The decreased availability of food and water in arid deserts limited the birds' investment in current reproduction and the authors inferred that larks in arid environments would show a shift toward investment in self-maintenance (Tielemans et al. 2004, Tielemans 2005). Similarly, differences in reproduction and apparent survival were found for horned larks in high versus low elevation environments in the current study.

Although the breeding season was more than twice as long for *E. a. strigata* in Washington, *E. a. articola* in British Columbia produced almost twice as many fledglings per

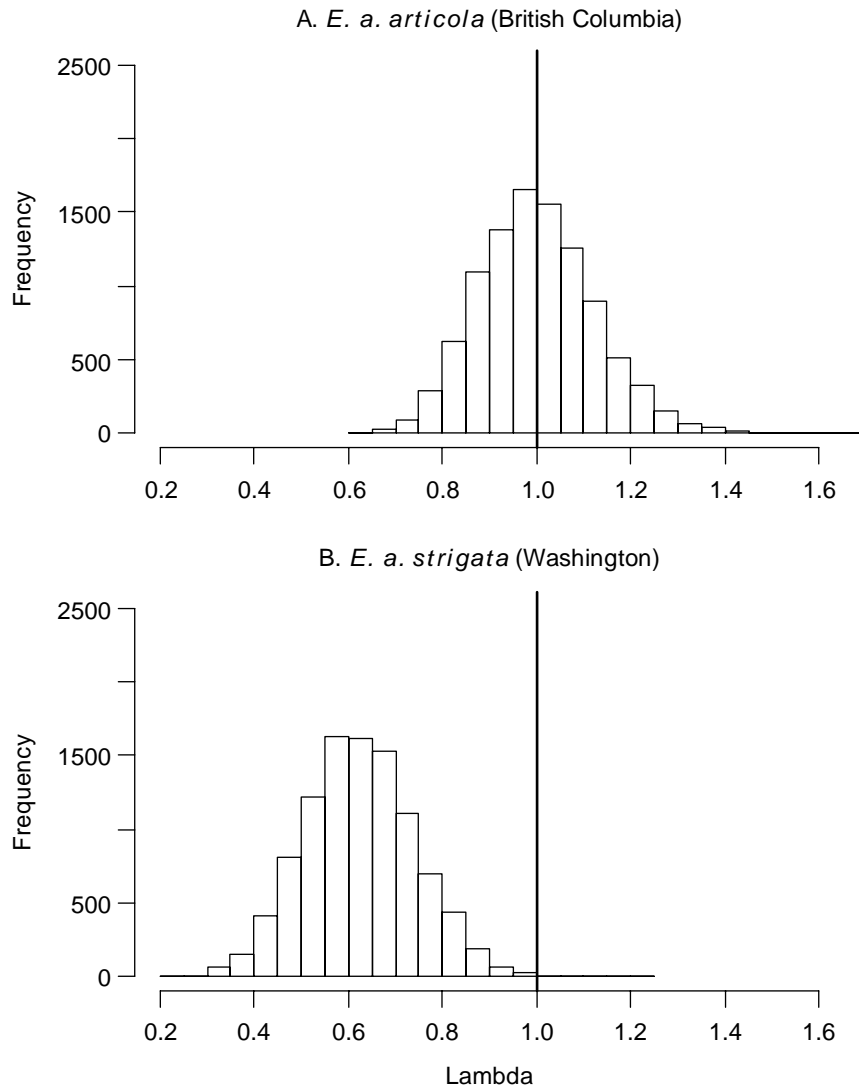


Figure 1. Frequency distribution of estimates of lambda (λ) for two horned lark subspecies, (a) *E. a. articola* at high elevation in alpine habitat in British Columbia, Canada, 2003–2006, and (b) *E. a. strigata* at low elevation in grasslands and sandy shorelines in Washington, USA, 2002–2005. The bold line indicates $\lambda = 1$, values to the right of the line show the proportion of simulations that predicted a growing population.

year. Season length, re-nesting frequency and the production of multiple broods can have large influences on annual fecundity and may explain as much variation in annual fecundity as nest success (DeCecco et al. 2000, Underwood and Roth 2002). Although the sample size was small, *E. a. strigata* had re-nesting and interbrood intervals that were more than three times longer than *E. a. articola* and the minimum observed re-nesting interval for *E. a. articola* was 3 days while the minimum observed re-nesting interval for *E. a. strigata* was 10 days. In effect, the potential benefits of the longer breeding season for *E. a. strigata* were negated by their prolonged re-nesting intervals. Clutch size was also significantly larger and rates of nest depredation lower for *E. a. articola* than for *E. a. strigata* and may have allowed *E. a. articola* to further compensate for the short breeding season by increasing investment in each nesting attempt.

Horned larks feed primarily on insects during the breeding season (Beason 1995). In the spring and summer large numbers of insects are carried on winds from lower

elevations and deposited on snowfields in alpine habitats where they are easily captured by foraging birds (Crawford and Edwards 1986, Antor 1995). Abundant food and lower nest depredation rates may allow *E. a. articola* to compensate for the short breeding season by producing larger clutches with shorter re-nesting intervals which led to higher fecundity for *E. a. articola* than *E. a. strigata*.

