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Physiological life history and behavioral responses of a breeding bird community to experimentally reduced nest predation risk

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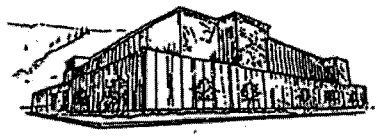

PHYSIOLOGICAL, LIFE HISTORY, AND BEHAVIORAL RESPONSES OF A BREEDING BIRD COMMUNITY TO EXPERIMENTALLY REDUCED NEST PREDATION RISK

by

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The role of nest predation in shaping avian life history strategies remains conspicuously untested by broad experiments that alter environmental risk of nest predation; despite the fact that nest predation is a major source of reproductive failure. We examined whether parents preferentially settle in safer nesting environments and adjust their reproductive strategies to local risk. We experimentally reduced nest predation risk and show that 8 species of migratory passerines prefer to nest in areas with reduced risk of nest predation. Parents of 12 species of passerines nesting in these safer environments increased investment in their young through increased egg size, clutch mass, and the rate they fed nestlings, and also increased investment in female condition by increasing the rates that males fed incubating females at the nest, and decreasing the time that females spent incubating. Although nest predation risk decreased with predator reduction, it did not decrease as significantly as predicted. We show that reproductive potential was not limited by the increased expression of risky behaviors as theory may have predicted, and suggest compensatory mortality as a likely alternative. Despite clear changes in reproductive strategies, we failed to find any influence of nest predation risk on baseline corticosterone levels either between treatments or across species that differ in risk. These results demonstrate that birds can assess nest predation risk at large and that nest predation plays a key role in the expression of avian habitat selection and reproductive strategies, but the physiological mechanisms regulating these changes remain unclear. Finally, in hope of imparting our understanding of the natural world to the next generation we designed an innovative lesson plan to teach children about microclimate, an important abiotic influence on natural communities.

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Table of Contents

List of Tables

List of Figures

CHAPTER 1

PARENT BIRDS ASSESS NEST PREDATION RISK AND ADJUST THEIR REPRODUCTIVE STRATEGIES

Abstract

Avian life history theory has long assumed that nest predation plays a minor role in shaping reproductive strategies. Yet, this assumption remains conspicuously untested by broad experiments that alter environmental risk of nest predation, despite the fact that nest predation is a major source of reproductive failure. Here, we examined whether parents can assess experimentally reduced nest predation risk and alter their reproductive strategies. We experimentally reduced nest predation risk and show that in safer environments parents increased investment in young through increased egg size, clutch mass, and the rate they fed nestlings. Parents also increased investment in female condition by increasing the rates that males fed incubating females at the nest, and decreasing the time that females spent incubating. These results demonstrate that birds can assess nest predation risk at large and that nest predation plays a key role in the expression of avian reproductive strategies.

Introduction

Past attention to putative causes of variation in avian reproductive strategies has focused extensively on variation in the abundance of food (Lack 1948, Martin 1987). Indeed, experimental tests of food limitation abound in the literature (see Martin 1987). Yet, food does not explain considerable variation in reproductive strategies within and among species (Martin 1995, Martin et al. 2000a, Ferretti et al. 2005). As a result, the environmental causes of broadly differing reproductive strategies observed in nature remain unclear.

Nest predation is the primary cause of reproductive failure for most birds and, thus, represents an important source of natural selection (Ricklefs 1969, Martin 1995). Correlative evidence suggests that this source of selection can influence the expression of reproductive strategies (Lack 1948, Slagsvold 1982, Martin 1995, Martin et al. 2000a). Yet, the causal influence of nest predation risk on the expression of reproductive strategies by diverse species remains largely untested experimentally. Moreover, the ability of birds to assess variation in nest predation risk in the environment at large and adjust their reproductive strategies remains untested and unknown. Here we reduce nest predator populations to directly test the ability of 12 coexisting passerine species (Table 1) to assess variation in background levels of nest predation risk and whether they alter their reproductive strategies in response.

If individuals can assess nest predation risk in the environment, phenotypic responses to varying risk can shed light on the role of nest predation in the expression of reproductive strategies (West-Eberhard 1989; Ghalambor and Martin 2001, 2002). For example, greater risk of nest predation may favor reduced investment in current clutches

as a means of bet-hedging to allow increased energy for re-nesting (Slagsvold 1984, Roff 1992, Martin 1995). As a result, clutch size, egg mass, and clutch mass, all of which contribute directly to fitness (Roff 1992, Williams 1994, Saino et al. 2004), might be reduced in the face of high nest predation risk. Similarly, nest attentiveness (percentage of time females spend incubating) is a major energetic investment (Williams 1996), and might also be reduced under elevated nest predation risk as a means of bet-hedging. Alternatively, greater nest predation risk may favor increased attentiveness because of the potential benefits from camouflaging the nest contents or being present to deter predators that discover the nest (Marzluff 1985, Montgomerie and Weatherhead 1988, Kleindorfer and Hoi 1997). Finally, nest predation can favor reduced activity at the nest to reduce the probability of nest detection by predators (Skutch 1949; Martin et al. 2000a, b; Ghalambor and Martin 2002). Thus, rates of mate-feeding (males feeding incubating females at the nest) and nestling feeding (both parents feeding young) might decrease under high nest predation risk. The potential consequences of nest predation risk for this broad suite of traits that comprise an individual's reproductive strategy remain untested experimentally. We experimentally tested all of the above predictions by removing the primary nest predators of a community of passerine birds to study the reproductive response of birds nesting in reduced nest predation environments.

Methods

Study Area and Species

From 2001-2004, we studied a bird community breeding in snowmelt drainages along the Mogollon Rim in central Arizona at approximately 2,300m in elevation. The habitat in these drainages is typical of a western mixed conifer forest (Martin 1998).

Our study included 12 species of coexisting passerines representing four nesting guilds that experience different nest predation risk (Table 1, Martin 1995). Nesting begins in early May and extends into July. Species were included in analyses only when we could obtain samples (Table 1); for example, we could not obtain samples of egg mass and clutch mass for cavity-nesting birds.

Field Techniques

Nests were located using long-standing techniques (Martin and Guepel 1993). Incubating females were not flushed from nests to limit human disturbance, which birds may perceive as a predation threat. Instead, nests were either checked from afar by parental behavior, or contents were checked when females were off during normal foraging bouts.

We measured egg mass for nests located during nest building or egg-laying, and measured all eggs within two days of clutch completion using a calibrated digital scale accurate to 0.001 g. We only included nests know to be first attempts. These nests were also used in determining clutch mass (sum of total egg mass for a nest). Clutch size was taken from all nests found prior to hatching because partial loses are virtually never observed in this system. Again we only included nests known to be first attempts.

Clutch size did not differ between the limited sample used for mass determination where we observed the complete clutch being laid and the broader sample in an analysis of variance that included species as a random factor ($F_{1, 638} = 1.867$, $p = 0.172$).

