

An ‘ecological trap’ for yellow warbler nest microhabitat selection

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Contrary to assumptions of habitat selection theory, field studies frequently detect ‘ecological traps’, where animals prefer habitats conferring lower fitness than available alternatives. Evidence for traps includes cases where birds prefer breeding habitats associated with relatively high nest predation rates despite the importance of nest survival to avian fitness. Because birds select breeding habitat at multiple spatial scales, the processes underlying traps for birds are likely scale-dependent. We studied a potential ecological trap for a population of yellow warblers *Dendroica petechia* while paying specific attention to spatial scale. We quantified nest microhabitat preference by comparing nest- versus random-site microhabitat structure and related preferred microhabitat features with nest survival. Over a nine-year study period and three study sites, we found a consistently negative relationship between preferred microhabitat patches and nest survival rates. Data from experimental nests described a similar relationship, corroborating the apparent positive relationship between preferred microhabitat and nest predation. As do other songbirds, yellow warblers select breeding habitat in at least two steps at two spatial scales; (1) they select territories at a coarser spatial scale and (2) nest microhabitats at a finer scale from within individual territories. By comparing nest versus random sites within territories, we showed that maladaptive nest microhabitat preferences arose during within-territory nest site selection (step 2). Furthermore, nest predation rates varied at a fine enough scale to provide individual yellow warblers with lower-predation alternatives to preferred microhabitats. Given these results, tradeoffs between nest survival and other fitness components are unlikely since fitness components other than nest survival are probably more relevant to territory-scale habitat selection. Instead, exchanges of individuals among populations facing different predation regimes, the recent proliferation of the parasitic brown-headed cowbird *Molothrus ater*, and/or anthropogenic changes to riparian vegetation structure are more likely explanations.

Habitat selection is the behavioral process by which animals choose where to live and breed. Theory assumes that animals will prefer habitats that maximize their fitness (Fretwell and Lucas 1970). However, field studies providing evidence for ‘ecological traps’ challenge this basic theoretical assumption. Members of several populations across a variety of animal taxa appear to favor poor-quality habitats despite the availability of better-quality habitats (reviewed by Battin 2004). Ecological traps have the potential to threaten population persistence particularly when a substantial fraction of population members select poor quality habitats (Kristan 2003). Thus, the presence of traps raises an important question for conservation and evolutionary ecologists: why do the members of some populations favor habitats that confer lower fitness than available alternatives?

Studies of birds have provided much of the empirical evidence for ecological traps. Nest survival is an important component of avian fitness (Clark and Martin 2007) and predation is typically the main cause of nest failure (Martin 1993). Given the importance of predation, ornithologists expect birds to select breeding habitats that minimize predation risk (Martin 1998). However, several studies document preferences for breeding habitat associated with elevated

predation rates and reduced nest survival (Misenhelter and Rotenberry 2000; additional studies reviewed by Robertson and Hutto 2006). These purported traps may have arisen because anthropogenic disturbance has disrupted nest predator behavior, distributions, or community composition in ways that are not recognized by birds selecting nest sites. Alternatively, despite the obvious importance of nest predation, other selective agents acting upon other fitness components could still balance out costs incurred by utilizing high-predation habitats. Thus, why some birds continue to prefer high-predation breeding habitats is not well understood.

Since birds select habitat at multiple spatial scales (Wiens et al. 1987) and since habitat-specific predation patterns arise at multiple scales (Thompson 2007), the processes underlying ecological traps for birds are likely scale-dependent. At a relatively coarse scale, birds select breeding territories to accommodate multiple activities, including foraging, roosting, and nesting. At a finer scale, birds select microhabitats from within their territories for particular activities, including microhabitats for nest establishment. With respect to predation risk, habitat at coarse scales can influence predator numbers and/or distributions, whereas at finer scales, microhabitat can influence predator hunting strategies and/or nest

detection rates (Thompson 2007). Coarse-scale predation patterns would have a greater bearing on territory selection, but territory selection may also be shaped by other factors, such as food availability (Shochat et al. 2005, Chalfoun and Martin 2007). By contrast, fine-scale, microhabitat-related patterns should strongly influence birds during nest site selection, especially since other agents of natural selection are less likely to have any bearing on this phase of habitat selection. Indeed, most purported traps for birds (reviewed by Robertson and Hutto 2006) are observed at coarser scales, so most populations purportedly 'trapped' by predation may in reality be favoring territories for their food resources, the benefits of which may or may not outweigh apparent predation costs.

Here, we studied the processes underlying an apparent ecological trap for a population of yellow warblers *Dendroica petechia*. First, we compared microhabitat use versus availability to quantify nest microhabitat preferences, and we demonstrated that nests in preferred sites suffer higher predation rates than nests in less preferred sites. Next, since we expect birds to be most responsive to predation risk during nest site selection, we compared use versus availability within individual territories to determine if apparent maladaptive preferences arose during nest site selection. Finally, we analyzed data from both natural and experimental nests to examine the mechanistic underpinnings of microhabitat-predation relationships. This information allowed us to consider both the relative predator-avoidance benefits associated with alternative microhabitat choices and when during the habitat selection process yellow warblers chose nest microhabitats. In light of our findings, we considered various alternative explanations for apparently maladaptive nest microhabitat preferences, including tradeoffs between nest survival and other fitness components.

Methods

Study species and location

The yellow warbler *Dendroica petechia* is an open-cup, shrub- and tree-nesting neotropical migrant passerine that breeds mainly in riparian areas/vegetation across North America (Lowther et al. 1999). In the Mono Lake Basin of east-central California, breeding male yellow warblers arrive and begin establishing territories by mid-May (PRBO Conservation Science unpubl.). Females arrive subsequently, begin nesting in late May, and continue initiating new attempts following nest failure through the first week of July. Individual yellow warbler pairs occupy exclusive territories encompassing a substantial area of riparian habitat (0.29 ± 0.17 ha (SD) on Rush Creek) from which they select nest sites.

A variety of vertebrates depredate nests of riparian songbirds in the Mono Lake basin (Latif 2009). Based on observations from this system, the principal egg predators are birds (mainly corvids such as Steller's jays *Cyanocitta stelleri*, and black-billed magpies *Pica hudsonia*, and the brood-parasitic brown-headed cowbird *Molothrus ater*), although rodents (least chipmunks *Tamias minimus*, and murid and cricetid mice) also pose a substantial threat. Snakes (mainly garter snakes *Thamnophis* spp.) are the principal

predators of nestlings in our study system, although corvids and mice have also been observed taking chicks. Cowbirds depredate nests in conjunction with brood parasitism (49% of yellow warbler nests were parasitized in our study area; Heath 2008).

