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How Predation Risk Shapes Avian Nest Site Selection and
Processes Underlying Nest Predation Patterns

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Quresh S. Latif

December 2009

Dissertation Committee:
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ABSTRACT OF THE DISSERTATION

How Predation Risk Shapes Avian Nest Site Selection and
Processes Underlying Nest Predation Patterns

by

Quresh S. Latif

Doctor of Philosophy, Graduate Program in
Evolution, Ecology, and Organismal Biology
University of California, Riverside, December 2009
Dr. John T. Rotenberry, Chairperson

Given the importance of nest predation to avian fitness, ornithologists expect birds to

select nest sites that minimize predation risk. Despite numerous studies contributing to a

wide body of literature, how predation shapes avian nest site selection is still not well

understood largely because studies rarely examine the processes underlying either nest

site selection or predation risk. I investigated how predation shapes nest site selection for

a population of Yellow Warblers with an eye for the processes underlying observed

patterns. From 2000-2008, 728 Yellow Warbler nests were monitored regularly until they

either succeeded or were depredated (fieldwork was collaborative with PRBO

Conservation Science). I measured microhabitat at nest sites (habitat use) and at

randomly located sites (habitat availability) for analyses of habitat preference (use versus

availability). I also monitored experimental nests (2006-2008) in sites that typically and

atypically characterized Yellow Warbler nest sites, and I identified nest predators from

video footage recorded at nests and observations of predation recorded directly by field workers.

I found conflicting evidence regarding the role of predation in shaping avian nest site selection. On the one hand, Yellow Warblers preferred high-predation nest microhabitat patches; preferred willow-dominated patches were positively correlated with predation rates (Chapter 2). On the other hand, Yellow Warblers preferred concealment levels (> 30%) that avoided predation risk, and even dynamically changed their selection patterns to favor low-predation sites when predation pressure changed (Chapter 3). Microhabitat-predation patterns primarily arose during the egg period (laying and incubation; Chapters 2, 3, 4) as a direct result on the predatory behaviors of either avian (mainly cowbird; *Molothrus ater*) and/or rodent (chipmunks and mice) egg predators (identified in Chapter 1). Microhabitat-predation patterns were not confounded by coarser-scale predation patterns, which arose from different processes than did microhabitat-predation patterns (Chapter 4). These results suggest that Yellow Warblers are more capable of recognizing predator-free nest space with respect to nest concealment than microhabitat patch structure. Future research should examine the specific cues used by birds to select nest sites. Such research would further elucidate the limitations on the ability for nesting birds to recognize predator-free space.

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General Introduction

Habitat selection is the behavioral process by which mobile animals choose where to live and breed. The term *habitat* refers to sets of physical and biological features of the environment that characterize particular locations (i.e., habitat features). Animals presumably recognize habitat features and select locations based on the presence or absence of particular features (Cody 1985, Block and Brennan 1993). Furthermore, in so far as different locations confer different survival and reproductive rates, individuals would enhance their fitness by selecting high-fitness habitats, and natural selection should favor such individuals (Thorpe 1945, Rosenzweig 1981). Indeed, heritable variation in habitat selectivity has been documented in a variety of taxonomic groups (Jaenike and Holt 1991), providing a foundation for natural selection to shape habitat selection. Being particularly mobile animals, birds make numerous habitat selection decisions over the course of their lives, and are therefore useful for studying the habitat selection process (Svardson 1949, Cody 1985, Block and Brennan 1993).

Nest survival is the limiting fitness component (Saether and Bakke 2000, Clark and Martin 2007) and predation the main cause of failure for many bird species (Nice 1957, Ricklefs 1969, Martin 1993), so ornithologists expect such species to favor habitats that minimize the risk of nest predation. Numerous studies examine the relationship between preferred habitat features (i.e., features used at a higher frequency than they are available; Block and Brennan 1993, Jones 2001) and nest predation rates. As expected, some populations do prefer low-predation habitats (Bekoff et al. 1989, Martin 1998).

Furthermore, most open-cup nesting birds place their nests in sites that are at least partially concealed by surrounding vegetation, suggesting some attempt to hide their nests from visually-oriented nest predators (Martin 1993). However, many studies fail to detect correlations between either preferred habitat features or vegetation density and variation in natural predation rates (Hoover and Brittingham 1998, Wilson and Cooper 1998, Boulton et al. 2003, Rangel-Salazar et al. 2008). Even more perplexing, some populations apparently prefer breeding habitats associated with elevated nest predation rates (i.e., "ecological traps"; Gates and Gysel 1978, Misenhelter and Rotenberry 2000, Part et al. 2007). These findings have led some researchers to suspect a greater role of selective pressures other than predation risk in shaping avian habitat selection (Hoover and Brittingham 1998, Filliater et al. 1994). However, most studies simply document preference and predation patterns without substantive examination of the processes underlying these patterns. An understanding of why birds may not prefer low-predation habitats likely requires some consideration of the processes giving rise to both habitat preference and habitat-predation relationships.

Because birds are so mobile, avian habitat selection is comprised of multiple steps that take place over various spatial scales (Wiens et al. 1987, Chalfoun and Martin 2007). Some species select different habitats during breeding versus non-breeding seasons (i.e., migrants), but nest predation occurs during breeding, so it should mainly influence breeding habitat selection. At relatively coarse spatial scales, birds select regions in which to breed, and within the selected region each individual either selects a home range or a territory to defend. At finer scales, birds select microhabitats for specific activities

within their chosen home range or territory. For instance, microhabitats are selected for nest sites at a fine-scale from within individual territories. An important distinction between territory selection and nest site selection is that territories are selected for multiple activities so territory selection is likely shaped by multiple factors (e.g., food availability, as well as the availability of adequate nesting and roosting sites). By contrast, nest locations are selected specifically for nesting and should therefore be chosen mainly on the basis of whether nests in those locations are likely to succeed. Most ecological traps reported for birds involve preferences for high-predation territories, and therefore may arise because birds are selecting territories on the basis of food availability at the expense of nest survival (reviewed by Robertson and Hutto 2006). By contrast, preferences for nest sites in high-predation microhabitats are less common (except see Crabtree et al. 1989). Furthermore, even though preferred nest microhabitat features are often uncorrelated with predation risk, most studies only measure natural variation in predation rates, and may therefore lack the power necessary to detect habitat-predation relationships shaping nest site selection particularly if birds only occupy low-predation nest sites (Schmidt and Whelan 1999a). Thus, nest site preferences may reduce predation risk more often than is currently apparent, although measurements of relative predation risk outside microhabitats normally occupied by nesting birds are necessary to fully examine the adaptive significance of avian nest site selection.

The ability of birds to respond to predation pressure when selecting nest sites depends on how habitat relates to predation risk. Generally, habitat can influence predation risk by affecting predator ecology, but such effects may take place over various

spatial scales (Thompson 2007). Habitat effects on predator population densities or distributions can cause coarse-scale variation in predation risk (Chalfoun et al. 2002), whereas finer-scale habitat-predation relationships can arise when microhabitat features affect foraging patch quality for predators (Schmidt and Ostfeld 2003) or the capability for predators to locate nests (Mullin et al. 1998). Habitat may also influence predation risk indirectly by influencing food availability for nesting birds, which can influence the time and energy available for nest defense (Martin 1992). At coarse spatial scales, predator-free space would be easiest to track if predation risk is linked to food resources, whereas habitat effects on predators independent of food would be more difficult to track. As stated previously, birds should be most responsive to fine-scale microhabitat effects on predator foraging behavior, since birds can focus exclusively on avoiding predators when selecting nest sites.

The processes by which habitat can affect predation risk depends largely on which species principally depredate nests (Thompson 2007). Consequently, nest predator identification is a necessary step towards elucidating these processes. Of additional value is identification of non-habitat predation patterns and their underlying processes. At the very least, non-habitat spatiotemporal patterns should be accounted for when analyzing habitat-predation effects since they may confound habitat-predation patterns. Additionally, non-habitat patterns may provide insight into predator ecology which may provide a useful context for understanding habitat-predation effects. For example, a positive correlation between nest density and predation risk may arise if predators focus their hunting efforts where nests are most abundant (Schmidt and Whelan 1999b).

Therefore, given such "density-dependent" predation, active nest-searching by predators may be an important factor contributing to elevated predation rates in habitats preferred by breeding birds.

FIELD GUIDE TO THIS DISSERTATION

This dissertation investigates the relationship between nest predation and nest site selection exhibited by a population of Yellow Warblers (*Dendroica petechia*) that breed along Rush Creek, a tributary of Mono Lake, CA. Chapter 1 focuses on identification of the principle nest predators of Yellow Warblers and other songbird species in Mono Basin riparian habitats. Using various techniques, including video and direct observations of predators at nests, I identified cowbirds and rodents as the principle egg predators and snakes as the principle nestling predators in this system. Because of the particular theoretical importance of predation to birds during nest site selection, I mainly focused on how nest predation shapes this aspect of habitat selection (Chapters 2, 3). In Chapter 2, I present evidence that Rush Creek provides a trap for Yellow Warblers selecting nest sites. Yellow Warblers prefer microhabitat patches associated with higher nest predation rates than available alternatives, and subsequent analyses demonstrate that this trap arises from fine-scale processes. Despite the presence of this trap, in Chapter 3, I present evidence showing that Yellow Warbler nest site selection is adaptive in the context of nest concealment. Nest concealment was not correlated with natural variation in predation rates, but experimental nests measured higher relative predation rates outside the typical concealment range occupied by nesting warblers. These results demonstrate

how the range of nest site choices made currently can limit the measurement of habitat-predation relationships that may have shaped those choices. Finally, Chapter 4 examines non-habitat nest predation patterns and the processes underlying these patterns. Specifically, I examined patterns related to bird density, within-seasonal timing, and timing within the nesting cycle (from laying to fledging). Additionally, I examined the extent to which parent birds contribute to these patterns by examining the same patterns for nests without parents (i.e., experimental nests). The non-habitat predation patterns documented from these analyses provide insight into the hunting behaviors of nest predators, how nesting birds interact with predators, and consequently how and why nest predation influences Yellow Warbler nest site selection to the extent that it does.

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Chapter 1: Nest predators in Mono Basin riparian systems and what happens when they visit nests

ABSTRACT

Nest predation places substantial limits on avian fitness but predation risk is generally difficult to predict in part because predator communities vary among systems and nest predators vary in their hunting behavior. Predator identification is therefore an important step towards understanding how and why nest predation occurs. In partnership with PRBO Conservation Science, I identified nest predators for riparian breeding songbirds along tributaries of Mono Lake, CA. We identified nest predators using a variety of methods: field workers directly observed predators at nests, cameras recorded video footage of nest predation, and clay eggs in experimental nests recorded distinctive bite impressions of certain types of egg predators. Using these methods, we identified 10 distinct predator types at natural nests of three songbird species and at experimental nests. Video observations identified Brown-headed Cowbirds (*Molothrus ater*) as the predominant egg predator in this system, although clay egg bites indicated that rodents also represented a substantial threat to nests with eggs. By contrast, we identified snakes as the predominant predator of nestlings. Finally, a substantial portion of predator visitations to nests resulted in either partial predation or no predation of clutches or broods. I argue that the observed differences in egg versus nestling predators and the low proportion of predator visitations resulting in complete predation are unlikely to be artifacts of sampling error but instead likely reflect real patterns in predator ecology.

INTRODUCTION

Nest survival is an important component of avian fitness (Ricklefs 1969, Lack 1966, Saether and Bakke 2000, Clark and Martin 2007) and predation is the main cause of nest failure for most terrestrial bird species (Nice 1957, Ricklefs 1969, Martin 1993). Thus, nest predation strongly influences the evolution and ecology of birds (Collias and Collias 1984, Lima and Valone 1991, Martin 1995, Saether and Bakke 2000) and the study of nest predation is an important field in ornithology (Lima 2009). Most studies of nest predation document patterns of variation in nest survival rates with little knowledge of which predators are responsible for nest failure (Best and Stauffer 1980, Filliater et al. 1994, Wilson and Cooper 1998, Ricketts and Ritchison 2000, Grant et al. 2005, Aguilar et al. 2008). However, because patterns differ among locations, a general theory capable of explaining and predicting predation risk remains undeveloped (Lahti 2009). Differences in patterns among localities arise largely because predators vary in morphology and hunting strategies and because predator communities differ among habitats and bioregions. Therefore, identifying nest predators is critical for elucidating the factors determining predation risk (Thompson 2007).

Recent technological developments have vastly improved our ability to study nest predation. Lately, researchers have employed video cameras to directly observe the predation process, allowing frequent and reliable identification of nest predators (reviewed by Thompson 2007, Richardson et al. 2009), as well as observation of key behaviors exhibited by predators when depredating nests. Identification with cameras is more accurate than examination of nest remains (Lariviere 1999) and video cameras are

less intrusive than trigger-based still cameras (Liebezeit and George 2003). Camera-facilitated observations of nest predation are of additional value because they allow researchers to observe behaviors typical of specific types of predators. For instance, eggs may be vulnerable to different types of predators than nestlings, in which case the prevalence of egg versus nestling predators would contribute to variation in predation risk within the nesting cycle (Nur et al. 2004, Grant et al. 2005). Certain predators may upon visiting a nest commonly depredate some but not all of its contents (i.e., partial predation; Lariviere and Messier 1997), and this behavior may impose selective pressures not imposed by the risk of complete nest predation (Halupka 1998, Nielsen et al. 2008).

I identified nest predators and observed their behavior in riparian habitats along tributaries of Mono Lake, CA. I focused my observations on which predators visited nests during the egg versus nestling stages, as well as whether predator visitations resulted in complete, partial, or no loss of the clutch or brood from each nest. I report observations of predatory events recorded with video cameras, as well as those recorded directly by workers in the field. We identified a variety of predators depredating nests along Mono Basin tributaries. In addition, our observations suggested some predator-specific tendencies towards depredating either eggs or nestlings, and a surprising number of observed predator visits to natural nests resulted in either partial loss or no loss of eggs or nestlings. Given the frequent occurrence of incomplete predation observed in this and other systems (Lariviere and Messier 1997, Halupka 1998, Small 2005), further study of the implications of incomplete predation on avian fitness and the evolution and ecology of birds is warranted.

METHODS

I observed nest predation experienced by birds breeding in riparian habitats along tributaries of Mono Lake, CA. I primarily used continuous-recording video cameras to observe nest predation. From 2002-2004, I deployed cameras at nests built by one of three nesting species: Yellow Warblers (*Dendroica petechia*), Song Sparrows (*Melospiza melodia*), and a Lazuli Bunting (*Passerina amoena*). During this period, I found and monitored nests built by these species in collaboration with PRBO Conservation Science's riparian songbird monitoring program (www.prbo.org/cms/359, cited 2009). Additionally from 2007-2008, I deployed cameras at natural Yellow Warbler nests and experimental nests as part of a larger study investigating patterns of predation risk for this species (Chapters 2-4). Experimental nests consisted of previously used Yellow Warbler nests, each containing a real passerine egg and a clay egg. In addition to observations recorded by cameras, PRBO workers directly observed and reported cases of nest predation while monitoring natural nests in the field, and I identified bite impressions left by predators in clay eggs when possible.

Video cameras used to monitor nests consisted of "bullet" security cameras either wired or wirelessly connected to 24-hour time-lapse video cassette recorders (VCRs). Recorders and cameras were powered by battery/solar-panel arrays. Cameras were also capable of recording nocturnal predators by recording in the infrared spectrum. Cameras recorded continuously once deployed (King et al. 2001). I mounted cameras < 1 meter from nests so that the nest and any visitors were easily discernible in the resulting video

footage, and I placed VCRs, solar panels, and batteries > 10 meters from the nest to avoid drawing attention to nests. Additionally, I covered cameras in camouflage-patterned duct tape to minimize their conspicuousness (Figure 1.1). I attempted to deploy cameras at natural nests as early as possible in the nesting cycle to maximize the probability of recording predation events. However, cameras were often deployed late in the nesting cycle (e.g., during the nestling stage) due to unavailability of early-stage nests. I deployed cameras at experimental nests when nests were first placed in the field. All nests were checked and their contents were recorded in-person at least once in four days. I reviewed footage recorded between any two nest checks during which the number of eggs or nestlings were reduced to identify the predator or predators responsible for the change. I also reviewed all video footage obtained at natural nests to look for predator visitations that had not resulted in clutch or brood losses. For each predator visitation recorded, I noted whether eggs or nestlings had been depredated and whether the predator had partially or completely depredated the nest. Given my interest in predator behavior, I considered nests retaining only parasitic eggs or nestlings following a predation event to have been partially depredated. I do not report observations of visitations during which brood parasitic eggs were laid since they are reported elsewhere (Latif et al. 2006).

I report two types of observations recorded directly by workers in the field. I report all observations of predators in the act of consuming either eggs or nestlings at nests, and I report observations likely implicating particular species as nest predators. The latter included (1) observations of predators at a nest or within 5 meters of a nest during the same observation interval that the nest was depredated (i.e., within a 4-day period),

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(2) predators observed with either eggs or nestlings in their mouth or bill, or (3) fresh sign of a particular predator (i.e., a new cowbird egg) appearing at a nest during the same observation interval the nest was depredated.

Clay egg impressions were identified by comparing impressions recorded in the field to impressions made with specimens in the lab. Experimental nests containing clay eggs were placed in numerous sites representative of the microhabitat range occupied by Rush Creek Yellow Warblers as part of multiple studies (Chapters 2-4, unpublished studies). Only rodent and avian predators left identifiable bite impressions in clay eggs. I created impressions with either skulls or preserved heads of a series of rodent and avian predators representing most of those found along Rush Creek (where experimental nests were monitored). These included Western Scrub-jay (*Aphelocoma californica*), Black-billed Magpie (*Pica hudsonia*), Brown-headed Cowbird (*Molothrus ater*), Red-shafted Flicker (*Colaptes auratus*), Bewick's Wren (*Thryomanes bewickii*), House Wren (*Troglodytes aedon*), least chipmunk (*Tamias minimus*), deer mouse (*Peromyscus maniculatus*), pinyon mouse (*Peromyscus truei*), and bushy-tailed woodrat (*Neotoma cinerea*). Impressions made with these lab specimens fell into four distinct categories (two rodent and two avian categories) distinguishable via ocular examination without subsequent reference to the specimens initially used to make the impressions. The pointed bills of the cowbird and flicker specimens (1) left narrow, sharp-tipped impressions distinct from the (2) broad, blunt-tipped impressions made with the corvid specimens (i.e., scrub-jay and magpie). The (3) incisor marks made with the woodrat specimen were distinctly larger than (4) those made with the chipmunk and mice

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specimens. I classified impressions recorded at experimental nests into one of these four categories when possible. Avian predators in the field often left scratches or poke marks in clay eggs, but since equivalent marks made with lab specimens were not distinctive (including those made with wren specimens), I simply classified these types of marks as avian (data analyzed in Chapters 2, 3, 4).

Observations of nest predators were recorded along each of four tributaries of Mono Lake: Rush Creek, Lee Vining Creek, Mill Creek, or Wilson Creek. The first three are natural tributaries and have been subjected to varying degrees of water diversions, livestock grazing, and subsequent ecological restoration (Hart 1996, SWRCB 1994). Wilson Creek is a man-made channel, so the habitat associated with this tributary developed only recently (1911). Descriptions of the habitat along these tributaries are detailed by Heath et al. (2006a, b, c, d). In brief, Mono Basin riparian habitats are dominated by either willow (*Salix exidua*, *Salix lucida*, and *Salix lutea*) or black cottonwood (*Populus trichocarpa*) and are interspersed with Woods' rose (*Rosa woodsii*), which grows both in the understory of willow or cottonwood stands and in relatively contiguous, monotypic stands. Sagebrush (*Artemisia tridentata*) dominates the landscape surrounding these riparian systems, but sagebrush also occurs within the riparian corridor due to recent fluctuations in water availability and consequent fluctuations in riparian habitat extent.

RESULTS

Over the entire study period, a total of 10 distinct nest predator types (identified minimally to family) were identified. These were garter snake (*Thamnophis couchii*), gopher snake (*Pituophis catenifer*), mouse (*Peromyscus maniculatus* or *Peromyscus truei*), chipmunk (*Tamias minimus*), raccoon (*Procyon lotor*), ermine (*Mustela erminea*), Stellar's Jay (*Cyanocitta stelleri*), wren (either *Troglodytes aedon* or *Thyomanes bewickii*), Bullock's Oriole (*Icterus bullockii*), and Brown-headed Cowbird. Species designations for garter snake, mouse, chipmunk, and ermine were based on a previously conducted Mono Basin biological inventory (Jones and Stokes Associates 1993). To capture footage of these predators, I video-monitored 29 Yellow Warbler nests, 15 Song Sparrow nests, one Lazuli Bunting nest, and 10 experimental nests for a total of 519 days (natural: 486, experimental: 33). From this effort, I obtained footage of 23 nest visitations made to 18 nests (9 natural and 9 experimental nests) along two creeks (some nests were visited on multiple occasions by different predators; Table 1.1). PRBO workers directly observed seven predation events, as well as five observations likely implicating particular species as nest predators (Table 1.3). The latter suggested Western Scrub-Jays (*Aphelocoma californica*) and Black-billed Magpies (*Pica hudsonia*) as nest predators in addition to predators identified using video cameras.

A number of clay egg impressions recorded at experimental nests were distinguishable more specifically than simply as rodent or avian marks. On 17 occasions, avian predators attempted to forcefully grab or bite clay eggs, leaving more distinctive impressions than scratches or pokes. Fourteen of these were made by pointy-bills similar

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to those made with cowbird or Red-shafted Flicker specimens in the lab. The remaining three were made by stouter-billed avian predators more akin to those made with the magpie and scrub-jay specimens. Incisor marks made by rodents in the field were all closer in size to chipmunk and mouse incisors and clearly smaller than woodrat incisor impressions made in the lab.

PRBO and I observed 17 instances of egg-related predatory behavior. Video cameras recorded 13 predator visitations to nests with eggs (5 at natural nests, 8 at experimental nests), of which 12 resulted in some loss or damage of eggs (weasel visit to natural nests resulted in no egg loss; Table 1.2). In addition, PRBO workers recorded at least five direct observations of egg predation (2 conclusive, 3 suggestive; Table 1.3). We observed female cowbirds (males were never observed) depredating eggs on numerous occasions, and less commonly we observed events implicating five other types of egg predators: Black-billed Magpie, Stellar's Jay, wren, Bullock's Oriole, and chipmunk.

PRBO and I observed 17 instances of nestling-related predatory behavior. Video cameras recorded 10 visits by predators to nests post-hatching, of which seven resulted in either partial or total brood loss (Table 1.2). In addition to video observations, PRBO workers recorded nine events implicating specific nestling predators (5 conclusive, 4 suggestive; Table 1.3). Our most frequently observed nestling predators were snakes (particularly garter snakes). In addition to snakes, we conclusively identified four other types of nestling predators (Stellar's Jay, mouse, raccoon, and ermine; Tables 1.2, 1.3) and our observations suggested two more (Western Scrub-jay, Brown-headed Cowbird; Table 1.3).

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A majority of observed predator visits to natural nests recorded by video cameras resulted in either no predation or partial predation (not examined at experimental nests; Table 1.2). We observed seven visits by predators resulting in partial clutch or brood loss at five nests, of which two subsequently produced fledgelings. None of the observations of clutch predation by cowbirds resulted in complete clutch loss. On Lee Vining Creek, a garter snake visited a Song Sparrow from which it consumed a cowbird nestling but left the remaining Song Sparrow nestling. Finally, a wren visited a Lazuli Bunting nest and poked a hole in one egg but left the second intact, after which the female bunting returned, ate the contents of the damaged egg, and removed the shell from the nest. An ermine depredated only one of two cowbird chicks from a Song Sparrow nest (i.e., the one visited previously during the egg period), and the remaining cowbird chick died of unknown causes. Finally, a mouse depredated only one of two 10-day old cowbird nestlings from a Song Sparrow nest. Although both nestlings attempted to escape (i.e., jumped out of the nest), only one survived while the devoured carcass of the second was found next to the nest just outside the camera's field of view. We observed only four occasions during which predators consumed either an entire clutch or an entire brood at a natural nest, including one visit by a raccoon to a Song Sparrow nest that resulted in the depredation the only nestling (cowbird) present (i.e., partial predation was not possible).

Four predator visits to natural nests resulted in no predation (Table 1.2). Two of these were made by snakes to nests after chicks had fledged. The Song Sparrow nest from which a garter snake had depredated a cowbird nestling was not re-visited by the garter snake, but a gopher snake visited the nest 1:15 (min: sec) after the surviving Song

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Sparrow nestling left. The timing of these events suggests that the chick was "force-fledged" by the gopher snake, i.e., induced to leave the nest early in response to the threat presented by the snake. On Rush Creek, a garter snake visited a Yellow Warbler nest the day after all the chicks had fledged. Two additional visits were made by predators that chose not to depredate any of the nests' contents. One visit was made by an ermine during the egg period to the same Song Sparrow nest from which an ermine later depredated a cowbird nestling. During another event, a cowbird visited a Yellow Warbler nest with seven-day-old nestlings but left all the nestlings untouched.

DISCUSSION

We identified a variety of nest predators in riparian habitats along Mono Lake tributaries. Given our sample size, we are unlikely to have identified the full range of nest predators present in Mono Basin riparian systems. However, our dataset is probably large enough to identify the dominant nest predator types (Weidinger 2008). A recent meta-analysis found that cameras tend to lower predation rates and therefore may deter predators (Richardson et al. 2009). In our Mono Basin study, natural camera nests were depredated at lower rates than non-camera nests (analysis presented in Richardson et al.'s review), and cameras recorded no egg predators at natural Yellow Warbler nests despite the high egg predation rates experienced by this species (Chapters 2-4). Direct observations and clay egg impressions implicate corvids as nest predators (Table 1.3), but video cameras rarely recorded corvids at nests (only once depredating Yellow Warbler nestlings). Thus, corvids may avoid cameras and be under-represented by video observations. However,

the cameras recorded very little of the earliest part of the nesting cycle (only 4 cameras

deployed at Yellow Warbler nests before incubation day 4), which is when predation

rates were highest (Figure 4.3). Furthermore, we observed more egg predators at

experimental Yellow Warbler nests, where cameras were deployed immediately. Finally,

examination of clay egg impressions indicated that corvids are not the dominant nest

predator in this system. Thus, a lack of camera deployment during laying and early

incubation is the most likely cause for the paucity of egg predators recorded at natural

nests.

Video observations indicated cowbirds were particularly important egg predators,

and the information acquired from examining clay egg bites was consistent with this

conclusion. Although we only directly observed partial clutch predation by cowbirds, a

large portion of complete clutch losses are also probably caused by cowbird predation.

We only observed cowbird predation at nests with parasitized clutches, which are least

likely to be completely destroyed by cowbirds since at the very least they are unlikely to

destroy their own eggs and because leaving some host eggs reduces the probability of

host abandonment (Lowther 1983, Arcese et al. 1996). By contrast, cowbirds may destroy

non-parasitized clutches to force hosts to re-nest, thus creating new opportunities for

parasitism (Arcese et al. 1996). As predicted by the "forced re-nesting hypothesis," non-

parasitized Yellow Warbler clutches were more likely to be completely depredated than

parasitized clutches along Rush Creek (Chapter 4). Cowbirds are also known to force re-

nesting by depredating non-parasitized broods (Arcese et al. 1996), and we observed

some evidence for this behavior (Table 1.3). However, we also recorded a cowbird

visiting a non-parasitized Yellow Warbler brood (7-days old) during which nestlings were not depredated. This observation, the lack of nestling destruction by cowbirds, and the frequent observations of nestling depredation by other predators (see below) together suggest that cowbirds may be less likely to depredate nestlings than clutches. Given their life history, cowbirds are probably the most effective of any predator at finding nests, and Yellow Warbler nests (those most commonly monitored) are particularly easy to find (personal observation). Consequently, cowbirds may locate most nests (including those discovered too late to parasitize) during the egg period. Thus, cowbirds may usually decide whether to force a host to re-nest prior to hatching. Comparisons of cowbird-specific brood predation rates experienced by conspicuous versus cryptic host species would provide information necessary to test this hypothesis.

