

How avian nest site selection responds to predation risk: testing an ‘adaptive peak hypothesis’

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Summary

1. Nest predation limits avian fitness, so birds should favour nest sites that minimize predation risk. Nevertheless, preferred nest microhabitat features are often uncorrelated with apparent variation in predation rates.
2. This lack of congruence between theory-based expectation and empirical data may arise when birds already occupy ‘adaptive peaks’. If birds nest exclusively in low-predation microhabitats, microhabitat and nest predation may no longer be correlated even though predation ultimately shaped microhabitat selection.
3. This ‘adaptive peak hypothesis’ was tested for a population of Yellow Warblers (*Dendroica petechia*) focusing on two nest microhabitat features: concealment and height. Experimental nests measured relative predation risk both within and outside the microhabitat range typically occupied by natural nests to examine whether nest site choices made by birds restricted our ability to detect microhabitat effects on predation.
4. Within the natural range (30–80% concealment, > 75 cm height), microhabitat–predation relationships were weak and inconsistent, and similar for experimental and natural nests. Over an extended range, however, experimental predation rates were elevated in exposed sites (< 30% concealed), indicating a concealment-related ‘adaptive plateau’.
5. Clay egg bite data revealed a concealment effect on avian predators, and the abundance of one avian predator group correlated with nest concealment among years, suggesting these predators may cue birds to modulate nest concealment choices.
6. This study demonstrates how avian responses to predation pressure can obscure the adaptive significance of nest site selection, so predation influences may be more important than apparent from published data.

Key-words: adaptive landscape, *Dendroica petechia*, habitat selection, Mono Lake, nest predation, nest site preference, riparian, Yellow Warblers

Introduction

Among the most important decisions a bird makes is where to build its nest. For open-cup nesting terrestrial species, nest survival is an important component of fitness and predation the predominant cause of failure (Martin 1993). To the extent that careful attention to the details of a nest site’s microhabitat characteristics reduces the likelihood of predation, we expect to find strong selection gradients (*sensu* Lande & Arnold 1983) resulting in a positive association between preferred microhabitat features and reproductive success. Thus, researchers expect preferred microhabitat features to posi-

tively correlate with nest survival and negatively with predation risk. Although some studies do find such relationships (Bekoff, Scott & Conner 1989; Martin 1998), many others do not, leading to some doubt of the adaptive significance of nest site selection for minimizing predation risk (Wilson & Cooper 1998; Rangel-Salazar *et al.* 2008).

Field studies often fail to detect statistically significant relationships between phenotype and fitness (Kingsolver *et al.* 2001), in part because of the evolutionary response of wild populations to natural selection. Given a strong adaptive response, all phenotypes expressed in a population may occur close to an adaptive peak (Fisher 1930), such that the fitness variation necessary to measure natural selection would not exist in nature. Therefore, by only measuring

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natural variation in predation rates, many studies may limit their power to detect important selection gradients if birds completely avoid high-predation microhabitats (Schmidt & Whelan 1999). Therefore, to comprehensively investigate the adaptive significance of nest site selection, researchers should measure predation risk outside the normal microhabitat range occupied by nesting birds.

In this study, phenotypic engineering, i.e. experimental expansions of natural phenotypic distributions (Sinervo & Basolo 1996), was employed to examine the adaptive significance of nest microhabitat selection for a population of Yellow Warblers (*Dendroica petechia*) focusing on nest concealment and height. Despite their potential influence (Martin 1993), studies commonly fail to detect concealment–predation and height–predation relationships (Filliater, Breitwisch & Nealen 1994; Chase 2002). To begin, concealment and height preferences were examined, and microhabitat range limits for natural nests were identified. Next, nest survival rates were correlated with concealment and height (a selection gradient analysis) within this ‘natural microhabitat range’. Having documented microhabitat preferences but no microhabitat–predation relationships within the natural range, experimental nests measured relative predation risk across an extended microhabitat range. We expected to record higher predation rates outside this range. Finally, bite impressions in clay eggs measured predator-specific microhabitat relationships, suggesting potential mechanisms underlying the observed adaptive landscape.

Materials and methods

STUDY SYSTEM

Yellow Warblers are shrub- and tree-nesting, neo-tropical migrant songbirds that breed in riparian habitat across North and Central America (Lowther *et al.* 1999). From 2000 to 2008, Yellow Warblers were studied at Rush Creek, a tributary of Mono Lake, California, USA (1995 m elevation, 37°56′20″N, 119°03′50″W). From 2000 to 2005, data were collected from two Rush Creek study plots totalling 39 ha and 2 stream-kilometre (Heath, McCreedy & Latif 2006) as part of a multispecies demographic monitoring programme. From 2006 to 2008, Yellow Warbler studies continued at the upper plot (20 ha, 1 stream-kilometre), during which time the hypothesis-driven components of this study were conducted. Three willow species (*Salix exigua*, *Salix lucida* and *Salix lutea*) were the principal woody plants within the study area, but substantial stands of Woods’ rose (*Rosa woodsii*) and big sagebrush (*Artemisia tridentata*) were also present.

Nest predators within our study area are identified in detail elsewhere (Latif 2009). In brief, Brown-headed Cowbird (*Molothrus ater*; hereafter cowbird), wrens (Troglodytidae), Bullock’s Oriole (*Icterus bullockii*), least chipmunk (*Tamias minimus*) and Corvidae [Black-billed Magpie (*Pica hudsonia*) and/or Western Scrub-Jay (*Aphelocoma californica*)] were the egg predators identified at Rush Creek. Avian predators probably posed the greatest threat to songbird eggs, although which species were most important remains uncertain. Garter snakes (*Thamnophis* spp.) were most frequently observed depredating nestlings along Rush Creek and other Mono

Lake basin tributaries. Steller’s Jay, gopher snake (*Pituophis catenifer*), mouse (Muridae/Cricetidae), raccoon (*Procyon lotor*) and weasel (*Mustela* spp.) were also confirmed predators of nestlings, and Western Scrub-Jay and cowbird were likely nestling predators. Cowbirds depredate nests in conjunction with brood parasitism (49% of Yellow Warbler nests were parasitized in our study area (Heath 2008); Sealy 1992, describes additional cowbird predation of Yellow Warbler nests; Ortega 1998, reviews cowbird nest predation).

IDENTIFICATION OF NEST SITE PREFERENCES AND THE NATURAL MICROHABITAT RANGE

Nest-searching and microhabitat measurements

Yellow Warbler nests were searched for during the Yellow Warbler breeding season (May 15–July 31, 2000–2008). Additionally, season-long observations of Yellow Warbler territorial behaviours (e.g. singing, counter-singing, simultaneous nesting) were mapped to identify distinct breeding territories for unmarked Yellow Warblers (Robbins 1970). As many nests for as many territories as possible were located (Martin & Geupel 1993). Nests were found for 70–94% of territories in any given year, so we are confident that the nests found adequately sampled the range of nest microhabitats occupied by the study population.