We assessed parental behaviors by videotaping nests starting within 30 minutes of sunrise for four to six hours (Martin et al. 2000a). When ever possible we recorded nests once in early incubation and once in late incubation and averaged to determine incubation behaviors. Tapes were scored for behaviors including: percentage of time females spent on the nest (nest attentiveness), the rate that males visited the nest to feed incubating females (mate-feeding rate) and the rate that both parents feed the young (nestling feeding rate) (Martin et al. 2000a). Nestling feeding rates were measured only once at nests videotaped within one day of nestlings breaking primary pinfeathers to control for the influence of nestling development on feeding rates.

Nest Predator Removals

Based on population densities and video evidence of nest predation events the primary predator community in this system is limited to five species: red squirrel (*Tamiasciurus hudsonicus*), gray-collared chipmunk (*Tamias cinereicollis*), deer mouse (*Peromyscus maniculatus*), white-footed mouse (*P. leucopus*), and Steller's Jay (*Cyanocitta stelleri*) (Martin 1998). Additional nest predators exist within the community, but at such low densities that their effect on nesting productivity is likely minimal.

We removed nest predators from 10 plots (removal plots) to compare with 10 neighboring plots with intact predator communities (control plots). We primarily

removed mammalian predators from selected drainages through live trapping and translocation, but supplemented these efforts with lethal removals when necessary. Sherman and Tomahawk live-traps were baited with peanut butter and sunflower seeds and checked daily. All captures were transported 10 km to similar habitats separated from the study area by large canyons. Because of their increased mobility it was necessary to lethally removal all Steller's jays. All removal methods followed national guidelines and were approved and monitored under permits from the Arizona Game and Fish Department (SP635085), the U.S. Fish and Wildlife Service (MB791101-3), and The University of Montana Institutional Animal Care and Use Committee (01-04-TMCWR-033105-01). Removals for all predator types began the second week of April, before the arrival of female migrant birds to the study site, and because plots were not fenced, we continued removal efforts through mid July each year to offset immigration from surrounding source populations. We assessed the effectiveness of removals by comparing capture rates throughout the season.

To control for additional sources of variation in habitat quality we paired control and removal plots based on data from previous years that suggested similar bird, nest predator, and plant assemblages. We removed nest predators from ten, 5-10 hectare drainages. Control and removal plots were spatially paired (within 1 km) to minimize possible spatial influences, but separated by at least one intervening drainage to buffer against possible carryover effects of removals on control plots. We removed predators from the same plots each of the four years to maximize effect size.

We conducted aural surveys for jays and squirrels throughout the season as a index of predator abundance. Sampling consisted of a one-minute survey to determine

the presence or absence of each predator. Tape recorders were paired and randomly placed on both control and removal plots every fourth day of the season for a total of 23 sampling days per year. Because squirrels and jays, as well our study species are most active in the morning, tapes were sampled starting at sunrise and every half-hour after for a total of 6 samples. Thus, we sampled 6 times per day for 23 days each year across all four years.

Analyses

We examined capture rates of nest predators across the season using a simple linear regression. For nest predator surveys, we paired data by date and compared between treatments using a paired t-test. Mayfield estimates of daily predation rates were compared between treatments by species and year using a paired t-test (Mayfield 1961, 1975; Hensler and Nichols 1981). In examining parental responses, individual pairs and their nests were used as independent sample points for the analysis of behavioral and life history data. We used an analysis of covariance that included species as a random factor to test for overall differences between treatments in life history and parental care behaviors while controlling for potentially confounding effects. We excluded non-significant variables or interactions from trial models. Analyses were conducted on raw data, but differences represented in graphs are percent change [(removal-control)/control*100)] to standardize changes for ease of visual comparison.

Results

Over four years we removed 3791 predators from removal plots (769 – red squirrel, 45 – Steller's jay, 531 – gray-collared chipmunk, 2446 – mice spp.), and found and monitored 410 nests on removal plots and 850 nests on control plots. Differences in nest numbers reflect differences in renesting rates after nest failure between treatments and not increased densities on control plots (Chapter 2). Experimental removals resulted in a reduction in capture rates on removal plots across the breeding season (Fig 1a; $F_{1, 84}$= 81.969, $p < 0.001$), which foreshadowed the change in nest predator detections between treatments (Fig. 1b; red squirrel $t_{58} = -7835$, $p < 0.001$; Steller's jay $t_{58} = -6.058$, $p < 0.001$). The reduction in vocalizations of two major predators is important because it reflects a reduction in predator cues and activity that might be key for assessment of risk by birds, but also telegraphs a strong reduction in actual nest predation rates (Fig. 1c; $t_{44} = -2.02$, $p = 0.025$).

The reduction in actual and perceived nest predation risk yielded significant changes in reproductive strategies by the diverse array of species that we studied. Parents increased investment in offspring. Mean egg mass was larger on plots with reduced nest predation risk, as predicted (Fig. 2a; Treatment: $F_{1, 249} = 54.205$, $p < 0.001$; Initiation date: $F_{1, 249} = 16.772$, $p < 0.001$; Species: $F_{8, 249} = 1475.825$, $p < 0.001$; Treatment by species: $F_{8, 249} = 12.622$, $p < 0.001$). Yet, clutch size, a trait that other studies have found can be influenced by variation in nest predation risk (Julliard et al. 1997, Ferretti et al. 2005) showed a clear lack of response among the diverse array of species that we studied (Fig 2b; Treatment: $F_{1, 748} = 0.745$, $p = 0.388$; Initiation date: $F_{1, 748} = 65.831$, $p < 0.001$; Species: $F_{11, 249} = 75.283$, $p < 0.001$). Nonetheless, the increase in egg mass led to an

increase in clutch mass (Fig. 2c; Treatment: $F_{1, 250} = 13.106$, $p < 0.001$; Species: $F_{8, 250} = 350.804$, $p < 0.001$; Treatment by species: $F_{8, 250} = 5.267$, $p < 0.001$). Moreover, parents also increased investment in hatched young by feeding nestlings at a higher rate on removal plots (Fig. 2d; Treatment: $F_{1, 189} = 14.458$, $p < 0.001$; Number of nestlings: $F_{1, 189} = 18.722$, $p < 0.001$; Species: $F_{8, 189} = 15.842$, $p < 0.001$; Treatment by species: $F_{8, 189} = 2.277$, $p = 0.031$).

The reduced risk of nest predation also caused parents to invest in traits that enhance female condition. The rate that males fed incubating females increased on removal plots (Fig. 3a; Treatment: $F_{1, 598} = 162.429$, $p < 0.001$; Species: $F_{12, 598} = 360.612$, $p < 0.001$; Treatment by species: $F_{12, 598} = 53.428$, $p < 0.001$), as predicted. Increased mate-feeding (Fig. 3a) is known to reduce the energy constraints placed on females by the time and energy costs of incubation, and previous studies have found an increase in nest attentiveness with increased mate-feeding (von Haartman 1958, Lyon and Montgomerie 1985, Smith et al. 1989, Halupka 1994). However, we found the opposite pattern of decreased nest attentiveness (Fig. 3b; Treatment: $F_{1, 581} = 6.284$, $p = 0.012$; Year: $F_{1, 581} = 10.489$, $p < 0.001$; Species: $F_{12, 581} = 18.896$, $p < 0.001$) despite increased mate-feeding. Females on removal plots reduced nest attentiveness and accepted the double benefits of increased mate-feeding and increased time off the nest caring for themselves when nest predation risk was low.