We identified a somewhat different suite of predators as nestling predators compared to egg predators. Snakes were the most commonly observed nestling predator, which is in contrast with our failure to observe any egg predation by snakes. Both species of snakes observed in the Mono Basin are documented egg predators in other systems (Thompson and Burhans 2003, Peterson et al. 2004). Nevertheless, our observations suggest that snakes in the Mono Basin most commonly depredate nestlings and rarely depredate eggs. Snakes can use parental activity as a visual cue for finding nests (Mullin and Cooper 1998), so snakes may be more capable of finding nests during the nestling period when parental visitation rates are highest. Additionally, our observation of a gopher snake which left three un-hatched eggs intact in a nest after missing the Song Sparrow nestling, suggests an actual preference for nestlings and a lack of interest in

eggs. Our observations also suggest that ermine prefer nestlings. Since the two observed ermine visits were made to the same Song Sparrow, it is possible that both visits were made by the same ermine. If so, this weasel relinquished an opportunity to consume eggs in exchange for the potential opportunity to depredate nestlings. Although snakes do eat eggs, researchers more frequently observe snakes depredating nestlings (Morrison and Bolger 2002, Stake and Cimprich 2003, Thompson and Burhans 2003, Stake et al. 2004), so snakes may generally either locate nests more easily during the nestling period or prefer nestlings over eggs. More observations are necessary to evaluate whether weasels generally prefer nestlings (see studies reviewed by Thompson 2007, Richardson et al. 2009). Eggs represent a smaller source of calories than nestlings, particularly in comparison to older nestlings, but if a predator chooses to wait for eggs to hatch, another predator may depredate the nest in the ensuing period. In addition, if a predator waits too long, nestlings may be old enough to leave the nest in response to a predatory visit (observed here in response to visits by gopher snake and mouse; see also Halupka 1998). A cost-benefit analysis would help elucidate whether and how long predators should wait to depredate nests.

Our video observations indicate partial predation to be a common result of predator visits to nests in Mono Basin riparian areas. As discussed previously, partial clutch predation by cowbirds can be readily understood in light of their life history. Non-cowbird predators may only partially depredate a nest for several reasons. First, many of the observed predators were small and therefore more likely satiated by only a portion of a nest's contents. Since nestlings are larger than eggs, predator satiation is particularly

likely during the nestling stage and may explain observed partial depredations of Song Sparrow nests by an ermine and a garter snake. Older nestlings are even more likely to satiate predators, and additionally may flee the nest in response to a predator's visit (Halupka 1998). Either or both of these factors may explain the observed partial mouse depredation of a Song Sparrow nest. Whereas portions of larger birds' clutches (e.g., duck clutches) may satiate larger predators (Lariviere and Messier 1997), portions of small birds' clutches would most easily satiate small predators. Therefore, consistent with these observations, small predators would be most likely to partially depredate nests of small birds such as passerines (but see observations by Small 2005). Why wrens depredate nests is less understood, although resource competition has been proposed as a determining factor (Bellesisles and Picman 1986, Simons and Simons 1990). Partial nest predation could alleviate resource competition by reducing the overall number of neighboring consumers, but our observation of a wren partially depredating a Lazuli Bunting nest did not occur within or near any established wren territories (PRBO unpublished data), so the purpose behind this predatory act was not apparent. Given these reasons for the occurrence of partial predation, our observations are unlikely to be an anomaly of the Mono Basin, and indeed partial predation has been observed sometimes frequently in other systems (Lariviere and Messier 1997, Halupka 1998, Small 2005). A high risk of partial predation may favor bet-hedging egg-laying strategies not necessarily favored by a high risk of complete predation (i.e., conspecific brood parasitism; Nielsen et al. 2008), potentially explaining behaviors exhibited by Mono Basin birds not

exhibited elsewhere (Latif et al. 2006). Further research on the particular fitness costs

imposed by partial predation is warranted.

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TABLES

Table 1.1. Predator visitations by nesting species recorded with video cameras.

Site	Predator Species	# nests visitations by nesting species				
		YWAR	SOSP	LAZB	EXP	Total
Rush Creek	Brown-headed Cowbird	1_N	3_E		5	9
	Bullock's Oriole				1	1
	garter snake	2_N				2
	chipmunk				1	1
	mouse		1_N			1
	raccoon		1_N			1
	weasel		$1_E, 1_N$			2
	wren				1	1
Lee Vining Creek	garter snake		1_N			1
	gopher snake		1_N			1
	unidentified snake	1_N				1
	Stellar's Jay	1_N				1
	wren			1_E		1

Nesting Species visited by predators included Yellow Warbler (YWAR), Song Sparrow (SOSP), Lazuli Bunting (LAZB), Experimental nest simulating Yellow Warbler nests (EXP). Subscripts denote the stage (E = egg, N = nestling) during which visits were made.

Some natural nests were visited on multiple occasions by the same or different predators. Predator visitations were observed at a total of nine natural and nine experimental nests. To capture these observations, I video-monitored 29 Yellow Warbler nests, 15 Song Sparrow nests, one Lazuli Bunting nest, and 10 experimental nests for a total of 519 days (natural: 486, experimental: 33).

Table 1.2. Timing and outcome of predator visitations to video-monitored nests

Predator Type	# visits observed by portion of clutch/ brood depredated			Exp
	none	partial	complete	
Brown-headed Cowbird	1_N	3_E		5
Bullock's Oriole				1
Stellar's Jay			1_N	
wren		1_E		1
raccoon			1_N	
weasel	1_E	1_N		
chipmunk				1
mouse		1_N		
garter snake	1_N	1_N	1_N	
gopher snake	1_N			
unidentified snake			1_Y	

Subscripts denote the stage (E = egg, N = nestling) during which visits were made. Experimental nests were considered depredated when finch eggs were damaged or removed, or if impressions were left in clay. Since experimental nests (Exp) could not be "partially depredated" and never contained nestlings, visits to experimental nests were tallied separately.

Visits were often made to natural nests previously visited either by the same or different predator type. Predator visitations were recorded at a total of nine natural and nine experimental nests. To capture these observations, I video-monitored 29 Yellow Warbler nests, 15 Song Sparrow nests, one Lazuli Bunting nest, and 10 experimental nests for a total of 519 days (natural: 486, experimental: 33).

Table 1.3. Direct observations of predatory behavior made in the field.

Predator Species	Observation
Brown-headed cowbird	▪ A dead Yellow Warbler nestling was ejected and found outside the nest. A cowbird egg was left in the nest (LVC, 2004). ▪ On multiple occasions, one or more cowbird eggs were left in a nest during the same observation interval that the entire clutch had been depredated (multiple sites, multiple years).
Black-billed magpie	● Observed depredating eggs from an American Robin nest (MC, 2003). ▪ Observed caching a duck egg in lawn clippings in neighborhood adjacent to riparian (MC, 2001).
Stellar's Jay	● Observed eating eggs from a Yellow Warbler nest (LVC, 2003). ▪ Observed leaving the vicinity of a Yellow Warbler nest with eggs (LVC, 2003). ▪ Observed on several occasions flying with either an egg or a nestling in bill (LVC, 2004).
Western Scrub-jay	▪ Nestlings in a Yellow Warbler nest (both host and cowbird) were found pecked to death but not consumed. Concurrent with this observation, two adult and two juvenile scrub-jays were observed within 20 meters of the nest calling for 1.5 hours while multiple bird species scolded and mobbed them (Rush Creek, 2003).
chipmunk	▪ Observed leaving partially depredated magpie nest while on eggs. The nest was completely depredated by the subsequent nest check (Rush Creek, 2005).
garter snake	● Observed depredating nestlings from a Song Sparrow nest (LVC, 2002). ● Observed depredating Brewer's Blackbird nestlings (LVC, 2001). ● Observed in a second Song Sparrow nest, from which the snake had eaten either a cowbird egg or a recently hatched nestling (based on nest history; LVC, 2005). ● Observed eating a Savannah Sparrow nestling (WC, 2002). ▪ Observed 2 meters from a Song Sparrow nest with young the day before they were depredated (LVC, 2004).
gopher snake	● Observed depredating young from a Spotted Towhee nest (MC, 2002).

● denotes observations that unequivocally identify nest predators.

▪ denotes suggestive observations: (1) predators observed at the nest or within 5 meters of the nest during the same observation interval a nest was depredated (within 4 days), (2) predators observed with either eggs or nestlings in mouth/ bill, (3) fresh sign of a particular predator (i.e., cowbird eggs) appearing at a nest or within 5 meters of a nest during the same observation interval the nest was depredated (within 4 days).

Observations recorded along Rush Creek (RC), Lee Vining Creek (LVC), Mill Creek (MC), or Wilson Creek (WC).

FIGURE LEGENDS

Figure 1.1. Camera at nest (photo by Arya Degenhardt).

Chapter 2. An "ecological trap" for Yellow Warblers and its underlying processes

ABSTRACT

According to habitat selection theory, animals should select habitats that promote their fitness. Because nest survival is a major component of avian fitness and predation the main cause of nest failure, we expect birds to place their nests in sites where they are least likely to be depredated. I tested this hypothesis for a population of Yellow Warblers (*Dendroica petechia*) that breed in riparian vegetation along Rush Creek, a tributary of Mono Lake, CA. I quantified nest habitat preference by comparing microhabitat structure at nest sites (microhabitat use) versus random sites (microhabitat availability). Additionally, since territories are selected for factors other than nest survival (e.g., food availability), I controlled for habitat variation among territories when analyzing preference. To analyze preference relationships with nest survival, I fit generalized linear models to data from monitoring both natural and experimental nests. Yellow Warblers preferred nest sites in willow-dominated (*Salix sp.*) microhabitat patches despite the higher predation rates experienced there in comparison to predation rates in alternative microhabitats. This preference clearly arose during within-territory selection for nest sites, when birds should pay the closest attention to predation risk. At least two different predators with very different hunting strategies (cowbirds and rodents) depredated experimental nests at elevated rates in willow microhabitats. The nest site selection strategy that would most effectively avoid predation risk probably depends upon which of these predators are more important. Nevertheless, I conclude that the current strategy employed by Yellow Warblers is not optimal for avoiding nest predation.

INTRODUCTION

Habitat selection is the central behavioral process by which animals choose where to live and breed. Theory predicts that animals will prefer those habitats that confer the greatest benefits to fitness (Rosenzweig 1981, Svardson 1949, Thorpe 1945). Furthermore, since habitat preference is heritable in a variety of taxonomic groups (Jaenike and Holt 1991), we expect such "adaptive" habitat preferences to be maintained by natural selection in wild populations. However, contrary to this basic theoretical expectation, studies of a variety of taxonomic groups provide substantial evidence for maladaptive preferences (reviewed by Battin 2004). These empirical observations have given rise to the "ecological trap" concept.

The term "ecological trap" was originally used to describe locations in which populations favor less than optimal habitats despite the availability of better habitats (Gates and Gysel 1978, Misenhelter and Rotenberry 2000). Recent interest in ecological traps has focused on the potential implications of traps to conservation biology (Battin 2004, Schlaepfer et al. 2002), which arises from their potential to threaten population persistence particularly for populations that favor extremely poor quality habitats (Delibes et al. 2001, Donovan and Thompson 2001, Kokko and Sutherland 2001, Kristan 2003). However, regardless of the impact of traps on population dynamics, the presence of traps raises an important question for evolutionary ecologists: why do some populations favor non-optimal habitats? Due to the strong interest in the consequences of traps to conservation, some authors restrict their definitions of "ecological trap" to describe situations either where populations favor sink habitats (Battin 2004, Part et al.

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2007), or where maladaptive preferences are caused by anthropogenic disturbance (Schlaepfer et al. 2002). However, any system in which populations favor relatively low quality habitats is of interest to evolutionary ecology, so I use the original, more inclusive, definition of an ecological trap (in sensu Gates and Gysel 1978, Misenhelter and Rotenberry 2000) in this paper.

Studies of birds have provided much of the empirical evidence for ecological traps. Nest survival is an important component of avian fitness (Ricklefs 1969, Lack 1966, Saether and Bakke 2000) and predation is usually the main cause of nest failure (Martin 1993, Nice 1957, Ricklefs 1969). Consequently, predation is an important agent of natural selection that has strongly shaped the evolution of avian traits (Collias and Collias 1984, Martin 1995), so ornithologists expect birds to select nest habitats that maximize nest survival and minimize predation risk (Bekoff et al. 1989, Martin 1998). However, a number of studies document preferences for habitat associated with reduced nest survival and elevated predation rates (Gates and Gysel 1978, Misenhelter and Rotenberry 2000, Shochat et al. 2005). These traps are generally thought to 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 (Chalfoun et al. 2002). However, why these populations of birds continue to prefer high-predation habitats is not well understood.

Some consideration of spatial scale is likely necessary to understand ecological traps for birds, since both habitat selection and processes underlying habitat-predation patterns arise at multiple spatial scales (Wiens et al. 1987, Chalfoun et al. 2002, Chalfoun

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and Martin 2007). When considering habitat selection, at least two spatial scales are of interest. 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, such as nest site microhabitat in which nests are established. Nest predation should most strongly influence nest microhabitat selection, whereas territory selection may be shaped by other factors, such as food availability (Shochat et al. 2005). Indeed, many purported traps for birds (reviewed by Robertson and Hutto 2006) may arise because birds select territories on the basis of food availability at the expense of nest survival (Shochat et al. 2005, Chalfoun and Martin 2007). Habitat can also influence nest predation at either coarse scales by influencing predator number and distributions (Chalfoun et al. 2002), or at finer scales by influencing their hunting strategies and/or nest detection (Martin 1993, Schmidt et al. 2001). Birds should pay the greatest attention to fine-scale habitat predation patterns while selecting nest sites from within their territories, whereas coarse-scale habitat-predation patterns are more relevant to territory selection and should therefore have a greater potential for "trapping" birds.

Here, I present evidence for an ecological trap for a population of Yellow Warblers (*Dendroica petechia*) that breed along Rush Creek, a tributary of Mono Lake, CA. I found nest site selection to be "trapped" by predation risk despite the expected importance of predation to habitat selection at this scale. Yellow Warblers preferred to nest in willow-dominated microhabitat patches even though birds that built their nests in non-willow microhabitats experienced lower predation rates. This maladaptive preference

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was apparent over a substantial time period (nine years). Given the relatively fine spatial scale at which this trap arises, trade-offs between predation risk and other agents of selection are unlikely. By considering important nest predators and how they contribute to habitat-predation patterns, I explore the extent to which alternative nest site selection strategies would be more effective for avoiding nest predation. However, regardless of which strategy would be most adaptive, the nest site selection strategy currently employed by Yellow Warblers does not minimize nest predation risk.

METHODS

Study Species and Location

Yellow Warblers are an open-cup, shrub and tree-nesting neotropical migrant passerine that breeds mainly in riparian habitat across North America (Lowther et al. 1999). Yellow Warblers are the *D. p. brewsteri* (considered synonymous with *D. p. morcomi*, see review in Heath, 2008). Males establish territories, females select nest sites, build nests, and incubate the eggs, and both parents feed the young. Numerous predator species prey on Yellow Warbler nests, and they are also a common host of the brood-parasitic Brown-headed Cowbird (Lowther 1983). Although this species is of minimal conservation concern of globally (IUCN 2008), Yellow Warblers are a California State Species of Special Concern (Shuford and Gardali 2008).

I conducted this study along lower Rush Creek, the largest tributary of Mono Lake, east of the Sierra Nevada mountain range in California (2020 m, 38°04'N, 119°10'W). A detailed description of the historic and current vegetative, hydrologic and

management conditions of lower Rush Creek are provided by McCreedy and Heath (2004). In summary, the riparian habitat along Rush Creek has been recovering from decades of extreme water diversions that ended in 1990 and livestock grazing that ended by 1994 (Hart 1996, SWRCB 1994).The lower reach of the stream is now dominated by three species of willow (*Salix exidua*, *S. lucida*, *S. lutea*) and interspersed by Woods' rose (*Rosa woodsii*), which forms large, continuous stands (as much as 50-100 meters across) in various locations scattered throughout the riparian corridor. The extensive pre-diversion canopy layer dominated by cottonwoods (*Populus balsamifera* ssp. *trichocarpa*) is now mostly absent, but willows do grow as high as 6-8 meters in some areas. The adjacent upland is dominated by big sagebrush (*Artemisia tridentata*), but also includes bitterbrush (*Pursia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus.*). The recovery of riparian vegetation has partially reversed the encroachment of sagebrush into the riparian corridor. However, sagebrush still forms a substantial component of the shrub layer along Rush Creek (McBain and Trush 2003).

Along Rush Creek, male Yellow Warblers arrive and establish territories in early May, and females initiate nests starting in late May and continue initiating new attempts following nest failure through the first week of July. Predators either observed depredating nests along Rush Creek (either directly or with video monitoring) or suspected of depredating nests include garter snakes (*Thamnophis* sp.), mice (Muridae/ Cricetidae), least chipmunks (*Tamias minimus*), raccoons (*Procyon lotor*), weasels (*Mustela* sp.), Western Scrub-Jay (*Aphelocoma californica*), Black-billed Magpie (*Pica hudsonia*), wrens (Troglodytidae), and Bullock's Oriole (*Icterus bullockii*; Chapter 1). In

addition, Brown-headed Cowbirds parasitize ca. 50% of Yellow Warbler nests in our study area and are also documented nest predators (Arcese et al. 1996, Chapter 1). Second brood attempts after successful first broods (as opposed to re-nesting after nest failure) were rarely observed in the Mono Basin (PRBO unpublished data) and were not observed along Rush Creek during this study. Individual Yellow Warbler pairs occupy exclusive territories encompassing a substantial area of riparian habitat (0.29 ± 0.17ha) from which they select nest sites.

Fieldwork

Yellow Warbler nest monitoring, demography, and habitat measurements. Yellow Warbler nesting demography was monitored along Rush Creek from 2000-2005 as part of a wider riparian songbird monitoring program conducted by PRBO Conservation Science. The study plot during this period consisted of a 39 ha. plot of riparian habitat along 2.3 km of Rush Creek. From 2006-2008, I continued studying Yellow Warbler demography along Rush Creek focusing specifically on the relationship between nest habitat preference and predation risk for Yellow Warblers. During this period, I monitored nests on the upper half (1.0 km) of the Rush Creek study plot, encompassing 20.3 ha of riparian habitat. During the entire study period, PRBO and I determined the location and number of all distinct breeding territories within the study plot using season-long observations of territorial behavior (singing behavior, simultaneous nesting, aggressive behavior), and found and monitored as many nests as possible within these territories (Martin and Geupel 1993, Robbins 1970). We found nests for 70-94% of all

territories in any given year. We visited each nest at least once every four days and recorded contents until the nest failed or fledged young. We minimized disturbance to vegetation near nests and avoided attracting predators to active nests. Specific precautions included minimizing observer contact with vegetation surrounding nests to avoid leaving scent trails, checking multiple locations in addition to the nest location to confuse any predators potentially following observers, spending as little time as possible at the nest when checking it, and avoiding checking nests when potential nest predators were within line-of-site of the observer (Martin and Geupel 1993, Robbins 1970).

We measured Yellow Warbler nest habitat use by measuring microhabitat at nest sites, focusing on metrics of shrub structure and composition. These metrics included (1) overhead cover, (2) willow cover, (3) willow stem counts, (3) Woods' rose cover, and (5) non-riparian shrub cover (mainly sagebrush). Following Martin et al. (1997), we measured overhead cover with a densiometer and the other four measurements across 5-meter radii circles centered on each nest. In addition, we recorded *nest substrate* (i.e., whether willow, Woods' rose, or sagebrush supported the nest) at nest sites, and we also estimated concealment and nest height which I described and analyzed in more detail in a separate, parallel study (Latif Dissertation Ch.2). I focused my study mainly on the structure and composition of the shrub layer because previous work on Yellow Warblers (Knopf and Sedgewick 1992) demonstrated structural features of the shrub layer to be of primary importance to Yellow Warblers selecting nest sites.

We measured habitat availability by measuring microhabitat at random sites using the same metrics applied to nest sites. From 2001-2005, PRBO measured nest habitat

available to all riparian bird species along Rush Creek by measuring microhabitat at sites centered on each of 30 random points per year. They generated these points within the boundaries of the study plot using ArcGIS software (ESRI 1996). From 2006-2008, I focused availability measurements along Rush Creek specifically on nest habitat available to Yellow Warblers by centering my measurements on potential nest shrubs nearest to each random point generated during this period along Rush Creek. Potential nest shrubs included any shrub capable of supporting a Yellow Warbler nest (verified with previously-used nests) except for rabbitbrush, since we never found nests in rabbitbrush probably due to its inadequate structural integrity.

In addition, for an analysis of Yellow Warbler nest habitat preference that controlled for variation in habitat availability amongst territories (see below), I needed to measure habitat availability within individual territories, which required measuring multiple random sites per territory. In 2006, I digitized each Yellow Warbler territory, randomly selected thirty of these territories, and randomly generated three random points within each of these thirty territories (90 points total). In 2007 and 2008, I generated a grid of 514 points spaced ~20 meters apart spanning the entire portion of the study plot (in these years the upper sub-plot), and we took measurements at 431 sites randomly selected from this grid. I then overlaid digitized territories over grid-sites in ArcGIS and assigned each measured site either to the territory within which it was contained or to the nearest territory. Grid sites located more than 20 meters outside any territories were not assigned to any territories. This process was repeated for each year, so each measured grid site was linked to up to three territories (i.e., one per year from 2006-2008).

Experimental nest monitoring. In addition to monitoring natural nests, I also monitored experimental nests along Rush Creek from 2006-2008 to elucidate the mechanisms underlying habitat-predation relationships. Because habitat can be manipulated for experimental nests (i.e., I selected experimental sites), habitat-predation relationships for experimental nests allowed me both to infer causal relationships between habitat and predation rates and to investigate which habitat features were most closely related with predation risk. In addition, since experimental nests lack parents and since parental behavior can also influence predation risk, experimental nests allowed me to measure the direct effects of habitat on predators while controlling for any potential indirect habitat effects that could arise from effects on parental behavior (Martin 1992, Weidinger 2002). Finally, I placed clay eggs in experimental nests that recorded bite impressions useful for distinguishing between avian versus rodent predators (Dion et al. 2000, Weidinger 2002). I used these to determine which of these two predators were most influenced by habitat features of interest. Because avian and rodent predators differ in behavior, morphology, and natural history, they can be affected by habitat in different ways, so information on predator-specific habitat-predation relationships also provides useful information for identifying the most likely mechanisms linking habitat with predation risk.

I ensured that data from experimental nests were relevant to predation risk experienced by Yellow Warblers by constructing experimental nests that simulated Yellow Warbler nests as closely as possible. Each experimental nest consisted of a previously-used Yellow Warbler nest containing one passerine egg (from a Zebra Finch

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(*Taeniopygia guttata*)) and one clay egg, which I monitored for a maximum of 14 days (i.e., the average Yellow Warbler egg period) using the same protocol as I used to monitor natural nests. I considered nests depredated when finch eggs were either damaged or removed and/or if bite impressions were left in clay eggs. After monitoring, I measured habitat characteristics using methods identical to those performed for natural nests, and identified the predators responsible for clay egg bite-marks when possible.

In 2006-2007, I monitored experimental nests in 140 sites representing a broad range of microhabitats most commonly used by nesting Yellow Warblers (i.e., in rose and willow) from June to early July. To allow us to distinguish between the effects of patch structure on predation risk and the effects of other nest habitat features, I minimized the correlation between microhabitat variation and variation in other nest site attributes (i.e., concealment, nest height, and substrate) by stratifying experimental nest placement among both levels of site-scale attributes (i.e., >80%, 30-80%, and <30% concealed sites; < 75cm and > 75cm sites; rose and willow nest shrubs), and classes of patch-scale microhabitat structure (i.e., willow-dominated and rose-dominated patches).

In 2008, I used experimental nests to determine if habitat was correlated with predation risk at a spatial scale that would allow Yellow Warblers selecting nest sites to mitigate predation risk. Since nest sites are chosen from within territories, Yellow Warblers can only use nest habitat selection to evade predators if predation is affected by microhabitat at a within-territory scale. However, since Woods' rose grows in large contiguous patches along Rush Creek, rose-dominated microhabitat patches are not evenly distributed across the riparian landscape. Consequently, larger scale habitat effects

on predator densities could potentially drive microhabitat-predation relationships, in which case Yellow Warblers could only evade predators by selecting low-predation territories. At the territory scale, factors such as food availability may trump the influence of predation risk on habitat selection since territories are selected for activities other than nesting (e.g., foraging; Shochat et al. 2005).

To examine the spatial scale of habitat effects on predation, I monitored 30 pairs of experimental nests (60 nests total) arranged to distinguish microhabitat-predation effects from territory-scale effects. For each pair, one nest was placed in a site characterized by preferred habitat (i.e., a willow-dominated patch) and the other was placed in less preferred habitat (i.e., a patch dominated by either Woods' rose or sagebrush; see results of preference analysis). In addition, I placed members of each pair ca.10-30 meters apart, which is a distance smaller than the diameter of most Yellow Warbler territories. Therefore, sites occupied by members of each pair represented two alternative choices that an individual nesting female could have made. Furthermore, this distance is probably smaller than the home ranges of two predator types of particular interest: chipmunks and corvids (Bowers et al. 1990, Lacher and Mares 1996, Curry et al. 2002, PRBO unpublished data, Trost 1999), so sites occupied by each nest pair also represented alternative foraging locations for individual predators.

Data Analysis

Habitat Preference. I identified preferred nest habitat features and quantified Yellow Warbler nest habitat preference by analyzing differences between nest site habitat

measurements (i.e., habitat use) and random site measurements (i.e., habitat availability).

I analyzed these differences primarily using Multiple Analysis of Variance (MANOVA)

and discriminant function analyses (DFA). MANOVA tested for differences between nest

and random sites with respect to variables describing microhabitat patch structure. Given

significant differences, I used DFA to calculate linear functions of habitat variables that

best discriminated between nest and random sites (i.e., discriminant functions;

Tabachnick and Fidell 2001). Discriminant functions essentially described habitat

gradients associated with preference, or *preference gradients* (Misenhelter and

Rotenberry 2000), and the value of any individual site calculated using such a function

was a *preference score* (i.e., the location of a site along a preference gradient; *abbrev*.

PrefScr). I identified preferred and avoided habitat features by referring to *loadings* (i.e.,

correlation coefficients between raw habitat variables and preference scores), referring

only to loadings > 0.32 (Tabachnick and Fidell 2001).

   To control for variation in observers and measurement protocol among years, I

separated the data into three time blocks, 2001-2003, 2004-2005, and 2006-2008, and I

carried out separate preference analyses for each of these periods. Because of the

difference in protocol used to sample habitat availability in 2006-2008 (i.e., random site

measurements were centered on shrubs instead of points in space), I analyzed preference

for this period separately from the other periods. In addition, from 2001-2005, different

observers measured random sites each year, so I divided this dataset into two similarly

sized subsets collected by different sets of observers by separating 2001-2003 data from

2004-2005 data. Because I analyzed preference separately for these three time periods, I

generated three preference gradients: PG1 from 2001-2003 data, PG2 from 2004-2005 data, and PG3 from 2006-2008 data.

I also analyzed preference exhibited by Yellow Warblers on Rush Creek from 2006-2008 using a procedure that controlled for variation in habitat availability amongst territories. This procedure was based on analyzing the differences between nest and random sites within individual territories. First, I identified major axes of habitat variation using a principal components analysis (PCA; Tabachnick and Fidell 2001) applied to grid site habitat measurements (2007-2008 sites only). I retained all components (PCs) with eigenvalues > 1 (Tabachnick and Fidell 2001). I scored all nest sites and random sites along retained PCs. I then calculated the mean score for nest sites (i.e., habitat use by individual birds) and the mean score for random sites (i.e., within-territory habitat availability) for each territory along each habitat gradient. Finally, I used factor loadings (correlations between PC axes and raw variables) to interpret which habitat gradients were described by the PCs, focusing specifically on loadings > 0.32 (Tabachnick and Fidell 2001). I analyzed within-territory differences between mean scores along PC axes for nest versus random sites using randomized-complete-block ANOVA models (one analysis per PC). Each ANOVA model included a territory parameter (i.e., block) and a Preference parameter (the difference between nest means and random site means within territories; i.e., treatment) as sources of variation (Sokal and Rohlf 1995).

In addition, I included two parameters that accounted for the effects of sampling effort when measuring habitat availability as covariates in ANOVA models. Inadequate

sampling effort when measuring habitat availability (i.e., random sites) would elevate sampling error, which could give rise to spurious differences between nest and random sites particularly for those territories within which habitat availability was sampled the least. As an index of sampling effort, I computed the percent area of individual territories sampled (PAS) by random site measurements (PAS = (# random sites $\times$ 78.5 [the area of a 5-meter radius circle]) / area of the territory (m^2)), and I included PAS as well as an interaction term, PAS*Preference, as sources of variation in randomized-complete-block ANOVA models. I calculated F-values using Type III Sums of Squares, so by including PAS and PAS*Preference as covariates in ANOVA models, the Preference parameter only accounted for the contribution of pair-wise differences between nest and random site PC score means after controlling for the potential influence of sampling effort.

Nest survival. My analysis of nest survival was based on calculating daily survival rates (DSR), so I assessed the fate of a nest each time a nest was checked by an observer. I considered natural nests to have "failed" when no Yellow Warbler eggs or nestlings remained in the nest, the nest was abandoned by the parents, or eggs remained un-hatched substantially past the normative incubation period (11.3 days; PRBO unpublished data). I considered nests that contained only Brown-headed Cowbird eggs or nestlings as having failed. I considered nests that initially contained both Yellow Warbler eggs and cowbird eggs but subsequently hatched only cowbird eggs as having failed on hatch day. I defined failure for experimental nests previously.

To analyze the relationship between habitat preference and nest survival, I fit generalized linear models describing DSR as a function of preference scores (PScr's) and

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covariates to data from nest monitoring using *proc genmod* (SAS 9.1; Shaffer 2004).