Our study spanned 2000–2008. From 2000–2005, we collected data as part of an all-species riparian bird monitoring program along the lower reaches of four tributaries to Mono Lake, Mono County, California, USA: Rush, Lee Vining, Mill, and Wilson creeks (1972–2020 m, $37^{\circ}56'N$, $119^{\circ}04'W$ – $38^{\circ}04'N$, $119^{\circ}09'W$). Two study plots along each creek ($n = 8$) encompassed a total of 39, 30, 15 and 15 ha of riparian floodplain vegetation respectively (Heath et al. 2006). From 2006–2008 we studied the processes contributing to nest habitat preference and predation patterns at one Rush Creek study plot ($n = 1$; 20 ha). A strong xeric – mesic gradient characterized floodplain vegetation, with mixed willow (*Salix* spp.) and black cottonwood *Populus balsamifera* ssp. *trichocarpa* at the mesic extreme, non-riparian shrubs big sagebrush/ bitterbrush/rabbitbrush (*Artemisia tridentata*/ *Purshia tridentata*/ *Chrysothamnus* spp.) at the xeric extreme, and Woods' rose *Rosa woodsii* in between (McBain and Trush 2003). This gradient has been influenced by decades of anthropogenic habitat alterations. Water diversions and livestock grazing (Stine et al. 1984), followed by grazing cessation and stream re-watering (Kauffman et al. 2000), have caused substantial fluctuations in the extent of riparian vegetation within the floodplains. Sagebrush-associated vegetation remained a substantial component of the floodplain shrub layer during our study (McBain and Trush 2003). Yellow warbler densities ranged from 2.2 pairs ha⁻¹ on Rush to 0.4 pairs ha⁻¹ on Mill creeks (Heath et al. 2006).

Yellow warbler nest microhabitat use, availability and preference

Nest microhabitat use

We located yellow warbler nests during alternate-day visits to all plots (2000–2005) or daily visits to the single Rush Creek plot (2006–2008) throughout the nesting season. Concurrently, we identified distinct breeding territories and located their approximate boundaries on our study plots by mapping season-long observations of territorial behavior and by comparing simultaneous nest cycle timing of neighboring pairs (Robbins 1970). Most individuals were unmarked, but after initiating color-banding in 2005, 17% of 2005 territories across all plots contained at least one marked individual, as did 17% of 2006–2008 territories at Rush Creek. We located nests for 70–94% of all territories in any given year.

After monitoring nests to determine their fate, we measured microhabitat structure at each nest site to assess microhabitat use. A previous study demonstrated shrub features to be of primary importance to yellow warblers selecting nest sites (Knopf and Sedgewick 1992) and 96% of nests in our study were placed in shrubs and saplings that met our 'shrub layer' criteria ($n = 1067$ nests, 2000–2005; PRBO unpubl.). We therefore focused on habitat preference and predation patterns with respect to the shrub layer (woody vegetation <5.0 m in height, or saplings of any height with stems <8 cm diameter at breast height). In the field, we estimated absolute total percent shrub cover, estimated relative percent

cover for each shrub species, and counted the total number of shrub stems by species within a 5-m radius circle centered on each nest. We derived absolute species-specific shrub covers (total cover \times relative cover/100), which we used along with stem counts as explanatory variables in habitat preference and nest survival models. We also used a spherical densiometer (Martin et al. 1997) to measure the upper portion of the shrub layer and the tree canopy. We took readings at each of four cardinal directions 1 m from each nest and averaged the four readings to obtain an index of upper-shrub and tree density, referred to as overhead cover. In addition to measurements of microhabitat patch structure, we recorded nest substrate (the plant species supporting the nest) and estimated concealment (the mean ocular estimate of the percent nest-cup concealed when viewed 1 m from the nest in six directions: above, below, N, S, E, W; used only as a covariate in this study) (Martin et al. 1997).

Microhabitat availability

We measured microhabitat availability at random sites located within study plot boundaries. From 2000–2005, we measured microhabitat availability at ca. 30 randomly-placed points per year along each creek. We generated these points within study plot boundaries both within and outside known yellow warbler territories (671 points total) using ArcGIS 9.2 (ESRI 2006). From 2006–2008, we measured microhabitat availability within yellow warbler territories at the single Rush Creek plot. Although color-marked individuals' nesting sites shifted spatially between attempts, territory boundaries inferred from season-long observations included the range of microhabitat choices within reach of individual females selecting nest sites. We digitized 2006–2008 territory boundaries and identified multiple random sites per territory in which natural nests were also located. In 2006, we located three random sites within each of 30 randomly selected territories (90 points total). Within territories from all years (2006–2008), we identified additional random sites located at grid points spaced 20 m apart. We randomly selected 331 candidate random sites from a total of 514 grid points located within the study plot. For each year, we assigned each candidate site to the territory containing it or to the nearest territory within 20 m. Using these procedures, we assigned 6.8 ± 3.8 (SD) random points to each of 56 territories in 2006 and 5.0 ± 3.3 random points to each of 113 territories from 2007–2008.

We measured the same microhabitat-patch-structure variables at random sites as at nest sites. From 2000–2005, we centered measurements on random-site coordinates. From 2006–2008, focusing specifically on microhabitat availability for yellow warblers, we centered measurements on the potential nest shrub nearest to each random point. Potential nest shrubs were shrubs of any species yellow warbler nests were known to occupy and structurally capable of supporting a nest. GPS units located points in the field with a ca 5-m margin of error. Assuming no bias towards particular microhabitat values, this error should not have influenced our characterization of microhabitat availability.

Microhabitat preference analysis

We identified preferred nest habitat features and quantified preference by analyzing differences between nest site habitat measurements (i.e. microhabitat use) and random

site measurements (i.e. microhabitat availability). We used multiple analysis of variance (MANOVA) to test for significant multivariate differences between nest and random sites with respect to microhabitat patch structure measurements. Given significant differences, we used discriminant function analyses (DFA) to calculate linear functions of microhabitat variables that best discriminated between nest and random sites (Tabachnick and Fidell 2001, Misenhelter and Rotenberry 2000). Discriminant functions essentially described preference gradients, and the value of any individual site calculated using such a function is a preference score (the location of a site along a preference gradient). We referred to loadings (correlation coefficients between raw habitat variables and preference scores) to interpret preference gradients and identify preferred and avoided microhabitat features. Due to the differences in sampling protocol (i.e. random site measurements), we analyzed preference for the 2006–2008 period separately. We also divided 2000–2005 data from plots with adequate sample sizes (Rush and Lee Vining creeks) into two equivalent sized subsets (2000–2003 data and 2004–2005 data) to control for inter-annual variation in observers (Table 2).

Since preference gradients were potentially influenced by territory selection and/or territory density (especially given an uneven spatial distribution of microhabitats; Supplementary material Appendix 1), we analyzed nest microhabitat preferences while controlling for the influence of territory location. We compared nest to random sites within individual 2006–2006 Rush Creek territories (i.e. territories containing multiple random sites). We first identified major axes of microhabitat variation by applying a principal components analysis (Tabachnick and Fidell 2001) to 2007–2008 random grid point habitat measurements. We retained components (PCs) with eigenvalues >1 (Tabachnick and Fidell 2001) and scored all nest sites and random points along retained PCs. Along each PC axis, we calculated each territory's mean nest site score (individual/territory-specific microhabitat use) and mean random site score (territory-specific microhabitat availability). We used randomized-complete-block ANOVA models (one analysis per PC) to analyze territory-specific differences in use versus availability. Each ANOVA model included a territory parameter (the block) and a preference parameter (the treatment). The preference parameter's F-statistic tested for territory-specific differences.