Microhabitat structure at each nest site was measured from 1 July to 31 August following completion of the nesting cycle. The per cent of the nest concealed was visually estimated when standing 1 m from the nest in each of six directions: above the nest, below the nest and from each cardinal direction (N, S, E and W). Extremely high nests were accessed either by climbing adjacent branches or with a ladder. A mirror was held above nests too high to stand over, or as a last resort (<20% of occasions), above-nest vegetation density was scrutinized from below to estimate above-nest concealment. The mean of the six concealment estimates served as an overall index of concealment for each nest. Nest height was measured from the ground to the base of the nest-cup. The structure and composition of the shrub layer was measured for microhabitat patches (i.e. 5-m radius circles) surrounding each nest, and the species and height of the individual shrub supporting each nest (hereafter referred to as ‘substrate’ and ‘shrub height’, respectively; Martin *et al.* 1997) was recorded. To minimize interobserver variation, field crews taking these measurements participated in numerous calibration sessions throughout each season. For ocular percentage estimates (i.e. shrub coverage and raw concealment measurements), a maximum of 20% interobserver error was considered acceptable following calibration. Concealment was not strongly correlated with measurement date ($r = 0.04$, $n = 209$ natural- and experimental-nest site measurements collected 3 July–31 August, 2006–2007), so our measurements strictly captured spatial variation in nest concealment independent of shrub phenology. Given significant effects of phenology, concealment measurements may not represent sites as they were when selected by nesting birds or when depredated (Vega Rivera *et al.* 2009). Nevertheless, our measurements should index relative concealment of sites selected by birds (nest sites) or available to them (random sites), assuming that phenology does not cause rank reversals (i.e. sites most concealed at the beginning of the season becoming least concealed at the end). As individual birds ultimately select sites from a set of spatially distributed choices (i.e. they do not wait for concealment to improve before initiating nests), our measurements were appropriate for this study.

Preference analysis and identification of the natural microhabitat range

In 2006–2008, concealment and height at random sites were measured to assess microhabitat availability for preference analyses (Jones 2001). Twenty-nine points were selected from a grid of points spaced 20 m apart generated within the study plot. Most of the 29 points fell within the boundaries of an active territory from each year (two points fell only within 2006 and 2008 territories). The potential nest shrub nearest to each selected point deemed structurally capable of supporting a Yellow Warbler nest was identified and its height measured. Each potential nest shrub was visually scanned for the most concealed site. A previously used Yellow Warbler nest was placed in each of these sites, verifying the shrub's structural integrity and allowing nest concealment and nest height to be measured. Although not a completely random process (i.e. concealment was maximized within the selected shrub), random selection of shrubs meant these sites were selected less purposefully than a bird attempting to maximize concealment and/or height from the range of options available within its territory. Therefore, random-site measurements provided a useful point of reference for assessing Yellow Warbler preferences for concealment and height. All random sites were measured from 15 August to 31 August well before the onset of autumnal defoliation.

Yellow Warbler nest microhabitat preferences were examined by comparing nest microhabitat scores (i.e. microhabitat use) to random site scores (i.e. availability). To prevent biased sampling of low-predation microhabitats, only nests found during the building phase were analysed to characterize microhabitat use. As the random-site selection process upwardly biased concealment availability measurements, higher-than-random nest concealment scores indicated a positive concealment preference, whereas lower-than-random nest scores were ambiguous. Height availability measurements were not inherently biased, so as long as height did not correlate with concealment, nest-versus-random-site height differences were interpreted as a preference. Two-factor ANCOVAs (analyses of covariance) were used to test nest-versus-random-site differences in concealment and height. Shrub-related nest site preferences are documented (i.e. for willow; Latif, Heath & Rotenberry in press) and shrub species differ in physical structure (willow are taller with sparser foliage than Woods' rose and sagebrush). ANCOVAs therefore included metrics of shrub structure as covariates: (i) scores along a principle component axis (PC1) describing microhabitat patch structure and (ii) substrate (three classes: willow, rose and sagebrush). PC1 was generated from a principal components analysis applied to measurements of 5-m radii patches centred on random sites describing overhead cover (based on densiometer measurements), percent coverages of three shrub types [willow (*Salix sp.*), rose (*R. woodsii*) and nonriparian shrubs (mainly *A. tridentata*)] and the number of willow stems. PC1 was strongly positively correlated with willow variables and thus described a willow–nonwillow gradient in microhabitat patch structure (Latif, Heath & Rotenberry in press). Preferences for shrub height and relative nest height (nest height/shrub height) were also considered as possible cues for height selection.

The 'natural microhabitat range' was identified by examining Yellow Warbler nest microhabitat distributions. Natural range boundaries were identified at steep distributional drop-offs (identified from visual inspection of histograms) or, if such drop-offs were not apparent, at positions such that $\leq 10\%$ of nests occurred outside the identified range at either end. Although somewhat arbitrary, these criteria allowed identification of the tails of nest microhabitat distributions, which experimental nests sampled more intensely.

NATURAL NEST MONITORING AND SELECTION GRADIENT ANALYSIS WITHIN THE NATURAL MICROHABITAT RANGE

Natural nest monitoring

Once Yellow Warbler nests were located, their contents were recorded at least once every four days [mean check interval = 3.1 ± 1.1 (SD) days] until they failed or fledged young. Nests were considered failed (i) when no Yellow Warbler eggs or nestlings remained in the nest prior to the earliest potential fledge date, (ii) when the nest was abandoned by the parents or (iii) on the expected hatch day if eggs remained un-hatched more than 8 days past the normative incubation period [10.4 ± 1.2 (SD) days after clutch completion; $n = 45$ nests whose clutch completion and hatch dates were known to the day]. Nest predation was considered the cause of failure given scenario 1 or when directly observed. Nests were also considered failed if and when they contained only cowbird eggs or nestlings. Nests were considered failed on hatch day if they initially contained both host and cowbird eggs but only hatched the latter. Nests that survived to potential fledging age (9.8 ± 0.9 days from hatching; $n = 29$ nests whose hatch and fledge dates were known to the day; Q. Latif and PRBO Conservation Science unpublished data derived from Mono Lake birds) were considered successful or failed based on additional field observations. For example, direct observation of fledglings or parents carrying food shortly after nest termination indicated success, whereas initiation of new attempts coupled with no apparent parental food carries indicated failure (Weidinger 2007). Fates of a minority of nests (2%) lacked evidence of success or failure and so were considered unknown. Standard precautions were used to avoid attracting predators to active nests (Martin & Geupel 1993).

Analysis of natural nest survival relationships with microhabitat

We analysed nest survival rates using logistic exposure, a discrete survival analysis that employs a modified logit link function with a binomial distribution to model daily nest survival rate (DSR) as a function of explanatory variables (Shaffer 2004). Logistic exposure treats the *observation interval* (the period between nest checks) as the sampling unit, accounts for nests being observed for different lengths of time and considers nest outcomes (success vs. failure) during each interval as independent events. Logistic exposure models (hereafter DSR models) were fitted using PROC GENMOD (SAS 9.1, SAS Institute, Cary, North Carolina, USA) to data from known-fate nests observed active with at least one Yellow Warbler egg or live nestling. DSR models included either linear (β_1x) or quadratic ($\beta_1x + \beta_2x^2$) microhabitat effects representing different forms of selection (i.e. directional, stabilizing, or disruptive; Lande & Arnold 1983).