Covariates included three temporal variables: *year*, *date* (within-season timing expressed

as the day of the year), and *stage* (egg vs. nestling (within-nest cycle timing)); one spatial

variable: *sub-plot* (upper vs. lower half of study plots); and *parasitism status* (i.e.,

whether the nest contained viable cowbird eggs or nestlings when observed). All of these

variables were found from preliminary analyses to be correlated with DSR, so I included

all these variables as covariates in DSR models, although only year and date were

included in DSR models fit to experimental nest data since only these variables applied to

experimental nests. In addition, I included parameters describing interactions between

PScr's and covariates in DSR models to look for spatial or temporal inconsistencies in

preference-survival relationships.

I analyzed the statistical evidence for preference-survival relationships by

comparing the fit of DSR models that included PScr's as a predictor variable to the fit of

models that included only covariates. I used one of two indices of model fit: Akaike's

Information Criterion corrected for sample size (AIC_c), or an equivalent variant that

corrected for over-dispersion ($QAIC_c$). From these indices, I calculated Akaike weights

(w_i), which provide the relative weight of evidence for individual models within a given

set of models on a scale from 0-1. Dividing the weight of one model by the weight of

another produces an evidence ratio (ERs), which provides the weight of evidence of one

model over another irrespective of the set of models used to calculate the Akaike weights

(Burnham and Anderson 2002). I calculated evidence ratios for preference models

compared to covariate-only models (ER = $w_{PScr-model}$ / $w_{Covariate-only-model}$) to examine the

weight of evidence for preference-survival relationships. An ER < 1 would indicate poor evidence for a particular preference effect, whereas an ER > 1 but < 2 would indicate marginal evidence and an ER > 2 would indicate relatively strong evidence for a particular preference effect. For each set of models fit to a particular dataset, I decided whether to derive model weights and evidence ratios from AIC_c or $QAIC_c$ depending upon a variance inflation factor (c) derived from a goodness of fit statistic ($c = \chi^2_{GOF} /$ d.f.; d.f. = 8) applied to a model containing the maximum number of explanatory variables appearing in the model set (i.e., the "global" model). When c > 1, I used $QAIC_c$ to calculate model weights, for which I divided log-likelihood value by 'c' and thus corrected for over-dispersion (Burnham and Anderson 2002). Finally, I tested for inconsistencies in habitat effects by examining evidence ratios for PScr*covariate interaction relationships ($ER = w_{PScr*covariate-model} / w_{additive-PScr-model}$).

In addition to examining the statistical evidence for preference-survival relationships, I also examined the relative magnitude and direction of habitat effects on nest survival by referring to parameter estimates and their standard errors and by graphing period nest survival rates ($NSR = DSR_{egg}^{14.3} \times DSR_{nestling}^{9.8}$; 14.3 = mean # days for laying + incubation, 9.8 = mean # days from hatching to fledging; $NSR = DSR^{14}$ for experimental nests) and their confidence intervals along preference gradients (Powell 2007, Shaffer and Thompson 2007). To facilitate comparisons of parameters, I standardized preference scores for nests (PScr = discriminant score – mean discriminant score) / s.d. of discriminant scores; where mean and s.d. were calculated from natural nest values) before fitting preference models to the data.

Fledge number. Fledge number is a component of fecundity that is not accounted for by my metric of nest survival, and therefore could trade-off with predation risk. I modeled fledge number for successful nests (FN = fledge number for nests that produced at least one Yellow Warbler fledgling) as a linear function of various combinations of preference scores and covariates using *proc genmod* (SAS 9.1). I modeled fledge number as a linear function of habitat variables and covariates, and calculated evidence ratios for habitat effects on fledge number using the same procedure employed to analyze habitat effects on nest survival. Fledge number models included all covariates that improved model fit in preliminary analyses. I examined evidence ratios, as well as parameter estimates and their standard errors for habitat effects on fledge number to evaluate the potential for trade-offs between fledge number and nest survival.

Mechanistic analyses. I conducted two mechanistic analyses of habitat-predation relationships. The first of these was aimed at determining which habitat features were most directly related with predation risk. I was interested in whether microhabitat patch structure or the shrub species supporting the nest (i.e., a site-scale feature) had a greater influence on predation risk. So, I fit models describing DSR as a function of all possible combinations of three variables to data from natural nests. These variables included scores along principle component axes retained from our within-territory preference analysis (PC1 and PC2; i.e., microhabitat patch structure) and the shrub species supporting the nest (i.e., Substrate). In addition, I also fit models describing DSR as a function of all possible combinations of PC1 and Substrate to data from 2006-2007 experimental nests (excluding PC2 from these models since these nests were not placed

in sagebrush). I calculated *variable weights* (i.e., the sum of the Akaike weights for models containing the variable of interest) to examine the relative importance of each variable for predicting nest (Burnham and Anderson 2002). In order to examine the magnitude of these relationships, I also calculated parameter estimates, NSR estimates at various points along habitat gradients, and standard errors. By averaging across models, I derived values that were independent of model structure (Burnham and Anderson 2002). In addition, shrub structure could affect nest predation by influencing nest concealment (Martin 1993, 1989), so to control for potentially confounding concealment effects, I included concealment parameters reflecting known relationships between concealment and DSR (i.e., a quadratic model for experimental nests and a concealment $\times$ *year* interaction model for natural nests; Dissertation Ch.2) as covariates in all of the models for this analysis. We did not include nest height as a covariate in these models because height was not found to be a good predictor of nest survival (Dissertation Ch. 2).

My second mechanistic analysis examined whether habitat affected predation risk at a within-territory spatial scale (i.e., the scale at which nest habitat selection could evade predators) by analyzing data from 2008 experimental nest pairs. I compared nest survival for experimental nests between habitats on a pair-wise basis. I computed the number of days each nest survived (survival time; *abbrev.* ST) assuming that depredated nests failed half-way between the penultimate and the ultimate nest check, and that successful nests survived for 14 days (the average length of the Yellow Warbler egg period). I used a randomized-complete-block ANOVA model to analyze variation in ST. In this model, I included a class variable that accounted for the contribution of the nest

pair to ST (i.e., the block), which I named Location, and a Habitat parameter (i.e., preferred or less preferred habitat), which accounted for pair-wise differences in ST (i.e., treatment; Sokal and Rohlf 1995). I also included Concealment as a covariate in this model to control for potentially confounding effects of nest concealment on predation risk.

Habitat effects on avian versus rodent predators. To examine the contribution of avian versus rodent predators to preference-survival relationships, I modeled predator-specific bite rates of clay eggs as a function of experimental nest preference scores and covariates using logistic exposure models (Shaffer 2000). For these models, I defined a nest as 'failed' only when a bite impression by the predator type of interest was left in the clay egg within the experimental nest being observed. For this analysis, I excluded data from observation periods during which the nest was depredated but no identifiable bite impressions were left in the clay. For models of avian bite rates, I considered nests depredated by rodents to have 'survived,' but I truncated the data from these nests at the point of depredation, and I did the opposite for rodent models. I used these models to calculate predator-specific bite rates (PSBR = 1 - DSR[14]) along preference gradients. I only modeled the relationship between PSBR and PG3, since this preference gradient had the strongest relationship with nest survival (see below).

RESULTS

Habitat Preference. During the study period, nest sites were generally associated with more willow and less non-riparian shrubs when compared to random sites. In addition,

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Woods' rose did not differ as substantially between nest and random sites, and these patterns were generally consistent across time periods. Multivariate F-values testing for differences between nest and random sites were significant for all time periods and overhead cover was associated with the largest positive loadings on all preference gradients (Table 2.1). Across all nest and random sites ($n = 1614$), overhead cover was positively correlated with willow variables (willow cover: $r = 0.64$; willow stems: $r = 0.20$), and negatively with non-willow variables (rose cover: $r = -0.26$; non-riparian cover: $r = -0.31$; all $P < 0.001$), so higher overhead cover at nest sites was probably a consequence of the presence of more willow shrubs at nest sites. The positive loadings of willow cover and stem counts on preference gradients support this interpretation. Preference gradients were negatively loaded by non-riparian cover and had weaker loadings with rose cover, indicating an avoidance of sagebrush and relative ambivalence towards Woods' rose. The three preference gradients for Rush Creek were all highly correlated with each other (for nest and random sites, among $PScr_{PG1}$, $PScr_{PG2}$, and $PScr_{PG3}$ all r's > 0.80), so Yellow Warbler preference was generally consistent across time. The distributions of nest and random sites along preference gradients were clearly different but also overlapped substantially (Figure 2.1), so I was confident that random sites could have been occupied by nests and were therefore available to nesting Yellow Warblers.

When comparing nest versus random sites within territories, I also found that relative to random sites, nest microhabitats were characterized more by willow than non-willow and more Woods' rose than sage brush. From the PCA applied to 2007-2008 grid

site measurements, two components had eigenvalues > 1 (Table 2.2). The first component (PC1) was loaded positively by willow variables and negatively by non-willow variables, indicating that this axis describes a habitat gradient ranging from willow-dominated microhabitats at its positive end to non-willow microhabitats at its negative end. The second component (PC2) was most strongly positively loaded by sagebrush cover and negatively by rose cover, so this axis describes a gradient from microhabitats characterized more by Woods' rose to those characterized more by sagebrush. Mean differences within territories (nest site means - random site means) were positive for PC1 (0.36) and negative for PC2 (-0.29), indicating that mean PC scores for nests favored the willow end of the PC1 gradient and the Woods' rose end of the PC2 gradient (Figure 2.2). F-values associated with within-territory differences were both highly significant (Preference parameters; Table 2.3). On average, 19.6% (s.d. = 8.2%) of individual territories were sampled by random site measurements. PAS and PAS*Preference were marginally significant sources of variation in mean scores along the PC1 axis, but Preference was still a significant source of variation even when controlling for the effects of sampling effort.

The relationship between preference and nest survival. I found consistently negative relationships between nest survival and habitat gradients associated with preference. From 2000-2008, we found and monitored 728 active nests along Rush Creek in which we observed at least one Yellow Warbler egg or nestling. Of these, 481 failed and 247 succeeded. We attributed 374 (78%) failures to nest predation making predation the predominant cause of failure for natural nests. For both experimental and natural

nests, evidence ratios for two out of three preference-survival (PG-DSR) relationships were > 2 and all estimates for parameters describing PG-DSR relationships were negative (Table 2.4). From the parameter estimates for relationships on Rush Creek, I calculated NSR estimates for natural nests ranging from 0.29 ± 0.07 s.e. to 0.14 ± 0.06 s.e., 0.27 ± 0.07 s.e. to 0.16 ± 0.06 s.e., and 0.32 ± 0.07 s.e. to 0.12 ± 0.05 s.e. from the less preferred ends (PScr = -2) to the more preferred ends (PScr = -2) of PG1, PG2, and PG3 respectively. Experimental nest NSR ranged from 0.22 ± 0.05 s.e. to 0.10 ± 0.03 s.e., 0.19 ± 0.05 to 0.12 ± 0.04, 0.24 ± 0.05 s.e. to 0.07 ± 0.03 s.e. from the less preferred (PScr = -1) to the more preferred (PScr = 1) ends of PG1-R, PG2-R, and PG3-R respectively. Thus, from preference-survival models, I calculated 40-64% decreases in NSR (period survival) for natural nests and 39-72% decreases in NSR for experimental nests from less preferred to more preferred ends of preference gradients, with the largest decreases found along PG3 (Figure 2.3). I also found little evidence for PG*covariate interactive relationships with DSR (all ERs < 1), so preference-survival relationships were fairly consistent across time, space, and parasitism status.

Fledge number. Fledge number was not related with nest habitat preference. I found little evidence for relationships between PGs and fledge number, and parameter estimates for these relationships were small and their standard errors were large (Table 2.5).

Mechanistic analyses. The shrub feature that was most strongly and consistently related with predation risk for both natural and experimental nests was the degree to which microhabitat patches were characterized by willow. From DSR models fit to

natural nest data, PC1 (representing a gradient from willow-to-non-willow dominated patches) was associated with the largest variable weight, and model-averaged parameter estimates for this relationship were negative (Table 2.6). Model-averaged NSR estimates for natural nests decreased by 53% from the negative to the positive end of the PC1 gradient (from PC1 of -2 to 2, NSR decreased from 0.32 ± 0.07 s.e. to 0.15 ± 0.05 s.e.). From models fit to 2006-2007 experimental nest data, variable weights for PC1 versus *substrate* did not differ as substantially as they did for natural nests models, probably because of a stronger correlation between *substrate* and PC1 among experimental nests ($r = 0.58$). However, model-averaged parameter estimates clearly indicated lower nest survival rates in willow compared to rose, and model-averaged NSR estimates for experimental nests during these years decreased by 38% from the negative end (PC1 = -1.5) to the positive end (PC1 = 1.5) of this gradient (NSR decreased from 0.24 ± 0.07 s.e. to 0.15 ± 0.06 s.e.). Finally, since all models contained concealment parameters as a covariate, relationships between structure and nest predation were not explained by differences in concealment among shrub types.

For experimental nest pairs monitored in 2008, survival time was substantially lower for nests placed in willow microhabitats. Within-pair difference in PG-0608 scores between willow nests minus non-willow nests were all positive (min = 0.02; max = 3.53; mean = 1.76), so willow nests consistently occupied the preferred end of this gradient. Nests in willow microhabitats were depredated substantially faster than their counterparts in either rose-dominated or sagebrush-dominated microhabitats ($ST_{preferred} - ST_{non-preferred}$ = -6.5 days, *sd* = 5.8), and these pair-wise differences contributed significantly to

variation in ST among nests (Table 2.7). Furthermore, ST did not differ substantially between rose nests (9.6 ± 4.8 s.d.; *n* = 15) and sagebrush nests (10.1 ± 4.7 s.d.; *n* = 15; P = 0.67), so the presence of willow was the main habitat feature associated with variation in ST among 2008 experimental nests.

Avian and rodent predation along a preference gradient. Clay eggs were bitten at higher rates by both avian and rodent predators in preferred, willow microhabitats. In 2006 and 2007, out of 140 experimental nests monitored, 77 clay eggs were bitten by nest predators. Of these, 50 were distinguishable as avian bite marks, 23 as rodent, and 4 marks were not identifiable. Avian predators left scratches, pokes, and/or bite impressions that were clearly shaped like the inside of the upper and lower mandibles of a bird bill. Rodent bite impressions were also discernable by the distinctive double-tooth impressions left by their incisors. Since my experimental design in 2008 differed from 2006 and 2007, I generally analyzed the data from 2008 separately (i.e., previous analysis). However, to compensate for low sampling of rodent bites, I supplemented the rodent dataset with data from nests monitored in 2008 (6 additional rodent bites were recorded out of 60 nests monitored in 2008). I found strong evidence for a relationship between PG3 and bite rates for both predator types and model parameters associated with these effects were both negative (Table 2.8), translating into substantially higher estimates of avian and rodent bite rates in preferred microhabitats (Figure 2.4).

DISCUSSION

Evidence for an ecological trap

I found substantial evidence that Rush Creek represents an ecological trap for Yellow Warbler nest habitat selection. Yellow Warblers showed a preference for microhabitats characterized by willow, which was positively associated with predation risk, and this preference was apparent even when I controlled for variation in habitat availability among territories. Although, not all preference gradients had statistically strong relationships with nest survival (i.e., PG2; Table 2.4), preference-survival relationships were consistently negative. In addition, PG3 had the strongest negative relationship with nest survival, and this gradient was particularly relevant to Yellow Warbler nest habitat preference, since random site measurements upon which this gradient was based (i.e., from 2006-2008) were centered on potential nest shrubs. In addition, preference was generally consistent across time periods, and was also consistent with preference patterns found on the other creeks in the Mono Basin (Latif et al. In Prep.), so nest habitat preference appears to be relatively stable for this population and consistent across the Mono Basin. I also found very little evidence for heterogeneity in the relationship between preferred habitat features and predation risk across time or space. Thus, within the time-frame of this study, Yellow Warblers continually preferred nest habitats that were consistently associated with relatively high predation risk.

I used non-random habitat use (i.e., a difference between habitat use and availability) to document habitat preference (Jones 2001), which has been challenged as a tool for documenting maladaptive habitat preference (Robertson and Hutto 2006). The

major problem with using non-random use as a metric of preference is that variation in territory density, which is not necessarily an index of preference (Bock and Jones 2004), may drive non-random use patterns. However, since I controlled for variation in habitat availability among territories, nest habitat use patterns documented in this study are not likely driven by variation in density at the territory scale.

Willow habitats are the most mesic, whereas Woods' rose habitats are more xeric, and sagebrush is the most xeric (McBain and Trush 2003), so Yellow Warblers essentially prefer the most mesic microhabitats for nesting. Data on Yellow Warblers gathered from the three neighboring riparian systems in the Mono Basin also indicated a preference for mesic nest habitats (i.e., characterized by willow or cottonwood (*Populus trichocarpa*)), and these habitats were also associated with lower nest survival rates and high predation risk (Latif et al. in Prep.). Thus, this ecological trap reflects a general pattern for the Mono Basin.

Trade-offs between predation and other agents of natural selection
Yellow Warblers may continue to prefer high-predation habitats if preferred habitats benefit fitness components other than nest survival enough to outweigh costs incurred by predation risk. Adult mortality may be elevated at the nest site since the attention of adults are focused on nest attendance or if vegetation surrounding the nest obscures approaching predators (Gotmark et al. 1995). However, preference (PG3) was only weakly correlated with vegetation density at the nest site (i.e., concealment) among natural nests ($r = -0.11$, $n = 665$), and to my knowledge, nest habitat relationships with

adult songbird mortality are not documented. Furthermore, I could think of no reason why predation risk would be lower for adults attending nests in willow microhabitats, and variation in fecundity is generally more important than adult survivorship to relative overall fitness for small passerine birds (Clark and Martin 2007, Saether and Bakke 2000). Therefore, a trade-off between nest survival and adult survivorship seems unlikely to shape nest habitat preference.

Two additional agents of natural selection that may trade-off with predation risk are food availability and brood parasitism by cowbirds. Both of these factors are documented to influence brood size (Hoover 2003, food limitation reviewed by Martin 1987, brood parasitism effects: Lowther et al. 1999), but I found no trends in brood size along preference gradients. Predation rates may also co-vary with brood parasitism (Arcese et al. 1996, Tewksbury et al. 2002), and I did find marginal evidence for habitat-parasitism relationships (Q. Latif and PRBO unpublished data), allowing for potential interactions between parasitism and predation, but I found no evidence for such interactions in these analyses. Food availability could also influence the ability of birds to re-nest following failure, which is an important component of fecundity (Powell et al. 1999, Powell and Knutson 2006), and nestling mass at fledging, which may affect juvenile survivorship (a less studied but potentially important component of fecundity; Powell et al. 1999). However, since Yellow Warblers do not feed from the nest site, habitat selection at the territory level or at larger spatial scales should have a much greater influence on food availability than microhabitat selection for nest sites (Chalfoun and Martin 2007, Shochat et al. 2005).

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Could optimal microhabitat selection mitigate predation risk?

Depending upon which habitat features affect predation risk and how these features are related to predator behavior, Yellow Warblers may be incapable of using nest habitat selection to effectively evade predators. Since preferred habitat increased predation for experimental nests, these habitats are clearly influencing predators directly, either by attracting predators to them or by hindering their ability to detect or access nests. However, unlike in other systems (Chalfoun et al. 2002), predators were clearly being influenced at a within-territory scale, given the higher predation rates the willow members of 2008 experimental nest pairs (Table 2.7), and this is the spatial scale at which nest habitat selection can mitigate predation risk. In addition, microhabitat patch structure was most closely related with predation risk. Elements of patch structure could increase predation risk either by increasing the quality of foraging opportunities for predators or by presenting physical obstacles that impede predator movement (Crabtree et al. 1989, Bowman and Harris 1980, Schmidt and Ostfeld 2003). Thorns associated with Woods' rose could impede predator movement, however the willow-to-non-willow gradient (PC1) was more closely associated with predation risk for natural nests than the rose-sagebrush gradient (PC2), and 2008 experimental nests survived just as long in sagebrush as they did in rose. Sagebrush habitat is not particularly dense, so the most likely factor attracting predators to willow is increased foraging opportunities.

Recent studies demonstrate that birds are capable of adjusting nest habitat selectivity in response to direct experiences with predators (Peluc et al. 2008; Chapter 3, Eggers et al. 2006, Forstmeier and Weiss 2004), so a greater encounter rate with

predators has the potential to cause birds to avoid willow. However, if predators actively search for nests, avoiding willow may simply cause predators to shift their foraging effort to whichever habitats Yellow Warblers favor. Active nest-searching by predators would cause predation to be positively correlated with nest density since predators would search more intensely where nests are more abundant (Schmidt and Whelan 1999). However, predation rates on natural nests are negatively related with Yellow Warbler territory density, contradicting the predicted pattern given nest-searching by predators (Chapter 3).

In addition, some predator types are more likely to nest-search than others, so we can consider which predators are depredating nests at higher rates in preferred habitats. Predators with large home ranges are more likely to search for nests since home ranges would contain enough nests to make nest-searching a viable foraging strategy for individual predators. Being obligate brood parasites, cowbirds probably exhibit the most sophisticated nest-searching behaviors of any nest predator (Lowther 1983, Banks and Martin 2001), and corvids and medium-sized mammalian predators are also thought to display nest-searching behavior on a facultative basis (Schmidt and Whelan 1999, Vigallon and Marzluff 2005). Brown-headed Cowbirds were the predominant avian predator, but corvids (e.g. Clark's Nutcracker, American Magpie, Western Scrub Jay and Common Raven) also posed a substantial threat to nests in this system (Chapter 1). These predators may look more intensely for nests in preferred microhabitats where they probably encounter them more frequently. However, small ground predators such as rodents are less likely to search for nests since their home ranges are relatively small (Schmidt et al. 2001). Therefore, since willow microhabitats were associated with higher

predation rates on experimental nests by both avian and rodent predators, the nest-searching hypothesis alone is not sufficient to explain why predation rates are higher in preferred microhabitats. The most likely explanation for higher rodent predation rates in willow microhabitats is that these habitats are relatively productive, especially in contrast with the available alternatives, and therefore offer a variety of predators the best foraging opportunities for favored food items.

Population consequences of this trap

According to theory, a potential consequence of an ecological trap is either population extinction, or the formation or exacerbation of a sink such that the population is sustained by immigration (Donovan and Thompson 2001, Kristan 2003, Delibes et al. 2001). From nine years of observation (PRBO and Latif unpublished data), I found no evidence that Yellow Warbler population densities are declining along Rush Creek; ~ 85-100 breeding territories consistently occupied the study plot through 2005 and ~ 60-70 territories have occupied the upper sub-plot through 2008. Furthermore, preliminary results of a population viability analysis, which accounts for apparent adult survival calculated from the return rates of banded birds, indicate this population to be self-sustaining (Heath et al. in progress), so Rush Creek does not appear to constitute a severe enough trap to threaten population persistence.

The likely origins of maladaptive preference and how it is maintained

The most likely explanation for why Yellow Warblers prefer high-predation habitats is that nest habitat preference is shaped in other parts of the Yellow Warbler range. Contrary to patterns found in the Mono Basin, studies in two other locations in California found higher nest survival rates in mesic microhabitats. Nest survival is relatively high in White Alder microhabitats in Shasta County (reviewed by Heath 2008), and in "core riparian habitats" in montane wet meadows in the northern Sierra Nevada Mountain region (Cain et al. 2003). The latter study finds that predators invade riparian habitats from surrounding conifer forests, so nests in the riparian core are relatively inaccessible to these predators. Furthermore, not all mesic microhabitats may be associated with high predation rates even in xeric landscapes. Heltzel and Earnst (2006) did find higher predation rates in willow habitats within another sagebrush landscape, but they also found relatively low predation rates and high nest survival in aspen (*Populus tremuloides*) habitats, which may result from the unique physical features of aspen that reduce nest accessibility to predators (Richardson and Vander Wall 2007). Gene flow and/or intermixing of individuals among populations that experience different predation regimes may counteract the ability for individual populations to adapt to local conditions. The relatively high predation regime observed in the Mono Basin may arise in part because predators focus their foraging efforts in relatively mesic and productive microhabitats while avoiding the relatively xeric alternatives. This xeric-mesic gradient is probably less pronounced in other systems. Variation in the strength of this gradient would be less likely to influence cowbird nest predation, but differences in predation

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regimes among systems suggests that cowbird nest predatory behavior does vary among localities.

The propensity for birds to adapt their nest habitat preferences to local conditions may be further modulated by their life history. The importance of life history is apparent by comparing Yellow Warbler behavior to the nest habitat selection behavior of Willow Flycatchers (*Empidonax traillii*), a species that also breeds along Rush Creek and builds nests similar in structure to Yellow Warblers. Whereas Yellow Warblers along Rush Creek prefer willow, Willow Flycatchers in this system build their nests exclusively in Woods' rose (McCreedy and Heath 2004). Given their similarities in nest structure, experimental nests simulating Yellow Warbler nests also simulate Willow Flycatcher nests, so Willow Flycatchers would probably also experience higher predation rates in willow if they nested there. The exclusive use of Woods' rose as a nesting substrate is an aberrant behavior for Willow Flycatchers (McCreedy and Heath 2004), so this preference may arise from local adaptation or from an adaptive behavioral response to the local predation regime. Strong site fidelity (nesting in the habitat in which one was raised) could also give rise to a preference for rose (i.e., where more nests survive), but I am unaware of any studies documenting an influence of site fidelity on nest site selection of songbirds.

In contrast with Yellow Warblers, Willow Flycatchers may favor low-predation habitats because they have less opportunity to re-nest following nest failure. Whereas Yellow Warblers will initiate nests over a six week period (late May to early July) and a 24 day nesting cycle, Willow Flycatchers have only four weeks to initiate nests (mid-June

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to mid-July) and a 30 day nesting cycle. Because of their high, within-season re-nest rates (up to 6 attempts; PRBO unpublished data), strong differentials in nest survival may not translate to equally strong differentials in fecundity for Yellow Warblers, so natural selection favoring preference for low-predation nest habitats may not be particularly strong. By contrast, nest predation probably imposes relatively higher costs on Willow Flycatcher fecundity and overall fitness, so there is probably greater selective pressure on Willow Flycatchers to select low-predation nest habitats.

One caveat to this hypothesis is that due to high rates of brood parasitism by cowbirds and consequently high nest abandonment rates by host females, Rush Creek currently represents a sink for Willow Flycatchers (PRBO unpublished data). Therefore, the data necessary to measure nest predation rates for Rush Creek Willow Flycatchers in any microhabitats are not available since nests do not survive long enough for predators to find them. However, considering the differences between Yellow Warblers and Willow Flycatchers with respect to both nest habitat selection behavior and life history, larger differentials in predation risk may be necessary to shape nest habitat preference in Yellow Warblers than are present in this system.

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TABLES

Table 2.1. MANOVA results and preference gradient loadings. P-values for all three time-blocks were < 0.001.

| | Preference Gradients | | |
	PG1	PG2	PG3
Multivariate F-values	18.1	12.8	17.08
degrees of freedom	5, 388	5, 309	5, 704
Loadings			
Overhead Cover	0.71	0.88	0.78
Willow Cover	0.39	0.56	0.50
Willow Stems	0.39	0.27	0.57
Rose Cover	0.28	0.01	-0.16
Non-riparian Cover	-0.70	-0.71	-0.48

Table 2.2. Eigenvalues, percent variation explained, and factor loadings for the two principal components retained from a PCA applied to grid sites from 2007-08. -- denotes loadings < 0.32.

	PC1	PC2
Eigen Value	2.49	1.20
% variation accounted for	49.8	24.0
Loadings		
Overhead Cover	0.81	--
Willow Cover	0.94	--
Willow Stems	0.65	--
Rose Cover	-0.62	-0.66
Non-riparian Cover	-0.39	0.80

Table 2.3. Analysis of within-territory preference. *Preference* parameters represent pair-wise differences between mean PC scores for nest versus random sites within territories. *PAS* and *PAS*Pref*erence account for the effects of sampling effort on observed microhabitat variation.

PC	Source	df	Sum of Squares	MS	F-value	p-value
1	**Preference**	**1**	**6.31**	**6.31**	**22.04**	**< 0.001**
1	Territory	168	169.80	1.01	3.53	< 0.001
1	PAS	1	0.91	0.91	3.17	0.08
1	PAS*Preference	1	0.90	0.90	3.14	0.08
2	**Preference**	**1**	**2.90**	**2.91**	**16.49**	**< 0.001**
2	Territory	168	128.81	0.77	4.34	< 0.001
2	PAS	1	0.33	0.33	1.89	0.17
2	PAS*Preference	1	0.29	0.29	1.62	0.20

Table 2.4. Nest survival along preference gradients. $ER_{PScr} = w_{PScr} / w_{Covariates\ only}$. K = # parameters in each model. The natural nest data set included 6,803 observation days (n effective) taken from 732 nests; experimental nest data included 764 observation days from 141 nests. The variance inflation factor (c) for natural nest models = 1.45 (based on the PG-0405 model), and c = 0.43 for experimental nest models (based on the PG-0103 model), so model weights are based on $QAIC_c$ for natural nest models and on AIC_c for experimental nest models.