Natural nest monitoring and analyses of preference relationships with nest survival

Nest monitoring

Once located, we visited yellow warbler nests at least once every four days and recorded their contents until they either failed or fledged young. We considered nests failed when (1) no yellow warbler eggs or nestlings remained in the nest prior to the earliest potential fledge date, (2) the nest was abandoned by the parents, or (3) eggs remained un-hatched substantially past the normative incubation period (11.3 days; PRBO unpublished data derived from Mono Lake birds). We considered nest predation the cause of failure given scenario 1 and/or when we observed predation directly. We considered nests failed if and when they contained only brown-headed cowbird eggs or nestlings. We considered nests failed

Table 1. Nest microhabitat preference gradients from discriminant function analyses calculated for yellow warblers along four creeks in the Mono Lake basin. All MANOVA p-values were < 0.001. Positive loadings indicate preference. Negative loadings indicate avoidance.

	Rush			Lee Vining		Mill	Wilson
	2001–2003	2004–2005	2006–2008	2000–2003	2004–2005	2000–2005	2000–2005
No. nests, no. random sites	304, 90	261, 60	290, 421	173, 117	182, 60	61, 178	51, 166
MANOVA F-values	18.1	12.8	17.08	19.3	8.3	16.1	17.4
Degrees of freedom	5, 388	5, 309	5, 704	8, 281	7, 234	10, 228	4, 212
Discriminant function Loadings							
Overhead cover	0.71	0.88	0.78	0.67	0.60	0.73	0.99
Willow cover	0.39	0.56	0.50	0.52	0.33	0.14	0.79
Willow stems	0.39	0.27	0.57	0.29	0.16	0.02	0.56
Rose cover	0.28	0.01	-0.16	0.31	0.39	0.50	n/a
Rose stems	n/a	n/a	n/a	n/a	n/a	0.60	n/a
Non-riparian cover	-0.70	-0.71	-0.48	0.08	0.01	-0.53	-0.31
Cottonwood sapling cover	n/a	n/a	n/a	-0.07	-0.19	0.41	n/a
Cottonwood sapling stems	n/a	n/a	n/a	-0.08	-0.23	0.37	n/a

n/a denotes where variables were not included in models either because the shrub type was rare along the corresponding creek, or because of extreme non-normality in the variable's distribution (i.e. a long upper tail for rose stem counts recorded along Rush and Lee Vining creeks).

on hatch day if they contained both host and cowbird eggs but only the latter hatched. Nests with uncertain fates were assigned fates using published criteria (Martin and Geupel 1993, Weidinger 2007). For a small minority of nests (2%), we found no evidence of either fledging or failure so we considered the fates of these nests unknown and excluded these nests from our analyses. We used standard precautions to avoid attracting predators to active nests (Martin and Geupel 1993).

Analysis of microhabitat-preference-survival relationships

We built logistic exposure models (Shaffer 2004) to analyze daily nest survival rates (DSR) in relation to variables of interest. We fitted logistic exposure models using PROC GENMOD in SAS 9.1 (SAS Inst.). We truncated the final intervals of fledged nests on the estimated fledge day (ca day 10, PRBO unpubl.; follows recommendation by Weidinger 2007).

We constructed DSR models that included preference scores as explanatory variables to investigate preference-survival

Table 2. Preference-survival relationships and nest survival estimates along preference gradients. $n_{\text{effective}}$ = number of observation-days represented in the data. k = number of parameters in each model. $\beta \pm \text{SE}$ = preference parameter estimate \pm their standard errors. Δ_{Pref} = reduction in AIC_c or QAIC_c with preference parameters in nest survival models (negative values indicate a reduction; see Appendix 4 for model log-likelihood values [-LL] and model weights [w_i]). Nest survival rates (NSR) were calculated at preference gradient scores = -2 and +2 for Rush Creek natural nests and Lee Vining Creek nests (i.e. larger datasets), and -1 and +1 for the remaining datasets. Covariates were Year, Date, Stage, and Plot in Rush Creek natural nest models; Year and Date in experimental nest models; Stage only in Lee Vining and Mill creek models; and no covariates in the Wilson Creek model (covariate effects on DSR presented in Supplementary material Appendix 3). Models included covariates that reduced AIC_c for preliminary, univariate models.

Dataset	Preference gradient	$n_{\text{effective}}$	k	Δ_{Pref}	Evidence ratio	$\beta \pm \text{SE}$	NSR \pm SE	
							at preference gradient score = -1 or -2	at preference gradient score = 1 or 2
Rush Creek natural nests (2000–2008)	2006–2008	6803	14	-2.9*	4.3	-0.16 \pm 0.07**	0.33 \pm 0.10**	0.12 \pm 0.07**
	2004–2005	6803	14	0.6*	0.7	-0.08 \pm 0.07**	0.27 \pm 0.10**	0.16 \pm 0.08**
	2001–2003	6803	14	-0.9*	1.6	-0.13 \pm 0.07**	0.30 \pm 0.10**	0.14 \pm 0.08**
Rush Creek experimental nests (2006–2007)	2006–2008	764	4	-4.2	8.2	-0.34 \pm 0.14	0.24 \pm 0.05	0.07 \pm 0.03
Lee Vining Creek natural nests, (2000–2005)	2004–2005	2799	4	0.9*	0.6	-0.14 \pm 0.13**	0.41 \pm 0.18**	0.22 \pm 0.16**
	2000–2003	2799	4	1.8*	0.4	-0.06 \pm 0.13**	0.35 \pm 0.18**	0.26 \pm 0.18**
Mill Creek, natural nests (2000–2005)	2000–2005	618	4	-2.7	3.9	-0.43 \pm 0.20	0.51 \pm 0.19	0.21 \pm 0.17
Wilson Creek, natural nests (2000–2005)	2000–2005	507	2	2.0*	0.37	-0.03 \pm 0.29**	0.39 \pm 0.21**	0.37 \pm 0.21**

Δ_i = AIC_c or QAIC_c for a model with the preference parameter minus AIC_c or QAIC_c for the equivalent model with only covariates.

$\text{AIC}_c = -2 \times \text{LL} + 2k + 2k(k + 1)/(n_{\text{effective}} - k - 1)$

*indicates ΔQAIC_c values; $\text{QAIC}_c = -2 \times \text{LL} / c + 2(k + 1) + 2(k + 1)(k + 2)/(n_{\text{effective}} - (k + 1) - 1)$, where $c = 2.0, 2.2$ and 1.7 for Rush Creek natural nest models, Lee Vining Creek models, and Wilson Creek models, respectively.