Discussion

The influence of food abundance on investment in eggs and reproductive behaviors like mate-feeding and nest attentiveness has been studied extensively (von

Haartman 1958, Lyon and Montgomerie 1985, Martin 1987, Smith et al. 1989, Halupka 1994, Sanz 1996). While food is obviously important, nest predation is the primary source of reproductive mortality in many systems (Ricklefs 1969, Martin 1995) and therefore may impose strong direct selection on the expression of reproductive traits. We found such direct effects for a broad array of traits including the first experimental demonstration that nest predation risk may play a pivotal role in determining maternal investment in eggs, which may yield significant fitness benefits to young (Tinbergen et al. 1990, Williams 1994, Smith et al. 1995, Styrsky et al. 1999, Pelayo and Clark 2003). Furthermore, the fact that this increased investment was not limited to egg laying, but was maintained throughout the nesting cycle emphasizes the importance of nest predation in shaping many aspects of reproductive investment.

Equally as interesting as change in egg size was the lack of response in clutch size. Clutch size is known to correlate with nest predation risk across species (Martin 1995, Martin et al. 2000a), and has been shown to change with differences in nest predation risk across habitat gradients (Ferretti et al. 2005) and among years (Julliard et al. 1997). However, increases in clutch size represent an incremental increase in investment (i.e. from 1 to 2 to 3 eggs) that may require females to invest more in a clutch than small, continuous changes in individual eggs. Increases in clutch size also require continued investment throughout the nesting cycle (i.e. more eggs to heat, and more nestlings to feed), whereas increased egg size does not require such clear increases in future investment. Clutch size increases, therefore, require considerably more investment than egg size increases, which may be particularly important if females make mistakes in assessing nest predation risk or if risk can change within a nesting cycle. Changes in egg

size rather than clutch size may represent a conservative response to relatively small changes in a strong and rapidly variable selection agent, nest predation.

In addition to showing the direct effects of nest predation risk, we also show that nest predation risk can create an indirect effect of food limitation by restricting the ability of adults to acquire food resources for themselves and their young. In particular, the reduction in nest attentiveness by incubating females despite increased mate-feedings highlights the complex indirect effects of nest predation on food limitation in these systems. These results imply that females on control plots increase incubation effort in response to greater nest predation risk even when energy is more limited by reduced mate-feeding. Such responses are opposite to those expected by bet-hedging. Although initially surprising, these results follow theory that suggests females should increase investment in themselves and enhance opportunities for future reproduction when the cost to current young is minimal (Roff 1992), as can be expected in low offspring mortality environments.

The fitness consequences of both direct and indirect effects of nest predation risk are clearly substantial, and emphasize the importance of considering responses to variation in nest predation risk in a relatively complete array of traits comprising reproductive strategies (Ferretti et al. 2005). Previous experiments that have attempted to explore the influence of nest predation risk on reproductive strategies have provided useful information on the short-term reactions of parents to the immediate threat imposed by a predator at the nest in a restricted subset of traits (Ghalambor and Martin 2001, 2002). However, when a predator is at the nest, the primary concern of the parents is deterring a predation event. Such studies do not address whether birds can assess

variation in nest predation risk in the environment at large and modify their broader reproductive strategies based on such assessments. We have demonstrated here for the first time that parents can assess risk in the environment at large and adjust their reproductive strategy as a function of environmental risk of juvenile mortality. These findings highlight the importance of nesting mortality in shaping reproductive strategies both within and among species well beyond anything appreciated previously.

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Table 1 | Study species differ in background nest predation risk.

Species Code*	Nest Predation Rate**	Nest Site***	Study Species		Number of Nests (control, removal)				
			Common Name*	Scientific Name	Egg Mass	Clutch Size	Clutch Mass	Nstl Feed	Attent./ Mtfd
howr	0.005	Cavity	House Wren	*Troglodytes aedon*	5, 8	18, 12	5, 8	8, 6	30, 22
rbnu	0.008	Cavity	Red-breasted Nuthatch	*Sitta canadensis*					7, 5
brcr	0.012	Cavity	Brown Creeper	*Certhia americana*					9, 6
wbnu	0.014	Cavity	White-breasted Nuthatch	*Sitta carolinensis*					4, 4
moch	0.014	Cavity	Mountain Chickadee	*Poecile gambeli*					11, 5
ocwa	0.028	Ground	Orange-Crowned Warbler	*Vermivora celata*	21, 22	76, 48	21, 22	16, 21	52, 32
viwa	0.030	Ground	Virginia's Warbler	*Vermivora virginiae*	16, 10	70, 34	16, 10	23, 22	37, 18
cofl	0.033	Niche	Cordilleran Flycatcher	*Empidonax occidentalis*	21, 6	81, 15	21, 6	4, 6	62, 17
rfwa	0.040	Ground	Red-Faced Warbler	*Cardellina rubrifrons*	27, 5	62, 8	27, 5	27, 7	43, 9
ghju	0.041	Ground	Gray-Headed Junco	*Junco hyemalis caniceps*	37, 18	120, 55	37, 18	29, 19	50, 42
amro	0.046	Subcanopy	American Robin	*Turdus migratorius*	7, 6	25, 16	7, 6	5, 8	34, 25
heth	0.085	Subcanopy	Hermit Thrush	*Catharus guttatus*	23, 11	41, 24	23, 11	5, 3	29, 13

* Species codes used for labels in all figures are from the American Ornithological Union and are based on common names.

** Mean daily probability of nest failure 1985-2004.

*** Nest predation rates differ among species related to their nest site.

Figure Legends

Figure 1 | Predator removals resulted in a reduction in nest predators and ultimately nest predation rates. Capture rates (**a**) on removal plots fell across the season and (**b**) vocalization rates of red squirrels and Steller's Jays, as well as (**c**) nest predation rates were substantially reduced on removal plots when compared to control plots. Error bars indicate s.e.m. across years.

Figure 2 | Life history traits and parental care behaviors affecting offspring were altered by predator removals. Responses are illustrated by percent change [(removal-control)/control*100]. Females nesting on plots with reduced nest predation risk **(a)** laid larger eggs, (**b**) did not change their clutch size, but **(c)** increased clutch mass. Both parents (**d**) increased the rate they fed nestlings. Error bars indicate s.e.m. across years.

Figure 3 | Behaviors affecting female parents were altered by predator removals. Responses are illustrated by percent change [(removal-control)/control*100]. Females nesting on plots with reduced nest predation risk (**a**) were fed more at the nest by their mates, and **(b)** reduced the percentage of time they spent incubating. Error bars indicate s.e.m. across years.