Nest Type	Model	K	$\Delta AIC_c/ \Delta QAIC_c$	w_i	ER_{PScr}	$\beta_{PScr} \pm se$
	PG-0608	14	0.0	0.69	10.4	-0.16 ± 0.05
	PG-0103	14	2.8	0.17	2.6	-0.12 ± 0.05
Natural	Covariate-only	13	4.6	0.07		
	PG-0405	14	4.7	0.07	0.98	-0.08 ± 0.05
	Intercept-only	1	52.6	< 0.01		
	PG-0608	4	0.0	0.65	8.2	-0.34 ± 0.14
	PG-0405	4	2.2	0.21	2.7	-0.23 ± 0.12
Experimental	Covariate-only	3	4.2	0.08		
	PG-0103	4	5.2	0.05	0.6	-0.14 ± 0.14
	Intercept only	1	7.4	0.02		

Table 2.5. Fledge number and nest habitat preference. Evidence ratios, parameter estimates and standard errors for linear regression models relating fledge number to preference gradients (FN; ER = $w_{PScr+covariates}$ / $w_{covariates\ only}$). $n = 246$. Date and parasitism status were the only covariates that related strongly with FN.

Preference Gradient	ER$_{PrefScr}$	β$_{PrefScr}$ ± se
PG1-R	0.36	0.001 ± 0.061
PG2-R	0.36	-0.013 ± 0.059
PG3-R	0.36	0.001 ± 0.061

Table 2.6. The relative importance of particular shrub features for predicting nest survival. Variable weights ($w_{variable}$) and model-averaged parameter estimates (β) for two patch-scale variables: PC1 and PC2, and one site-scale variable: *substrate.* Models contain *concealment* covariates, so these values control for known effects of concealment on nest survival (a quadratic relationship for experimental nest models, and a *concealment**year interaction for natural nests). β$_{substrate}$ for *willow* was set to zero. Parameter estimates were averaged across models that contained the parameter of interest. Experimental nests from 2006-2007 were not placed in sagebrush, so PC2 was not included as a predictor variable in experimental nest models. For the global experimental model, c = 1.50, and for the global natural nest model, c = 1.26, so variable weights for all models were based on QAIC$_c$.

Nest Type	Variable	$w_{variable}$	Model-averaged β ± s.e.
Natural	PC1	0.76	-0.17 ± 0.08
	PC2	0.39	-0.09 ± 0.09
	Substrate	0.41	Rose: -0.35 ± 0.20 Sagebrsuh: -0.01 ± 0.27
Experimental	PC1	0.50	-0.35 ± 0.20
	Substrate	0.66	Rose: 0.44 ± 0.29

Table 2.7. Pair-wise habitat effects on survival time for 2008 experimental nests. The Habitat parameter tests for a significant within-pair difference in ST controlling for variation in ST among nest pairs and the effects of concealment.

Source	df	Sum of Squares	MS	F-value	p-value
Habitat	**1**	**633.8**	**633.8**	**22.0**	**< 0.001**
Location	29	501.7	17.3	3.5	0.47
Concealment	1	26.4	26.4	1.6	0.22

Table 2.8. Models examining variation in predator-specific bite impressions in clay eggs. N effective (n_eff) provides the number of observation days included in the datasets to which these models were fit.

Predator Type	n_eff	Model	k	ΔAIC_c	w_i	$ER_{PScr-0608}$	β_{PG_0608}	β_{PG}_se
Avian	741.5	PG3	4	0.0	0.94	20.3	-0.56	0.20
		Covariates only	3	6.0	0.05			
		Intercept only	1	8.6	0.01			
Rodent	1149.5	PG3	4	0.0	0.87	10.3	-0.58	0.23
		Covariates only	3	4.7	0.08			
		Intercept only	1	5.7	0.05			

FIGURES

Figure 2.1. Frequency distributions of nest and random sites along three preference gradients generated for three time periods: 2001-2003, 2004-2005, 2006-2008.

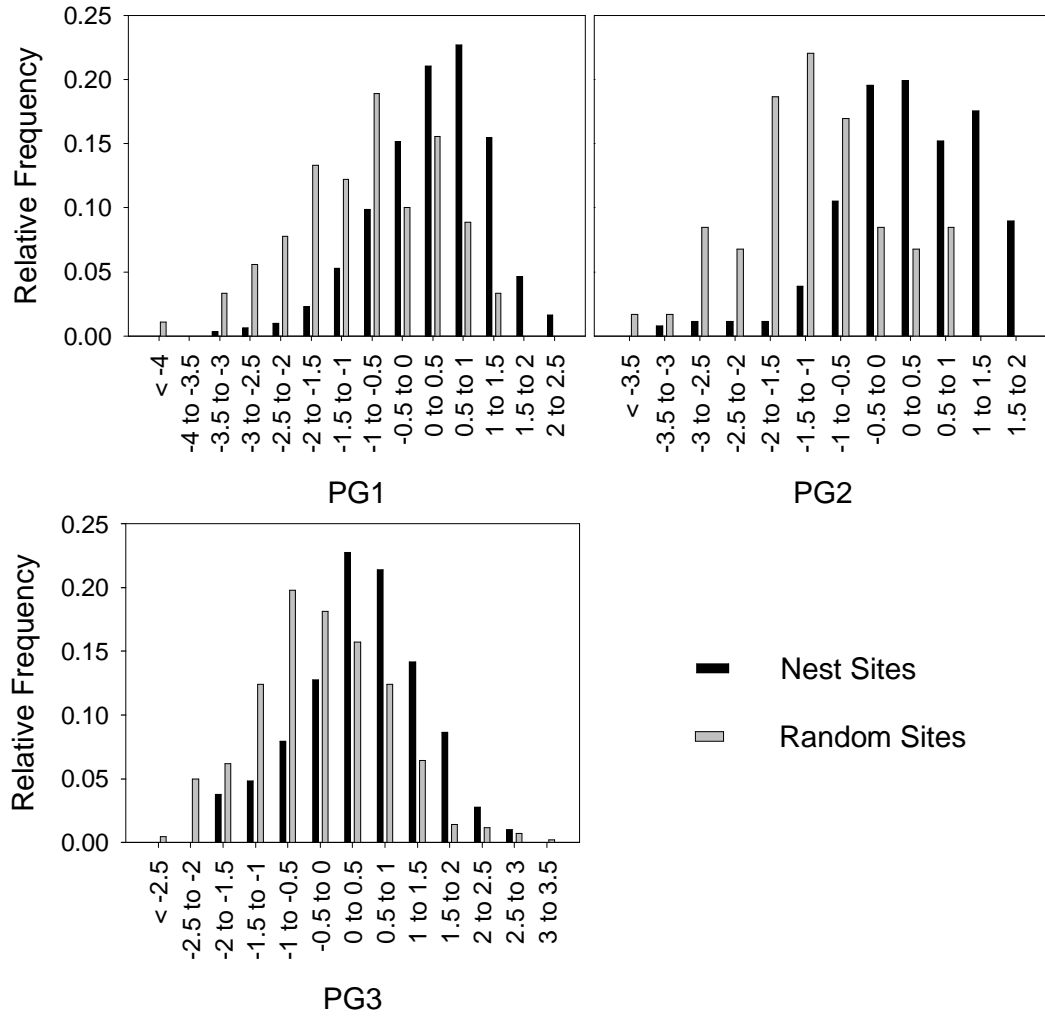Figure 2.2. Within-territory differences between nest and random sites. Each point shows the difference between the mean score for nest sites and the mean score for random sites within a particular territory from 2006 to 2008 along Rush Creek.
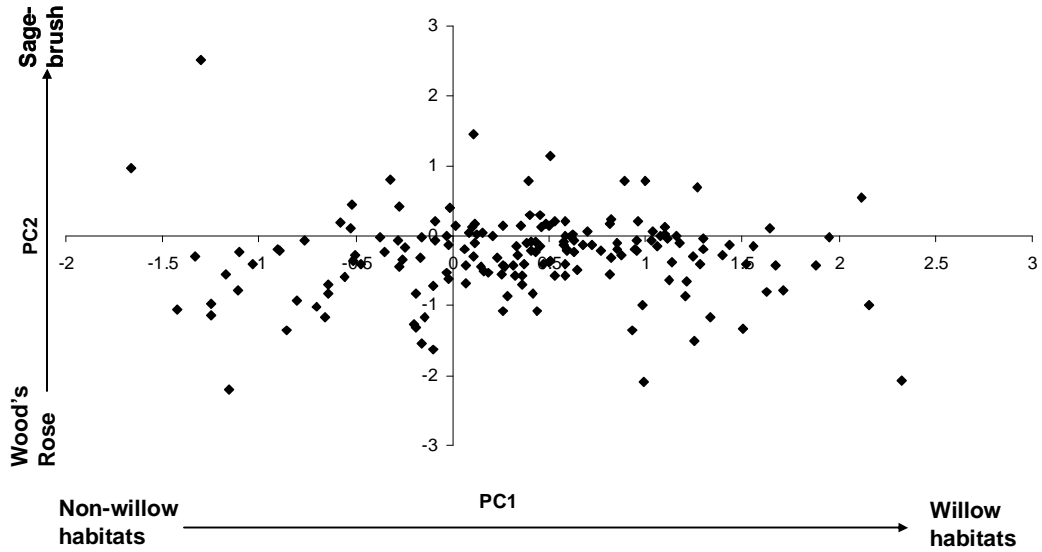

Figure 2.3. Estimates and 95% confidence bands for nest survival rate (*NSR*) for natural and experimental nests along three population-level preference gradients.
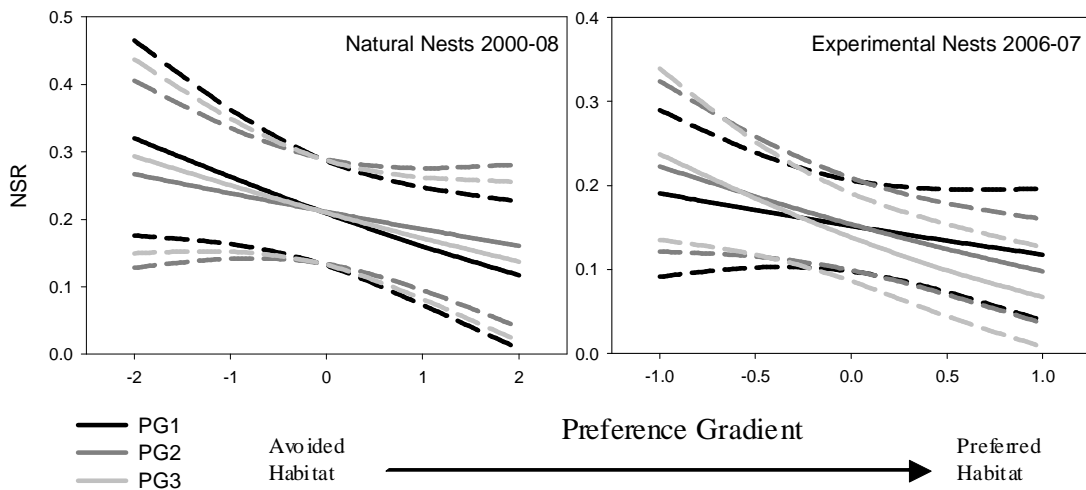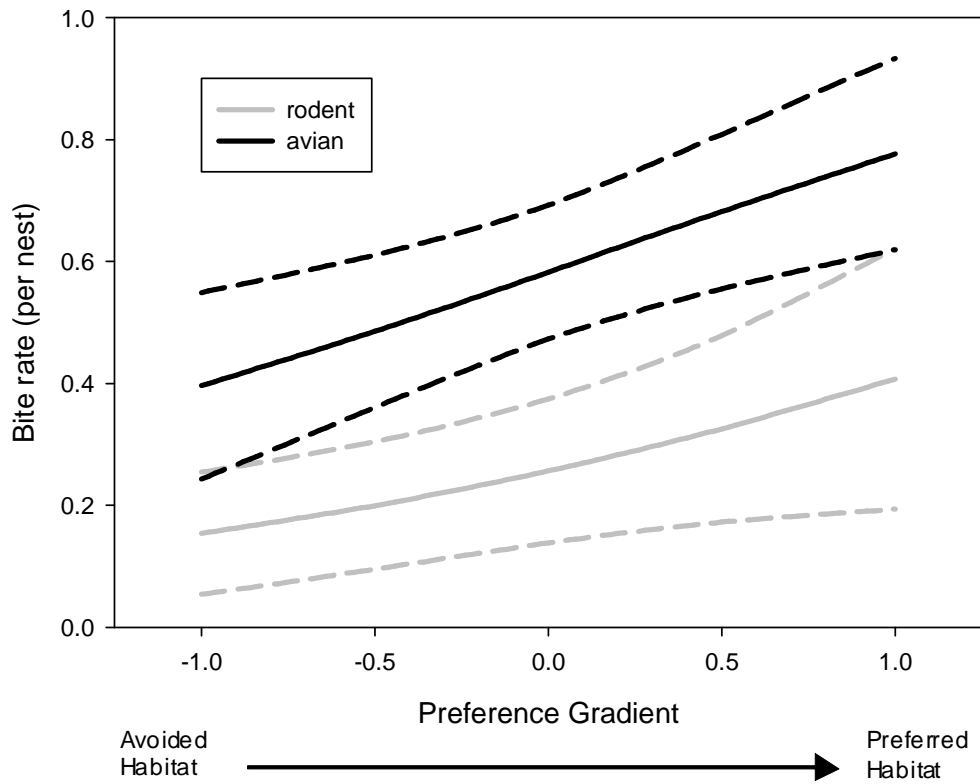
Figure 2.4. Avian and rodent bite rates (an index of predation rates) along a preference gradient (PG3).

Chapter 3. Evidence that "adaptive peaks" shape Yellow Warbler nest site selection

ABSTRACT

Nest predation is a major limitation to avian fitness, so birds should select nest sites that minimize predation risk. However, many empirical studies fail to find significant relationships between natural variation in predation risk and preferred nest habitat features. Such findings may be explained if birds occupy "adaptive peaks." Birds may exclusively select nest site features that confer minimal-predation risk, making predation rates constant with respect to natural variation in nest site structure, despite elevated predation rates in unoccupied nest sites. I tested this "adaptive peak hypothesis" for a breeding population of Yellow Warblers with respect to two nest site features: concealment and height. I monitored experimental nests within and outside concealment and height ranges naturally occupied by Yellow Warbler nests. I found particularly strong evidence for a concealment-related adaptive peak, or rather an "adaptive plateau." Predation rates for both natural and experimental nests were unrelated with concealment among nests within the natural concealment range, but experimental predation rates were much higher in extremely exposed sites (< 30% concealed) rarely occupied by natural nests. Furthermore, in 2001 the location of this adaptive plateau shifted, and during this year, Yellow Warblers adjusted their nest site selectivity in favor of low-predation concealment levels. Clay egg bite data identified avian predators as contributing the most to concealment-predation relationships, making the presence of avian predators a potentially useful cue for Yellow Warblers to track changes in predation pressure. The nest height relationship with predation risk interacted with microhabitat patch structure,

making a height a poor predictor of predation risk and therefore relatively useless as a cue for nesting birds attempting to locate predator-free nest space.

INTRODUCTION

Selection gradient analysis provides a tool for visualizing the relationship between phenotype and selection in nature. It represents the first step in the selection process, which is differential fitness (i.e., reproductive success) of individuals as a function of their phenotype (Lande and Arnold 1983). The second step lies in the phenotypic distribution of the offspring that are produced. Given differential fitness, the distribution of phenotypes in successive generations should shift towards the nearest *adaptive peak*, a region in trait space where fitness is locally maximized (Fisher 1930). However, many field studies fail to detect statistically significant relationships between phenotype and fitness (Kingsolver et al. 2001), perhaps in part because of the evolutionary response of natural populations to selection. Given a strong adaptive response, all the phenotypes expressed in a population may occur close to an adaptive peak, in which case the fitness variation necessary to document the process of natural selection would not exist in nature. As a consequence, researchers often experimentally expand natural phenotypic distributions (i.e., phenotypic engineering), thereby improving their power to document the adaptive process (Anholt 1991, Sinervo et al. 1992).

Ornithologists have used selection gradient analysis extensively to study the adaptive significance of avian nest habitat selection. For open-cup nesting terrestrial species, nest survival is an important component of fitness and predation the predominant

cause of nest failure (Martin 1993, Lack 1966, Ricklefs 1969). Thus, ornithologists look for positive correlations between preferred nest habitat features and nest survival, as well as negative correlations between these features and predation risk. Although many studies do find such relationships (Bekoff et al. 1989, Martin 1998, Kelly 1993, Martin and Roper 1988), numerous studies fail to detect significant microhabitat-predation relationships, leading some researchers to doubt the importance of predation pressure in shaping nest site selection (Hoover and Brittingham 1998, Wilson and Cooper 1998, Bisson and Stutchbury 2000, Boulton et al. 2003, Rangel-Salazar et al. 2008). However, most studies may fail to document an adaptive significance of nest site selection in because they only measure natural variation in predation rates. If birds only nest near adaptive peaks and thus avoid high-predation nest habitats, predation patterns that have shaped nest site selection would not be adequately represented by natural variation in predation rates (Schmidt and Whelan 1999). Therefore, to thoroughly examine the adaptive significance of nest site selection, researchers must measure predation risk outside the microhabitat range normally occupied by nesting birds.

I examined the adaptive significance of nest habitat selection for a population of Yellow Warblers (*Dendroica petechia*) by measuring relative predation risk outside the natural nest habitat range occupied by this population. I focused on correlating predation with gradients in two nest site features: concealment and height. Although we expect these habitat features to influence predation risk from a mechanistic view (Martin 1993, Schmidt 1999), many studies fail to detect correlations between these features and natural predation rates (Chase 2002, Murphy 1983, Best and Stauffer 1980, Filliater et al. 1994,

rewiew in Martin 1989). Similar to findings in other studies, in this study natural predation rates for Yellow Warblers were generally not correlated with either concealment or height, yet Yellow Warblers did occupy distinct height and concealment ranges that differed from the range of sites available to them. To unveil potential adaptive peaks in the context of predation risk, I monitored experimental nests within and outside the concealment and height ranges occupied by natural nests. To ensure that experimental patterns of predation risk across an extended range were relevant to Yellow Warblers, I designed experimental nests that mimicked natural Yellow Warbler nests as closely as possible and calibrated experimental predation patterns to natural patterns recorded within the natural habitat range. I supplemented experimental manipulations with an examination of inter-annual variation in both nest habitat use and selection gradients. Recent work documents the ability of birds to assimilate information from observations of predators into nest site selection decisions (Eggers et al. 2006, Peluc et al. 2008) allowing for responses to temporal variation in predation pressure when selecting nest sites (Forstmeier and Weiss 2004). Therefore, I examined whether nest habitat use along concealment and height gradients responded to inter-annual variation in the form of predation-based selection gradients. Finally, I analyzed data from bite impressions left in clay eggs to investigate predator-specific habitat relationships. These data allowed me to consider the potential mechanisms underlying the adaptive landscape unveiled by experimental nests.

METHODS

Study System.

Yellow Warblers are a shrub-nesting neo-tropical migrant passerine that breeds in riparian habitat across North and Central America (Lowther et al. 1999). Males establish territories, females select nest sites, build nests, and incubate the eggs, and both parents feed the young. For this study, Yellow Warblers were studied along Rush Creek, a tributary of Mono Lake, CA. This study was a collaborative effort that spanned from 2000-2008. From 2000-2005, PRBO Conservation Science monitored Yellow Warblers as part of an all-species riparian songbird monitoring program. PRBO's study area included a 38.4 ha., 2.0 km-long section of Rush Creek (Heath et al. 2006a, Heath et al. 2006b). In 2006 - 2008 I continued monitoring Yellow Warblers along the upper 20.3 ha, 1.0 km-long sub-plot of the PRBO study area. The shrub layer along Rush Creek is dominated by three species of willow (*Salix exidua*, *Salix lucida*, and *Salix lutea*), but is also characterized by a substantial component of Wood's rose (*Rosa woodsii*), as well as a somewhat smaller sagebrush component (mainly big sagebrush (*Artemisia tridentata*); further details in Chapter 2). Predators observed depredating nests along Rush Creek (either directly or with video monitoring) included garter snakes (*Thamnophis* sp.), mice (Muridae and Cricetidae), least chipmunks (*Tamias minimus*), raccoons (*Procyon lotor*), weasels (*Mustela* sp.), wrens (Troglodytidae), and Bullock's Oriole (*Icterus bullockii*; Chapter 1). In addition, Western Scrub-Jays (*Aphelocoma californica*) and Black-billed Magpies (*Pica hudsonia*) commonly breed along Rush Creek. Magpies are documented nest predators elsewhere in the Mono Basin (Chapter 1), and both these species are

documents predators of open-cup nests in other systems (Peterson et al. 2004, Preston and Rotenberry 2006, additional studies reviewed by Richardson et al. 2009). Additionally, brood parasitic Brown-headed Cowbirds (*Molothrus ater*) parasitized 49.5% of Yellow Warbler nests along Rush Creek (PRBO and Q. Latif unpublished data), and are also a documented nest predator (Arcese et al. 1996, Chapters 1, 4).

Natural nest monitoring and habitat measurements

PRBO and I monitored Yellow Warbler nests from May 1 through August 15 in all years (2000 – 2008). We relied on behavioral cues to find as many nests for as many breeding territories as possible within the study site (Martin and Geupel 1993). We used observations of territorial behavior to locate all breeding territories within the study area (Chapter 2), and we found nests for 70-94% of all territories located in any given year. Thus, I am confident that the nests we monitored adequately sampled the population members breeding within our study site. Furthermore, by maximizing the number of territories sampled, we distributed our nest-searching efforts evenly across space and microhabitat types. Once a nest was located, we visited the nest at least once every four days and recorded its contents until its fate (i.e., failure or success) was determined. We considered nests to have "failed" when no Yellow Warbler eggs or nestlings remained in the nest, the nest was abandoned by the parents, or eggs remained un-hatched substantially past the normative incubation period (11.3 days; PRBO unpublished data derived from Mono Lake birds). We considered nests that contained only Brown-headed Cowbird eggs or nestlings to have failed and nests that initially contained both Yellow

Warbler and cowbird eggs but subsequently hatched only cowbird eggs to have failed on hatch day. We took various precautions to avoid leading predators to nests under observation (Martin and Geupel 1993, Robbins 1970).

Once nest fate was determined, PRBO and I measured the microhabitat structure at each nest site. We measured concealment by visually estimating the percent of the nest concealed while standing one meter from the nest in each of six directions: above the nest, below the nest, and from each of the four cardinal directions. For the analysis presented here, we calculated the mean of the resulting six estimations to obtain an overall index of concealment. We measured nest height from the ground (or water surface for nests over standing water) to the base of the nest-cup. We also measured the structure and composition of the shrub layer for microhabitat patches (i.e., 5-meter radii circles) surrounding each nest, and identified the species and measured the height of the individual shrub supporting each nest. Prior to measuring habitat in the field, observers participated in numerous calibration sessions aimed at maximizing inter-observer measurement consistency. Following training, estimates of percent shrub coverage and concealment varied no more than 20% between observers.

To provide habitat availability measurements for analyses of habitat preference (i.e., for comparisons with nest habitat use; Jones 2001), I measured concealment and height at random sites. I measured sites at 30 points randomly chosen from a grid of points spanning the 2006-2008 study plot (point generation protocol provided in Chapter 2). I identified the shrub nearest to each point and capable of supporting a nest, and visually scanned each of these shrubs for the most concealed site. I recorded the height of

the shrubs associated with random points and the height of selected sites within each

shrub. I also placed a previously used Yellow Warbler nest at each site, which I used to

measure concealment. Selection of these sites was not a completely random process since

concealment was maximized within the selected shrub. However, since shrub selection

was random, I was less selective than a bird attempting to maximize concealment from

the range of sites available within its territory. Therefore, random site measurements

provided a useful point of reference for assessing concealment and height preferences for

Yellow Warblers.

Experimental nest placement and monitoring

I monitored experimental nests for this study during two breeding seasons: 2006 and

2007. Experimental nests consisted of previously used Yellow Warbler nests each

containing a real passerine egg and a clay egg. Passerine eggs were similar in size to

Yellow Warbler eggs and were obtained from captive Zebra Finch (*Taeniopygia guttata*)

colonies and stored according to standard protocol (DeGraaf and Maier 2001) until

deployed in the field. Clay eggs were made by hand to resemble the size and shape of real

eggs using modeling clay (Figure 3.1) and recorded distinguishable bite impressions of

either avian or rodent predators (also used by Dion et al. 1999, Weidinger 2002). When

considering differences in morphology, foraging behavior, and natural history between

these two types of predators, information regarding which of these predators contributed

to observed habitat-predation relationships helped to elucidate the mechanistic basis for

these relationships. To facilitate their recovery, I formed clay eggs around fishing weights

anchored with fishing line to woody stems near the nest site. Unlike Yellow Warbler eggs, finch eggs and clay eggs were not speckled, but available evidence suggests no effect of egg coloration on predation risk (Major et al. 1996, Major and Kendal 1996). I monitored experimental nests according to the same protocol used to monitor natural nests for a length of time equivalent to the average egg period (i.e., the combined laying and incubation period) for Yellow Warblers in the Mono Basin (~14 days; PRBO unpublished data). I considered nests depredated when finch eggs disappeared or were damaged, or when bite impressions were left in clay eggs. I monitored experimental nests for a maximum of 14 days, after which I recorded any predator types identifiable from clay egg bites, and measured habitat using a protocol identical to the one applied at natural nest sites.

I placed and monitored 140 experimental nests from 2006-2007. I distributed these nests among sites both within and outside height and concealment ranges typically occupied by Yellow Warbler nests. I relied on previous observations of Yellow Warbler nests to identify typical and atypical sites in which to place experimental nests. However, I ultimately categorized nests as occurring within or outside natural habitat ranges based on *a posteriori* analyses of nest site measurements. In addition, because microhabitat shrub-species composition is correlated with nest predation risk in this system, I distributed experimental nests between the two major microhabitats known to differ predation risk; i.e., willow-dominated and rose-dominated microhabitats (Chapter 2).

Data Analysis

Nest habitat selection. To identify natural height and concealment ranges for Yellow Warblers, I referred to relative frequency distributions of natural nests along habitat gradients. Before generating distributional plots, I used one-way ANOVA models fit to the data using PROC GLM in SAS 9.1 (SAS 9.1; Cary, North Carolina) to examine the significance of variation in concealment and height scores among years. Given significant variation ($p < 0.05$), I examined yearly means and standard errors to identify atypical years. Ignoring atypical years, I then generated frequency distributions for natural nests for the entire study period (2000-2008), and I identified the "natural habitat range" as the range within which $\geq 80\%$ of Yellow Warbler nests were found. In addition, where apparent, I identified steep drop-offs in nest distributions as natural range limits. Finally, I gauged the extent to which the range occupied by Yellow Warblers during the experimental period (2006-2007) represented typical habitat use patterns by gauging the extent to which 2006-2007 distributions fell within the natural range identified from 2000-2008 distributions.

To determine if nest habitat use was a product of active Yellow Warbler preferences, I compared concealment and height scores for natural nest sites (i.e., habitat use) to random site scores (i.e., habitat availability; Jones 2001). Since the process used to select random sites upwardly biased concealment measurements, nest concealment scores significantly higher than the random site scores would indicate a positive preference for concealment, whereas nest concealment scores equal to or lower than random site scores would constitute ambiguous results. Height was not inherently biased

at random sites, so in so far as height was uncorrelated with biased random site features (i.e., concealment), random site height scores served as a useful point of reference for identifying preferences in either direction. Additionally, the two major shrub types occupied by Yellow Warbler nests along Rush Creek differ in physical structure. Specifically, willow are taller and have a sparser leaf structure than non-willow shrubs (i.e., Woods' rose and sagebrush; Latif pers. obs.) and Yellow Warblers prefer willow (Chapter 2). Therefore, I had an *a priori* reason to expect nests to be less concealed and higher than random sites even if Yellow Warblers paid no direct attention to concealment or height when selecting nest sites. Therefore, to allow assessment of the actual importance of concealment and height to Yellow Warbler nest site selection, I analyzed concealment and height relationships with the shrub type in which nests were found. If height or concealment preferences were potentially confounded with the known preference for willow, I separated preference analyses by shrub type. I used t-tests (assuming equal variances) to examine the significance of differences between nest versus random site mean scores (Sokal and Rohlf 1995).

Nest survival analyses. I analyzed habitat relationships with nest survival for both natural and experimental nests using logistic exposure, which models daily nest survival rate (DSR) as a function of one or more explanatory variables (Shaffer 2004). Logistic exposure is a discrete survival analysis that uses a modified logit link function with a binomial distribution. The time period between nest checks was treated as the observation interval and accounted for nests being observed for different lengths of time. I assumed that individual nests were independent samples, and logistic exposure models were fit to

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the data using PROC GENMOD (SAS 9.1). To determine the form of natural selection (i.e., directional, stabilizing, or disruptive; Lande and Arnold 1983), I modeled DSR as a function of parameters describing both linear and quadratic relationships with height and concealment scores.