**indicates standard error values inflated by a factor of \sqrt{c} .

$$W_i = e^{0.5 \Delta_i} / \sum_{0-j} e^{0.5 \Delta_j}$$

$$\text{Evidence ratio} = w_{\text{preference_model}} / w_{\text{covariate-only_model}}$$

relationships, and we included a series of covariates to control for other sources of variation. Covariates included three temporal variables: Year, Date (the within-season timing of observation intervals expressed as day-of-year), and Stage (egg vs nestling); one spatial variable: Plot (compared the two study plots at each creek); and Parasitism status (whether the nest contained viable cowbird eggs or nestlings when observed).

We used an a priori information-theoretic approach (Burnham and Anderson 2002) to analyze whether the data supported preference–survival effects. We used one of two indices of model fit: Akaike’s information criterion corrected for sample size (AIC_c), or an equivalent variant that also corrected for un-modeled heterogeneity in the data ($QAIC_c$). From AIC_c or $QAIC_c$ differences, we calculated Akaike model weights (w_i), and from these, evidence ratios to examine the statistical support for preference–survival relationships ($ER = w_i$ for a preference model/ w_i for the equivalent covariate-only model). We also calculated evidence ratios for preference score \times covariate interactions to look for inconsistencies in preference effects. For any given model-set, we used $QAIC_c$ to quantify relative model-fit given the presence of un-modeled heterogeneity in the data as indicated by a variance inflation factor $c > 1$ calculated for a global model (the model with the maximum number of explanatory variables that best-fit of the data; Burnham and Anderson 2002).

To examine the relative magnitude and direction of preference–survival relationships, we report model-predicted nest survival rates and their confidence intervals along preference gradients (Shaffer and Thompson 2007), as well as model parameter estimates and standard errors. The overall nest survival rate ($NSR = DSR_{egg}^{14.3} \times DSR_{nestling}^{9.8}$; $14.3 =$ mean number days for laying plus incubation, $9.8 =$ mean number of days from hatching to fledging). To allow comparison of preference parameter estimates, we standardized preference scores (standard preference score = discriminant score – mean discriminant score)/SD of discriminant scores, where mean and SD were calculated for natural nests) before fitting models. Given un-modeled heterogeneity in the data ($c > 1$), we multiplied standard errors by \sqrt{c} (Burnham and Anderson 2002).

Experimental nests and the underlying relationship between microhabitat and predation risk

Experimental nest monitoring

From 2006–2008, we placed and monitored experimental nests in the 20.3-ha Rush Creek sub-plot to provide supplemental nest predation data. Each experimental nest consisted of a yellow warbler nest (collected after use) containing one passerine egg (zebra finch; *Taeniopygia guttata*) and one clay egg, and was monitored for a maximum of 14 days (the average yellow warbler egg laying and incubation period) using the same protocol described for natural nests. We considered experimental nests depredated once finch eggs were either damaged or removed and/or when bite impressions were left in clay eggs. After monitoring, we identified the predators (avian or rodent) responsible for clay egg bite-marks (Latif 2009).

Determination of which microhabitat features affected predation risk

We used multi-model inference (Burnham and Anderson 2002) to identify which microhabitat features were most directly correlated with nest survival along Rush Creek. We fitted DSR models with all possible combinations of three microhabitat explanatory variables to data from both natural and experimental nests monitored along Rush Creek. These explanatory variables were scores along the two retained principal component axes describing major axes of habitat variation and nest substrate (the shrub species supporting the nest; hereafter Substrate). All DSR models contained applicable spatial and temporal covariates. In addition, since concealment was known from a separate analysis to influence yellow warbler nest predation (Latif 2009), we included important concealment effects as covariates in DSR models here, allowing examination of how other aspects of microhabitat structure influenced nest predation. To examine the magnitude of microhabitat effects, we referred to model-averaged parameter estimates and standard errors, and model-averaged NSR estimates calculated for differing microhabitat values (accounting for model-selection uncertainty; Burnham and Anderson 2002). As described for the preference–survival analysis, we corrected standard errors and indices of model-fit by the variance–inflation factor when $c > 1$ for the global model.

For this analysis, we used data from experimental nests monitored in 2006–2007. During this period, we selected sites for experimental nests stratified among nest site microhabitats to minimize correlations between microhabitat gradients (microhabitat patch structure, Substrate, and concealment). We placed nests in 140 sites stratified among substrate levels (rose vs willow nest shrubs), microhabitat patch types (willow-dominated vs rose-dominated patches), and concealment levels ($>80\%$, $30\text{--}80\%$, and $<30\%$). We monitored no more than 30 experimental nests at any one time (fewer than half the number of active yellow warbler territories on the study plot), and we spaced experimental nests simultaneously monitored ≥ 20 m apart.

Verification that microhabitat–predation relationships arose at within-territory scales

In 2008, we used experimental nests to verify the fine-scale nature of microhabitat–predation relationships, and thus the availability of low-predation alternatives to individual birds selecting nest sites from within their territories. We monitored 30 experimental nest pairs (60 nests total), each of which consisted of one nest in high-predation microhabitat (a willow-dominated patch) and another nest in low-predation microhabitat (a Woods’ rose- or non-riparian-dominated patch). We placed members of each pair 15 ± 8 (SD) meters apart, a distance smaller than the diameter of most yellow warbler territories (Q. Latif and PRBO unpubl.). We distributed nest pairs as evenly as possible throughout the study plot surveyed in 2008 (nearest neighbor distances between pair mid-points were 55 ± 21 m [min = 27 m]). We compared the survival of these nests on a pair-wise basis. We computed the number of days each nest survived (survival time, ST) assuming depredated nests failed half-way between the penultimate and ultimate nest checks (max ST = 14 days). To analyze variation in ST, we used a randomized-complete-

block ANCOVA including a factor identifying the nest pair (the block) and a factor identifying microhabitat type (high-predation vs low-predation habitat; the treatment), the latter of which accounted for pair-wise differences. We included concealment as a covariate as above.

Analysis of predator-specific contributions to microhabitat–predation relationships

We constructed logistic exposure models describing avian- and rodent-specific clay-egg bite rates as a function of experimental nest preference scores to examine microhabitat relationships with these predator types. For avian bite rate models, we deemed nests failed when we recorded avian bite impressions, and we considered nests rodent-depredated to have survived, but we truncated data from the latter at the time of rodent predation (midpoint of rodent-depredated observation interval). We did the opposite when modeling rodent bite rates. We excluded observation intervals during which nests were depredated without recording identifiable clay-egg bite impressions. We compiled the avian dataset strictly from 2006–2007 observations of experimental nests. However, to compensate for low sampling of rodent bites in 2006–2007, we included 2008 data in the rodent dataset (six additional rodent bites were recorded out of the 60 nests monitored in 2008). We calculated predator-specific bite rates (PSBR) along a preference gradient (PSBR = $1 - \text{DSR}^{14}$; DSR from predator-specific logistic exposure models), as well as their standard errors (Shaffer and Thompson 2007). Though common during our study, snake predation only occurred during the nestling stage (Latif 2009) and was thus not observable with our experimental nests.