An information theoretic framework (Burnham & Anderson 2002) was used to examine the relative evidence for particular models. Upon fitting DSR models to the data, model weights (w_i) were calculated from AIC_c (Akaike Information Criterion corrected for sample size) differences between focal models and the best-fit model (lowest AIC_c). Evidence ratios ($ER = \Sigma w_{\text{models-with-effect}} / \Sigma w_{\text{models-without-effect}}$; Burnham & Anderson 2002) and likelihood ratio tests quantified the statistical support for microhabitat effects. Covariate effects (effects not of direct interest) in DSR models were year, date (day-of-year), stage (egg vs. nestling), plot ($n = 2$), parasitism (brood parasitism status) and microhabitat patch composition (PC1 effect identified by Latif 2009). Concealment-or-height $\times$ covariate interactions ($ER = w_{\text{interaction-model}} / w_{\text{additive-model}}$) were tested to look for hetero-

geneity in the strength and direction of selection gradients. Only interactions and covariates that reduced AIC_c in preliminary tests were included in final model comparisons. Goodness-of-fit tests were performed for the global model in each model set ($\hat{c} = \chi^2_{\text{goodness-of-fit}}/\text{d.f.}$; $\hat{c} > 4$ indicates poor model structure; Burnham & Anderson 2002). Comparison of model-based nest survival estimates to class-based estimates for microhabitat gradient partitions also allowed a qualitative assessment of goodness-of-fit (Shaffer & Thompson 2007). Model-predicted nest survival estimates ($NSR = DSR_{\text{egg}}^{13.2} \times DSR_{\text{nestling}}^{9.8}$ [natural nests] or DSR^{13} [experimental nests]; exponents = the length of egg and nestling periods) and their 95% confidence bands were calculated following established procedures (Powell 2007; Shaffer & Thompson 2007).

EXPERIMENTAL NESTS AND TESTS FOR 'ADAPTIVE PEAKS'

Experimental nest placement and monitoring

Experimental nests were previously used Yellow Warbler nests each containing a real passerine egg [obtained from captive Zebra Finches (*Taeniopygia guttata*) and stored following established protocol until deployed in the field; DeGraaf & Maier 2001] and a clay egg. Clay eggs were shaped from modelling clay to resemble the size and shape of real eggs (Fig. 1). Avian- and rodent-predator bite impressions left in clay eggs were distinguishable from each other. To facilitate their recovery, clay eggs were formed around fishing weights anchored with fishing line to woody stems at the nest site. Unlike Yellow Warbler eggs, finch eggs and clay eggs were not speckled, although previous study did not find evidence for egg-coloration effects on predation (reviewed by Major, Gowing & Kendal 1996). The same protocol employed for natural nests was used to monitor experimental nests for 13 days (i.e. the combined laying and incubation period for Yellow Warblers in the Mono Lake basin; PRBO Conservation Science unpublished data) [mean check interval = 3.5 ± 0.9 (SD) days]. Experimental nests were considered depredated when finch eggs disappeared or were damaged, or when predators bit clay eggs.

Concurrent with natural-nest monitoring in 2006–2007, 140 experimental nests were monitored after being distributed among sites within and outside natural microhabitat range limits and in the two substrates typically occupied by natural nests (rose and willow). When placing experimental nests, sites typical and atypical for Yellow Warblers were identified based on previous experience,

although during data analysis, nest sites were classified based on microhabitat scores derived from field measurements. Experimental nests were also distributed between willow- and rose-dominated microhabitat patches, which are known from separate analyses to differ in predation risk (Latif, Heath & Rotenberry 2011). No more than 30 experimental nests were monitored at a time (fewer than half the number of active Yellow Warbler territories and thus active nests on the study plot), and experimental nests monitored simultaneously were spaced ≥ 20 m apart.

Calibration of experimental predation patterns with natural patterns

To validate experimental-nest data for analysing relative predation risk over an extended microhabitat range, natural and experimental predation patterns were first compared within the natural microhabitat range. DSR models were fitted to two data sets that included 2006–2007 data from both natural and experimental nests: one excluded data from outside the natural concealment range ($> 80\%$ and $< 30\%$) and the other excluded data from outside the natural height range (< 75 cm; see Results of natural-microhabitat-range analyses). To ensure comparability of predation patterns, natural nest data from the nestling stage and from nests that experienced fates not observable at experimental nests (e.g. abandonment) were excluded from these data sets. DSR models included year, date, and nest type (natural vs. experimental) as covariates. Model fit was compared for models with and without linear or quadratic microhabitat effects and their interactions with nest type. Evidence ratios for interactions ($ER = w_{\text{interaction-model}}/w_{\text{additive-model}}$) tested for differences in natural vs. experimental patterns. Experimental data were considered appropriate for investigating adaptive peaks when neither additive nor interactive microhabitat effects were supported ($ERs < 1$). Height and concealment values were not strongly correlated (natural nests: $r = -0.09$, $n = 141$; experimental nests: $r = -0.07$, $n = 140$) and follow-up analyses showed no support for height $\times$ concealment interactions ($ER < 1$), so only independent analyses of microhabitat effects were reported.

Predation patterns over an extended microhabitat range

Having verified their validity, experimental data were used to investigate adaptive peaks and identify predators contributing to the adaptive landscape. DSR models with all possible combinations of linear and quadratic, height and concealment effects, as well as year, date and PC1 covariates were fitted to all available data from experimental nests. Clay-egg-bite rates were analysed to determine how avian and rodent predators contributed to predation patterns. Two data sets were compiled, one corresponding to avian and the other to rodent predators, and for which nests were considered failed if and when clay eggs were bitten by the predator type of interest. Observation intervals were truncated half-way between the ultimate and penultimate nest checks when depredated by the predator type not of interest, and observation intervals were excluded when nests were depredated by unidentified predators (37% of cases). DSR models that best fit these data (based on AIC_c) were used to calculate predator-specific bite rates ($PBR = 1 - DSR^{13}$) along concealment and height gradients. To compensate for relatively low sample sizes, the rodent data set was supplemented with data from nests monitored for a separate experiment conducted in 2008, in which the members of 30 pairs of nests (60 nests total) were monitored in alternate shrub types (willow vs. rose; Latif *et al.* 2011). We recorded six additional rodent bites at these nests.

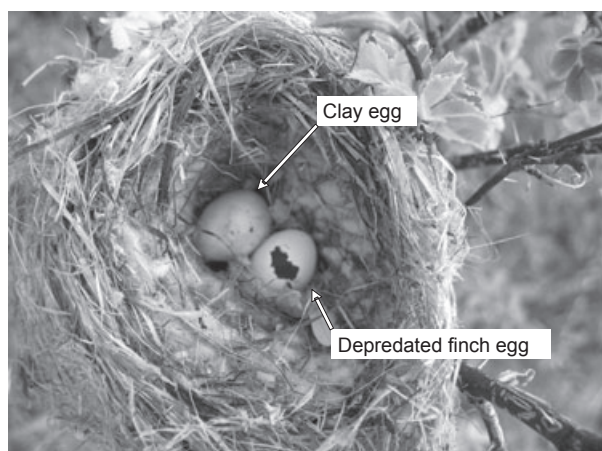


Fig. 1. A depredated experimental nest.