I analyzed the statistical evidence for DSR-habitat relationships using evidence ratios derived from comparing the fit of logistic exposure models (hereafter DSR models) to data from nest monitoring within an information theoretic framework (Burnham and Anderson 2002). I first calculated model weights (w_i) from differences in AIC_c scores (Δ_i) between a given model and the best-fit model ($w_i = e^{\Delta_i} / \sum_{0-j} e^{\Delta_i}$; where j = the total # of models in a set of models). I then calculated evidence ratios to compared the fit of models with a parameter of interest to equivalent models without that parameter ($ER = \Sigma w_{model(s)-with-parameter} / \Sigma w_{model(s)-without-parameter}$). Thus, an $ER < 1$ would indicate no improvement in fit with the parameter and thus a lack of evidence for the effect of interest, whereas $1 < ER < 3$ would indicate marginal evidence, and an $ER > 3$ would indicate strong evidence for a particular habitat parameter (Burnham and Anderson 2002). As a supplement to marginal evidence ratios ($1 < ER < 3$), I provide p-values from likelihood ratio tests (χ^2_{df}) comparing models with versus without parameters of interest. I verified the adequacy of model structure by examining the goodness-of-fit of models. I relied partially on a variance inflation factor ($c = \chi^2_{Goodness-of-fit} / df$) calculated for the model with the most parameters within each set of candidate models (i.e., the global model), where $c > 4$ would indicate poor model structure (Burnham and Anderson 2002). In addition, I

supplemented this quantitative goodness-of-fit criterion with estimates of nest survival within discrete categories along habitat gradients of interest. This procedure is analogous to comparing plots of observed versus predicted values for ordinary linear regression (Shaffer and Thompson 2007). To examine the direction and strength of selection gradients, I plotted model estimates and 95% confidence bands for nest survival rates along habitat gradients (NSR = DSR_egg$^{14.3}$ × DSR_nestling$^{9.8}$ (natural nests) or DSR^{14} (experimental nests); exponents = the length of either egg or nestling periods). Confidence bands were calculated by applying the delta method to standard errors for logit estimates from logistic exposure models (Powell 2007, Shaffer and Thompson 2007).

All DSR models included a suite of covariates to control for heterogeneity in nest survival not of direct interest. From preliminary analyses and from previous work (Chapters 1 & 3), I found substantial effects (ER > 1) of Year, Date (day of the year), Stage (egg vs. nestling), Plot (the upper vs. the lower half of the study site), Parasitism (i.e., brood parasitism status), and microhabitat structure on DSR, so I included all these variables as covariates in DSR models where applicable (e.g., only Year and Date for experimental nests). Microhabitat structure was represented by nest scores along a principle component axis (PC1) that represented a gradient from willow-dominated (positive) to non-willow dominated (negative) microhabitat patches. I looked for heterogeneity in the strength and direction of selection gradients by examining the improvement of model-fit with concealment or height × covariate interactions (ER =

$w_{\text{interaction-model}}$ / $w_{\text{additive-model}}$). Only interactions that improved model fit (ER > 1) are discussed.

My examination of the role of adaptive peaks in shaping nest site selection began with an analysis of DSR-habitat relationships within the natural habitat range. If adaptive peaks shape Yellow Warbler nest habitat selection, natural nest survival should be uncorrelated with habitat within the natural range. To test this prediction, I analyzed concealment and height relationships with natural nest survival for the entire study period (2000-2008) using the procedure just described. In addition, I verified the utility of experimental nests for exploring the predation-based adaptive landscape by comparing experimental predation patterns with natural patterns within the natural range. I considered experimental nests useful for measuring relative predation risk outside the natural habitat range in so far as experimental predation patterns paralleled natural patterns within the natural range. Since my main objective was to measure relative predation rates along habitat gradients, absolute differences in predation rates between natural and experimental nests did not invalidate the use of experimental nests as a tool for unveiling adaptive peaks (Figure 3.2).

To compare natural and experimental predation patterns within natural microhabitat ranges, I fitted logistic exposure models to two datasets that included data from both natural and experimental nests monitored during the experimental period (2006-2007). One of these datasets excluded data from outside the natural concealment range (i.e., > 80% and < 30%) and the other excluded data from outside the natural height range (i.e., < 75cm). I made natural and experimental DSR estimates from this analysis

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comparable by excluding observations of natural nests from the nestling stage and from nests that experienced fates not observable at experimental nests (e.g., abandonment). Logistic exposure models fit to these data included Year, Date, and the categorical covariate, Type, which accounted for absolute differences in DSR between natural and experimental nests. I fitted model sets that included all possible combinations of either linear or quadratic habitat effects as well as habitat $\times$ Type interaction effects on nest survival. I fitted a model set describing various combinations of concealment-DSR models to the 30-80% concealment dataset and a set of height-survival models to the > 75 cm data set. I calculated evidence ratios for interaction parameters (ER = w_{intxn_model}/ $w_{additive\_model}$) to examine the extent to which experimental versus natural habitat-predation relationships differed. Height and concealment values were not strongly correlated (natural nests: $r = -0.09$, $n = 141$; experimental nests: $r = -0.07$, $n = 140$) and I found no evidence for height $\times$ concealment interactions (ER < 1). Thus, independent analyses of DSR-concealment and DSR-height relationships were warranted.

Habitat-predation relationships across an extended range. Having verified the relevance of experimental predation patterns to Yellow Warblers, I analyzed habitat-predation relationships across the entire range sampled by experimental nests to determine if Yellow Warblers occupied adaptive peaks. I fitted DSR models to experimental data that included Year, Date, and PC1 covariates, as well as all possible combinations of linear and quadratic, height and concealment effects on nest survival. In addition, I analyzed habitat relationships with bite impressions left by avian and rodent predators by fitting DSR models to two derived datasets (one dataset corresponding to

each predator type) for which nests were only identified as 'failed' when clay eggs were bitten by the predator type of interest. Additionally, I excluded observation intervals during which nests were depredated by unidentified predators and truncated observations of nests that were depredated by the predator type not-of-interest half-way between the ultimate and penultimate nest checks. I used DSR models fit to avian- and rodent-specific data to calculate predator-specific DSR estimates, from which I calculated predator-specific bite rates ($PBR = 1 - DSR^{14}$) along concealment and height gradients. To compensate for a low sampling of rodent bites, I supplemented the rodent dataset with data from nests monitored for a separate study in 2008 (6 additional rodent bites were recorded out of 60 nests monitored in 2008; Chapter 2).

RESULTS

Nest habitat use and preference

I identified 30-80% as the "natural concealment range" for Yellow Warblers. I found significant inter-annual variation in concealment of natural nest sites ($F_{8,658} = 9.2$, $p < 0.001$; sample for this and subsequent analyses excluded observations with missing values). Nest concealment was atypical during 2001 (compare 2001 mean = 73.3% ± 17.0 (s.d.) to yearly means from 53.6% ± 17.7 to 61.9% ± 22.1 in other years), so I ignored 2001 data when identifying the natural concealment range for Yellow Warblers. In 2000 and from 2002-2008, > 80% of nest sites (500 of 595 nests) were between 30-80% concealed (Figure 3.3A). On average, willow shrubs provided less concealment than non-willow shrubs. From 2000-2008, mean concealment for nests placed in non-willow

shrubs (65.4%) was higher than for nests in willow shrubs (55.5%; $t_{656} = 7.0$, $p < 0.001$), and PC1 (i.e., the presence of willow at the patch-scale) was negatively correlated with concealment ($r = -0.33$, $n = 665$, $p < 0.001$).

I identified sites > 75cm as the "natural height range" for Yellow Warblers. From 2000-2008, 94.7% of nests (673 of 711 nests) occurred at or above 75cm. On average, nests in willow shrubs were higher (181cm) than in non-willow shrubs (126 cm; $t_{704} = 8.6$, $p < 0.001$), and PC1 was positively correlated with height ($r = 0.27$, $n = 711$). This difference mainly arose because the height range for willow nests was more extensive at the upper end of the height gradient (Figure 3.3B). Willow shrubs at random sites were on average taller (330 cm) than non-willow shrubs (133 cm; $t_{476} = 17.0$, $p < 0.001$), and nest-shrub height was highly correlated with nest height ($r = 0.73$, $n = 710$). Since nest height increased with increasing nest-shrub height, the upper nest height range was likely constrained more by site availability than by Yellow Warbler site selectivity. By contrast, nests rarely occurred below 75 cm regardless of microhabitat structure, so this lower bound is more likely a product of Yellow Warbler behavior. Therefore, I only identified a lower limit to the natural height range. I found significant variation in nest height among years ($F_{8,706} = 5.5$, $p < 0.001$). Mean nest height in 2008 was especially high as was the variance (compare 2008: 216 cm ± 126 (s.d.) to other years ranging from 138 cm ± 82 (2006) – 170 cm ± 84 (2007)). However, since I only identified a lower limit to the natural height range, 2008 nest heights were not considered aberrant in the context of this study.

Yellow Warblers occupied sites that were more concealed and higher than random sites. Concealment and height scores for natural nests were significantly higher than random site scores (Table 3.1). As was the case for nest sites, random site height and concealment scores were not strongly correlated ($r = 0.26$, $n = 30$, p = 0.16), a non-linear relationship was not apparent from a scatter-plot, and the difference in the average concealment for sites below 75 cm (Mean = 42.1%) and above 75 cm (Mean = 41.2%) were not significantly different ($t_{27} = 0.14$, P = 0.88). Thus, nest height preference was not confounded with preference for concealment. Nest height selection was probably shaped by a preference for relatively tall nest shrubs. Nest shrubs were significantly taller than randomly located shrubs regardless of the shrub type in which nests were placed. Thus, Yellow Warbler preference for high nest sites was not exclusively a consequence of their preference for willow (Table 3.1).

Nest predation within the natural habitat range

Predation rates for natural nests were generally unrelated with concealment, but the data did provide evidence for a difference in the natural concealment-predation relationship during 2001. I fitted DSR models to data from 665 natural nests found and monitored from 2000-2008. Of these, 422 nests failed and 324 of observed failures (77%) were attributed to nest predation, so nest predation was the predominant cause of failure. The data provided little evidence for an overall relationship between concealment and nest survival ($ER_{Concealment} = \Sigma w_{M2+M5+M8} / \Sigma w_{M3+M6+M9} = 1.3$; M2 vs. M3 $\chi^2_{1(df)} = 2.5$, p = 0.11; (M2 = abbrev. for model 2); Table 3.2), but the data did provide evidence for a

concealment $\times$ year interaction ($ER_{Conc + Conc \times Year} = \Sigma w_{M1+M4+M7} / \Sigma w_{M3+M6+M9} = 4.6$; M1 vs. M3 $\chi^2_9 = 21.3$, p = 0.01; Table 3.2). The year associated with the largest concealment parameter estimate was also the year in which nests were concealed at aberrantly high levels (i.e., 2001: $\beta_{Concealment} = 0.027$; β_{Conc} ranged from -0.012 (2005) to 0.018 (2003) in other years). NSR estimates based on a Concealment $\times$ Year model (Model 1; Table 3.2) increased substantially with increasing concealment in 2001. By contrast during other years, when Yellow Warblers occupied their normal concealment range, NSR was not on average correlated with concealment (Figure 3.3C).

Across the entire study period, natural nest survival co-varied with height, but the slope of this relationship depended upon microhabitat patch structure. Natural nest data provided evidence for an overall DSR-height relationship, but the data provided stronger support for a height $\times$ PC1 interactive relationship with DSR ($ER_{Ht} = \Sigma w_{M4+M5+M6} / \Sigma w_{M7+M8+M9} = 4.8$, M4 vs. M7 $\chi^2_1 = 5.1$, p = 0.02; $ER_{Ht \times PC1} = \Sigma w_{M1+M2+M3} / \Sigma w_{M4+M5+M6} = 5.9$, M1 vs. M4 $\chi^2_1 = 5.9$, p = 0.02; Table 3.2). This interaction effect translated into a positive relationship between NSR and nest height in willow-dominated microhabitats (positive PC1 scores), in contrast with an apparent negative DSR-height relationship in non-willow microhabitats (negative PC1 scores). However, very few data were collected from high sites (> 300cm) in non-willow microhabitats, and this limitation in the data is reflected in the relatively wide NSR confidence band for high, non-willow nest sites (Figure 3.3D). Therefore, the height $\times$ PC1 interactive effect documented here mainly reflects a higher overall nest survival rate in non-willow microhabitats (further

documented in Chapter 2) coupled with a positive DSR-height relationship in willow (the microhabitat in which natural nest sites spanned a wide range of heights).

From 2006-2007, I monitored 141 natural nests during their egg period along with 140 experimental nests. During this period, the natural nests occupied the relatively exposed end of the natural concealment range (2006: 55.7% ± 18.3 (s.d.); 2007: 53.7% ± 16.1). However, only 9.9% of these nests (14) were < 30% concealed and 4.3% of these nests (6) were > 80% concealed. By contrast, a substantially greater proportion of experimental nests occupied the lower end (29 nests; 20.7% of total) and the upper end (18 nests; 12.8% of total) of the concealment gradient (Figure 3.4A). Heights for natural nests were relatively low in 2006 (138 cm ± 82) and high in 2007 (170 cm ± 84), but only 7.8% of natural nests (11) were placed below 75 cm. By contrast, I placed 31.4% of experimental nests (44) below 75 cm.

2006-2007 experimental and natural nest data from within the natural range (30-80% concealed; > 75 cm) did not provide evidence for a correlation between predation rates and either concealment or height. None of the concealment models fit these data any better than covariate-only models (Table 3.3), and the evidence for a within-range Type×concealment interaction was also very low ($ER_{(M3+M5)/(M2+M4)} = 0.34$, M3 vs. M2 $\chi^2_1 = 0.06$, p = 0.81; Table 3.3). I found marginal evidence for a Height × Type interaction ($ER_{(M8+M11)/(M9+M10)} = 1.05$, M8 vs. M9 $\chi^2_1 = 2.7$, p = 0.10), but all height models were weighted substantially less than the Covariate-only model (largest $ER_{M8/M7}$ = 0.52; Table 3.3), and class-based NSR estimates did not suggest a notable difference in experimental versus natural height-survival relationships (Figure 3.4D). Unlike evidence

obtained from across the entire study period, these data provided no evidence for a Height $\times$ PC1 interaction ($ER_{Ht \times PC1} = 0.5$, $\chi^2_1 = 0.59$, p = 0.44; Ht$\times$PC1 model compared to model 8, Table 3.3).

Nest predation over an extended habitat range

Data from experimental nests monitored over extended ranges provided strong evidence for concealment and height relationships with predation risk. The data supported both linear and quadratic concealment-DSR relationships ($ER_{(M2+M4+M6)/(M7+M8+M9)} = 88.7$, $ER_{(M1+M3+M5)/(M7+M8+M9)} = 112.7$; Table 3.4). The evidence for a quadratic over a linear effect was not particularly strong ($ER_{(M1+M3+M5)/(M2+M4+M6)} = 1.3$, M1 vs. M2 $\chi^2_1 = 2.6$, p = 0.11; Table 3.4). However, the quadratic model was more consistent with the pattern indicated by class-based NSR estimates, i.e., a sharp decline in NSR below 30% coupled with constant NSR above 30% (Figure 3.4C). Experimental nest data also provided substantial evidence for a relationship between nest height and predation risk across an extended height range. Both linear and quadratic height models were supported (linear: $ER_{(M1+M2+M7)/(M5+M6+M9)} = 3.6$, M1 vs. M5 $\chi^2_1 = 4.7$, p = 0.03; quadratic: $ER_{(M3+M4+M8)/(M5+M6+M9)} = 2.1$, M3 vs. M5 $\chi^2_2 = 5.5$, p = 0.06), but class-based NSR estimates were not particularly suggestive of a non-linear effect (Figure 3.4D). Experimental NSR decreased with increasing height, and I found relatively high NSR and lower predation rates below the natural height range (75 cm; Figure 3.4B). Experimental nest data did not provide evidence for a Height $\times$ PC1 interaction ($ER_{Ht \times PC1} = 0.44$, $\chi^2_1 = 0.40$, p = 0.53; Ht$\times$PC1 model compared to model 7, Table 3.4).

In 2006 and 2007, of the 140 experimental nests monitored, 77 clay eggs were bitten by nest predators. Of these, 50 were distinguishable as avian bite marks, 23 as rodent, and 4 marks were not identifiable. Avian predators left scratches, pokes, and/or bite impressions that were 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 left by rodent incisors.

Clay egg data provided evidence for strong effects of concealment on avian predation, whereas the data did not provide strong evidence for a concealment relationship with rodent predation. The data provided strong support for both a linear relationship and a curvilinear relationship between avian predation and concealment (linear: $ER_{(M10+M12)/(M14+M15)} = 43.9$, quadratic: $ER_{(M11+M13)/(M14+M15)} = 28.3$; Table 3.4), translating into substantial decreases in avian bite rates with increasing concealment (Figure 3.4E). The data did not provide strong evidence for a concealment relationship with rodent predation (linear: $ER_{(M22+M19)/(M20+M17)} = 0.5$, quadratic: $ER_{(M21+M23)/(M20+M17)} = 0.3$, M19 vs. M17 $\chi^2_1 = 0.67$, p = 0.41; Table 3.4). However, the class-based RBR estimate for nests < 30% concealed was notably higher than RBR for nests > 30% concealed, suggesting a possible non-linear relationship detectable with greater statistical power (Figure 3.4E).

Clay egg data also provided strong evidence for a height relationship between avian predation and nest height, but no evidence for a height relationship with rodent predation. Evidence ratios for this relationship were fairly large (ER_{Ht} for models 8, 9, and 12; Table 3.5), and model-based and class-based ABR estimates increased with

increasing height (Figure 3.4F), although the differential in ABR along a height gradient was not as large as the differential associated with concealment. By contrast, I found no evidence for a relationship between nest height and rodent predation from these data (ER_{Ht} for models 4, 6, and 7; Table 3.5), and model-based and class-based RBR estimates along a nest height gradient did not show any strong trends (Figure 3.4F).

Avian predator territories and nest concealment

Since concealment was especially correlated with predation by avian predators, and since previous studies document the ability of songbirds to adjust their nest site selectivity in response to the presence of avian predators (Peluc et al. 2008), we analyzed the relationship between yearly nest concealment means and the number of avian predator territories. In addition to locating Yellow Warbler territories, PRBO and I used observations of behavior and nest locations to locate breeding territories for two species of avian nest predators. We mapped a total of 12 American Magpie territories and one Western Scrub-jay territory from 2001-2005 (the Western Scrub-jay in 2005). Although our sample size was low ($n = 5$ years), I found a statistically significant correlation between mean concealment of Yellow Warbler nests and the number of avian predator territories documented within the study area ($r = 0.91$, p = 0.03; Figure 5).

DISCUSSION

An adaptive plateau shapes nest concealment

I found strong evidence that Yellow Warblers occupy an adaptive plateau with respect to nest concealment. During two years of study, nest sites within the natural concealment range occupied by Yellow Warblers were associated with lower predation risk and higher nest survival than sites just below this range ($< 30\%$; measured by experimental nests), whereas predation risk did not vary substantially among sites within the natural range (Figure 3.4C). Since Yellow Warblers preferred concealed sites (Table 3.1) and since concealment was not positively correlated with other preferred features (i.e., concealment was negatively correlated with preferred willow shrubs), Yellow Warblers selected nest sites based directly on concealment level and actively avoided highly exposed sites. By favoring sites that were at least moderately concealed, Yellow Warblers avoided the high predation risk associated with more exposed sites. However, predation risk neither decreased nor increased substantially above the natural range ($> 80\%$), so predation did not restrict the use of highly concealed sites (Figure 3.4C). However, since Yellow Warblers do not usually benefit from concealing their nests more than at a moderate level, the time required to find highly concealed sites may instead shape the upper limit of the natural concealment range. Indeed, finding highly concealed sites for experimental nests was especially time consuming (Q. Latif personal observation).

I used measurements of relative predation risk using experimental nests to investigate adaptive peaks shaping Yellow Warbler nest habitat selection. Differences often measured between experimental and natural nests in both absolute predation rates,

as well as in the slopes of their habitat-predation relationships (Major and Kendal 1996, Moore and Robinson 2004), give rise to concerns about the utility of experimental nests for measuring predation risk relevant to natural populations (Faaborg 2004, King et al. 1999, Part and Wretenberg 2002). However, in this system, natural and experimental habitat-predation patterns were concordant within natural ranges along concealment and height gradients, as well as along a willow-rose microhabitat gradient studied previously (Chapter 2). Additionally, experimental nests were depredated by nest predators that are known to depredate open-cup nests including those built by Yellow Warblers (Chapter 1). Given the concordance of within-range natural and experimental patterns and the vulnerability of experimental nests to known songbird nest predators, experimental nests in this study likely recorded relative predation patterns that would be experienced by Yellow Warblers if they extended their natural nest habitat range.

The mechanistic basis for selection gradients with respect to nest concealment
Differences between avian versus rodent predator relationships with concealment may help explain the shape of observed concealment-predation relationships. I found a strong negative relationship between nest predation by avian predators and concealment, in contrast with a weak concealment relationship with rodent predation (Figure 3.4E). Cowbirds were probably the predominant avian predator of natural and experimental nests in this system, although predators from the family Corvidae (Western Scrub-jay and Black-billed Magpie; hereafter corvids) also pose a substantial threat to nests in this system (Chapter 1). The results of this study are consistent with those of other studies

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(Dion et al. 2000, Liebezeit and George 2002, Martin and Joron 2003). Relatively weak effects of vegetation density on rodent predation may arise from a trade-off between two conflicting effects. Although dense vegetation reduces the ability of rodents to detect nests, rodents may also favor dense microhabitats to avoid predation from higher trophic levels (Brown 1999, Brown and Kotler 2004, Schmidt et al. 2001, Dion et al. 2000). Thus, the difference in concealment effects on avian versus rodent predators may reflect a fundamental difference in habitat responses.

Snakes also commonly depredated Yellow Warbler nests along Rush Creek (mainly garter snakes (*Thamnophis* sp.); Chapter 1). Unfortunately, snakes did not leave distinct bite marks in clay eggs, nor are they likely to depredate experimental nests, since they have only been observed depredating nestlings (Chapter 1). Thus, I am uncertain of the relationship between snakes and concealment in this system. However, the likely stage-specific increase in the importance of snakes did not translate into a stronger effect of concealment on predation of nestlings from natural nests ($ER_{Stage \times Conc} = 0.4$, $\chi^2_1 = 0.06$; from comparison to model 8, Table 3.2). In addition, Mullin et al. (1998) provide evidence for non-linear effects of vegetation density on snake foraging efficiency purportedly resulting from trade-offs between foraging efficiency, suggesting a habitat response more similar in form to the one documented for rodents than for avian predators.

The relative abundance of avian predators versus small-ground-predators may be a key factor shaping the relationship of concealment-related predation pressure. The potential importance of this aspect of predator community composition is apparent when

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contrasting circumstances documented in 2001 with those of other years. In 2001, PRBO

and I recorded the highest number of corvid predators (Figure 3.5) coupled with the

strongest positive correlation between concealment and natural nest survival (2001: β_{Conc}

= 0.027 compared to β_{Conc} from -0.012 (2005) – 0.018 (2003); from Model 1, Table 3.2),

suggesting a potential positive influence of avian predator numbers on the effect of

concealment on predation. That said, corvid numbers were not a good predictor overall of

yearly concealment-survival parameters ($r = -0.01$, $n = 5$), probably in part because

corvid numbers do not account for the relative abundance or predatory behavior of

cowbirds, an even more important avian predator (Chapter 1, 4). In addition to corvid

numbers, relative abundances of cowbirds, small ground predators, as well as aspects of

predator foraging ecology (Mullin et al. 1998, Schmidt and Ostfeld 2003) may all need to

be quantified to predict concealment-predation relationships. Nevertheless, the data

collected in this study suggest that corvid numbers may be a significant contributor to

concealment-related nest predation pressure.

How does concealment selection adapt to predation risk?

A mechanism for a phenotypic response to predation pressure is required for predation

risk to shape nest habitat selection. Habitat selection may become adaptive if natural

selection acts on heritable variation in habitat preference (Jaenike and Holt 1991).

However, numerous studies document avian nest habitat selection to be behaviorally

plastic (Peluc et al. 2008, Forstmeier and Weiss 2004, Eggers et al. 2006), so natural

selection more likely shapes genetic variation for plasticity in nest habitat selection

including the behavioral responses of birds to nest predators. Birds may respond adaptively to previous experiences with predation (Marzluff 1988, Powell and Frasch 2000) or to observed changes in local predator abundance (Peluc et al. 2008, Forstmeier and Weiss 2004, Eggers et al. 2006). Two longitudinal studies found increased selectivity across years by birds for denser vegetation in response to a perceived increase in avian predators (Eggers et al. 2006) and for higher sites in response to an actual increase in rodent predators (Forstmeier and Weiss 2004). A third study documents an immediate, within-season reduction in nest height and increase in concealment by Orange-crowned Warblers (*Vermivora celata*) in response to a perceived increase in avian predator abundance during the nest site selection process (Peluc et al. 2008).

The close association between yearly nest concealment means and avian predator numbers, specifically those of the family Corvidae (i.e., American Magpies and Western Scrub-jays), across five years of study (2001-2005) suggest a response by Yellow Warblers to these predators in their selection of nest sites (Figure 3.5). Additionally, first-egg-date and concealment were not strongly correlated during 2001, the year with the strongest apparent response ($r = -0.10$, $p = 0.42$, $n = 70$) by Yellow Warblers, so Yellow Warblers are most likely responding immediately to observations of these predators during nest site selection rather than reacting to past experiences with predation. Observers did vary among years, but the relatively high 2001 concealment scores were recorded by two different observers (the lower section by Q. Latif, and the upper section by C. McCreedy), and one of those observers (Q. Latif) also collected a substantial portion of the data in subsequent years (2002-2004 and 2006-2008). Thus, divergent 2001

scores were not likely a product of measurement error. Inter-annual variation in territories may appear insubstantial (1-4), but individual magpie/ scrub-jay territories spanned substantial portions of the study plot (PRBO unpublished data), so individual predators could potentially influence the behavior of a substantial portion of the Yellow Warbler population. Specialized responses by birds to members of this family are documented (Peluc et al. 2008) and could be generally adaptive given the widespread importance of corvids as predators of open-cup nests (Sieving and Willson 1999, Santisteban et al. 2002, Preston and Rotenberry 2006). However, since corvid abundance did not correlate strongly with concealment-survival parameters for natural nests, the adaptive significance of the response observed in this study remains unclear. Information on the responses of birds to cowbirds and small ground predators would further inform our understanding of the adaptive significance of avian nest site plasticity.

Nest height selection and predation risk

The adaptive significance of Yellow Warbler nest height selection was not as apparent as was concealment selection in the context of nest predation risk. Yellow Warblers clearly preferred higher nest sites in higher shrubs regardless of the shrub type in which they nested (Table 3.1), and this preference was not confounded with their preference for concealment (i.e., among both nest and random sites, concealment and height were uncorrelated). Nest height did in part mitigate predation risk particularly in willow microhabitats, but high nests in non-willow microhabitats were not clearly favored by predation pressure (Figure 3.3D). Although experimental nests along an extended height

range recorded relatively low predation risk and higher nest survival rates below the natural height range (Figure 3.4D), these results should be interpreted with caution. Neither of the 2006-2007 datasets provided evidence for the Height × PC1 relationship supported by a larger dataset (i.e., 2000-2008), suggesting a lack of statistical power for detecting potentially important height-survival relationships during the experimental period. Nevertheless, since predation risk was not consistently higher in relatively low nest sites, nest heights selected by Yellow Warblers are not clearly adaptive in the context of predation risk nor did they clearly occupy an adaptive peak or plateau as do natural concealment levels. However, Yellow Warbler height preferences did conform to predation pressure experienced in willow microhabitats. Given that Yellow Warblers prefer willow (Chapter 2) and that higher nests experience lower predation risk in willow, a response to predation pressures most commonly encountered could result in a positive height preference.

Relatively weak and inconsistent effects of nest height on predators may also contribute to a lower response of Yellow Warblers to height-related predation pressures. Although nest height was correlated with avian predation, concealment effects were much stronger than height effects both in magnitude (i.e., compare the NSR differentials from negative to positive ends of concealment and height gradients; Figure 3.4E, 3.4F) and in statistical strength (Models 10-16, Table 3.4). These results parallel those of an experimental study of Fish Crows (*Corvus ossifragus*; Santisteban et al. 2002). A stronger effect of concealment on avian predation may explain why Yellow Warbler nest height did not track yearly changes in avian predator abundances ($r = -0.23$, $p = 0.71$, $n =$

5) nearly as closely as did nest concealment (Figure 3.5). Although Orange-crowned Warblers on Santa Catalina Is. reduced their nest heights in response to the simulated presence of Western Scrub-jays, sites selected by experimental females were also more concealed (Peluc et al. 2008), so concealment may be the primary feature used by birds to evade avian predators. Furthermore, even though rodent predation was not strongly correlated with concealment, the data did suggest the risk of predation by rodents to be elevated in extremely exposed sites (Figure 3.4E), suggesting concealment to be potentially useful for avoiding predation from multiple predator types. The effects of vegetation density on predation by rodents can be circumstance-dependent (Schmidt and Ostfeld 2003), but nest height does not appear to be any more useful as a cue for avoiding rodent predators (compare Figure 3.4E to results by Schmidt 1999, Forstmeier and Weiss 2004) and height may also be useless for avoiding snakes (Fischer 1981). Thus, concealment may offer the most reliable indicator of predator-free space, making concealment-based responses perhaps the most adaptive overall for avoiding nest predators.