The influence of anthropogenic habitat loss, habitat degradation and increased nest predator populations on the vital rates of *E. a. strigata* may explain the mismatch between the predicted and observed life history strategy for *E. a. strigata*. Our measure of lambda indicates that *E. a. strigata* is declining rapidly (38% year⁻¹) and therefore our estimates of current vital rates apparently do not reflect historic levels (or there would be no populations to study). Anthropogenic disturbance near breeding sites of *E. a. strigata* may have led to elevated rates of nest depredation as a result of increases in predator populations commonly associated with developed areas (i.e. domestic cat *Felis*

domesticus, northern raccoon *Procyon lotor*, striped skunk *Mephitis mephitis* and American crow *Corvus brachyrhynchos*; Marzluff et al. 2001). American crows have been observed deprelating two *E. a. strigata* nests (S. F. Pearson unpubl.). Alteration of habitat composition and structure caused by introduced non-native and invasive plants may also contribute to reduced fecundity and survival. The cumulative effects of anthropogenic disturbances around *E. a. strigata* breeding sites may be responsible for reducing annual fecundity in *E. a. strigata* to the point where it is almost half that of *E. a. articola* and may not accurately reflect historically divergent life histories between the two groups.

To further illustrate this point, using our estimates of apparent juvenile and adult survival and assuming immigration rates are low, in order for lambda to be stable for *E. a. strigata*, fecundity would need to equal 3.12 female fledglings female⁻¹ year⁻¹. If this estimate approximates historic levels of fecundity for *E. a. strigata*, then we would see differences in fecundity between the two subspecies in the direction predicted by life history theory.

Our estimates of apparent adult survival were in the direction predicted with a trend toward higher apparent adult survival in *E. a. articola* than in *E. a. strigata*. The higher apparent survival in *E. a. articola* may reflect a shift towards a high survivor life history, as has been shown in other high elevation vertebrate species (Dobson 1992, Sandercock et al. 2005, Bears et al. 2009, Martin et al. 2009). However, it is also possible that the lower estimate of apparent survival for *E. a. strigata* is a reflection that the population is under pressure and declining with no apparent compensatory evolutionary response to habitat degradation.

Apparent juvenile survival in *E. a. articola* was remarkably high (20%) and is likely an underestimate as we were not able to detect dispersal to other sites. Overwinter juvenile horned lark survival for a single year in shortgrass prairie in north-central Colorado was 4.4% (Boyd 1976) and median juvenile survival rates for migratory and non-migratory passerines typically range from 2.6 to 10.5% (Weatherhead and Forbes 1994). Badyaev and Ghalambor (2001) found that songbirds inhabiting high elevations have lower fecundity than low elevation birds, but invest more in parental care, and hence, their young have higher survival rates. It is possible that we observed a similar trade-off between offspring number and offspring quality for *E. a. articola*.

In addition to the difference in elevation between the two populations studied here, there was also a difference in latitude of 5–6°, and this latitudinal difference may provide an alternative explanation for the patterns we observed. As with differences across elevation, environmental and ecological variables also co-vary with latitude and are reflected in the life histories of the animals at low and high latitudes. For example, low latitude tropical passerines tend towards high survival life histories while high latitude temperate species tend towards high reproductive life histories (Martin 2004). Perhaps environmental factors such as increased day length, and thereby increased time available to forage (Lack 1947) for the higher latitude *E. a. articola*, contributed to their ability to produce more fledglings each year. Further studies across a range of latitudes

and elevations are required to tease apart the conflicting predictions of life history strategies across both latitudinal and elevational gradients (Tieleman 2009).

Our estimates of lambda assumed a closed population without immigration and may therefore be underestimates. However, our estimate of apparent juvenile survival used to calculate lambda for *E. a. strigata* does include juvenile dispersal among our 7 sites and adult dispersal is likely uncommon. Over four years we observed no instances of dispersal of the adult birds banded on our 7 study sites in Washington, even though we monitored a total of 21 sites in Oregon and Washington for returns. It is likely that we would have detected nearly all of the dispersal events because our detection probability was 1.0 for adults, because larks in western Washington only nest in discrete sites of appropriate habitat in a region dominated by conifer forests and because nearly all known breeding sites were monitored for banding returns. While there are no data on range-wide population trends for *E. a. strigata*, transect counts and data from territory mapping indicate rapid declines in their numbers (S. F. Pearson unpubl.). Therefore our estimates of lambda, while possibly underestimated, accurately reflect actual population declines for *E. a. strigata* and suggest that our estimated fecundity and/or survival values may not reflect historic values. It is also possible that the sites we studied are sink populations that are maintained by immigration of birds from other areas and the declining population does not necessarily indicate that historic levels of vital rates are not reflected. However, as discussed above, immigration rates into the study population are likely small, and given that *E. a. strigata* were historically present in the region, the rapid decline suggested here must not have been occurring over the long-term or the population would have disappeared some time ago.

Our results underscore the importance of including estimates of many traits in life history studies to provide insight into potential compensatory interactions among components of vital rates. Our results also indicate the need to estimate lambda when comparing the life histories of two or more groups. If a population is either declining or increasing rapidly (as indicated by lambda) as a result of modified habitat or increased predator populations, then its current demographic rates may not reflect their long term mean values and the result will be a mismatch between observed and predicted life history strategies. The human footprint is expanding rapidly and leaves very few habitats unmodified (Leu et al. 2008), as a result it will become increasingly important to understand how anthropogenic change is affecting vital rates and ultimately comparisons of life history trade-offs.

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