Potential for fledge number to compensate for preference effects on nest survival

Fledgling number is a component of fecundity that is not accounted for by the nest survival metric, and therefore could compensate for preference effects on predation risk. We modeled fledgling number (FN) for successful nests on Rush Creek (2000–2008) as a linear function of preference scores and covariates using PROC GENMOD in SAS. We only used data from nests whose fledglings were counted within four days of the fledge date. For this analysis, we used data from Rush Creek plots since these plots yielded the most data and provided the strongest evidence for an ecological trap. Fledgling number models included covariates (spatial/temporal variables described previously) that improved model fit in preliminary analyses. We calculated evidence ratios for preference effects on FN, and we examined parameter estimates and standard errors for these effects to evaluate the potential for FN to compensate for predation costs in preferred microhabitats.

Results

Yellow warbler nest microhabitat preference

Microhabitat features at yellow warbler nest sites were significantly different from those at random points for all creeks during all time periods (Table 1). Yellow warbler preferences,

as indicated by patterns of discriminant function loadings on 2000–2005 gradients, were generally consistent across creeks and across time periods at Rush and Lee Vining creeks. Overhead cover was strongly and positively correlated with all preference gradients, in association either with increasing willow cover and/or number of willow stems (on Rush, Lee Vining and Wilson creeks), or with increasing cover and number of cottonwood stems (on Mill Creek). Nest sites were either negatively associated (on Rush and Mill creeks) or unassociated (weak loadings on Lee Vining and Wilson creeks) with the amount of non-riparian shrub cover. Rose-cover and rose-stem loadings on preference gradients were inconsistent among creeks. Despite differences in sampling protocol (Supplementary material Appendix 2), 2000–2005 nest sites along Rush Creek deviated from random sites in a similar direction as did 2006–2008 nest sites from random sites measured concurrently (Table 1).

Yellow warbler nest microhabitat preferences apparent along Rush Creek in 2006–2008 were attributable to within-territory nest site selection. Retained principal components described two fundamental microhabitat gradients characterizing the study plot. PC1 described 49.8% of variation in microhabitat among grid points (eigenvalue = 2.49) and was strongly and positively correlated with overhead cover (0.81) and willow variables (willow cover: 0.94, willow stems: 0.65), and negatively correlated with non-willow variables (rose cover: -0.62 , nonriparian cover: -0.39). Thus, PC1 described a non-willow- (negative) to willow-dominated (positive) gradient in microhabitat patch structure. PC2 described 24.8% of the variation among grid points (eigenvalue = 1.24), and was strongly and positively correlated with sagebrush cover (0.80), and negatively with rose cover (-0.66). Thus, PC2 described a gradient in non-willow shrubs from Woods' rose- (negative) to non-riparian-characterized patches (positive). Within-territory differences in nest-site mean PC scores versus random-site mean scores (nest site means – random site means) were positive for PC1 (0.36 ± 0.06 SE) and negative for PC2 (-0.29 ± 0.05 SE). Thus, yellow warbler favored willow over non-willow and Woods' rose over sagebrush. We found significant habitat variation among territories (PC1: $F_{168,169} = 3.4$; PC2: $F_{168,169} = 4.2$), but when controlling for this variation, nest and random sites still differed (PC1: $F_{1,169} = 35.4$; PC2: $F_{1,169} = 39.5$; all $p < 0.001$).

The relationship between preference and nest survival

Predation was the predominant cause of nest failure in the Mono Lake basin. From 2000–2008, we found and monitored 728 active yellow warbler nests along Rush Creek. Of these, 481 failed and 247 succeeded, and we attributed 374 (78%) failures to nest predation. In addition from 2000–2005, we found and monitored 339 active nests along Lee Vining Creek ($n = 247$), Mill Creek ($n = 52$), and Wilson Creek ($n = 40$), and of these 197 failed, of which we attributed 148 failures (75%) to predation.

Relationships between nest survival and microhabitat preference gradients were generally negative (Table 2). All parameter estimates describing preference relationships with natural nest survival were negative. Models

predicted decreases in nest survival rates of 26–60% for natural nests from less preferred to more preferred ends of preference gradients (Table 2, Fig. 1). Nest survival rates for experimental nests on Rush Creek were also negatively related with preference; experimental nest survival was 71% lower at the preferred end versus the less preferred end of the 2006–2008 Rush Creek preference gradient (Table 2, Fig. 1). Covariate effects accounted for substantial variation in nest survival rates (Supplementary material Appendix 3), but there remained unmodeled heterogeneity ($c \geq 1.7$ along three of four creeks; Supplementary material Appendix 4), necessitating some use of QAIC_c. Finally, we found no statistical support for preference gradient \times covariate interactive effects on nest survival (all interaction parameters increased AIC_c or QAIC_c, and ERs < 1).

Mechanisms underlying microhabitat–predation relationships

The microhabitat features that affected predation risk

The data most supported a negative relationship between nest survival and PC1, the dominance of willow at the microhabitat patch scale, along Rush Creek (Table 3). The model-averaged NSR estimate for natural nests at the willow end of this gradient (PC1 = 2; NSR = 0.15 \pm 0.06) was 47% lower than at the non-willow end (PC1 = -2;

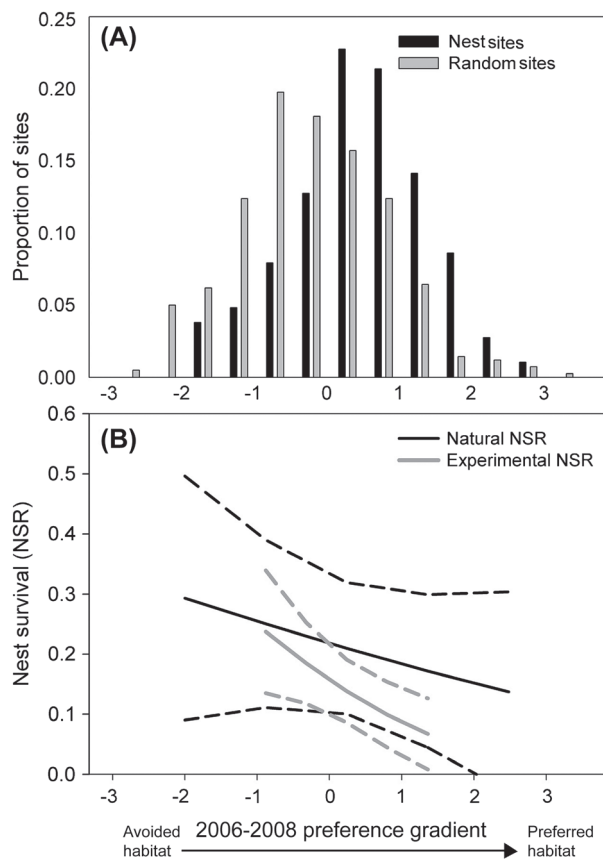


Figure 1. Frequency distributions of nest and random sites (A) and nest survival for all nests (2000–2008; B) along the 2006–2008 preference gradient. Dotted lines denote 95% confidence bands for NSR estimates.