YELLOW WARBLER CONCEALMENT AND AVIAN PREDATOR ABUNDANCE

Because experimental nest concealment correlated strongly with avian-predator clay egg bites (see Results), we were interested in how avian predators might influence Yellow Warbler nest concealment. An analysis relating among-year variation in nest concealment with predator numbers was conducted. Corvids were specifically examined because songbird responses to corvids during nest site selection are clearly documented (Peluc *et al.* 2008) and because abundance data were available for these predators. During 5 years of all-species monitoring (2001–2005), breeding territories for two corvid species (Black-billed Magpie and Western Scrub-Jay) were mapped using nest locations and behavioural observations (Martin & Geupel 1993). Among-year variation in concealment of nests found during building was analysed using ANOVA. Pearson's correlation coefficients related corvid abundance with yearly concealment means.

Results

Eight hundred and fifty-five natural Yellow Warbler nests were found from 2000 to 2008. Of these, 334 were found during building, providing data for microhabitat-use analyses. Of all nests, 676 nests were observed active (209 nests never observed with host eggs or nestlings). Outcomes were determined for 665 of these (11 nest fates were unknown), providing data for nest-survival analyses. Of nests used in survival analyses, 422 failed and 77% of failures were attributed to predation.

MICROHABITAT PREFERENCE AND THE NATURAL MICROHABITAT RANGE

Yellow Warblers selected nest sites more concealed and higher than random sites, indicating a positive preference for both these features (Table 1). With respect to both substrate and microhabitat-patch composition, nests in willow were less concealed than nonwillow nests (means for willow and nonwillow substrates = $53.5 \pm 1.1\%$ and $64.1 \pm 1.8\%$, respectively; $t_{295} = 4.9$, $P < 0.001$; concealment vs. PC1:

$r = -0.37$, $n = 297$, $P < 0.001$). Also with respect to both substrate and patch composition, nests in willow were higher than nests in nonwillow shrubs (heights in willow vs. nonwillow substrates = 172 and 136 cm, respectively; $t_{322} = 3.5$, $P < 0.001$; height vs. PC1: $r = 0.27$, $n = 322$, $P < 0.001$). Even when controlling for confounding effects of shrub type, however, nest-versus-random-site differences in concealment and height were significant (Table 1). Nest height correlated with shrub height ($r = 0.73$, $n = 325$, $P < 0.001$) and Yellow Warbler nests favoured tall shrubs (Table 1). In contrast, nest height was only weakly correlated with relative nest height ($r = 0.15$, $n = 299$, $P < 0.001$) and relative nest height did not differ as much between nest and random sites. Thus, nest height preferences apparently resulted mainly from preferences for tall shrubs. For random sites, height scores were not significantly correlated with concealment ($r = 0.26$, $n = 29$, $P = 0.16$), and for nest sites, height-related features were at most weakly correlated with concealment (nest height: $r = -0.06$, $P = 0.30$; shrub height: $r = -0.18$, $P = 0.002$; relative nest height: $r = 0.17$, $P = 0.003$; $n = 299$), and scatter-plots (not shown) did not suggest nonlinear relationships. Thus, height and concealment preferences did not appear confounded.

The 'natural concealment range' for Yellow Warbler nests was identified as 30–80%. From 2000 to 2008, 24 of 299 nests were $< 30\%$ concealed and 27 nests were $> 80\%$ concealed (Fig. 2a). The 'natural height range' for Yellow Warblers was identified as > 75 cm. Given shrub-specific height differences, height distributions for willow and nonwillow nests were examined separately. Maximum height was higher in taller, willow-dominated patches than in shorter, nonwillow-dominated patches (Fig. 2b), suggesting patch structure rather than nest site selection constrained the upper height limit. We therefore only identified a lower limit to the natural height range. Only 15 of 322 nests (eight of 99 nests in nonwillow patches; seven of 223 nests in willow patches) were < 75 cm high, and the distribution of natural nests dropped sharply at this height (Fig. 2b).

Table 1. Yellow Warbler nest microhabitat preferences at Rush Creek, Mono Lake basin, California 2006–2008

Habitat feature	Nest	Random	Covariates		
	Mean $\pm$ SE	Mean $\pm$ SE	Use $F_{1,138}$	PC1 $F_{1,138}$	Substrate $F_{2,138}$
Concealment (%)	51.9 $\pm$ 1.5	41.5 $\pm$ 3.0	13.5**	6.1	3.7
Nest height (cm)	171 $\pm$ 9	111 $\pm$ 13	5.6*	19.4	2.0
Relative height	0.51 $\pm$ 0.02	0.47 $\pm$ 0.03	3.7	16.7	14.2
Shrub height (cm)	350 $\pm$ 15	250 $\pm$ 32	4.6*	59.6	11.5
Willow height (cm)	395 $\pm$ 13 ($n = 101$)	330 $\pm$ 11 ($n = 248$) ^a	n/a		
Nonwillow height (cm)	175 $\pm$ 15 ($n = 95$)	141 $\pm$ 7 ($n = 232$) ^a	n/a		

Nest- versus random-site differences ($n = 114$ and 29, respectively, except for willow and nonwillow shrub heights) for nests found during the building phase are presented. 'Use' F statistics test microhabitat differences and are from two-factor ANCOVAs with two covariates: PC1 (an index describing a willow – nonwillow microhabitat gradient) and nest substrate (willow, rose or sagebrush). Relative height = nest height/shrub height.

* $P < 0.05$, ** $P < 0.001$.

^aAdditional data collected at random sites identified for another study (Latif *et al.* 2011).