Future Research

In conjunction with other approaches, phenotypic scaling represents a potentially powerful tool for further elucidating the adaptive significance of avian nest habitat selection. Given the widespread variation in predator community composition among systems, further attempts to apply phenotypic scaling to concealment would be beneficial. Other studies that have manipulated concealment have failed to either measure

predation risk explicitly outside the natural range (e.g., Howlett and Stutchbury 1996) or control for differences between experimental and natural nests within the natural range (e.g., Gotmark et al. 1995, see also Cresswell 1997, Weidinger 2002, Remes 2005), so additional study of concealment effects that incorporate these concepts into their design would be particularly beneficial. Measurements of selective pressures other than predation risk (e.g., microclimate: Marzluff 1988, Martin 2001, Kim and Monaghan 2005, or predation risk on adults: Gotmark et al. 1995) would also further our understanding of the overall importance of adaptive peaks, particularly since such studies could reveal trade-offs between fitness components. I found no relationship between concealment and fledge number for successful nests (i.e., a component of fitness not incorporated in the nest survival metric; $r = 0.02$, P $= 0.71$, $n = 240$), but the relationship between adult survivorship and concealment is unknown. Such a relationship has been hypothesized (Gotmark et al. 1995) but not documented. Unfortunately, abandonment by parents and ethical concerns limit the potential for manipulating concealment at active nests to measure its effects on adult predation.

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TABLES

Table 3.1. Differences in concealment, site height, and shrub height between nest versus random sites.

Habitat Feature	Site Type	n	mean	sd	t
Nest Height	random	29	111.2	72.6	2.6*
	nest	203	155.9	87.9	
Concealment	random	29	41.5	16.0	3.5**
	nest	202	53.8	17.6	
Shrub Heights					
Overall	random	480	238.9	169.3	5.3**
	nest	204	313.9	166.6	
Willow	random	248	330.4	169.8	3.3**
	nest	128	387.3	141.7	
Non-willow	random	230	133.3	47.7	6.7**
	nest	75	176.8	51.4	

$*p = 0.01$, $**p \leq 0.001$

Nests are from 2006-2007, concealment and non-use site heights were measured at 29 random points (2007), and shrub heights were measured at 480 random points (2006-2008). Observations with missing values were omitted.

Table 3.2. DSR models fit to 2000-2008 natural nest data. -LL = -Log-likelihood, w_i = model weights, k = # model parameters, Δ_i = ΔAIC_c; c = 1.5 (calculated for model 1). Covariates included Year, Date, Stage, Plot, Parasitism, and PC1. The 'Global' model includes all possible parameters, and the 'Constant Survival' contains only an intercept.

Model #	Model parameters	-LL	k	Δ_i	w_i
1	Global	945.1	25	0.0	0.57
2	Conc + Ht + Ht×PC1	954.5	17	2.7	0.15
3	Ht + Ht×PC1	955.7	16	3.2	0.12
4	Conc + Conc×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×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

Table 3.3. DSR models fitted to natural and experimental nest data within natural range. n eff = # observation days, -LL = -Log-likelihood, k = # model parameters, $\Delta_i = \Delta AIC_c$, w_i = model weight. 121 natural and 93 experimental nests provided data from the natural concealment range. 134 natural nests and 100 experimental nests provided data from above 75. For concealment models, c = 0.46 (calculated from model 5), and for height models, c = 0.56 (calculated from model 17). Covariates included Year, Date, Nest Type, and PC1. 141 experimental nests were monitored from 2006-2007. Dataset 3 included data from an additional 60 nests monitored in 2008.

Habitat Range	n_eff	Model #	Model parameters	-LL	k	Δ_i	w_i
30-80% concealed	1358	1	Covariates only	270.8	5	0.0	0.44
		2	Concealment	270.1	6	0.7	0.30
		3	Conc + Conc×Type	270.1	7	2.7	0.11
		4	Conc + Conc^2	270.1	7	2.8	0.11
		5	Conc + Conc×Type + Conc^2×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×Type	282.3	7	1.3	0.24
		10	Height	283.7	6	2.0	0.17
		12	Ht + Ht^2	283.2	7	3.1	0.10
		14	Ht + Ht^2 + Ht×Type + Ht^2×Type	282.1	9	5.0	0.04
		16	Constant Survival	299.3	1	23.1	< 0.01

Table 3.4. DSR models fitted to experimental nest data from extended habitat range. n eff = # observation days, -LL = -Log-likelihood, k = # model parameters, Δ_i = ΔAIC_c, w_i = model weight. For model set 1, c = 0.86 (based on model 3); model set 2, c = 0.55 (based on model 11); model set 3, c = 1.08 (based on model 23). Model sets 1 and 2 included Year, Date, Nest Type, and PC1 as covariates. Model set 3 included $Date^2$ and PC1 as covariates.

Model set	n_eff	Model #	Model parameters	-LL	k	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	10	$Conc + Ht$	-102.4	6	0.0	0.49
		11	$Conc + Conc^2 + Ht$	-101.8	7	0.9	0.32
		12	Concealment	-105.0	5	3.1	0.11
		13	$Conc + Conc^2$	-104.5	6	4.1	0.06
		14	Height	-107.1	5	7.4	0.01
		15	Covariates only	-110.3	4	11.7	< 0.01
		16	Constant Survival	-121.1	1	27.2	< 0.01
3. Failure = rodent bite	1150	17	Covariates only	-95.2	4	0.0	0.29
		18	Constant Survival	-98.4	1	0.4	0.24
		19	Concealment	-94.8	5	1.3	0.15
		20	Height	-95.0	5	1.6	0.13
		21	$Conc + Conc^2$	-94.4	6	2.4	0.09
		22	$Conc + Ht$	-94.7	6	3.0	0.06
		23	$Conc + Conc^2 + Ht$	-94.1	7	3.9	0.04

FIGURES
Figure 3.1. A depredated experimental nest.
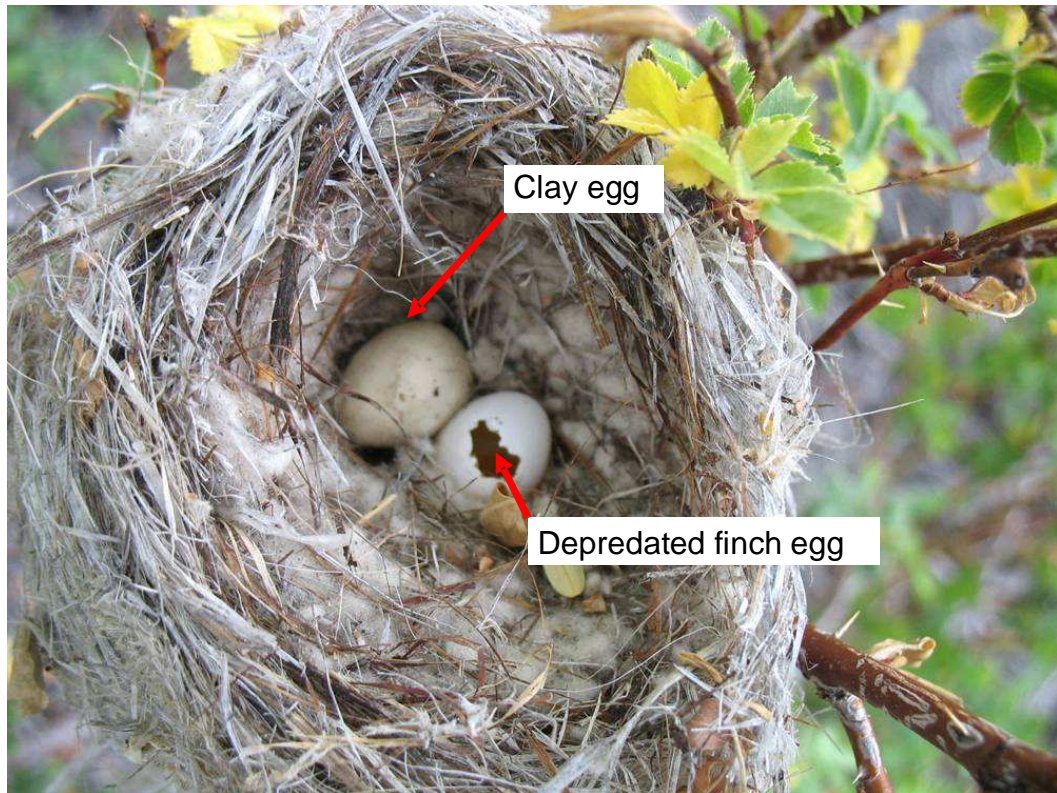

Clay egg

Depredated finch egg

Figure 3.2. Prediction generated from an adaptive peak hypothesis. If birds select nest sites along adaptive peaks, nest survival rates for both natural and experimental nests would be uncorrelated with habitat within the natural range, but experimental nests would record relatively high predation rates and lower survival rates outside natural habitat range limits.
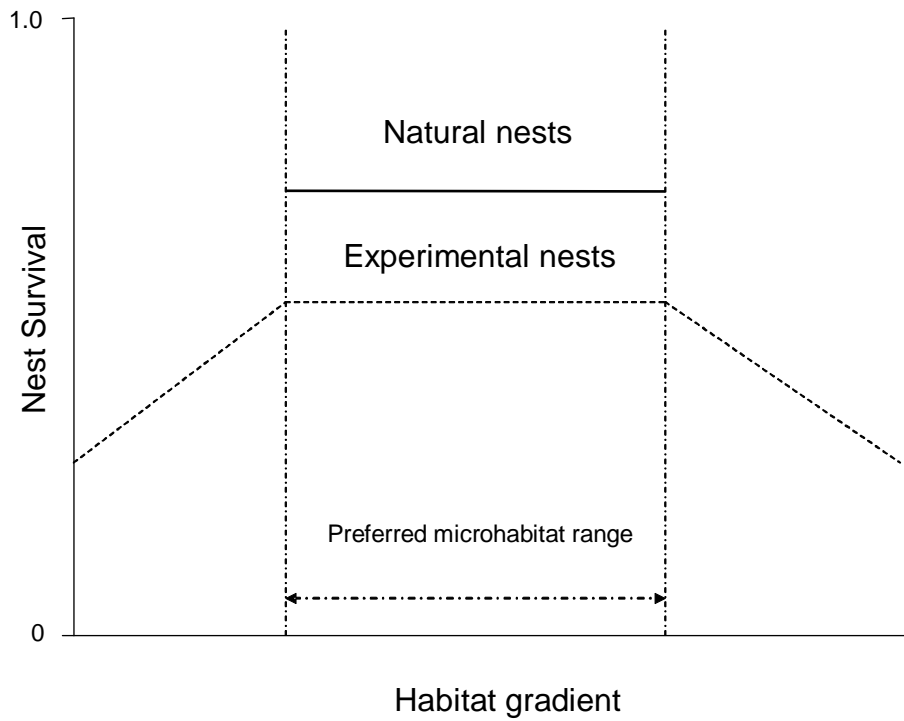
Figure 3.3. Frequency distributions and nest survival (NSR) for 2000-2008 natural nests along habitat gradients. For concealment distributions (3A), $n = 667$ and NSR. For height distributions (3B), $n = 706$. Nest height distributions and height-related NSR estimates are presented for nests in willow versus non-willow microhabitat patches as measured by scores along a principle component axis (PC1). Model estimates and 95% confidence bands are derived from Model 1, Table 2. NSR estimates for height and concealment classes are plotted at mean values for the nests within each of the following concealment classes: < 40, 40-50, 50-60, 60-70, $> 70\%$ for non-2001; < 50, 50-60, 60-70, 70-80, and $>80\%$ for 2001, and $> 70\%$ for 2001; and height classes < 100, 100-133, 133-166, 166-200, and > 200cm.
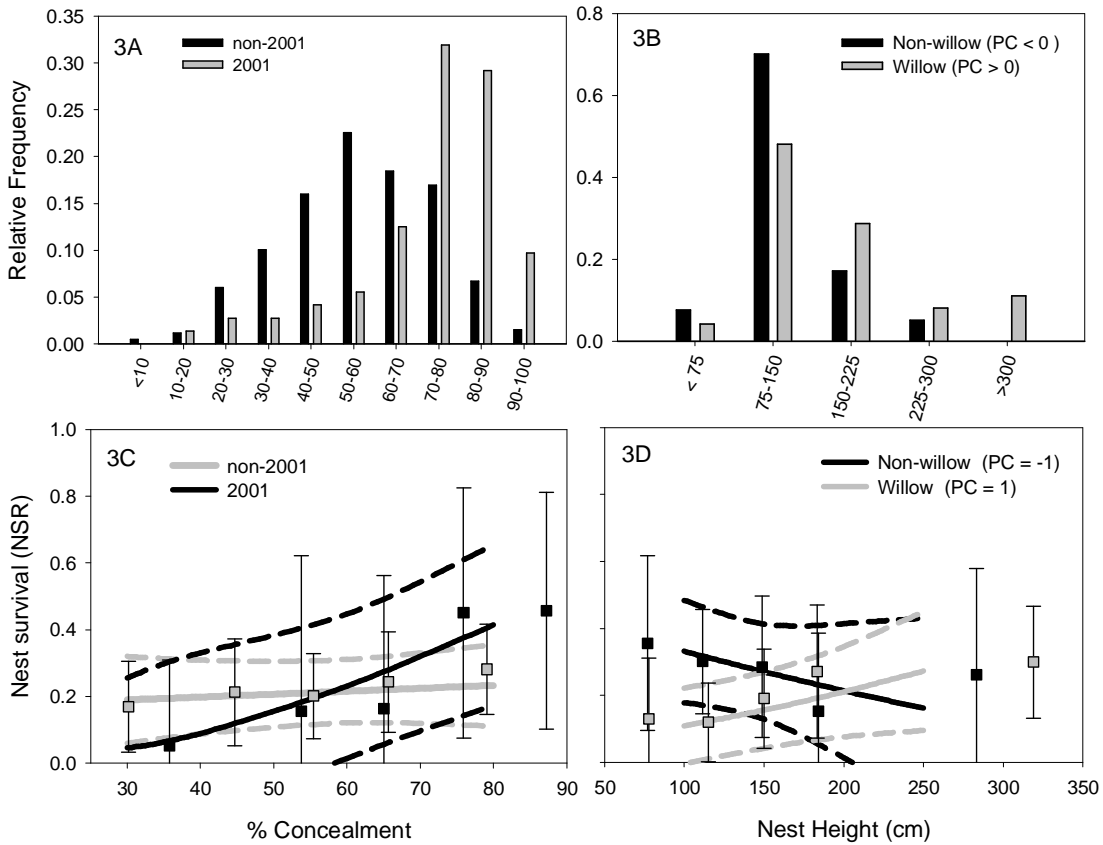
Figure 3.4. Relative frequencies of 2006-2007 natural ($n = 141$) and experimental nests ($n = 140$) along concealment (4A) and height (4B) gradients. Nest survival (NSR) estimates and 95% confidence bounds within natural concealment and height ranges for natural nests (class-based estimates only) and experimental nests (4C / 4D) and avian (ABR) and rodent (RBR) clay egg bite rates (4E / 4F) along experimentally extended concealment and height ranges. Model-based estimates were calculated from M1 (3C / 3D), M11 (ABR, 3E / 3F), M21 (RBR, 3E), and M20 (RBR, 3F) from Table 3.4. Class-based NSR estimates are plotted at mean values for nests $< 30\%$, 30-45%, 45-60%, 60-80%, $> 80\%$ concealed; and < 75cm, 75-150cm, 150-300cm, > 300cm high. Class-based ABR and RBR estimates are plotted at mean values for nests $< 30\%$, 30-55%, 55-80%, $> 80\%$ concealed; and < 75, 75-100, 100-140 (ABR), 100-150 (RBR), > 140 (ABR), and > 150 cm (RBR) high. Vertical dotted lines mark the limits of the natural concealment and height ranges.
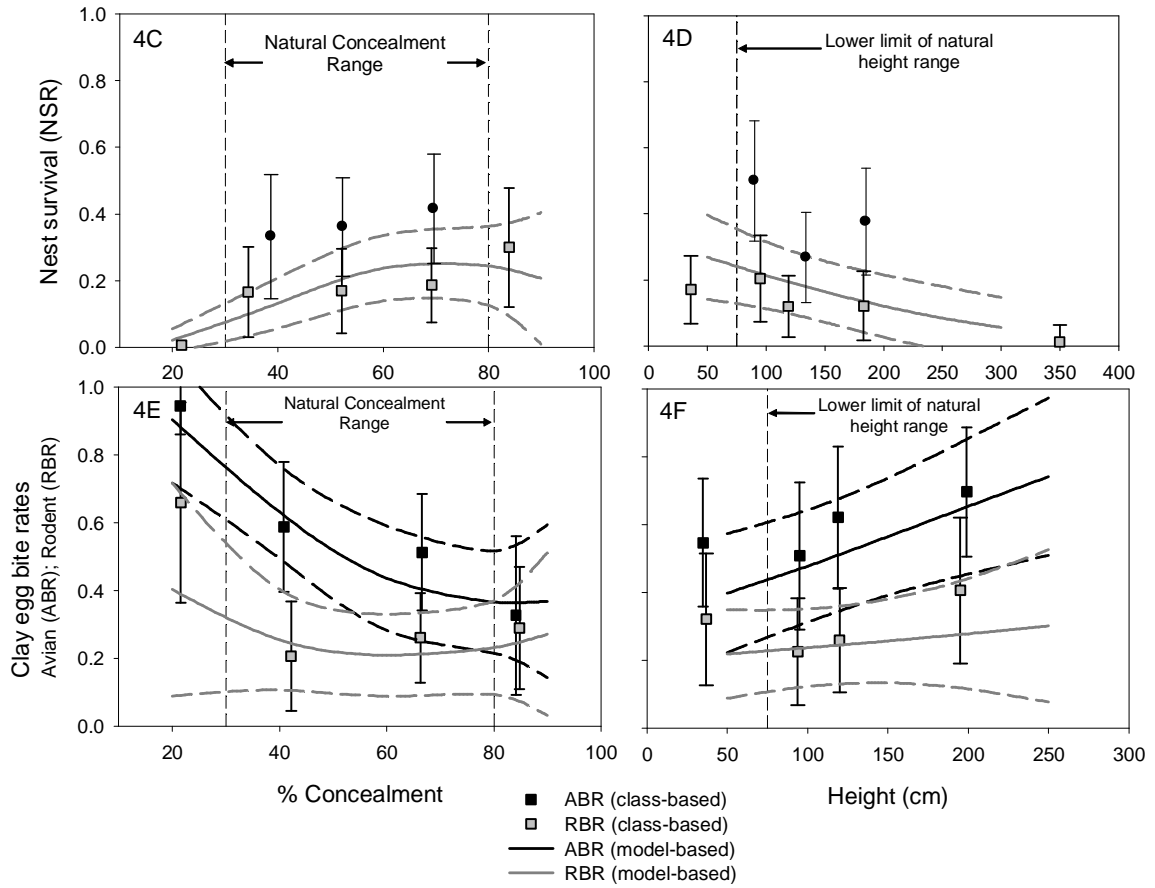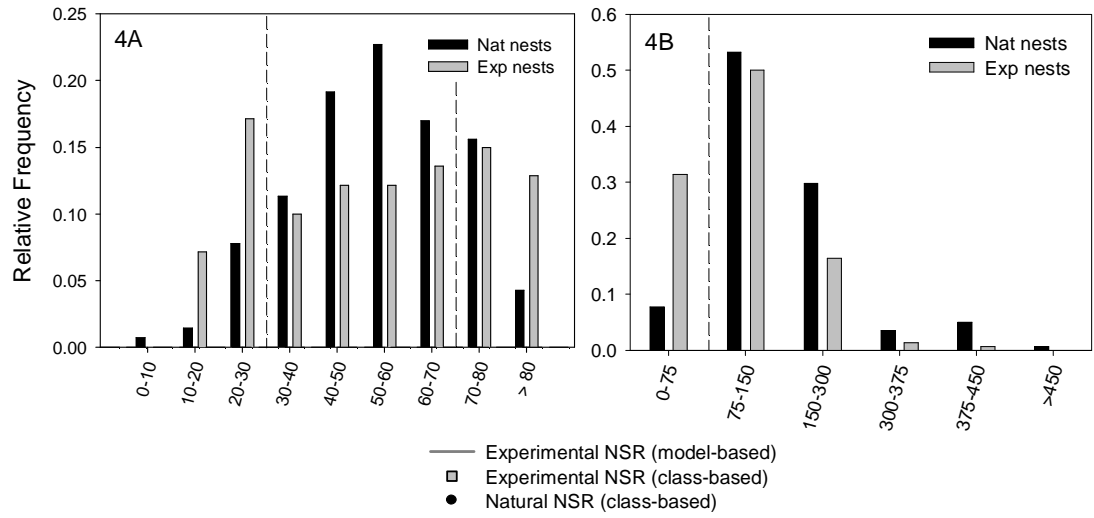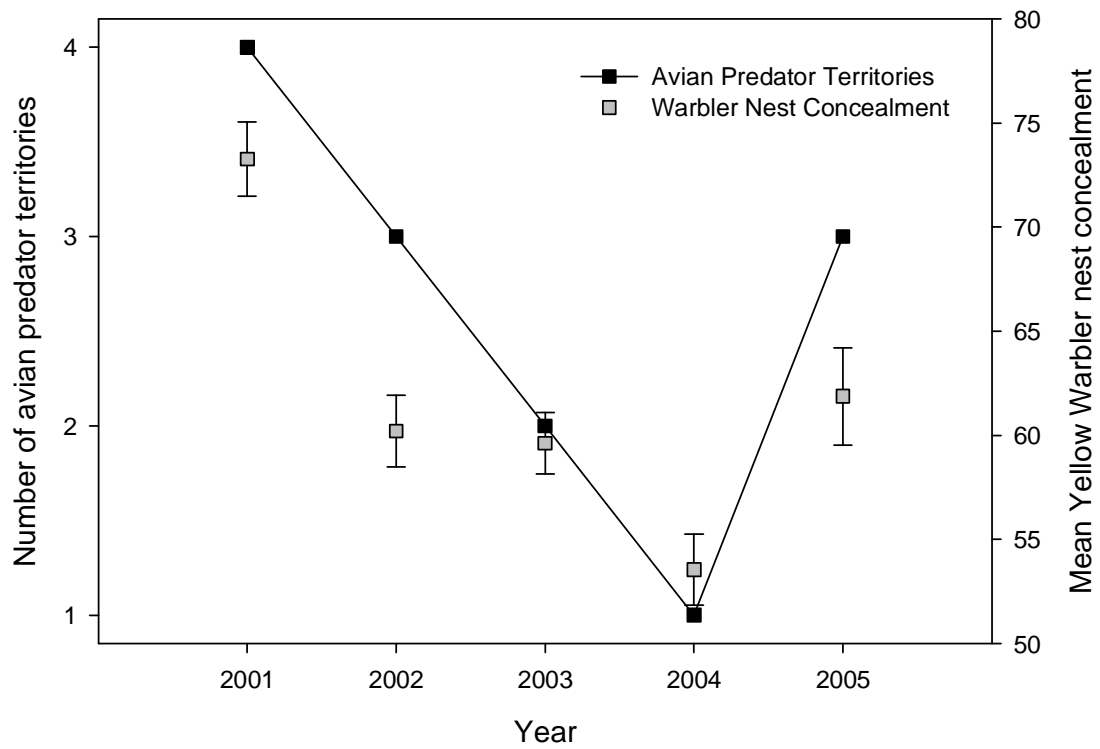
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Figure 3.5. Avian predator territories (black) and yearly concealment means (with standard error bars; grey) from 2001-2005. Avian predators consisted of members of the family Corvidae, which were mostly American Magpies but also included one Western Scrub-jay that established a territory in 2005.

Chapter 4: The role of Yellow Warbler parents in shaping spatiotemporal patterns of nest predation risk

ABSTRACT

Because nest predation limits fitness and therefore strongly shapes avian ecology and evolution, an understanding of nest predation would inform our understanding avian biology. However, field studies usually only document predation patterns without investigating the underlying processes necessary for a complete understanding of how and why predation occurs. I studied a population of Yellow Warblers, for which I documented nest predation patterns and examined how nesting parents contributed to variation in predation risk. I compared natural predation patterns to predation patterns experienced by nests without parents (i.e., experimental nests). I found a strong negative correlation between Yellow Warbler density and natural predation rates, and relatively low predation rates in the middle of the nesting season. Patterns during the egg period (laying and incubation) were similar to those apparent across the entire nesting cycle, yet overall egg predation patterns recorded at experimental nests, as well as predator-specific egg predation patterns (avian predator and rodent predator clay egg bite patterns), were relatively constant with respect to warbler territory density and date. I also found a decrease in daily predation rates over the course of the natural nesting cycle that was somewhat paralleled by experimental predation patterns. Comparisons of natural versus experimental predation patterns accounted for differences between natural and experimental nests other than the presence of parents. I concluded that parents played a critical role in producing natural predation patterns with respect to bird density and date,

but were less important for influencing variation in daily predation rates over the course of the nesting cycle.

INTRODUCTION

Nest predation is an important factor shaping the evolution and ecology of birds. Predation is the main cause of nest failure for a wide range of bird species (Martin 1993, Nice 1957, Ricklefs 1969), and nest survival is an important component of fitness (Ricklefs 1969, Lack 1966, Saether and Bakke 2000). Consequently, predation on nests has shaped the evolution of avian behaviors (Collias and Collias 1984, Peluc et al. 2008), life-histories (Martin 1988a, Martin 1995), and morphology (Kilner 2006), as well as avian population dynamics (Ricklefs and Bloom 1977, Robinson et al. 1995, Saether and Bakke 2000) and community composition (Martin 1988b, Lima and Valone 1991). Therefore, to understand multiple aspects of avian evolution and ecology we must be able to explain and predict predation risk. To this end, many studies document spatial and temporal correlates of predation risk (Best and Stauffer 1980, Filliater et al. 1994, Burhans et al. 2002, Grant et al. 2005).

A variety of spatial and temporal correlates of predation risk have been documented. Two commonly identified spatial correlates are habitat and nest density. The risk of nest predation in relationship to habitat (i.e., the physical environment) has been documented at multiple spatial scales (Hatchwell et al. 1996, Burhans and Thompson 1999, Chase 2002, Davis 2005, reviewed by Thompson 2007). Most studies document positive relationships between nest density and predation risk purportedly

caused by predators that focus their foraging efforts where nests are most abundant (Schmidt and Whelan 1999, Ackerman et al. 2004, Elmberg et al. 2009) but negative density-predation relationships are also possible (Hogstad 1995, Perry et al. 2008). Predation risk can also vary temporally, showing both large-scale, among-year patterns are documented (Bety et al. 2002, Chase et al. 2005), as well as finer-scale within-season patterns (Kroll and Haufler 2009, Fisher and Wiebe 2006, Nur et al. 2004, Grant et al. 2005). At the finest scale predation risk can vary over the course of the nesting cycle (Nur et al. 2004, Grant et al. 2005). Despite the large body of literature documenting predation patterns, these patterns often differ among studies, making a general theory capable of predicting predation risk difficult to develop (Lahti 2009). Therefore, elucidation of the processes underlying observed patterns is necessary to further our understanding of nest predation.

Two basic processes can potentially cause predation patterns. The most commonly held view is that spatiotemporal variation in either predator numbers or their behavior causes predation risk to vary (Thompson 2007). Less frequently recognized is the potential for parents to influence predation patterns. Parental behavior (e.g., nest defense or feeding nestlings) can influence predation risk either by deterring (Hogstad 1995, Sperry et al. 2008) or by attracting predators to nests (Mullin and Cooper 1998, Tewksbury et al. 2002). Thus, spatial or temporal variation in parental behavior or variation in parental influence over predation risk could also influence predation patterns (Weidinger 2002). If predators drive predation patterns directly, information regarding alternative prey for predators (Bety et al. 2002, Schmidt and Ostfeld 2003b) or habitat

relationships with predators (Chalfoun et al. 2002, Schmidt and Ostfeld 2003a) may be necessary to understand predation risk. Alternatively, if predation patterns arise from parental effects, variation in food availability for nesting birds (Martin 1992) or the presence of conspecifics (Hogstad 1995, Sperry et al. 2008) may be more relevant. By definition, nest predation must involve predators, but an understanding of how parents shape predation risk is crucial for understanding predation patterns.