NSR = 0.32 \pm 0.08). Experimental nest data also supported a PC1 effect on nest survival. The model-averaged NSR estimate for experimental nests in willow-dominated patches was 38% lower (PC1 = 1.5; NSR = 0.15 \pm 0.07) than in non-willow-dominated patches (PC1 = -1.5; NSR = 0.24 \pm 0.09). The relative support for the PC1 effect on nest survival for experimental nests was not as strong as the Substrate effect (Table 3). The direction of the Substrate effect, however, was opposite for experimental nests versus natural nests, indicating Substrate was a poor predictor of predation risk. Relatively low sample sizes and a correlation between Substrate and PC1 ($r = 0.57$, $n = 140$ experimental nests) limited our power to differentiate the relative strengths of Substrate versus PC1 effects with experimental nest data.

The spatial scale at which microhabitat influenced predation risk

For experimental nest pairs monitored in 2008, nests in willow were depredated substantially faster than their counterparts in either Woods' rose-dominated or non-riparian-dominated microhabitats ($ST_{\text{preferred}} - ST_{\text{non-preferred}} = -6.5$ days, SD = 5.8), and these differences contributed significantly to variation in survival time (ST) (Habitat parameter $F_{1,28} = 22.0$, $p < 0.001$). By contrast, ST did not vary significantly among nest pairs ($F_{29,28} = 3.5$, $p = 0.47$) or with concealment ($F_{1,28} = 1.6$, $p = 0.22$), so predation rates clearly varied at a within-territory scale. Furthermore, ST did not differ substantially between rose nests (9.6 \pm 4.8 SD; $n = 15$) and sagebrush nests (10.1 \pm 4.7 SD; $n = 15$; $p = 0.67$), so the presence of willow was the principal feature related to 2008 experimental nest survival. Differences in preference gradient scores (2006–2008 gradient) between willow nests minus non-willow nests were all positive (min difference = 0.02; max = 3.53; mean = 1.76), so willow nests were in relatively preferred microhabitat patches.

The contribution of avian and rodent predators to microhabitat effects

In 2006 and 2007, predators bit 77 clay eggs out of 140 experimental nests monitored. Of these bite marks, 50 were distinguishable as avian bites, 23 as rodent bites, and four were not identified. We found strong evidence for a relationship between the contemporaneous Rush Creek preference gradient and bite rates for both predator types (Supplementary material Appendix 6), and model parameters associated with these effects were both negative, reflecting substantially higher avian and rodent bite rates at the preferred end of that gradient (Fig. 2).

Microhabitat preference and fledgling number

The number of yellow warbler fledglings per successful nest was not related to nest microhabitat preference at Rush Creek. Evidence ratios for linear regression models relating fledgling number to the three Rush Creek preference gradients were all < 0.4 and parameter estimates for these relationships were small ($\beta_{\text{PC1}} \pm \text{SE}$: 0.001 \pm 0.061, -0.013 \pm 0.059 and 0.001 \pm 0.061 respectively).

Table 3. The relative importance of specific shrub features for explaining variation in yellow warbler nest survival. Variable weights and parameter estimates (β) were averaged across models (using weighted averaging; Burnham and Anderson 2002) that contained the explanatory variable of interest (Supplementary material Appendix 5). PC1 describes willow – non-willow gradient in microhabitat patch structure, PC2 describes a Woods’-rose – sagebrush microhabitat gradient, and Substrate describes the shrub species supporting the nest. All models contained concealment parameters as covariates (parameters were identified in a separate analysis; Latif 2009). Variable weights (w_v) for all models were based on $QAIC_c$. All standard errors were inflated by a factor of \sqrt{c} . $c = 1.3$ for natural nest models and 1.5 for experimental nest models ($c = \chi^2_{GOF}/DF$; χ^2_{GOF} = the Hosmer and Lemeshow goodness-of-fit statistic calculated for the maximally-parameterized model that best-fit the data).

Nest type	Variable ^E	w_v	Model-averaged $\beta \pm SE$
Natural	PC1 (non-willow → willow)	0.76	-0.17 ± 0.09
	PC2 (rose → sagebrush)	0.39	-0.09 ± 0.10
	Substrate*	0.41	Rose: -0.35 ± 0.23 Sagebrush: -0.01 ± 0.31
Experimental	PC1 (non-willow → willow)	0.50	-0.35 ± 0.24
	Substrate ^F	0.66	Rose: 0.44 ± 0.36

* $\beta_{Substrate}$ for Willow was set to zero.

^FPC2 was not included in experimental nest models since experimental nests (2006–2007) were not monitored in sagebrush.

Discussion

Evidence for an ecological trap

Yellow warblers that breed along the lower reaches of Mono Lake’s tributary streams apparently exhibit maladaptive nest microhabitat preferences, consistent with the classic definition of an ecological trap (Misenhelter and Rotenberry 2000). Yellow warblers preferred to nest in microhabitats dominated by the tallest woody riparian shrubs and saplings (willow and/or cottonwood) and these microhabitats tended to be associated with lower nest survival than available alternatives. Apparent microhabitat preferences were consistent across time periods and so appeared relatively stable for this population. On Rush Creek in particular, preferred nest microhabitat patches were dominated by willow shrubs and were associated with substantially higher predation rates and consequently lower nest survival than less preferred Woods’ rose- and non-riparian-dominated patches. We found the least evidence for maladaptive preferences along Wilson Creek. The relative homogeneity of the riparian shrub layer along Wilson Creek (virtually all willow and no Woods’ rose) probably limited our ability to detect those microhabitat–predation patterns central to the maladaptive preferences apparent on other creeks.