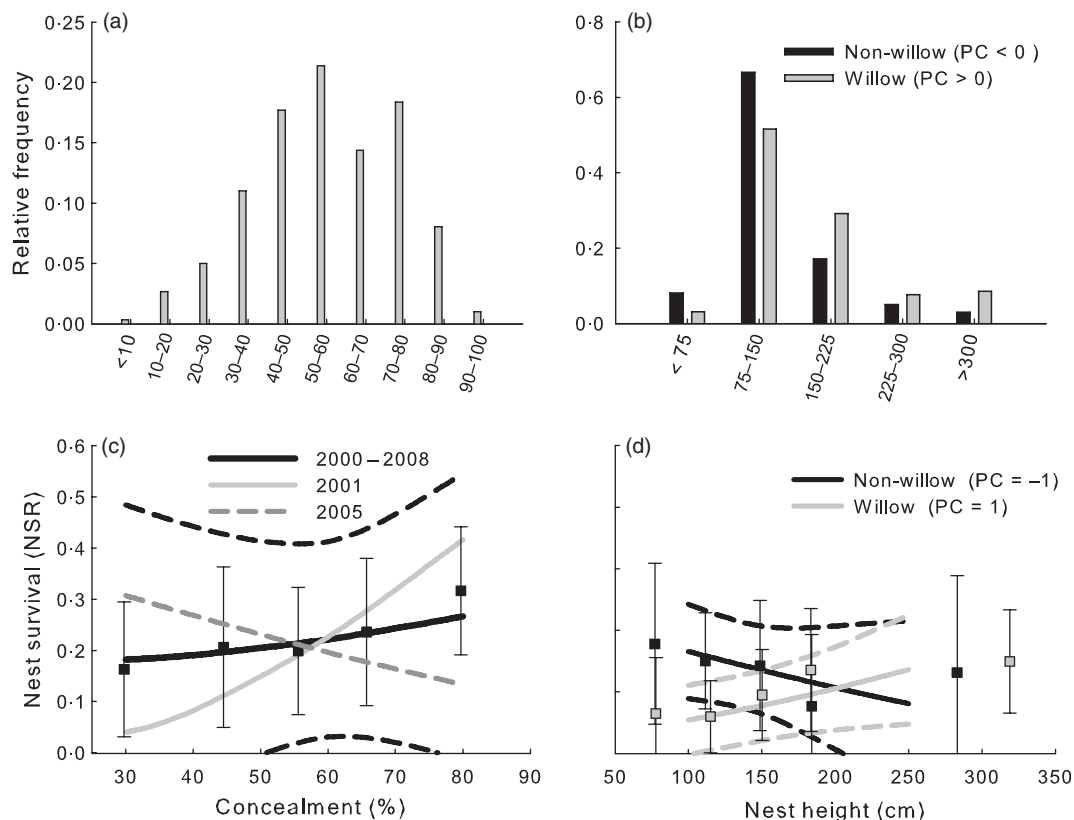


Fig. 2. Microhabitat distributions (a, b) and nest survival (c, d) for 2000–2008 Yellow Warbler nests. Microhabitat distributions are for nests located during building [$n = 299$ nests (a); $n = 322$ nests (b)]. Height-related estimates (d) compare willow (positive PC1 values) vs. nonwillow microhabitat patches (negative PC1 values; description of PC1 in text). Model estimates and 95% confidence bands are derived from Model 1, Table 3 and assume mean covariate values. Class-based estimates are plotted at mean values for classes: < 40%, 40–50%, 50–60%, 60–70%, > 70%; and height classes: < 100, 100–133, 133–166, 166–200 and > 200 cm.

SELECTION GRADIENTS WITHIN THE NATURAL MICROHABITAT RANGE

During the study period, concealment was not consistently correlated with natural nest survival. The data most supported a concealment $\times$ year interaction with nest survival (evidence ratio = 4.6; Tables 2 and 3). The concealment effect was the most negative in 2005 ($\beta_{\text{concealment}} = -0.01$) and most positive in 2001 ($\beta_{\text{concealment}} = 0.027$), but confidence intervals for these estimates included zero (95% CIs: -0.10 to 0.08 in 2005, -0.06 to 0.12 in 2001), so even the strongest yearly relationships were equivocal. On average, nest survival tended to increase with increasing concealment, but this relationship was weak and inconsistent (Fig. 2c). As 200 of the 665 monitored nests were found building, the microhabitat range sampled by nests monitored to measure survival [mean concealment = 59.1 ± 18.1 (SD) %; 6.4% and 11.5% of nests were < 30% and > 80% concealed, respectively; mean height = 161 ± 85 cm; 5.3% of nests were < 75 cm high] was similar to the range initially selected by nesting birds (i.e. nests found building).

The height–survival relationship interacted with microhabitat patch composition. Height $\times$ PC1 interaction models fitted the data best (ER = 5.9; Tables 2 and 3). Nest survival correlated positively with height in willow-dominated

patches but negatively in nonwillow patches (negative PC1 scores; Fig. 2d), and data were sparse from nonwillow nests > 300 cm, resulting in a wide confidence band for survival estimates for these nests (Fig. 2d).

MICROHABITAT DISTRIBUTIONS AND VALIDATION OF EXPERIMENTAL NESTS 2006–2007

In 2006–2007, 141 natural nests with eggs and 140 experimental nests were monitored. Ten per cent of 2006–2007 natural nests were < 30% concealed, 4% were > 80% concealed and 8% were below 75 cm. By contrast, 21% of experimental nests were < 30% concealed, 13% were > 80% concealed and 32% were below 75 cm (Fig. 3a,b).

Within these range limits, neither concealment nor height was correlated with either natural- or experimental- nest survival rates. Concealment parameters did not improve model fit to concealment-range-restricted data (Table 4), and a difference in concealment relationships with natural vs. experimental predation rates was not supported (Tables 2 and 4). Height-range-restricted data marginally supported a difference in height relationships with natural vs. experimental predation rates, but overall, height relationships were not supported (Tables 2 and 4; Fig. 3d).

Table 2. Evidence for concealment (Conc) and height (Ht) relationships with Yellow Warbler nest survival at Rush Creek, Mono Lake basin, California

Dataset	Effect	Evidence ratio	$\chi^2_{(d.f.)}$	$\beta \pm SE$
All natural nests (Table 3)	Conc + Conc $\times$ year	4.6	21.3 ₍₉₎ *	Range: -0.011 ± 0.044 (2005) -0.027 ± 0.047 (2001)
	Concealment	1.3	2.5 ₍₁₎	0.005 ± 0.003
	Ht $\times$ PC1	5.9	5.9 ₍₁₎ *	Range: -0.003 ± 0.002 (PC1 = -1.2) -0.004 ± 0.002 (PC1 = 1.7)
	Height	4.8	5.1 ₍₁₎ *	0.001 ± 0.001
Natural and experimental nests within natural concealment range (Table 4)	Concealment $\times$ nest type	0.3	0.1 ₍₁₎	Natural: 0.005 ± 0.010 ; Experimental: 0.009 ± 0.016
Natural and experimental nests within natural height range (Table 4)	Height $\times$ nest type	1.1	2.7 ₍₁₎	Natural: 0.001 ± 0.002 ; Experimental: -0.003 ± 0.003
Experimental nests throughout extended range (failure = any predation; Table 5)	Conc + Conc ²	112.7	13.4 ₍₂₎ **	Conc: 0.016 ± 0.005 ; Conc ² : -0.0004 ± 0.0002
	Concealment	88.7	10.8 ₍₁₎ **	0.017 ± 0.005
	Height	3.6	4.7 ₍₁₎ *	-0.003 ± 0.002
	Ht + Ht ²	2.1	5.5 ₍₂₎	Ht: -0.005 ± 0.002 ; Ht ² : 0.000 ± 0.000
Experimental nests throughout extended range (failure = avian predation; Table 5)	Concealment	43.9	9.4 ₍₁₎ **	0.022 ± 0.007
	Conc + Conc ²	28.3	10.6 ₍₂₎ **	Conc: 0.020 ± 0.007 ; Conc ² : -0.0004 ± 0.0004
Experimental nests throughout extended range (failure = rodent predation; Table 5)	Height	4.8	5.1 ₍₁₎ *	-0.005 ± 0.002
	Concealment	0.5	0.7 ₍₁₎	0.007 ± 0.010
	Conc + Conc ²	0.3	1.6 ₍₂₎	Conc: 0.002 ± 0.010 ; Conc ² : -0.0005 ± 0.0004
	Height	0.4	0.4 ₍₁₎	-0.002 ± 0.003

Evidence ratios ($\sum w_{\text{with-parameter}} / \sum w_{\text{without-parameter}}$) use model weights (w) and likelihood ratio tests use log-likelihoods (top models only) in referenced tables. PC1 describes microhabitat patch composition (see text). Parameter estimates (β) describe slopes of covariate relationships with the logit of daily nest survival.