Figure 1

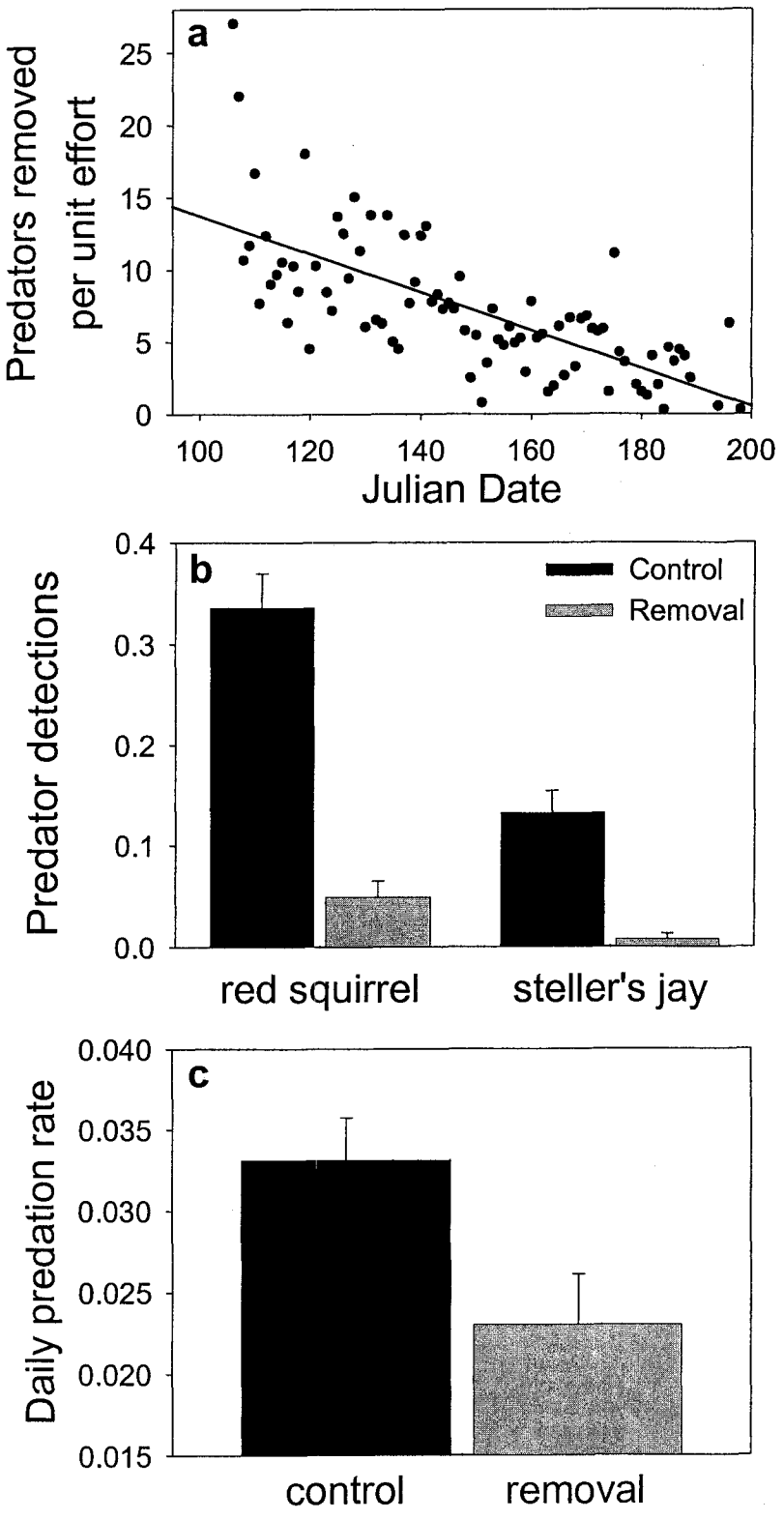


Figure 2

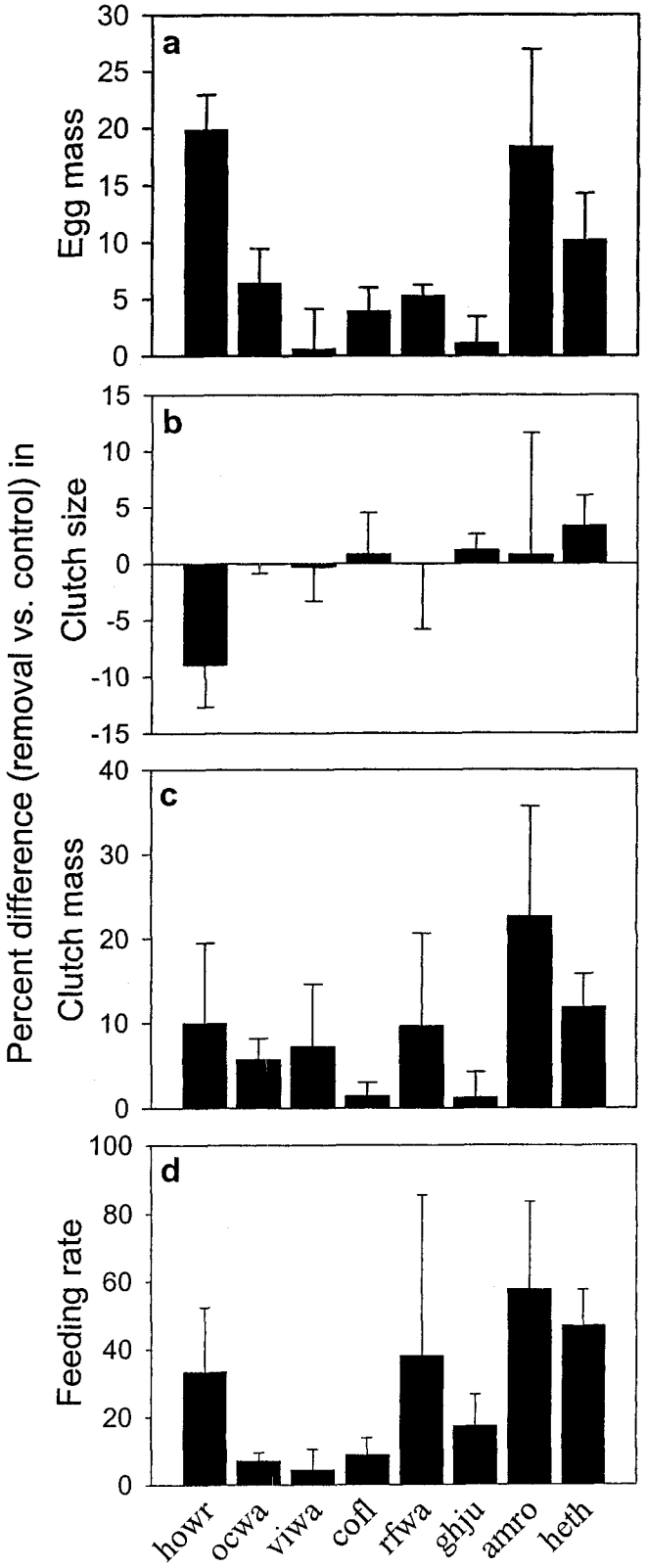
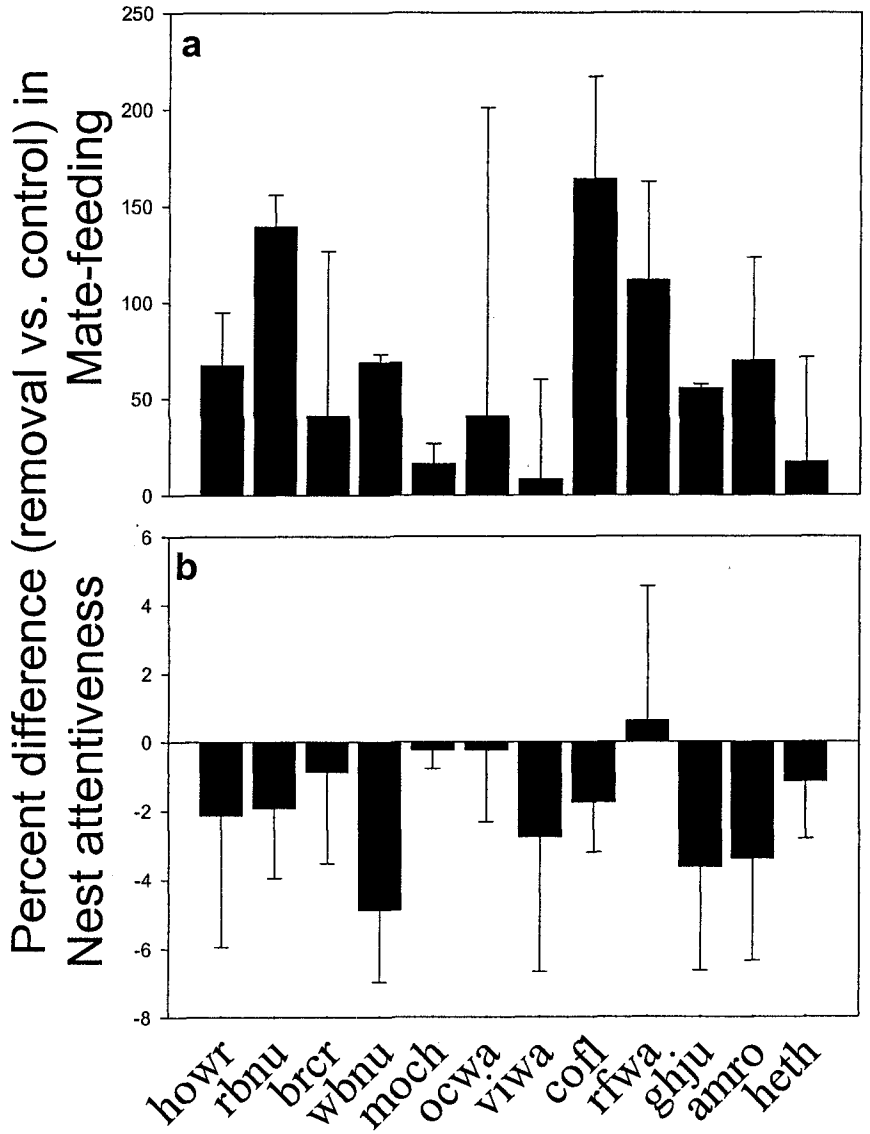