Although our natural nest data did not provide unanimous statistical support for preference–survival relationships, the data did support negative preference effects on natural nest survival along two of four creeks (Rush Creek and Mill Creek). Furthermore, Rush Creek experimental nest data corroborated this relationship and provided stronger statistical support. In addition, all preference–survival parameter

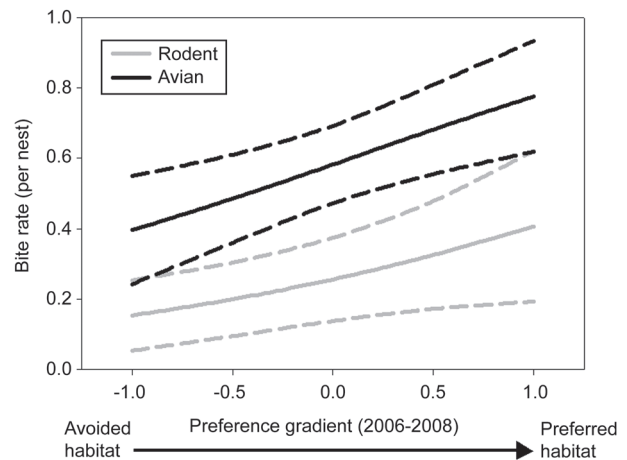


Figure 2. Avian and rodent bite rates (an index of predation rates on experimental nests) and their 95% confidence bands along the 2006–2008 preference gradient. Statistical evidence ratios (calculated from Akaike model weights) and parameter estimates for these relationships are provided in Supplementary material Appendix 2.

estimates were negative, so this relationship does not appear to be a stream-specific aberration. We found no evidence for heterogeneity in apparent preference–survival relationships (i.e. no evidence for preference \times covariate interactions), so these relationships apparently persisted throughout the time-frame of this study. Given some unmodeled heterogeneity in nest survival rates, we are uncertain of how much predation yellow warblers would avoid if they favored non-willow microhabitats. Nevertheless, our data indicate that nests in microhabitats that are less preferred by our study population are on-average more likely to succeed.

Why are yellow warblers attracted to high-predation nest microhabitats?

Yellow warblers could be induced to select high-nest-predation habitats if such habitats benefit fitness components other than nest survival and if those benefits outweigh nest-predation-related costs. Adult survivorship, brood size, and juvenile survival are fitness components that could potentially tradeoff with nest survival if any of these were sufficiently elevated for birds nesting in preferred habitats. Food availability could limit any of these fitness components (Martin 1987), and adults and juveniles can also be vulnerable to predation (Schmidt et al. 2008, Morosinotto et al. 2010). However, food availability is thought mainly to influence habitat selection at territory-or-larger spatial scales since adults forage in multiple locations distributed across their territories (Shochat et al. 2005, Chalfoun and Martin 2007). Similarly, since adults and juveniles (once they leave the nest) use multiple locations throughout their territories for various activities, they can be vulnerable to predators anywhere in their territories. Thus, coarse-scale habitat features and territory selection probably have a greater bearing on fitness components other than nest survival (Morosinotto et al. 2010). Most reported cases of maladaptive breeding habitat preferences exhibited by songbirds are apparent at territory-or-larger scales (Misenhelter and Rotenberry 2000, Shochat et al. 2005, Chalfoun and Martin 2007). Thus, traps apparent elsewhere

may potentially reflect tradeoffs between nest predation risk and either food availability or adult/juvenile predation risk. Alternatively, even if benefits to other fitness components do not outweigh nest predation costs, attraction to food resources and/or territories lacking adult/juvenile predators could explain why birds favor high-nest-predation territories. By contrast, yellow warblers in this study clearly favored high-predation nest microhabitats selected from within their territories and microhabitat–predation relationships arose at within-territory scales, so food and adult/juvenile predation are unlikely to shape this trap. Consistent with the notion that food availability should be more important at territory-or-larger-scales, we found no relationship between microhabitat preference and brood size, although we have no data on juvenile or adult survival.

Brood parasitism by brown-headed cowbirds could induce yellow warblers to favor high-predation, willow microhabitats if fitness costs due to parasitism were reduced enough in willow to offset high predation risk. Since brood parasitism reduces clutch and brood sizes in yellow warbler nests (Sealy 1992; Q. Latif and PRBO unpubl.), a tradeoff between parasitism and predation could result in a tradeoff between nest survival and brood size. However, we found no correlations between brood size and preference scores. In addition to brood size, parasitism can influence nest predation risk, in particular if cowbirds themselves depredate non-parasitized nests as part of their breeding strategy (Arcese et al. 1996). Indeed, we did measure lower predation rates on parasitized nests along Rush Creek (Latif 2009), which is consistent with a cowbird predation hypothesis. A tradeoff between cowbird predation and predation by conventional predators would tend to negate overall microhabitat–predation relationships, as well as induce interactions between microhabitat effects and parasitism effects on predation risk. Our data are not consistent with such patterns.

Microclimate may attract yellow warblers to nest in willow patches. Microclimate may be improved by the shelter from solar radiation provided by higher levels of overhead cover in preferred sites, and cooler microclimates may be especially desirable in high elevation desert environments like the Mono Lake basin. Hatchling number is the primary product of incubation efficiency, which could be affected by microclimate (Deeming 2002). In our study, we found no correlation between hatch number and preference scores (2006–2008 preference gradient) for nests that survived incubation ($r = -0.04$, $n = 303$). Energetic costs associated with microclimate could also influence other fitness components (e.g. nestling growth; Dawson et al. 2005), for which we have no data.

Finally, interspecific competition could limit avian nest site selection, particularly when nest site availability is limited (e.g. for cavity-nesting species; Stanback et al. 2009). Yellow warbler territories, however, each contained numerous suitable sites for open-cup shrub nests (we found plenty of sites for experimental nests). Members of open-cup nesting songbird communities may segregate along microhabitat gradients to minimize density-dependent predation pressures, which can arise from search-imaging by nest predators (Martin and Martin 2001). Other species with similar nest site placement, however, breed at relatively low densities (compare 85–100 yellow warbler territories to <10

willow flycatcher *Empidonax traillii* territories per year on Rush Creek study plots; McCreedy and Heath 2004, PRBO unpubl.), so interspecific competition for predator-free space is unlikely to shape yellow warbler nest microhabitat selection.

Where should yellow warblers nest? Are there better choices for avoiding predation risk?

An important consideration for understanding any ecological trap is whether the population of study could escape the trap if its members made different choices. Since yellow warblers select nest sites from within their territories, alternative low-predation nest sites would only exist if predation risk varies at a within-territory scale. Results from our 2008 experimental nest study indicate that such choices exist for individual yellow warblers. Furthermore, preference scores for 2006–2007 experimental nests were not spatially autocorrelated (Moran's $I = 0.02$; $n = 140$), so habitat–predation relationships for experimental nests generally reflect fine-scale patterns.

At a fine spatial scale, predator-specific hunting strategies likely give rise to microhabitat–predation relationships and thus determine whether yellow warblers would benefit by selecting different nest sites. Our data indicate that both avian and rodent predators are responsible for higher egg predation rates in willow, and these two predator types likely have very different hunting strategies. Cowbirds were probably the main avian predator represented by clay egg bites, and additional data indicate cowbirds often depredate eggs from natural nests in the Mono Lake basin in conjunction with their brood parasitic activities (Latif 2009). When hunting for nests, cowbirds and other avian predators may search specifically in microhabitats where nests are most frequently encountered (Salathe 1987, Robinson and Robinson 2001), potentially making avian predators difficult for yellow warblers to avoid via microhabitat selection. However, even if predators employ such a strategy, dispersion of nests among microhabitats is probably a better nest site selection strategy than the one that yellow warblers currently employ because microhabitat diversity limits search image formation by nest predators (Martin and Martin 2001).