Here, I examine the role of parents in producing patterns in predation risk for a population of Yellow Warblers (*Dendroica petechia*) studied over an 8-year period (2001-2009). Whereas separate studies examined fine-scale patterns (i.e., microhabitat relationships) and their mechanistic underpinnings (Chapters 2, 3), this study examined larger scale spatial patterns associated with territory density, as well as temporal variation in predation risk over the course of the nesting season and the nesting cycle. I first conducted an exploratory analysis of predation patterns experienced by natural nests and then compared natural patterns to patterns recorded by nests without parents (i.e., experimental nests) to investigate the role of parents in producing observed patterns. I designed experimental nests that mimicked natural Yellow Warbler nests as closely as possible and monitored them over a similar spatiotemporal extent over which natural nests were monitored. Furthermore, to isolate the role of parents in producing predation patterns, I accounted for differences between natural and experimental nests other than the presence of parents when analyzing natural and experimental predation patterns.

METHODS

Study system

I studied nest predation in a population of Yellow Warblers that breed along lower Rush Creek, the largest tributary of Mono Lake, east of the Sierra Nevada mountain range in California (2020 m, 38°04'N, 119°10'W). Yellow Warblers are an open-cup, shrub and tree-nesting neotropical migrant passerine that breeds mainly in riparian habitats across North America (Lowther et al. 1999). Yellow Warblers in the Mono Basin are the *D. p. brewsteri* (considered synonymous with *D. p. morcomi*, see review by Heath 2008). Male Yellow Warblers arrive along Rush Creek in early May and establish territories. Females select nest sites from within these territories, initiating nests from late May to early July. The habitat along lower Rush Creek is dominated by three species of willow (*Salix exidua*, *S. lucida*, *S. lutea*) and interspersed with patches of Woods' rose (*Rosa woodsii*). The adjacent upland vegetation is dominated by big sagebrush (*Artemisia tridentata*), but also includes bitterbrush (*Pursia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus.*). Rush Creek Yellow Warblers favor nest sites in willow, but also commonly nest in Woods' rose and occasionally in sagebrush (Chapter 2). A detailed description of the historic and current vegetative, hydrologic and management conditions of lower Rush Creek are provided by McCreedy and Heath (2004).

Numerous predator species prey on open-cup nests including those of Yellow Warblers in the Mono Basin. Species either observed depredating nests (i.e., directly or with video cameras) or suspected nest predators along Rush Creek include garter snakes (*Thamnophis* sp.), gopher snakes (*Pituophis catenifer*), mice (Muridae / Cricetidae),

chipmunks (*Tamias* sp.), raccoons (*Procyon lotor*), weasels (*Mustela* sp.), Western Scrub-Jay (*Aphelocoma californica*), Black-billed Magpie (*Pica hudsonia*), wrens (Troglodytidae), and Bullock's Oriole (*Icterus bullockii*; Chapter 1). In addition, Brown-headed Cowbirds (*Molothrus ater*) parasitized 43% of Yellow Warbler nests in our study area (*n* = 593 nests; PRBO and Latif unpublished data) and are also documented nest predators (Arcese et al. 1996, Chapter 1).

Data collection

Data for this study were collected over 8 years in collaboration with PRBO Conservation Science (formerly the Point Reyes Bird Observatory). From 2001-2005, PRBO monitored Yellow Warbler nests using standard methods (Martin and Geupel 1993) within a 38.4-ha section of Rush Creek as part of their long-term, riparian songbird monitoring program. From 2006-2008, I continued to monitor Yellow Warbler nests along the upper 20.3-ha portion of this site. Throughout this entire period, PRBO and I visited this site at least every other day for the duration of the nesting season (late May through late July). We relied on behavioral cues to find as many nests for as many breeding territories as possible within the study site (Chapter 2). We also used behavioral cues to map territories (Martin and Geupel 1993). By maximizing the number of territories sampled, we distributed our nest-searching efforts evenly across space. Once a nest was located, we visited the nest at least once every four days and recorded its contents until it was either completely depredated or all nestlings left the nest. Both numbers of Yellow Warbler and cowbird eggs and/or nestlings were recorded during each visit. We determined the age of

nestlings during each visit by comparing them to photographs of nestlings of known age. Additionally, in 2008 I candled eggs in the field (Lokemoen and Koford 1996) and determined their age by comparing them with images of candled eggs of known age. Finally, we measured the microhabitat structure at each nest site once nests were inactive (habitat measurement protocols in Chapters 2, 3).

In addition to monitoring natural nests, I also monitored experimental nests during two breeding seasons: 2006 and 2007. Experimental nests consisted of previously used Yellow Warbler nests each containing one passerine egg and one clay egg. I obtained passerine eggs similar in size to Yellow Warbler eggs from captive Zebra Finch (*Taeniopygia guttata*) colonies and stored them according to established protocol (DeGraaf and Maier 2001) until deployed in the field. I monitored experimental nests using the same protocol for monitoring natural nests until nests were either depredated (i.e., eggs were damaged or disappeared) or for 14 days (i.e., the length of the Yellow Warbler laying and incubation periods; PRBO unpublished data). I identified predators responsible for depredating experimental nests using video cameras (Chapter 1) and by examining bite impressions left in clay eggs by predators. Clay egg bite marks were discernable as either avian or rodent bites (Chapters 2, 3; see also Dion et al. 2000, Weidinger 2002). I monitored experimental nests over the season in which natural nests were active (i.e., from late May through early July) and over the same spatial extent across which I monitored natural nests (the upper 20.3-ha of the PRBO study plot). I monitored experimental nests across a somewhat wider range of microhabitats than is generally occupied by natural nests, (i.e., I extended natural concealment and height

ranges; Chapter 3), but most nests were monitored in microhabitats representative of those occupied by natural nests (i.e., in willow and rose, > 75cm, and from 30-80% concealed; Chapters 2, 3). Additionally for this study, I ignored experimental nests in non-natural microhabitats that suffered atypical predation rates (i.e., nests < 30% concealed) relative to rates suffered within the natural microhabitat range (Chapter 3).

Data Analysis

I analyzed nest survival using the logistic exposure method (Shaffer 2000), which relates daily nest survival rates (DSR) with either continuous or categorical explanatory variables. Logistic exposure is a discrete time-survival analysis that uses a modified logit link function with a binomial distribution. This method treats the time period between nest checks as the observation interval, accounts for nests being observed for different lengths of time between nest checks, and assumes that individual nests are independent samples. I analyzed data from all experimental nests and natural nests that were either successful or depredated and were observed with ≥ 1 Yellow Warbler egg and/or young. I excluded data from natural nests that were either abandoned or failed due to cowbird parasitism (i.e., cowbird eggs/young remained viable after host failure), which amounted to ca. 25% of failed nests (Chapter 2). When analyzing natural nest survival, I used one of two definitions of nest failure. For some analyses, I considered a nest failed when *completely depredated* or at *complete predation* (i.e., when no host eggs or young remained). Using this definition, a nest survived if it at least one chick fledged from the nest. For the remaining analyses, I considered a nest failed when *any predation* (i.e.,

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either partial or complete predation) was observed, so that a nest survived if it completely avoided predation. Since experimental nests could never be partially depredated, I used the latter definition when analyzing experimental predation rates and when comparing predation rates between natural and experimental nests.

All logistic exposure models (hereafter DSR models) described nest survival as a function of one or more factors of interest: Yellow Warbler territory density, date, nest age, and brood parasitism status. I generated a nest-specific index of territory density by counting the number of digitized territories that fell within a 150m-radius buffer centered on each nest using ArcGIS 9.2 software (ESRI 2006; Chapter 2), and subsequently dividing the number of territories by the area (ha) of the buffer (Density = # territories per ha). Buffer areas excluded any area falling outside the riparian corridor (i.e., outside the study plot). I initially used 50m-, 100m-, and 150m-radii buffers to generate multiple density indices, but these indices were highly correlated and preliminary analyses found the 150m-based index explained the most variation in nest survival, so I only included the 150m-buffer index in final DSR models. Timing within the nesting season was represented as the day-of-the-year (Date). Timing within the nesting cycle was represented as a continuous variable (Age: the number of days from the clutch completion date; i.e., clutch completion = 0 and laying days were negative), as a two-class variable ($Stage_{Egg/Nestling}$), or as a three-class variable ($Stage_{Laying/Incubation/Nestling}$). I represented brood parasitism status as a class variable (Parasitism = "parasitized" / "not parasitized"). Parasitism was evaluated for each observation interval (i.e., "parasitized" if the observed nest contained ≥ 1 cowbird egg or nestling during the interval). Parasitism

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was not of direct interest, but since cowbirds also depredate nests, effects of Parasitism and its interactions with other effects helped elucidate the processes underlying patterns of interest. Nonlinear versions of continuous effects interest were also represented in DSR models as either quadratic effects (e.g., $Date^2 = Date + Date^2$) or cubic effects (e.g., $Age^3 = Age + Age^2 + Age^3$).

In addition to effects of interest, all DSR models contained one or more effects of covariates. Covariates were correlates of DSR identified from previous analyses but not of direct interest. Each DSR model potentially contained one or more of the previously described variables as covariates. Additionally, DSR models contained Year (a categorical variable) and the microhabitat variable PC1 as covariates. PC1 is a nest's score along a principle component axis describing a willow-to-non-willow gradient in microhabitat patch structure (positive scores = more willow; Chapter 2). Concealment (the percentage of the nest-cup hidden by surrounding vegetation) and Height (the distance in centimeters between the ground and the bottom of the nest-cup) were usually not included as covariates in DSR models (except see analyses described in Table 4.3) because their effects on DSR (Chapter 3) are more complicated than the PC1 effect. However, to consider their potential confounding effects, I did examine inter-correlations between concealment/ height and effects of interest. Being spatial and temporal factors, microhabitat and Year effects are relevant to the subject matter at hand, but experimental nests did not control for among-year variation in parental effects (only monitored for two years), and microhabitat effects are explored in detail elsewhere (Chapters 2, 3).

Model comparisons and statistical analyses. To identify important factors shaping

nest survival, I compared the fit of DSR models with and without explanatory variables

of interest to data from nest monitoring. I fitted models to data using PROC GENMOD in

SAS 9.1 (SAS Institute, Cary, North Carolina) and compared their fit within an

information-theoretic framework (Burnham and Anderson 2002). I used Akaike's

Information Criteria (AIC_c) as an index of relative fit. Using AIC_c-difference scores (Δ_i =

difference scores between model *i* and the best-fitted model within a model-set), I

calculated model weights ($w_i = e^{\Delta_i} / \sum_{0-j} e^{\Delta_i}$) which provided the weight of evidence for

specific models. Additionally, I calculated evidence ratios to examine the evidence for

particular effects of interest (ER = $\Sigma w_{model(s)-with-effect}$ / $\Sigma w_{model(s)-without-effect}$). An ER < 1

indicates poor evidence, 1 < ER < 2 indicates marginal evidence, and an ER > 2 indicates

relatively strong evidence for a particular effect (Burnham and Anderson 2002). Having

identified important effects, I used best-fitting DSR models to estimate period nest

survival rates (NSR) along spatial or temporal axes to examine the shape of survival

patterns (Shaffer and Thompson 2007). For the entire natural nest period, NSR = $DSR^{24.1}$,

and for the egg period, as well as for experimental nest period, NSR = DSR^{14} (exponents

= length of the nest period in days). When calculating nest survival estimates, I assumed

mean covariate values for the observations to which DSR models were fitted. I used the

delta method applied to logit estimates and their standard errors to calculate standard

errors and 95% confidence intervals for nest survival estimates (Powell 2007, Shaffer and

Thompson 2007). Finally, I examined the adequacy of DSR models for predicting nest

survival rates by comparing model-based NSR estimates with class-based NSR estimates for partitions along continuous spatiotemporal axes. This procedure is analogous to plotting observed versus predicted values when conducting linear regression (Shaffer and Thompson 2007). I also calculated a quantitative measure of goodness-of-fit ($c = \chi^2_{GOF}$ / degrees-of-freedom) for models containing the maximum number of parameters ($c > 4$ indicates unacceptable model structure; Burnham and Anderson 2002).

I began with an exploratory analysis to identify natural patterns of predation risk. I constructed two sets of DSR models that contained all possible combinations of explanatory variables of interest, and fitted these models to data from natural nests. The first set contained all combinations of Date, Date^2, Density, Density^2, and Parasitism effects, with PC1 (i.e., microhabitat patch structure) and Stage$_{Egg/Nestling}$ as covariates. This model-set was fitted to data from all observations of natural nests. Because analyses of age effects require aging nests in the field (Nur et al. 2004, Grant et al. 2005), I fitted a second set of models describing candidate age effects to data derived from observations during which Age was known. These data included observations from nests that were found during the building, laying, or nestling stages in all years. Except for observations made in 2008 (i.e., when eggs were aged by candling in the field), I excluded observations of the incubation period of nests found after the laying stage. Candidate models for exploring age effects included one of five possible variables of interest: Age, Age^2, Age^3, the two-stage effect (Stage$_{Egg/Nestling}$), or the three-stage effect (Stage$_{Laying/Incubation/Nestling}$), and all models included PC1 and effects from the best-fitted model from the previous model-set as covariates. I fitted both of these model-sets to data

from observations made throughout the entire natural nest cycle for which failure =

complete predation, and to data collected during the egg period for which failure = any

predation.

I compared natural to experimental predation patterns by fitting DSR models to

datasets designed to control for differences between natural and experimental nests. By

accounting for differences other than the presence of parents, I isolated the effect of

parents on predation risk. Experimental nests differed from natural nests by (D1) never

containing nestlings, (D2) by never being parasitized by cowbirds, and (D3) by never

being partially depredated. Additionally, (D4) I monitored experimental nests for only

two years (2006-2007), and to accommodate a separate study (Chapter 2), (D5)

experimental nests occupied a wider microhabitat range than natural nests (i.e., sites <

30% concealed, > 80% concealed, and < 75cm high). My primary analyses consisted of

fitting models to two datasets that controlled for most of these differences (D1 and D3-

D5). These datasets included observations from experimental and natural nests monitored

in 2006-2007 (D4), but excluded observations of natural nests during the nestling period

(D1) and observations of experimental nests < 30% concealed (i.e., where experimental

nest survival rates deviated the most from natural rates; Chapter 2; D5). Additionally, one

of these two datasets excluded observations of natural nests following the first incidence

of partial predation (controlling for D3), at which point I considered natural nests to have

failed. All DSR models fitted to these two datasets included the class variable Type (i.e.,

experimental versus natural) as a covariate, and some models included spatiotemporal

effect × Type interaction parameters. Evidence ratios for interaction parameters tested for

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differences between experimental versus natural predation patterns. Additionally, I supplemented these analyses with qualitative comparisons of patterns apparent from analyzing natural-nest-only and experimental-nest-only data. Finally, I examined how parasitism (D2) influenced nest survival rates by calculating evidence ratios for Parasitism and Parasitism × spatiotemporal interaction effects on DSR for natural nests.

I also analyzed spatiotemporal patterns in predation rates specific to avian and rodent predators. I fitted DSR models to data from all experimental nests for which nest failure = predation by the predator type of interest (i.e., an avian or rodent bite in a clay egg; data compilation further described in Chapters 2, 3). To maximize my sample size, I included clay egg data from all experimental nests (i.e., including those < 30% concealed). I calculated avian predator bite rates (ABR) and rodent bite rates (RBR) along spatial or temporal axes of interest (PBR = 1 – DSR^{14}; PBR = predator-specific bite rate (ABR or RBR)) to evaluate the potential for these specific predator types to have shaped natural predation patterns.

RESULTS

Spatiotemporal patterns of variation in natural nest survival

I found substantial variation in survival rates for natural nests along spatiotemporal axes of interest. Of 596 Yellow Warbler nests monitored from 2001-2008, 239 succeeded and 357 were depredated. Of DSR models that included all possible combinations of Date, Date^2, Density, and Density^2 effects, the model with all these effects best fitted the data from natural nests (Model 1, Set 1, Table 4.1). The second-best-fit model was also

weighted substantially (Model 2, Set 1, Table 4.1) but differed from the best model only in the form of the Density effect (i.e., linear instead of quadratic). All other models were associated with relatively low weights ($w_i \leq 0.05$). Thus, although the data did not clearly distinguish the form of the Density effect on DSR (i.e., linear versus curvilinear), they did strongly support Density, Date, and Parasitism relationships with DSR. Areas surrounding nests varied in Density from 0.6 - 5.8 (mean = 3.1 ± 1.2 (s.d.)) territories/ ha. Nests in the most densely populated areas were more than twice as likely to survive as nests in least-populated areas (Figure 4.1A). Mean clutch completion dates (day 164 ± 10) varied significantly among years ($F_{8,721} = 8.8$, $P < 0.001$), but among-year variation accounted for only a small portion of the total variation in clutch completion dates among nests ($R^2 = 0.09$). The modal clutch completion date was 156 (ca. June 5). Nests whose clutches were completed in ca. mid-June were 2-3 times more likely to survive than nests initiated in late May or early July (Figure 4.1B). I found similar survival patterns within the egg period after equating failure with first predation (i.e., either partial or total; Set 2, Table 4.1; Figures 4.1C, 4.1D), although predictions based on DSR models fitted to these data were not as precise (c = 4.57).

Differences in natural versus experimental predation risk and spatiotemporal predation patterns

Natural nests monitored from 2006-2007 were more likely to survive the egg period than experimental nests even when controlling for differences between these nest types other than the presence of parents. I monitored 111 experimental nests > 30% concealed

concurrently with 141 natural nests. Regardless of how failure was defined for natural nests, the data strongly supported a difference in survival rates between natural and experimental nests ($ER_{M3/M5}$ = 2.9, Set 1; $ER_{M3/M8}$ = 4.3, Set 2; Table 4.2). When natural failure was defined comparably with experimental failure (i.e., first partial or complete predation), natural NSR_{Egg} (0.29 $\pm$ 0.04) was substantially higher than experimental NSR (0.18 $\pm$ 0.03; based on M3, Set 1, Table 4.2). When natural failure = complete predation, natural NSR_{Egg} was even higher (0.41 $\pm$ 0.05; calculated from DSR model with Year, PC1, and Type effects).

Survival patterns experienced by natural nests differed substantially from patterns for experimental nests (Table 4.2). The data most supported a Density $\times$ Type interaction ($ER_{M1/M3}$ = 3.1, $ER_{M1/M2}$ = 1.9, Set 1; $ER_{M1/M2}$ = 2.0, Set 2). From 2006-2007, natural NSR increased substantially, whereas experimental NSR remained relatively constant with increasing Density (Figure 4.2C). Although somewhat weaker, the support was still substantial for differences in Date-survival patterns between natural versus experimental nests. Analyses of 2006-2007 data did not strongly support Date-survival relationships ($ER_{M6/M3}$ = 0.2, $ER_{M7/M3}$ = 0.1, Set 1; $ER_{M4/M3}$ = 0.3, $ER_{M5/M3}$ = 0.02, Set 2; Table 4.2). However, 2001-2008 data from natural nests clearly supported a mid-seasonal peak in natural nest survival (Set 1, Table 4.1, Figure 4.1B), and this pattern remained strong within the egg period when natural nest failure was defined comparably with experimental failure (Set 2, Table 4.1, Figure 4.1D) and was reasonably consistent through time ($ER_{Date \times Year/Additive\ model}$ = 0.01, Δ_i = 8.6; Additive model = M1, Set 2, Table 4.1). By contrast, when analyzed alone, the data from experimental nests did not support

a Date-survival relationship ($ER_{M5/M1}$ = 0.16, Set 1, Table 4.3). Assuming a Date^2 × Type model (M7, Set 1, Table 4.2), mid-seasonal NSR was substantially higher than either early- or late-season natural NSR, as well as experimental NSR (Figure 4.2D). This model did not provide a particularly good fit to the data (based on the data to which this model was fitted, class-based NSR estimates increased rather than decreased at the end of the season). However, similar models (M4, Set 2, Table 4.2; M2, Set 2, Table 4.1) provided a better fit to larger datasets (compare class-based to model-based estimates in Figures 4.1B, 4.1D, and dotted plot in 4.2D), so the poor fit of the most restrictive model (solid black plot, Figure 4.2D) is likely a product of sampling error.

These patterns were not confounded with microhabitat effects. Since I included PC1 as a covariate in DSR models, the observed patterns account for any potential confounding PC1 effects. Neither Density nor Date were strongly correlated with Concealment among natural nests (Density: r = -0.25, Date: r = -0.06) nor among experimental nests (Density: r = -0.09, Date: r = 0.20), and scatter-plots did not suggest any non-linear relationships. Furthermore, for experimental nests > 30% concealed (i.e., the data included in this study), the concealment-predation relationship was weak (see Chapter 3), and unlike the Concealment × Year interaction effect detected for natural nests (Chapter 3), Density and Date effects did not interact with Year (both $ER_{\text{Interaction-model/Additive-model}}$ < 0.01; Additive model = M1, Set 1, Table 4.1). Including height as a covariate in DSR models did not unveil any within-season predation patterns for experimental nests ($ER_{M4/M1}$ = 0.4, $ER_{M3/M1}$ = 0.4, Set 1, Table 4.4), and scatter-plots did not suggest any non-linear relationships between height and Date. Furthermore, unlike

the Height $\times$ PC1 relationship detected for natural nests (Chapter 3), Density and Date effects did not interact with PC1 (both $ER_{Interaction-model/Additive-model} = 0.2$; Additive model = M1, Set 1, Table 4.1)

Predator-specific predation patterns

Avian and rodent predators left numerous, distinctive bite marks in clay eggs. From 2006-2007, I monitored 140 experimental nests containing clay eggs (including nests < 30% concealed) of which 77 received bite impressions. Of these, 50 were distinguishable as avian bite marks, 23 as rodent, and 4 marks were not identifiable. Avian predators left scratches, pokes, and/or impressions clearly shaped like the inside of the upper and lower mandibles of a bird bill. Rodent impressions were discernable by the distinctive double-tooth impressions left by their incisors.

Predator-specific bite rates were not strongly correlated with either Density or Date. Neither Date^2 nor Density effects on avian or rodent bite rates were strongly supported (avian: $ER_{M2/M1} = 0.7$, $ER_{M3/M1} = 0.2$, Set 2; rodent: $ER_{M5/M2} = 0.3$, $ER_{M3/M2} = 0.6$, Set 3; Table 4.4). Furthermore, class-based ABR and RBR estimates did not suggest any positive or negative trends in predator-specific predation rates along a Density axis (Figure 4.2E). Class-based ABR estimates could reflect a mid-seasonal peak in the risk of avian predation, whereas RBR estimates if anything suggested a decline in rodent predation as nesting seasons progressed (Figure 4.2F).

Brood parasitism and nest survival

Brood parasitism was correlated with both rates of partial and complete predation risk for natural nests. An effect of Parasitism on the likelihood of surviving complete predation was clearly supported for natural nests ($ER_{M1/M3} > 10$, Set 1, Table 4.1), parasitized nests being more likely to avoid complete failure (NSR = 0.30 ± 0.05 (s.e.)) than non-parasitized nests (NSR = 0.19 ± 0.04; estimates from M1, Set 1, Table 4.1). Similarly, from 2006-2007, a parasitized natural nest was more likely to avoid complete failure during the egg period (NSR = 0.54 ± 0.08) than a non-parasitized nest (0.32 ± 0.05; calculated using M3, Set 2, Table 4.2). However, brood parasitism did not reduce the likelihood of avoiding any and all predation. The data did not support a Parasitism effect on survival of *either* partial *or* complete predation ($ER_{(M3+M4)/M1+M2)} = 0.4$, Set 2, Table 4.1) and the likelihood of avoiding either type of predation was similar for parasitized (2001-2008: NSR = 0.23 ± 0.04, 2006-2007 NSR_{Egg}: 0.30 ± 0.06) and non-parasitized nests (2001-2008: 0.24 ± 0.04, 2006-2007 NSR_{Egg}: 0.29 ± 0.05) (2001-2008 estimates from M4, Set 2, Table 4.1, 2006-2007 estimates from a Year + Parasitism + Type model fitted to Dataset 1, Table 4.2). In short, these results indicate that parasitized nests were less likely to be completely depredated but more likely to be partially depredated than non-parasitized nests.

Despite the effect of Parasitism on partial and total predation rates, brood parasitism did not influence spatiotemporal predation patterns. Regardless of how nest failure was defined, all evidence ratios for interactions between spatiotemporal effects on

natural nest survival and Parasitism were < 1 (largest evidence ratio: $ER_{\text{Date}\times\text{Parasitism-model/Additive-model}} = 0.5$; Additive-model = Model 1, Set 1, Table 4.1).

Nest survival over the nest period

I found a substantial positive correlation between nest age and survival for natural nests. Age was known during 1,418 natural nest observation intervals (69% of all observation intervals). Of the models fitted to these data, a continuous, linear Age model received the most support (Table 4.1), and daily nest survival increased with nest age (Figure 4.3A). The data did not unequivocally support a continuous linear model over a two-stage model ($ER_{\text{M2/M3}} = 1.8$, Set 1, Table 4.4), but class-based DSR estimates along an Age axis did not suggest any threshold effects (hatching at Age = ca. 10.5, Figure 4.3A). Age effects were not dependent on brood parasitism status ($ER_{\text{Stage}\times\text{Parasitism/Additive-model}} = 0.16$, $ER_{\text{Age}\times\text{Parasitism/Additive-model}} = 0.39$, additive model = M2, Set 1, Table 4.4). However, the effect of nest age was somewhat dependent on microhabitat patch structure ($ER_{\text{M1/M2}} = 1.1$, Set 1, Table 4.4). Specifically, nests in willow-dominated microhabitats experienced much stronger age effects than in non-willow dominated microhabitats (Figure 4.3B). Age effects calculated within the egg period were not supported either for natural nests ($ER_{\text{M2/M1}} = 0.38$, Set 2, Table 4.4) or for experimental nests (equivalent ER = 0.42; models not presented). However, class-based NSR estimates suggest a positive DSR trend as experimental nests aged (Figure 4.3A).

DISCUSSION

How do parents influence predation risk?

I found substantial evidence that Yellow Warbler parents reduce the risk of nest predation. Egg predation rates at natural nests were consistently lower (i.e., survival rates were higher) than for experimental nests. When defining nest failure comparably (i.e., either partial or complete predation), 2006-2007 survival rates for natural nests (0.29 ± 0.04) were substantially higher than experimental rates (0.18 ± 0.03; see Results). Although experimental nests were never parasitized, complete avoidance of any predation was just as likely for natural nests whether or not they were parasitized. When using a comparable definition of failure, the difference in NSR between natural and experimental nests quantifies the influence of parents on predation risk. Yellow Warbler parents along Rush Creek reduced the risk of predation for their nests by ca. 11% overall during 2006 and 2007.

Nesting birds use various behaviors to reduce predation risk. Nest site selection is an important tool for reducing predation risk, but having controlled for microhabitat effects on predation risk (examined thoroughly in Chapters 2, 3), this study specifically documents the effects of parents after nest initiation. Post-initiation, birds can agonistically defend their nests (Blancher and Robertson 1982, Hogstad 2004) or employ more passive strategies, such as simply being present at the nest or using alarm calls or distraction displays to quiet begging nestlings or lure predators from the nest (Byrkjedal 1987, Winkler 1994, Halupka 1998). The presence of parents and/or the intensity of defensive behaviors are negatively related with predation risk for a variety of passerine

species (Greig-Smith 1980, Komdeur and Kats 1999, reviewed by Martin 1992), although the efficacy of defensive behaviors likely depends on which predators threaten nests (Schmidt and Whelan 2005). Yellow Warblers exhibit a variety of defensive behaviors, including agonistic behaviors, alarm calls, and distraction displays (Hobson et al. 1988, Hobson and Sealy 1989, Lowther et al. 1999, Latif pers. obs.). Given the variety of predators that threaten Yellow Warbler nests along Rush Creek (Chapter 1), it is highly plausible and apparent from the data that Yellow Warbler nest defense strategies reduce the threat imposed by at least some of these nest predators.

Predation pressure applied by cowbirds is an important determinant of nest predation risk for Yellow Warblers. Direct observations of nest predation implicate cowbirds as nest predators in this system (Chapter 1). Additionally, differences in complete and partial predation rates for parasitized versus non-parasitized natural nests suggest that cowbirds depredate a substantial portion of natural nests. The higher rate of partial clutch loss when nests are parasitized likely arises because cowbirds adjust clutch sizes by removing host eggs to favor their own fecundity (Lowther 1983, Tewksbury et al. 2002). The higher rate of total clutch loss when nests are not parasitized likely arises because cowbirds attempt to create new parasitism opportunities by depredating non-parasitized clutches and thereby forcing host females to re-initiate (Arcese et al. 1996, Hauber 2000). A positive correlation between parasitism and predation rates may arise from the simple fact that cowbirds are inherently less likely to discover nests in poor-quality sites, since these nests are likely to fail before they are discovered. However, I controlled for this effect by coding each observation interval according to the observed

nest's parasitism status during that interval. Selective parasitism by cowbirds of either high-quality nest sites or high-quality females could also explain positive correlations between parasitism and nest survival. Although I had no information regarding individual Yellow Warbler quality, cowbirds did not preferentially parasitize nests in low-predation microhabitats; parasitism was not correlated with microhabitat features known to affect nest survival (PC1: $r = -0.03$, Concealment: $r = 0.01$; $n = 2060$ observation intervals; microhabitat-predation effects described in Chapters 2, 3). Predators other than cowbirds could also differentially depredate parasitized versus non-parasitized nests if parasitism affects the cues that predators use to find nests. Tewksbury et al. (2002) attributed *higher* clutch predation rates from parasitized nests to higher visitation rates by males feeding tighter-sitting, parasitized females, but this effect cannot explain the *lower* predation rates on parasitized clutches found here. Thus, cowbirds are the likely culprit causing both higher total loss of non-parasitized clutches and higher partial loss of parasitized clutches.