Figure 3



CHAPTER 2

HABITAT SELECTION RESPONSES OF PARENTS TO OFFSPRING PREDATION RISK: AN EXPERIMENTAL TEST

Abstract

Habitat preferences are generally inferred from correlations between environmental cues presumed to indicate habitat quality and some component of population size or density. The causal relationship between agents of selection and habitat choice is rarely tested experimentally. In birds, the ability of nest predation to influence habitat settlement decisions is widely debated, despite the importance of nest predation in limiting fitness. Here, we experimentally manipulated nest predation risk across a landscape and asked the question: Do migratory birds assess and respond to spatial variation in nest predation risk when choosing breeding habitats? We examined preference for safer nesting habitat by quantifying the density of breeding pairs that settled in areas with and without intact nest predator communities and by examining the timing of habitat choice by nesting females. We found consistently more individuals nesting in areas with reduced nest predation risk than in areas with intact predator assemblages, although predation risk had no influence on settlement or breeding phenology. Additionally, those individuals occupying safer nesting habitats exhibited increased singing activity. These findings support a causal relationship between habitat choice and nest predation risk, and suggests the importance of nest predation risk in shaping avian community structure and breeding activity.

Introduction

Habitat decisions by females of all taxa preparing to rear offspring can influence individual reproductive success as well as population dynamics and community structure (Martin 1992, 1998; Smith et al. 2000; Kessler and Baldwin 2002; Blaustein et al. 2004; Tschanz et al. 2005). Resource limitation, predation, competition, and unfavourable climate can all influence offspring quality and survival (Casey 1976; Martin 1998, 2001; Kessler and Baldwin 2002). Theory predicts that females should choose sites to rear offspring that minimize these costs (Fretwell 1972; Jaenike and Holt 1991; Martin 1992, 1998; Morris 2003). Studies of oviposition and nest site selection suggest that females are particularly sensitive to predation risk to their offspring, and alter placement of their nests to minimize this risk (Martin 1998, 2001; Kessler and Baldwin 2002; Blaustein et al. 2004). Predation risk at particular oviposition and nest sites, however, is highly influenced by variation in risk at larger spatial scales (Martin 1992, Rieger et al. 2004, Lloyd et al. 2005). Although theory predicts that females should assess risk at these larger spatial scales to maximize the potential for safe nesting locations locally (Fretwell 1972; Jaenike and Holt 1991; Martin 1992, 1998; Morris 2003), few empirical studies have tested this prediction.

Variation in avian nest predation risk at the landscape, territory, and nest site level, for example, can have profound effects on population demographics and individual fitness, and thereby influence habitat choice (Martin 1992, 1998, 2001; Donovan et al. 1995; Lloyd et al. 2005). While there are clear examples of the influence of nest predation risk on decisions by females of where to nest locally (Martin and Martin 2001, Forstmeier and Weiss 2004), the influence of nest predation on habitat decisions at larger

spatial scales (i.e. territory choice) remains unclear, in part because direct experimental tests of its importance are conspicuously lacking.

Here, we examine whether individuals from twelve passerine species assess and choose habitats based on variation in nest predation risk across a landscape. Specifically, we experimentally reduced nest predation risk and measured subsequent settling patterns of returning migrants compared to resident species that settle prior to predator manipulations. We asked whether migratory birds make settlement decisions based on reliable cues such as nest predator abundance and /or vocalizations of predators independent from other agents of selection such as food availability or microclimate (Cody 1985, Martin 1995, Roos and Pärt 2004).

We utilized two metrics of habitat preference: order of occupation and population density (Fretwell 1972, Cody 1985, Petit and Petit 1996; but see Van Horne 1983). Each of these measures addresses different components of choice and may therefore enhance our understanding of habitat selection. Theory predicts that the first individuals to arrive in a landscape will choose to settle in areas of highest quality (Fretwell 1972). Thus, we assessed habitat choice by comparing the relative date that areas with and without nest predators were first occupied. This enabled us to determine the influence of nest predation risk on settlement choice independent of the confounding influences of conspecifics. Conspecifics may affect settlement decisions both positively (i.e. conspecific attraction; Ward and Schlossberg 2004) and negatively (i.e. territory defense, nest site limitation, food limitation; Fretwell 1972, Cody 1985, Martin 1995, Martin and Martin 2001, Richardson and Burke 2001), and obscure the importance of nest predation in determining where an individual would choose to settle given no other constraints or

biases. By examining settlement date of the first individuals to arrive in an area, we removed the potentially confounding effects of conspecifics. We predicted that individuals would settle first in areas with reduced nest predation risk to maximize their potential nest success.