* $P < 0.05$; ** $P < 0.01$.

Table 3. Models describing concealment (Conc) and height (Ht) relationships with daily nest survival rates fitted to 2000–2008 natural-nest data

Model No.	Model parameters	–LL	k	Δ_i	w_i
1	Global	945.1	25	0.0	0.57
2	Conc + Ht + Ht $\times$ PC1	954.5	17	2.7	0.15
3	Ht + Ht $\times$ PC1	955.7	16	3.2	0.12
4	Conc + Conc $\times$ year + Ht	948.0	24	3.9	0.08
5	Conc + Ht	956.8	16	5.4	0.04
6	Height	958.4	15	6.4	0.02
7	Conc + Conc $\times$ year	950.6	23	7.0	0.02
8	Concealment	959.5	15	8.7	< 0.01
9	Covariate-only	960.8	14	9.4	< 0.01
10	Constant Survival	1019.6	1	100.8	< 0.01

–LL = –Log-likelihood, w_i = model weights, k = No. of model parameters, Δ_i = ΔAIC_c . Covariates were year, date, stage, plot, parasitism and PC1 (an index of microhabitat patch composition). The ‘global’ model includes all possible parameters, and the ‘constant survival’ model contains only an intercept.

Δ_i = ΔAIC_c for the i th model – AIC_c for the best-fit model (lowest AIC_c).

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

$w_i = e^{-0.5 \Delta_i} / \sum_{j=1}^n e^{-0.5 \Delta_j}$; j = the total number of models (10).

$\hat{c} = 1.5$ (calculated for model 1); $\hat{c} = \chi^2_{\text{GOF}}/d.f.$

SELECTION GRADIENTS ACROSS AN EXTENDED MICROHABITAT RANGE

Of the 140 experimental nests monitored over a more expansive microhabitat range, 116 failed. The data from

these nests supported both linear and quadratic concealment relationships with predation risk (Tables 2 and 5; Fig. 3c).

Over the extended microhabitat range, experimental data also supported a height–predation relationship. Both linear

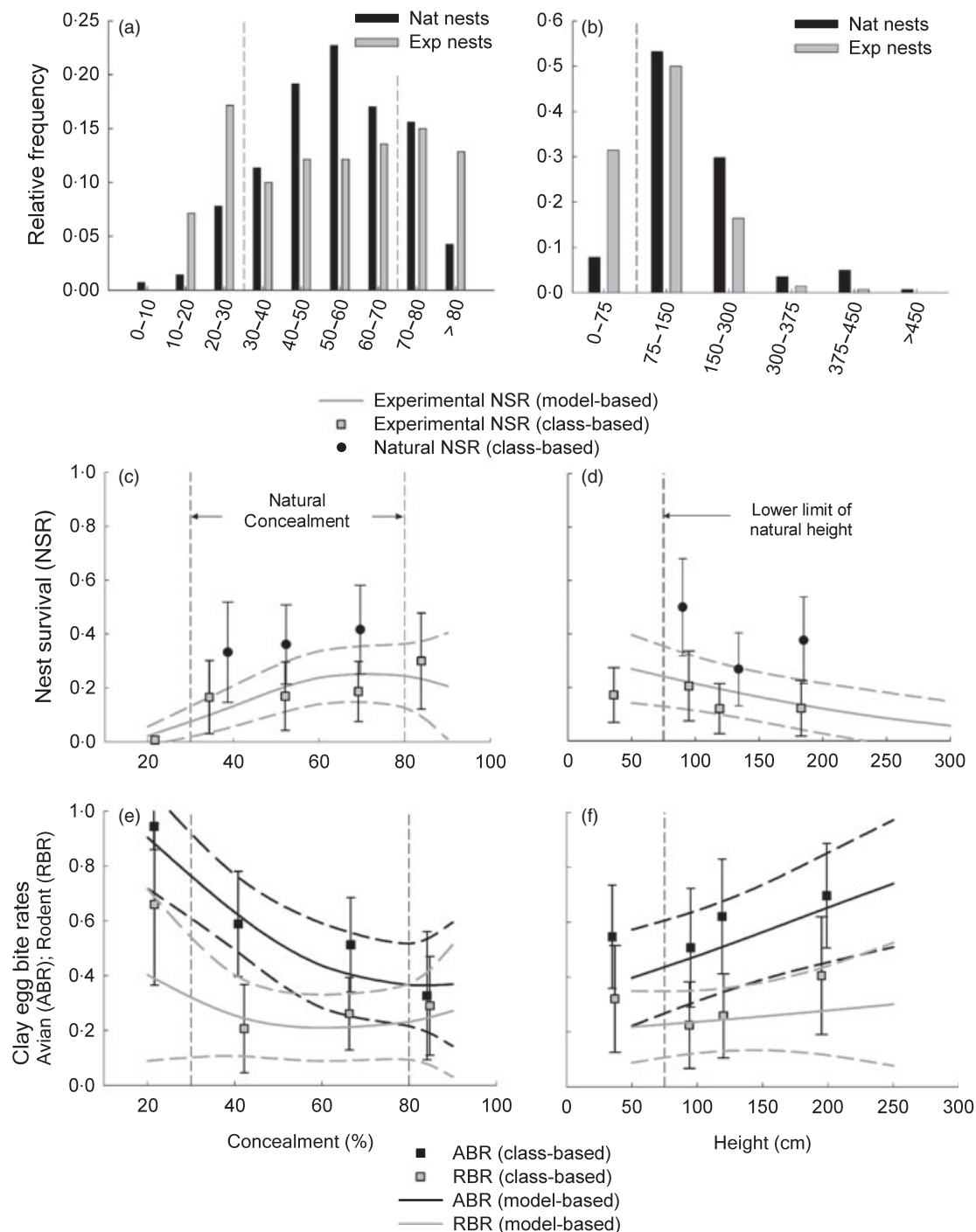


Fig. 3. Microhabitat distributions and nest survival (NSR) for 2006–2007 natural ($n = 141$) and experimental ($n = 140$) nests along concealment (a) and height (b) gradients. NSR estimates and 95% confidence bands are for natural nests (only class-based estimates within natural microhabitat range limits denoted by vertical dotted lines), experimental nests (c, d), and avian (ABR) and rodent (RBR) clay egg bite rates (e, f). Model-based estimates were calculated from Model 1 (c, d), Model 11 (e, f; ABR), Model 21 (e; RBR) and Model 20 (f; RBR) from Table 4 (average values assumed for covariates other than nest type). Class-based NSR estimates are plotted at mean values within classes: < 30%, 30–45%, 45–60%, 60–80%, > 80% concealed; and < 75, 75–150, 150–300, > 300 cm high. Class-based ABR and RBR estimates are for classes: < 30%, 30–55%, 55–80%, > 80% concealed; and < 75, 75–100, 100–140 (ABR), 100–150 (RBR), > 140 (ABR), and > 150 cm (RBR) high.

and quadratic height models were supported (Tables 2 and 5), and experimental nest survival decreased with increasing height (Fig. 3d). Class-based nest survival estimates, however, did not line up particularly well with model-based esti-

mates, indicating height was a poor predictor of nest survival.