In contrast to birds, rodents are thought to depredate nests when encountering them incidentally while foraging for more favored prey (Schmidt et al. 2001). Overall nest predation rates were most closely and consistently related to a willow – non-willow gradient in microhabitat patch structure. Willow foliage is less dense than both rose and sagebrush and therefore provides less concealment (PC1 correlation with concealment: $r = -0.33$, $n = 665$), which also influences predation risk (Martin 1993, Latif 2009). Our models, however, controlled for the potentially confounding effects of concealment on predation risk, and concealment was not as consistently related with natural predation rates on yellow warbler nests across years as was willow in this study (Latif 2009). Thorns associated with Woods' rose could impede rodent mobility. However, the willow – non-willow gradient (PC1) was more closely associated with predation risk for natural nests than the rose – sagebrush gradient (PC2), and experimental nests survived just as well in sagebrush as they did in rose (see Results for 2008 experiment). More

likely, willow may improve patch quality for rodents either by enhancing foraging opportunities or by providing more overhead cover and therefore refuge from their own predators. Our data did not account for differences among rodent species in microhabitat responses (documented by Schmidt and Ostfeld 2003), so data regarding microhabitat relationships with specific rodent predator species could provide further insight into the processes underlying this trap.

Origins of this trap, its maintenance and its population consequences

Regardless of whether higher nest predation rates in preferred willow microhabitats arise from incidental predation or from active nest-searching by predators, the current nest site selection strategy employed by yellow warblers is clearly not optimal for avoiding nest predation. Recent studies demonstrate that birds are capable of quickly adjusting nest site microhabitat selectivity in response to direct experiences with predators (Peluc et al. 2008). Nevertheless, despite substantial evidence for plasticity in avian nest site selection in response to predation pressure, our results suggest that this plasticity may be limited in our system.

Fundamentally, ecological traps are thought to arise when the usual relationship between habitat cues and fitness are disrupted (Kristan 2003, Battin 2004). The disruption underlying this trap could occur at a landscape scale. Gene flow and/or an influx of individuals from populations that experience different predation regimes may prevent the Mono Lake basin population from adapting to local predation pressures. Relatively high nest predation rates by rodents in mesic microhabitats characterized by riparian vegetation may arise because these microhabitats are more productive and therefore provide more foraging opportunities than relatively xeric microhabitats characterized by upland vegetation. By contrast, strong xeric–mesic gradients may be less characteristic of riparian systems in other parts of the yellow warbler's range, making the riparian-to-upland differential in foraging opportunities for incidental predators, such as rodents, less pronounced in those regions. Indeed, contrary to patterns found in the Mono Lake basin, studies in two other locations in California found higher yellow warbler nest survival rates in mesic habitats. Higher nest survival was correlated with white alder *Alnus rhombifolia* habitats in Shasta County (reviewed by Heath 2008), and nest survival in 'core riparian habitats' in montane wet meadows in the northern Sierra Nevada of California was higher than in other microhabitats used by yellow warblers at those sites (Cain et al. 2003). The latter study found that predators invade riparian habitats from surrounding conifer forests, so nests in the riparian core are less accessible to these predators. Furthermore, not all mesic microhabitats may be associated with high predation rates even in xeric landscapes. Within sagebrush-dominated landscapes similar to ours, Heltzel and Earnst (2006) did find higher predation rates in willow habitats, but they also found relatively low predation rates and high nest survival in aspen *Populus tremuloides*, which may result from the unique physical features of aspen that reduce nest accessibility to certain predators (Richardson and Vander Wall 2007). The xeric–mesic gradient is probably less relevant to cowbird predation and cowbirds occur throughout much of the

yellow warbler range (Lowther 1993). If cowbirds are driving this trap, however, the disruption of the typical habitat–cue–fitness relationship causing this trap may have occurred over a temporal rather than a spatial scale. Since cowbirds are motivated to depredate nests for very different reasons than the typical nest predator (Arcese et al. 1996), their proliferation in this system since the 1930s (Rothstein et al. 1980) may have disrupted the typical relationship between yellow warblers and their nest predators. Finally, recent human-caused habitat changes may contribute to this trap. Anthropogenic disturbance (e.g. water diversions and livestock grazing) has resulted in substantial destruction of riparian vegetation along Mono Lake tributaries (Stine et al. 1984). Although recent restoration efforts (mainly a return of minimum and peak water flows and removal of livestock grazing) have partially reversed this destruction, vegetation changes that persisted during this study (McBain and Trush 2003) may affect predator behavior or change predator communities in ways that disrupt the historic relationship between microhabitat cues and predation risk.

A full understanding of the processes maintaining this ecological trap will require an exploration of its potential demographic consequences. Given severe enough impacts on population growth, ecological traps can cause extirpation of local populations or induce sink dynamics, necessitating immigration to sustain a population (Kristan 2003). Based on nine years of observation (PRBO unpubl.), we found no evidence that yellow warbler densities are declining along Rush Creek; about 85–100 breeding territories consistently occupied both study plots through 2005 and about 60–70 territories consistently occupied the single plot through 2008. Either the population is being sustained by immigration, or productivity remains high enough to keep the population afloat despite maladaptive nest microhabitat preferences. At least two factors may modulate the impacts of maladaptive microhabitat preferences on overall fitness and population growth. Numerous non-microhabitat factors influence nest survival (i.e. both DSR-model covariates and un-modeled sources of variation), resulting in some uncertainty in nest survival probabilities (i.e. wide confidence intervals). Thus, a substantial number of individuals may successfully fledge young from willow nests even though willow nests are on average more likely to fail. In addition, the ability of birds to re-nest following failure modulates the relationship between nest survival and seasonal fecundity (Powell and Knutson 2006). Yellow warblers re-nest frequently following failure (as many as six attempts in a season; PRBO unpubl.), perhaps dampening the power of nest predation to shape nest site selection. To fully understand the demographic significance of this ecological trap, future investigations will need to employ population models that incorporate locally derived estimates of nest survival, adult survival, density, and other components of fecundity (Clark and Martin 2007).

This study provides evidence for an ecological trap for avian nest microhabitat selection at a within-territory scale. To our knowledge, this is the first study to document such a pattern despite numerous studies investigating microhabitat–preference relationships with nest predation rates (reviewed by Lima 2009). Thus, maladaptive nest microhabitat preferences appear rare, although reliance on natural-nest data may limit researchers' ability to fully explore the adaptive

significance of nest site selection (Schmidt and Whelan 1999, Latif 2009). Theoretical models of ecological traps mainly consider habitat selection at a single, territory-or-larger spatial scale (Donovan and Thompson 2001, Kristan 2003). Models that explicitly describe the effects of multi-scale habitat selection on avian population dynamics may help elucidate when maladaptive nest microhabitat selection is likely to arise. Populations that exhibit maladaptive preferences during both territory and nest-site selection would probably suffer much greater fitness losses, perhaps preventing their long-term persistence.

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Supplementary material (available online as Appendix O18835 at <www.oikosoffice.lu.se/appendix>). Appendix 1–6.