While settlement order may indicate the importance of nest predation in shaping settlement decisions under ideal conditions, these conditions are rare. Individuals arriving after the settlement of the first individual must also weigh the costs of settling with other conspecifics, including costs from competition for food, mates and nest sites, all known to increase with increasing density (Fretwell 1972, Cody 1985, Martin 1995, Martin and Martin 2001, Richardson and Burke 2001). Ultimately, individuals must balance nest predation risk against other costs in their choice of breeding habitats. To reduce other sources of environmental variation that could confound settlement decisions, we applied our predator removal treatment to ten plots paired with ten additional plots of historically similar bird and plant assemblages but with intact predator communities. We then tested whether birds would accept increased competition in favor of reduced nest predation risk by preferentially settling earlier and at higher densities in areas of reduced nest predation risk.

Methods

Study area and species

We studied the influence of nest predation risk on habitat preference of migratory birds breeding in 20 snowmelt drainages located along the Mogollon Rim in central Arizona from 2001-2004. Vegetation is typical of a western mixed conifer forest (Martin

1998). This system is particularly appropriate for examining habitat preference in relation to nest predation risk because nest predation accounts for 98% of nest failure (Martin 1998). Returning migrants are easily detected to measure settlement date, and densities are easily measured (Martin 2001). In addition, the predator community is simple making manipulation of nest predation risk feasible (Chapter 1).

We examined habitat preference for eight neotropical migrants that returned after nest predators had been experimentally reduced in portions of the landscape. These species represent a diverse continuum of ecological and behavioral characteristics, and are known to differ in nest predation risk (Martin 1995, 1998; Chapter 1). In all figures species will be referenced by their four-letter American Ornithological Union code: OCWA – Orange-crowned warbler (*Vermivora celata*), VIWA – Virginia's Warbler (*Vermivora virginiae*), RFWA – Red-faced Warbler (*Cardellina rubrifrons*), GHJU – Gray-Headed Junco (*Junco hyemalis caniceps*), HETH – Hermit Thrush (*Catharus guttatus*), AMRO – American Robin (*Turdus migratorius*), COFL – Cordilleran Flycatcher (*Empidonax occidentalis*), and HOWR – House Wren (*Troglodytes aedon*). We also examined the response of four resident species that chose nesting habitats prior to experimental reductions of nest predators and therefore should not respond to the experiment. This enabled us to use the density of these species as a control independent of our treatment. These species included: WBNU – White-breasted Nuthatch (*Sitta carolinensis*), RBNU – Red-breasted Nuthatch (*Sitta Canadensis*), MOCH – Mountain Chickadee (*Poecile gambeli*), and BRCR – Brown Creeper (*Certhia Americana*).

Nest predator removals

We conducted a predator removal experiment to alter nest predation risk across the landscape (see Chapter 1 for detailed description). We removed predators from 10 drainages (hereafter plots), 5-10 ha in size (removal plots) to compare with 10 neighboring and similarly sized drainages with intact predator communities (control plots). We paired plots based on 20 years of prior data that permitted us to match plots with similar bird, predator, and plant assemblages (Chapter 1). Control and removal plots were spatially paired to minimize possible spatial influences, but separated by at least one intervening drainage to buffer against possible carryover effects of removals on control plots. We removed predators from the same plots all four years of the study to maximize effect size.

Removals began before the arrival of any female migrant birds to the study site, and continued throughout the breeding season. The primary nest predators for which removals were conducted included: red squirrel (*Tamaiasciurus hudsonicus*), gray-neck chipmunk (*Eutamias cinereicollis*), deer mouse (*Peromyscus maniculatus*), white-footed mouse (*P. leucopus*), and Steller's Jay (*Cyanocitta stelleri*) (Martin 1992). Additional predators exist within the community, but at very low densities. To determine the effectiveness of removals we measured nest predation rates and assessed nest predator abundance throughout the breeding season by conducting aural surveys for jays and squirrels (Chapter 1).

Nest finding and monitoring

We located and monitored nests to determine nest initiation dates (day the first egg is laid in a nest) and nest predation rates. Nests on both control and removal plots were located using standard techniques (Martin and Guepel 1993). We determined the exact initiation dates for all nests found prior to clutch completion. Incubation periods are well established for all study species (Martin 2002), allowing us to increase our sample size by backdating nests found during the incubation period for which exact hatch date was observed. We used Mayfield estimates of nest predation rates (Mayfield 1961, 1975; Hensler and Nichols 1981), which we compared between treatments and across years using a repeated measures ANOVA.

Response Variables

We assessed habitat preference by comparing order of occupation and density (Fretwell 1972, Cody 1985, Petit and Petit 1996). Specifically we examined the date that the first female of each species arrived on each study plot and the density of breeding pairs for each species. We focused on female habitat preference because the risk of nest predation is greatest during the egg laying and incubation periods (Martin et al. 2000) when the majority of reproductive investment is by females. Selection should act strongly on females to choose nesting habitats that limit the risk of nest predation during these critical periods (Martin 1998, Martin et al. 2000).

We monitored plots daily from before any females arrived at the study site and recorded the date that the first female settled on each study plot. We considered females to have settled on a plot if a previously single male was verified to have paired with a

female and maintained that pairing for three consecutive days. Females that arrived on plots were easily detected because they are not particularly cryptic prior to nesting and males exhibit distinct changes in singing and courtship behaviors indicating the presence of a female (pers obs., Gibbs and Wenny 1993). Because of the intensity of these surveys we focused on two species, which we chose because they arrived early (OCWA) and late (COFL) at the study site. We also compared the nest initiation date of the first nest for each female on a plot as an indicator of when she arrived, settled and initiated breeding. These data may be particularly important because in passerines earlier nest initiation generally increases fitness (Arcese and Smith 1988, Nilsson 2000). We did not include the resident species in this analysis because of the difficulty in accessing cavity nests and determining exact nest initiation dates for these species. The arrival and nest initiation dates allow us to examine preference based on priority of settlement and breeding decisions, although both measures are potentially affected by issues of female site fidelity. Older females are usually the first to arrive in this system and are the most likely to be site faithful (pers obs., Switzer 1993). Thus, our examination of habitat choice is potentially conservative because of constraints from site fidelity.

We also assessed the density of breeding pairs as an index of habitat choice. Density may not always be a proper indicator of habitat quality, but it is a good indicator of preference (Van Horne 1983). In this experiment, density may indicate both preference and habitat quality because we altered an environmental factor known to affect fitness. We created territory maps for each species on each plot by intensively surveying the plots throughout the breeding season to assess breeding density. Maps included pairs of each species known to be breeding throughout the breeding season.