In 2006–2007, during 116 experimental-nest failures observed, 77 clay eggs were bitten by nest predators. Of

Table 4. Models describing concealment (Conc) and height (Ht) relationships with daily survival of natural and experimental nests within the natural microhabitat range for Yellow Warbler nests at Rush Creek, Mono Lake basin, California

Habitat Range	<i>n</i> eff	Model No.	Model parameters	–LL	<i>k</i>	Δ_i	w_i
30–80% concealed	1358	1	Covariates only	270.8	5	0.0	0.44
		2	Conc	270.1	6	0.7	0.30
		3	Conc + Conc $\times$ type	270.1	7	2.7	0.11
		4	Conc + Conc ²	270.1	7	2.8	0.11
		5	Conc + Conc $\times$ type + Conc ² $\times$ Type	269.6	9	5.7	0.03
		6	Constant survival	279.2	1	8.7	0.01
> 75 cm	1416	7	Covariates only	283.7	5	0.0	0.46
		8	Ht + Ht $\times$ type	282.3	7	1.3	0.24
		9	Ht	283.7	6	2.0	0.17
		10	Ht + Ht ²	283.2	7	3.1	0.10
		11	Ht + Ht ² + Ht $\times$ type + Ht ² $\times$ type	282.1	9	5.0	0.04
		12	Constant survival	299.3	1	23.1	< 0.01

n eff = No. of observation days, –LL = –Log-likelihood, *k* = No. of model parameters, Δ_i = ΔAIC_c , w_i = model weight. Data are from 121 to 93 natural and experimental nests, respectively, from the natural concealment range, and 134 and 100 natural and experimental nests, respectively, from the natural height range. Covariates were year, date, nest type and PC1 (a microhabitat-patch-composition metric).

Δ_i = ΔAIC_c for the *i*th model – AIC_c for the best-fit model (lowest AIC_c).

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

$w_i = e^{-0.5 \Delta_i} / \sum_{j=1}^6 e^{-0.5 \Delta_j}$; *j* = the total number of models (six each).

For concealment model 5, $\hat{c} = 0.46$; $\hat{c} = \chi^2_{\text{GOF}}/\text{d.f.}$

For global height model (not shown), $\hat{c} = 0.56$.

Table 5. Models describing concealment (Conc) and height (Ht) relationships with daily nest survival for all 2006–2007 experimental nests at Rush Creek, Mono Lake basin, California

Model set	<i>n</i> eff	Model No.	Model parameters	–LL	<i>k</i>	Δ_i	w_i
1. Failure = any depredation	764	1	Conc + Conc ² + Ht	176.9	7	0.0	0.31
		2	Conc + Ht	178.2	6	0.6	0.23
		3	Conc + Conc ² + Ht + Ht ²	176.5	8	1.2	0.17
		4	Conc + Ht + Ht ²	177.7	7	1.5	0.14
		5	Conc + Conc ²	179.2	6	2.6	0.08
		6	Concealment	180.5	5	3.1	0.07
		7	Height	183.6	5	9.4	< 0.01
		8	Ht + Ht ²	183.2	6	10.5	< 0.01
		9	Covariates only	186.4	4	12.8	< 0.01
		10	Constant survival	195.6	1	25.1	< 0.01
2. Failure = avian bite	742	11	Conc + Ht	102.4	6	0.0	0.49
		12	Conc + Conc ² + Ht	101.8	7	0.9	0.32
		13	Concealment	105.0	5	3.1	0.11
		14	Conc + Conc ²	104.5	6	4.1	0.06
		15	Height	107.1	5	7.4	0.01
		16	Covariates only	110.3	4	11.7	< 0.01
		17	Constant survival	121.1	1	27.2	< 0.01
		18	Covariates only	95.2	4	0.0	0.29
3. Failure = rodent bite	1150	19	Constant survival	98.4	1	0.4	0.24
		20	Concealment	94.8	5	1.3	0.15
		21	Height	95.0	5	1.6	0.13
		22	Conc + Conc ²	94.4	6	2.4	0.09
		23	Conc + Ht	94.7	6	3.0	0.06
		24	Conc + Conc ² + Ht	94.1	7	3.9	0.04

n eff = No. of observation days, –LL = –Log-likelihood, *k* = No. of model parameters, Δ_i = ΔAIC_c , w_i = model weight. The first and second model sets included year, date and PC1 (an index of microhabitat patch composition) as covariates. The third model set included date² and PC1 as covariates.

Δ_i = ΔAIC_c for the *i*th model – AIC_c for the best-fit model (lowest AIC_c).

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

$w_i = e^{-0.5 \Delta_i} / \sum_{j=1}^{10} e^{-0.5 \Delta_j}$; *j* = the total number of models (10).

For model 3, set 1, $\hat{c} = 0.86$; $\hat{c} = \chi^2_{\text{GOF}}/\text{d.f.}$

For model 11, set 2, $\hat{c} = 0.55$.

For model 23, set 3, $\hat{c} = 1.08$.

these, 50 were distinguishable as avian bite marks, 23 as rodent and four marks were not identifiable (six of 45 depredations were identified as rodent in 2008). Avian predators left scratches, pokes and/or bite impressions clearly shaped like the inside of the upper and lower mandibles of a bird bill. Rodent impressions were discernable by their distinctive double-tooth impressions corresponding to a rodent's incisors.

Clay egg data provided the strongest evidence for a relationship between concealment and avian predation, supporting both linear and curvilinear relationships (Tables 2 and 5). Model-based avian bite rate estimates decreased with greater concealment (Fig. 3e). Less support was found for a concealment relationship with rodent predation (Tables 2 and 5), although class-based rodent bite rate estimates were notably higher for nests <30% concealed (Fig. 3e), suggesting a possible nonlinear relationship. Nevertheless, parameter estimates describing the concealment relationships with avian vs. rodent bite rates did not differ significantly (Table 2).

Clay egg data supported a positive height relationship with avian predation (Tables 2 and 5). Avian bite rates increased with increasing height (Fig. 3f). A height relationship with rodent predation was not supported (Tables 2 and 5; Fig. 3f), but parameter estimates describing these relationships were not significantly different (Table 2).

CONCEALMENT AND AVIAN PREDATORS

From 2001 to 2005, 12 Black-billed Magpie territories and one Western Scrub-Jay territory were mapped (the latter observed in 2005). Interannual concealment variation was significant ($F_{8,290} = 3.8$, $P < 0.001$) and positively correlated with corvid abundance ($r = 0.89$, $n = 5$ years, $P = 0.04$; Fig. 4). Nests were most concealed in 2001 when corvids were most abundant, and the least in 2004 when corvids were least abundant (Fig. 4).