Yellow Warblers exhibit specialized behaviors for defending their nests against cowbirds (Tewksbury et al. 2002, Gill and Sealy 2004). Anecdotal observations suggest that even relatively small passerine birds can successfully chase off cowbirds (Strausberger 1998). In light of the likely threat of direct predation imposed by cowbirds, the lower natural predation rates relative to experimental predation rates strongly suggest that Yellow Warblers are capable of reducing this threat. The extent to which these data document parental effects depends upon the extent to which I have accounted for all differences between natural and experimental nests other than the presence of parents. Because I modeled experimental nest placement on natural nest site use patterns,

differences in experimental versus natural nest site selection processes are unlikely to confound post-selection parental effects on nest predation rates.

How does spatiotemporal variation in nest predator avoidance arise?

I found both spatial variation and within-season temporal variation in the ability of Yellow Warbler parents to mitigate nest predation risk. The natural predation patterns identified for the entire study period (Table 4.1, Figure 4.1) were reflected by variation in natural predation rates during the experimental period (2006-2007; Table 4.2, Figure 4.2). Given the relative lack of variation in predation rates for experimental nests, natural predation patterns were apparently caused by variation in parental effects. Parental effects on predation risk varied spatially with territory density and temporally over the course of the nesting season. Parents reduced predation risk the most in areas containing the highest densities of Yellow Warblers and mid-seasonally (Figures 4.2C, 4.2D). Therefore, the potential factors underlying observed predation patterns include any factors that give rise to spatial or temporal variation in either parental behavior or the influence of parents on predation risk.

One possible factor driving spatial or temporal variation in the influence of parents on predation risk is spatiotemporal variation in food availability. Greater food availability has the potential to decrease time spent foraging and thereby increase time spent near the nest where parents can employ predator avoidance strategies (Martin 1992). Studies in North America generally find bird density to be positively correlated with fecundity, probably because birds concentrate in high quality habitats where food is

most abundant (Bock and Jones 2004). Greater food availability where Yellow Warblers concentrate could cause a positive relationship between natural nest survival and territory density if greater food availability allowed warblers to defend their nests more effectively. Along Rush Creek, warblers were denser where willow was more prevalent (Density versus PC1: $r = 0.29$, P < 0.001; based on territory mean scores for non-use sites measured in 2006-2008, $n = 169$). Given their higher foliage volume and their association with relatively mesic sites (McBain and Trush 2003), willow shrubs likely provide the best foraging opportunities for leaf-gleaning birds, such as Yellow Warblers. High quality foraging sites provided by willow may be one factor attracting Yellow Warblers during territory selection, which may also be adaptive in the context of nest predation risk (unlike microhabitat selection for nest sites: Chapter 2). Higher breeding densities could also allow birds to work cooperatively to deter predators (Hogstad 1995, Perry et al. 2008), but cooperative defense should yield area-wide predator deterrence that should also reduce predation rates for experimental nests (Andersson and Wiklund 1978), but which has not been observed here. The seasonal peak in avoidance of nest predation by Yellow Warblers could be driven by a seasonal peak in arthropod abundance. Given the seasonality characteristic of temperate climates, within-year temporal variation in arthropod abundance is highly plausible. A peak in arthropods found on the surface of woody vegetation would be particularly relevant to leaf-gleaning birds such as Yellow Warblers (Lowther et al. 1999).

Predator numbers or functional variation in predator behavior could influence natural predation without affecting experimental predation rates if only predators that are

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immune to parental defense show numerical or behavioral fluctuations. Natural and experimental nests are both frequently depredated by cowbirds (see above discussion and Chapter 1), so cowbirds are unlikely to drive natural predation patterns without affecting experimental patterns. Indeed, avian clay egg bites were probably mainly caused by cowbirds (Chapter 1), and avian bites do not suggest any variation in cowbird predation pressure capable of explaining natural predation patterns (Figures 4.2E, 4.2F). However, since natural patterns were not dependent upon brood parasitism status, these patterns are unlikely to be solely a product of cowbird predation. Although important nestling predators, snakes rarely if ever depredate eggs (Chapter 1), so snakes are unlikely to drive egg predation patterns observed here. Although less frequent than avian predation, rodent bite rates were substantial and at least two types of rodent predators, chipmunks and mice, were observed depredating nests along Rush Creek (Chapter 1). These two types of predators can show very different ecological responses to environmental variation (Schmidt et al. 2001b, Schmidt and Ostfeld 2003a), and given differences in size, chipmunks and mice may be differentially susceptible to Yellow Warbler defensive behaviors. Chipmunks are larger than mice and therefore perhaps more capable of breaking through Yellow Warbler defenses. Furthermore, given lower population densities, chipmunks may be less accounted for by rodent predation of experimental nests (i.e., Figures 4.2E, 4.2F; see study by Schmidt and Ostfeld 2003a). Further study of chipmunk ecology and their susceptibility to songbird nest defense would be informative. However, even if chipmunk ecology drove the predation patterns observed here, parental defense against mice would be necessary for these patterns to be realized.

Why predation risk decreases with nest age

The positive nest-age relationship with daily survival of Yellow Warbler nests (Figure 4.3A) is most likely caused by microhabitat effects on predation risk. When predation risk varies among sites, nests in unsafe sites would be depredated more quickly, in which case most late-stage nests would be those located in safe sites. Such site effects can arise from microhabitat-predation relationships, such as those experienced by Yellow Warblers (Chapters 2, 3). Increases in daily survival rate with nest age have been attributed to post-initiation variation in parental behavior (Andersson and Waldeck 2006). However, the weaker age effects in unsafe nest sites (Figure 4.3B) and the apparent tendency for experimental nest survival to increase with age (Figure 4.3A) both suggest a greater role of site effects for causing age-related variation in nest survival for Yellow Warblers. Martin et al. (2000) unveiled a positive effect of post-initiation parental behavior on predation risk, resulting in a positive relationship between nest age and residual variation in predation risk when controlling for site effects. Interplay between microhabitat effects and parental effects may contribute to the variation in age effects on daily nest survival observed among systems (Grant et al. 2005, Nur et al. 2004, Franca and Marini 2009). In this system, microhabitat effects appear to be the predominant driver of age effects.

Broader implications

The processes determining spatiotemporal patterns in nest predation risk will depend upon the spatial or temporal scales at which patterns are observed (Thompson 2007). The results of this study are most informative for our understanding of within-season temporal

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patterns and mid-to-larger scale spatial patterns. Recent advances in analytic techniques have allowed researchers to document a variety of within-season temporal predation patterns for natural nests (Grant et al. 2005, Muellner and Linsenmair 2007, Kroll and Haufler 2009, Reidy et al. 2009). My results suggest that temporal variation in food availability could drive these patterns. Spatial variation in predation risk may be positively related with bird density if predators concentrate their foraging efforts where nests are most abundant (Elmberg et al. 2009, Niemuth and Boyce 1995, Schmidt and Whelan 1999). The lack of a relationship between nest density and experimental predation rates suggests that predators either only depredate nests incidentally while searching for their preferred prey (Vickery et al. 1992, Schmidt et al. 2001a) or search strategies are not correlated with density within the range of densities studied (e.g., cowbird search strategies; Norman and Robertson 1975, Robinson and Robinson 2001, Strausberger 1998). Rush Creek Yellow Warblers are therefore free to choose where to breed without apparent effects on predator behavior. As found by most studies of birds (Bock and Jones 2004), Yellow Warblers concentrate in areas conferring the greatest potential fecundity (i.e., highest nest survival rates). Also consistent with the results of other studies (Shochat et al. 2005, Chalfoun and Martin 2007), Yellow Warblers are not apparently responding to overall predator distributions, and are therefore most likely selecting breeding territories based on food abundance. Thus, this population could experience an ecological trap for territory selection (in addition to a trap for nest microhabitat preference; Chapter 2) if predators concentrated in areas with high food availability for Yellow Warblers (see results by Shochat et al. 2005, Chalfoun and Martin

2007). A review of available studies suggests anthropogenic disturbance to have a particularly strong potential for causing ecological traps in western North America (i.e., where disturbance is most recent; Bock and Jones 2004). Riparian habitat along Rush Creek is recovering from severe habitat degradation (Hart 1996, McBain and Trush 2003), but past disturbances do not appear to have been severe enough or of the necessary type to cause an ecological trap for Yellow Warbler territory selection. Rush Creek does provide an ecological trap for Yellow Warbler nest microhabitat selection, but this trap may involve natural processes independent of disturbance (Chapter 2).

Although the potential influence of parents has been recognized (Martin 1992), the prevailing view is that predator ecology generally drives variation in nest predation risk (Thompson 2007). This study demonstrates the importance of parents for influencing predation patterns through time and space. Experimental nests can provide useful tools to control for post-initiation parental effects when examining the processes underlying spatiotemporal patterns of nest predation risk.

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TABLES

TABLE 4.1. Models describing natural nest survival patterns for Yellow Warblers along Rush Creek (2001 – 2008; K = # of model parameters, -LL = -Log-likelihood, Δ_i = ΔAIC_c, w_i = model weights).

Dataset	Model #	Model	K	-LL	Δ_i	w_i
Set 1. Entire nest cycle (n-effective = 5587)	1	Parasitism + Date^2 + Density^2	15	749.3	0.0	0.62
	2	Parasitism + Date^2 + Density	14	751.1	1.7	0.27
	3	Date^2 + Density^2	14	752.9	5.2	0.05
	18	Covariates only (Year + PC1 + Stage$_{Egg/Nestling}$)	3	781.66	40.7	<0.01
	19	Constant Survival	1	808.59	90.5	<0.01
Set 2. Egg period only; failure = first predation (n-effective = 3181)	1	Date^2 + Density	12	617.5	0.0	0.22
	2	Date^2 + Density^2	13	616.6	0.2	0.20
	3	Parasitism + Date^2 + Density	13	617.5	2.0	0.08
	4	Parasitism + Date^2 + Density^2	14	616.5	2.2	0.07
	5	Density	10	620.6	2.2	0.07
	6	Date + Density	11	619.6	2.2	0.07
	7	Density^2	11	619.7	2.3	0.07
	8	Date + Density^2	12	618.7	2.4	0.07
	14	Covariates only (Year + PC1)	2	636.9	18.7	< 0.01
	19	Constant Survival	1	638.9	20.8	< 0.01

Only models with $w_i > 0.05$ shown. Covariate and Constant Survival models shown for comparison.

Models include all possible combinations of Date, Density, and Parasitism effects (19 models) fitted to data from natural nests monitored from 2001-2008 (n-effective = # observation-days represented). Date^2 = Date + Date^2. Density^2 = Dens + Dens^2. c = 1.46 for M1, Set 1; c = 4.57 for M4, Set 2.

TABLE 4.2. Models comparing natural versus experimental nest survival patterns (2006-2007; K = # of model parameters, -LL = -Log-Likelihood, Δ_i = ΔAIC_c, w_i = model weights).

Dataset	Model #	Models	K	-LL	Δ_i	w_i
	1	Dens + Type×Dens	6	320.3	0.0	0.54
	2	Density	5	321.9	1.1	0.31
Set 1. Natural nest failure = first predation; n-effective = 1503	3	Covariates only (Year + PC1 + Type)	4	324.2	3.7	0.08
	4	Covariates only (Year + PC1; no Type)	3	326.3	5.9	0.03
	5	Constant Survival	1	328.6	6.5	0.02
	6	Date^2	6	323.9	7.2	0.01
	7	Date^2 + Type×Date^2	8	323.0	9.4	< 0.01
	1	Dens + Type×Dens	7	309.8	0.0	0.58
	2	Density	6	311.4	1.2	0.32
Set 2. Natural nest failure = total predation; n-effective = 1637	3	Covariates only (Year + PC1 + Type + Parasitism)	5	314.2	4.7	0.06
	4	Date^2 + Type×Date^2	9	311.0	6.5	0.02
	5	Date^2	7	313.5	7.4	0.01
	6	No Type (Year + PC1 + Parasitism)	4	316.6	7.6	0.01
	7	Constant Survival	1	327.5	23.3	< 0.01

Model sets were fitted to data from 2006-2007 natural and experimental nests. n-effective = # observation-days represented. Only data from experimental nests > 30% concealed were included. Date^2 = Date + Date^2. Based on a Date^2 + Date^2×Type + Dens + Dens×Type model c = 0.94 for Set 1, and c = 0.95 for Set 2.

TABLE 4.3. Models fitted to data from experimental nests only (K = # of model parameters, -LL = -Log-Likelihood, Δ_i = ΔAIC_c, w_i = model weights).

Dataset	Model #	Models	K	-LL	Δ_i	w_i
Set 1. Experimental nests > 30% concealed; failure = any predation; n-effective = 699	1	Covariates only (Year+ PC1 + Height)	4	155.3	0.0	0.45
	2	Age	5	155.2	1.7	0.19
	3	Density	5	155.3	2.0	0.16
	4	Age + Dens	6	155.2	3.7	0.07
	5	Date^2	6	155.2	3.8	0.07
	9	Constant Survival	1	163.1	9.6	< 0.01
Set 2. All experimental nests; failure = avian clay egg bite; n-effective = 741.5	1	Covariates only (PC1 + Height + Concealment)	5	102.4	0.0	0.47
	2	Density	6	101.7	0.6	0.35
	3	Date^2	7	102.0	3.1	0.10
	4	Date^2 + Dens	8	101.3	3.9	0.07
	5	Constant survival	1	121.1	29.2	< 0.01
Set 3. All experimental nests, failure = rodent clay egg bite; n-effective = 767.5	1	Constant survival	1	74.3	0.0	0.74
	2	Covariates only (Year + PC1)	3	74.1	3.6	0.12
	3	Date^2	5	72.7	4.7	0.07
	4	Density	4	74.1	5.6	0.04
	5	Date^2 + Dens	6	72.5	6.4	0.03

For Set 1, only models with w_i > 0.05 and Constant Survival model shown. For Sets 2 and 3, all models were used to calculate evidence ratios (in text) so all are shown. Model sets fitted to data from experimental nests (n-effective = # observation-days represented). Date^2 = Date + Date^2. c = 0.31 for global model (M8; not shown), Set 1; c = 0.51 for M4, Set 2; c = 1.24 for M5, Set 3.

TABLE 4.4. Age-DSR models (K = # of model parameters, -LL = -Log-Likelihood, Δ_i = ΔAIC_c, w_i = model weights).

Dataset	Model #	Model	K	LL	Δ_i	w_i
Set 1. Entire nesting cycle (n-effective = 4021)	1	Age + Age×PC1	15	544.5	0.0	0.31
	2	Age	14	545.6	0.1	0.29
	3	Stage$_{Egg/Nestling}$	14	546.2	1.3	0.16
	4	Age + Age^2	15	545.4	1.7	0.13
	5	Age + Age^2 + Age^3	16	545.2	3.3	0.06
	6	Stage$_{Laying/Incubation/Nestling}$	15	546.3	3.6	0.05
	7	Covariates only	13	551.9	10.8	< 0.01
	8	Constant Survival	1	575.1	33.1	< 0.01
Set 2. Egg period only (n-effective = 1697)	1	Covariates only	13	324.5	0.0	0.60
	2	Age	14	324.4	1.9	0.23
	3	Constant Survival	1	338.6	3.9	0.08
	4	Age + Age^2	15	324.4	3.9	0.08

Model-sets describing Age effects fitted to data from natural nests (n-effective = # observation-days represented). Only observations of natural nests during which Age (# of days from clutch completion) was known in the field. Covariates included PC1, Date + Date^2, Dens + Dens^2, Year, and Parasitism. c = 0.97 for M5, Set 1; c = 1.10 for M4, Set 2.

FIGURES

Figure 4.1. Spatiotemporal variation in natural nest survival (2001-2008). Continuous NSR estimates for the entire nest period along territory density (A) and Date (B) axes were calculated using M1, Set 1, and for the egg period when equating nest failure with first partial or total predation (C, D) using M2, Set 2 (Table 4.1). Reference lines (B, D) mark ca. June 1 and July 1 respectively (May 31 and June 30 in leap years). Class-based NSR estimates along continuous axes are plotted at mean values for observations within each class.
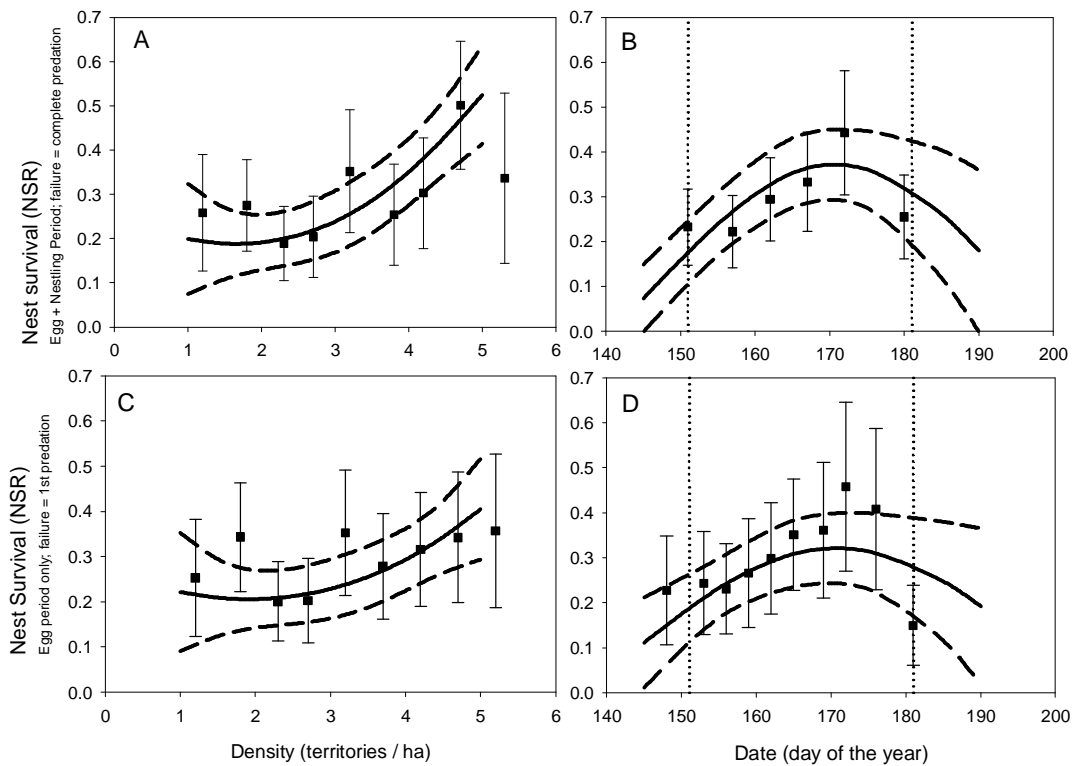
Figure 4.2. Comparison of experimental nest survival patterns to natural survival patterns (2006-2007). Natural and experimental nests were monitored along a similar spatiotemporal extent (A, B). Continuous NSR estimates along Density axis (C) were calculated using M1, Set 1, and along Date axis using M9, Set 1 (Table 4.2). When assuming natural nest failure = total predation (D), M5, Set 2, Table 2 was used. Reference lines (D, F) mark the 1st of June and July respectively. Class-based estimates are plotted at mean values for observation intervals within each class. Class-based estimates for avian bite rates (ABR) and rodent bite rates (RBR) are also presented (E, F). Although class-based estimates are not completely consistent with model-based estimates with respect to Date when failure = first predation (solid black plot, D), class-based estimates were more consistent with model estimates when similar models were fitted to larger datasets (dotted black plot, D; also see Figure 4.1D).
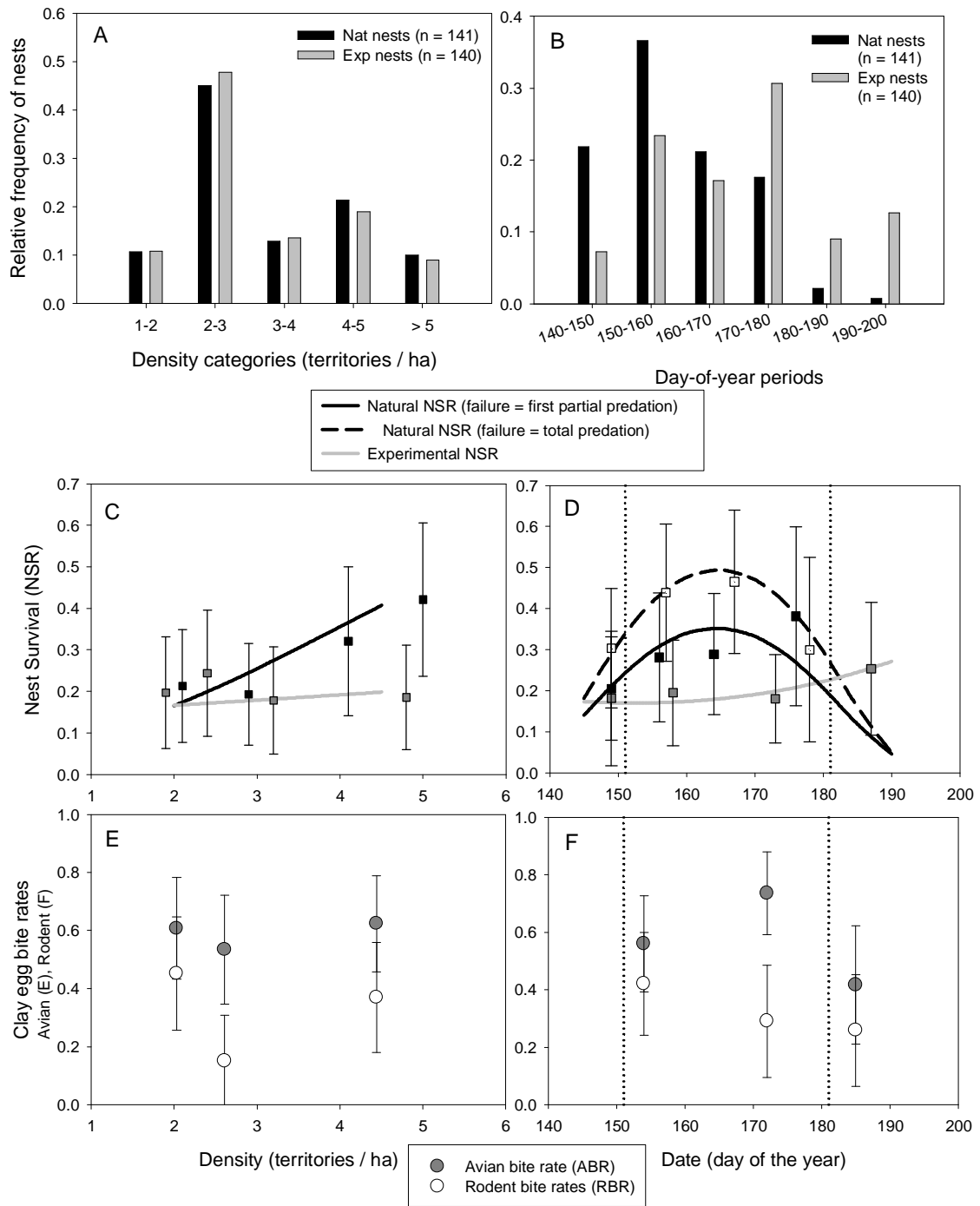
FIGURE 4.3. Daily survival rate (DSR) estimates and 95% CIs for natural nests along an Age axis (A) calculated using M2, Set 1, Table 5. Class-based estimates for natural (Black), as well as experimental nests (Grey) are plotted at mean values for observations within each class. DSR estimates along Age axis for nests in willow (Black, PC1 = 1.5) and for non-willow nests (Grey, PC1 = -1.5) were calculated using Model 1, Set 1, Table 5.
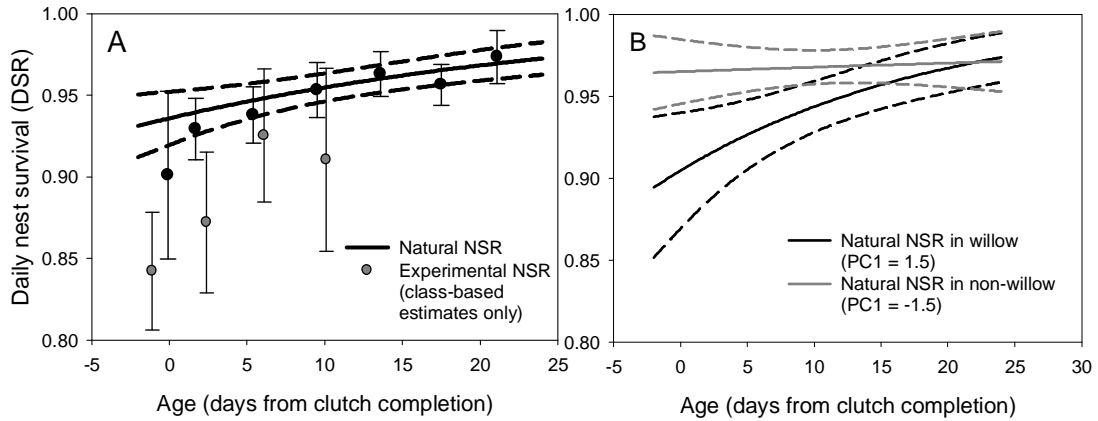
General Conclusion

The research reported in this dissertation provides important insights into how and why avian nest site preferences may or may not conform to apparent nest predation pressure. Clearly, birds do not always favor nest site microhabitats that minimize predation risk even when there are no apparent incentives capable of outweighing predation costs for selecting high-risk microhabitats. Nest predation by cowbirds and variation in the form of predation pressure across the landscape are two possible factors underlying maladaptive Yellow Warbler nest site selection. Furthermore, given the recent range expansion of cowbirds (Rothstein et al. 1980), their generalist brood parasitic strategy (Lowther 1983), and the lack of consistency in predation patterns among systems (Lahti 2009), these factors represent potential drivers of ecological traps for nest site selection in a variety of bird species. Nevertheless, this research shows how members of a population that suffer from a trap with respect to one microhabitat gradient may make adaptive decisions along other microhabitat gradients. More specifically, the effective use of concealment by Yellow Warblers to avoid nest predation contrasted with the inability for Yellow Warblers to identify predator-free space with respect to microhabitat patch composition may suggest a general organizing principle. In contrast with microhabitat patch effects, concealment effects on avian predation are probably relatively consistent among systems. Consequently, a concealment-based nest site selection strategy modulated by the presence of avian predators may be more tractable and more consistently favored by natural selection than potential strategies based on recognition of low-predation

microhabitat patches. That said, predator-free space with respect to patch structure is recognized and occupied by nesting birds in other systems (Martin 1998). Among-populational comparisons of microhabitat-predation relationships, as well as research aimed at elucidating the specific cues used by birds to identify predator-free nest space would contribute to a general understanding of how predation shapes avian nest site selection.

This research also demonstrates the potential utility of experimental nests (i.e., artificial nests) for examining the processes underlying nest predation patterns. Because of the differences between experimental and natural nests, monitoring of experimental nests does not provide a useful surrogate for monitoring natural nests when measuring natural predation rates (Major and Kendal 1996, Faaborg 2004, Moore and Robinson 2004). However, when monitored along with natural nests, experimental nests can provide a useful control for the effects of parental behavior on nest predation (Weidinger 2002). Using experimental nests, I have shown that microhabitat effects on predation risk (Chapters 2, 3) experienced by Yellow Warblers were not mediated by parental behavior, and are therefore the product of direct effects of microhabitat on predators. This information was critical for elucidating the processes likely underlying both adaptive and maladaptive nest microhabitat choices made by Yellow Warblers. In contrast with fine-scale spatial patterns, coarse-scale predation patterns *were* mediated by parents, making food availability a potential driver of these patterns. The greater influence of food on coarse-scale spatial patterns offers a potential explanation for why birds might pay less direct attention to the likelihood of nest success when selecting breeding habitat at

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territory-or-larger spatial scales (Shochat et al. 2005, Chalfoun and Martin 2007). When comparing natural versus experimental predation patterns, it was necessary to control for differences between natural and experimental nests other than the presence of parental behavior. Studies using experimental nests to control for parental effects on predation risk should therefore make every effort to design experimental nests that simulate the natural nests of particular study species as closely as possible.

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