As another index of density and breeding activity, we also randomly sampled plots for singing males throughout the breeding season. Tape recorders were paired and randomly placed on both control and removal plots every fourth day of the season for a total of 23 days and sampled starting at sunrise and every half-hour after for a total of six samples per day. Sampling consisted of a one-minute survey to determine the presence or absence of each species. We did not sample White-breasted Nuthatches or Brown Creepers for this comparison because they were rare and difficult to census accurately. For all of the response variables we tested for differences between treatments across years using a repeated measures ANOVA.

Results

Experimental nest predator removals resulted in a dramatic reduction in nest predator vocalization (Chapter 1). The reduction in vocalizations of the main predator community is important because it reflects a reduction in predator cues and activity that is likely used for risk assessment by birds. Moreover, it also foreshadows a strong reduction in actual nest predation rates for resident and migratory species (Fig. 1a, b; $F_{1, 22} = 5.092$, $p < 0.034$).

As expected, the density of resident species did not differ between treatments since residents established territories every year prior to our predator manipulations (Fig. 1c; $F_{1, 8} = 0.014$, $p = 0.909$). However, nesting densities of migratory species were significantly greater on removal versus control plots (Fig. 1d; $F_{1, 12} = 6.629$, $p < 0.024$). In addition, the singing activity of males of all species, both resident and migratory, was greater on removal plots (Fig. 1e, f; $F_{1, 18} = 17.166$, $p = 0.001$).

While predator removals influenced the density of nesting migrants, there were no differences between treatments for arrival dates of orange-crowned warblers and cordilleran flycatchers ($F_{1, 22} = 0.006$, $p = 0.939$). In addition, there were no clear treatment affects across all migrants for the date that the first nest of each species was initiated on each plot (Fig. 2a; $F_{1, 27} = 0.458$, $p = 0.504$), or the mean nest initiation date for each species on each plot (Fig. 2b; $F_{1, 26} = 0.732$, $p = 0.400$).

Discussion

Habitat selection studies in birds are generally correlational, often relating vegetation indices to timing of nest initiation or breeding density. These types of studies are useful for understanding habitat selection, but include at least two inherent problems. First, variation in vegetation at local and landscape levels is often associated with variation in a multitude of selection agents, including but not limited to: microclimate, food availability, adult predation risk, and nest predation risk. Distinguishing which of these is driving habitat selection can be nearly impossible using only vegetation correlates. Second, although vegetation may correlate with important sources of selection, this does not mean it is a perfect indicator given that food, predators, and microclimate can all vary within and among years independent of vegetation. Here we controlled these potential confounding effects by experimentally manipulating one particularly important agent of selection, nest predation, and testing its influence on habitat selection.

One of the most important components of selecting a habitat is using a cue that is readily available and reliably indicates habitat quality (Doligez et al. 2003, Danchin et al

2004). In this system, vocal cues of red squirrels and Steller's Jays are readily available and easy to assess. A reduction in frequency of these cues (Chapter 1) corresponded to a reduction in actual nest predation risk (Fig. 1a, b). This finding is important because it gives us a reasonable expectation that birds may distinguish between habitats of different quality based on such cues and choose habitats with reduced risk of nest predation.

Indeed, birds did respond to the experimentally induced landscape-level changes in nest predation risk. Although we failed to find any consistent patterns of settlement priority and nest initiation on removal plots (Fig. 2a, b), the strong increase in density of migratory species clearly suggests preference for plots with reduced nest predation risk (Fig. 1c, d), despite potentially increased costs of competition (Martin and Martin 2001). So why might we find a density response but no changes in when individuals settle and begin breeding? First, older and more successful individuals tend to arrive and settle first and are generally faithful to sites they occupied in previous years, especially if they were successful (pers obs., Switzer 1993, Haas 1998, Porneluzi 2003). Second, many individuals in this system arrive nearly synchronously, quickly exceeding the capacity of the removal plots and necessarily spilling into control plots (pers obs.). These natural patterns limit our ability to detect difference in arrival date and nest initiation date between treatments. Measures of density are not sensitive to these problems and therefore may better indicate true preference in this system.

The large increase in density of migratory species on plots with reduced nest predation risk (Fig. 1d) clearly indicates that birds are able to assess nest predation risk and modify habitat choice. As we expected, resident species (Fig. 1c) did not respond to the reduction in nest predation risk because they had already made habitat decisions prior

to the initiation of the experiment every year. The fact that we found no difference in resident abundance between treatments suggests that we chose well-paired study plots that eliminated many potential confounding variables. The lack of response to the treatment by resident species might also reflect a key difference between resident and migrant species in their nesting guilds. All of the resident species are cavity nesters, and may face greater limitation in nest site availability than the migratory species, which are mostly open-cup nesters (Martin 1993, but see Martin and Martin 2001). Nest site availability may ultimately constrain breeding density of cavity nesters even in desirable habitats (Martin 1993), because we know cavity nesters perceive and respond to variation in nest predation risk (Ghalambor and Martin 2002, Chapter 1).

We also found that male singing activity was higher on plots with reduced nest predation risk (Fig. 1e, f). Increased singing activity may simply reflect increased density and therefore increases in territory defense costs as males are forced to sing more in response to increased interactions between males (Penteriani 2003, Goretskaia 2004, but see Terof et al. 1998), but it may also reflect increased activity in safer environments (Martin et al. 2000). This latter possibility is further supported by the fact that singing activity increased for resident species that did not increase in density on removal plots (i.e. Fig. 1c, e), as well as species that increased in density (Fig. 3d, f). Alternatively, changes in singing activity by species that did not increase in density may reflect increased signaling of high quality territories, the importance of singing in limiting conspecific density in quality habitats (see above), or the potential for heterospecific competition with species that did increase in density. Regardless, increases in singing

activity signify the importance of nest predation in shaping community interactions, even among species that have limited overlap in nest sites or nest predation risk.

Our study has shown that the risk of nest predation can have profound effects on habitat selection decisions made by migrating birds. Moreover, the significant decrease in actual nest predation rates on individuals settling on predator removal plots suggests that these decisions represent adaptive responses to local variation in an important agent of selection. These findings reinforce the importance of variation in nest predation risk in shaping avian community structure and function through the process of habitat selection.

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Figure Legends

Figure 1 | Predator removals resulted in a reduction in nest predation rates which led to an increase in breeding density and singing rates. Responses are illustrated by percent difference [(removal-control)/control*100]. Predator removals resulted in a reduction in daily mortality rates for both resident (a) and migratory (b) species. Resident species (c) did not differ in density between treatments, but migratory (d) species preferentially settled on removal plots. Male song frequency was greater on removal plots than controls for both resident (e) and migratory (f) species. Data was not collected for all species for all variables as indicated by (n/a). Error bars represent s.e.m. across years.

Figure 2 | Predator removals did not lead to changes in phenology. Average relative date (removal – control) of first nest initiation (a) and mean nest initiation (b) did not differ between treatments. Error bars represent s.e.m. across years.