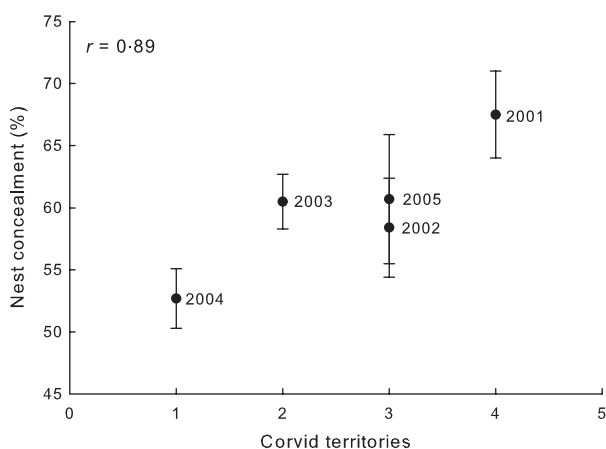


Fig. 4. Yearly nest concealment means (with standard error bars) vs. the number of corvid (members of the family Corvidae) territories from 2001 to 2005. The corvids represented are Black-billed Magpie except for one Western Scrub-Jay that established a territory in 2005.

Discussion

YELLOW WARBLERS OCCUPY AN ADAPTIVE PLATEAU

Our results support the 'adaptive peak hypothesis' with respect to nest concealment. Although the concealment-survival relationship for natural nests was generally weak and inconsistent, experimental data revealed higher predation risk in sites less concealed than sites typically occupied by natural nests. Nest- versus random-site differences indicated Yellow Warblers favoured concealed sites, and this behaviour was adaptive for reducing predation. Predation risk in highly concealed sites (>80%) did not differ from moderately concealed sites (30–80%), so the microhabitat space occupied by Yellow Warblers represents an adaptive plateau. Given the timing of our measurements, phenology-induced measurement error may have obscured concealment-related predation patterns. Furthermore, our experimental data sampled a spatially restricted area (i.e. the upper plot), and we expect that spatial variation in predator community composition will modulate predation patterns. Nevertheless, our results clearly demonstrate that sampling only within the natural microhabitat range can restrict statistical power for detecting important microhabitat-predation patterns, and conversely sampling across an extended range can improve our power to detect such patterns. Furthermore, goodness-of-fit indicators suggested our models did not exclude any major sources of variation in our data.

Artificial-nest predation patterns may not necessarily reflect natural predation pressures (Moore & Robinson 2004), but our experimental data were appropriate for unveiling the adaptive landscape for Yellow Warblers. Our analyses strictly examined microhabitat-related predation patterns. Within microhabitats containing both nest types, microhabitat effects on experimental predation mirrored natural predation patterns (see also; Latif et al. 2011). Experimental predation rates were higher overall than rates for natural nests (Fig. 3c,d) probably in part because parents may deter some nest predators (Latif 2009). Parents may be more capable of fending off certain predator types (Schmidt & Whelan 2005), so experimental predation may over-represent these predators. Nevertheless, most predators observed depredating our experimental nests are documented predators of natural songbird nests in the Mono Lake basin, and all are clearly capable of accessing songbird nests and removing their eggs (Latif 2009). Parents that select highly exposed nest sites may not actually suffer elevated predation rates if they defend their nests more vigorously in these sites, but such behaviour should nevertheless induce higher energetic costs in exposed sites. Experimental nests only recorded egg predation. Most predation of natural nests occurred during the egg period (Latif 2009), and many egg predators also depredate nestlings (e.g. rodents, corvids, and cowbirds; Latif 2009). Therefore, overall nest predation pressures experienced by Yellow Warblers are unlikely to deviate substantially from the egg predation patterns measured in this study.

HOW CONCEALMENT INFLUENCES PREDATION

The concealment effect on avian predation reported here is consistent with patterns reported elsewhere (Liebezeit & George 2002; Martin & Joron 2003). Concealment is likely effective for hiding nests from visually oriented avian predators (Santisteban, Sieving & Avery 2002). Thus, concealment effects on avian predators could drive concealment effects on nest survival. Concealment may also hide nests from rodents, although rodents also favour dense microhabitats, which provide higher levels of nest concealment, to avoid being depredated themselves (Schmidt *et al.* 2001). Further research examining how concealment affects predation by rodents would be of interest.

AN ENVIRONMENTAL CUE POTENTIALLY MODULATING CONCEALMENT SELECTION

Birds can vary their nest site choices in response to shifts in predation pressure (Eggers *et al.* 2006; Peluc *et al.* 2008). Interannual patterns suggest that Yellow Warblers may respond to the presence of corvids when selecting nest sites. Although observers varied among years, a single observer (Q. Latif) collected most 2001–2004 data and all 2006–2008 data. In the year of highest corvid abundance (2001), nest concealment did not correlate with nest initiation date (i.e. first-egg date; $r = -0.10$, $n = 70$ nests), suggesting an immediate response to corvids by nesting birds during the nest site selection process. Experimental evidence supports such behaviour in another warbler species (*Vermivora celata*; Peluc *et al.* 2008). Interannual variation in corvid abundance may appear insubstantial (1–4 territories), but each corvid territory spanned a considerable portion of the study plot (PRBO unpublished data), potentially influencing numerous Yellow Warblers. More corvids in 2001 could be the cause of the apparent upward shift in nest concealment if exposed nests were depredated prior to our discovering them, but because numerous nests were discovered during building, this scenario seems unlikely. That Yellow Warblers selected less-concealed nest sites when corvids were fewer raises the question of whether there might be costs associated with greater concealment, a question we are unable to address with our data. Nevertheless, the suggested response by Yellow Warblers to corvids is consistent with songbird behaviour reported elsewhere and merits further study.

NEST HEIGHT SELECTION AND PREDATION

Nest height preference was apparently not adaptive for avoiding nest predation. Yellow Warblers clearly preferred high nest sites in tall shrubs, but nest-survival rates were not consistently higher in these sites. Although possibly adaptive within willow microhabitats, Yellow Warbler preferences were apparently maladaptive in nonwillow microhabitats. Experimental data also suggested maladaptive nest height selection, but model predictions did not fit the data particularly well. In short, height was a poor predictor of nest

survival, perhaps making it difficult for Yellow Warblers to locate height-related predator-free space. Regardless, local nest predation pressure does not appear to shape height-related preferences in this system.

BROADER IMPLICATIONS

Phenotypic engineering could provide a powerful tool for elucidating the adaptive significance of avian nest microhabitat selection. The frequent lack of apparent relationships between nest microhabitat and predation risk has been attributed to the presence of multiple predator species differing in their individual habitat responses (Filliater, Breitwisch & Nealen 1994). This study demonstrates how parent birds can also contribute to variation in observed microhabitat-predation patterns by exhibiting the very predator avoidance behaviours expected of them. Given these findings, studies that only examine variation in predation rates among natural nests are unlikely to unequivocally demonstrate that nest site preferences are nonadaptive. This study, in conjunction with others, also suggests a potential role of behavioural plasticity in shaping nest site preferences. Additional research elucidating nesting bird responses to specific types of predators would improve our understanding how adaptive microhabitat preferences arise.

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