Figure 1

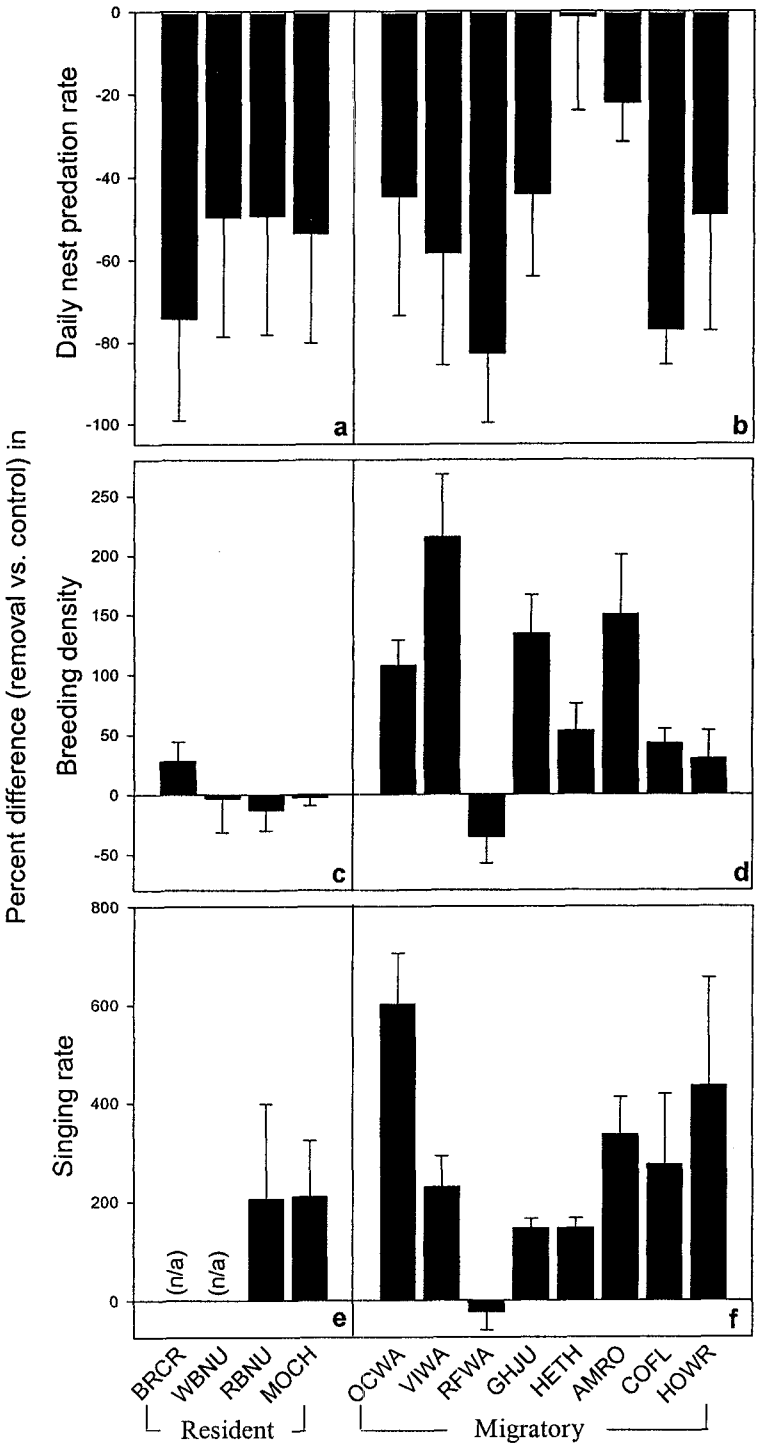
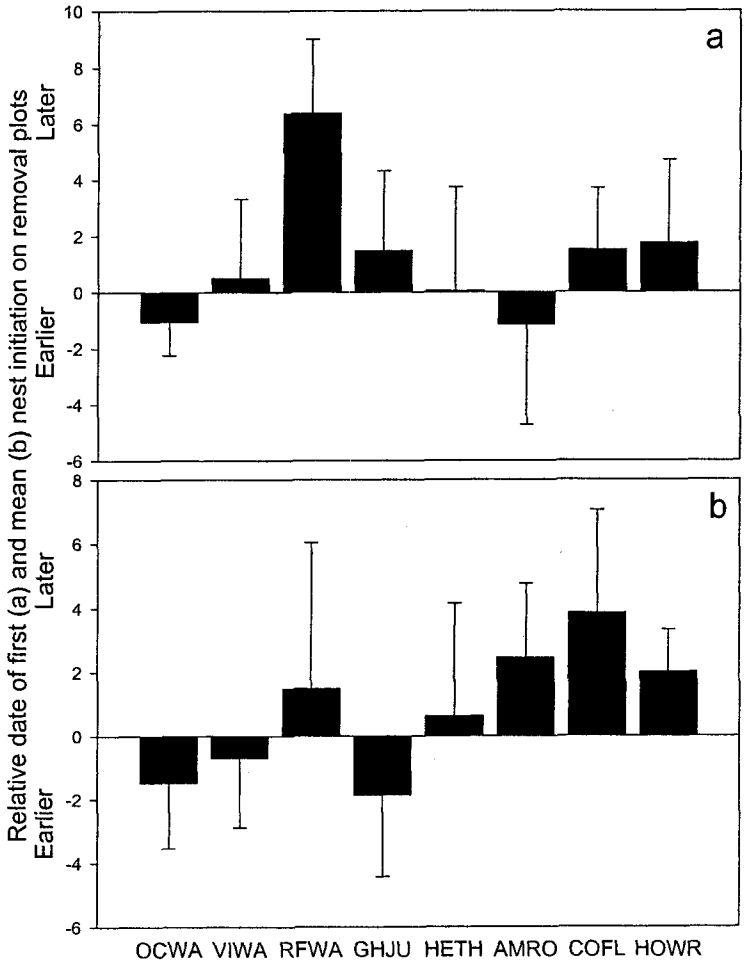


Figure 2



CHAPTER 3

TESTING ECOLOGICAL AND BEHAVIORAL CORRELATES OF NEST PREDATION

Abstract

Differences in nest predation rates among species in different nesting guilds or different habitats are generally assumed to result from inherent differences in risk that are specific to particular nest sites. Theoretical and empirical studies suggest that parental care behaviors evolve in response to nest predation risk and thereby differ among ecological conditions that vary in inherent risk. However, parental care also can influence nest predation risk. Separating the effects of nest predation risk inherent to a nest from the risk imposed by parental strategies is difficult, but imperative if we are to understand the evolution of parental care strategies. We used artificial nests to experimentally remove the effects of parental behavior, enabling us to assess inherent differences in nest predation risk across nest types and between habitats that differed in the abundance of nest predators. Risk of nest predation increased across nest types and between predator treatments in the same order for real and artificial nests. Thus, inherent differences in nest predation risk related to nest type and predator abundance influence nest predation rate independent of parental care behavior. However, despite similar patterns of nest predation, artificial nests experienced greater predation rates than real nests for all nest types and in both predator communities. Greater predation rates on artificial nests could reflect lower quality of nest sites chosen by investigators compared to birds. Yet, the extent to which predation rates on artificial nests exceed rates for real nests differed among nest types and predator treatments, suggesting that additional factors (i.e. functional or numerical responses of predators, or parental care behaviors) influence predation risk.

Introduction

Predation is a major evolutionary and ecological process that can shape both individual behaviors and community structure and function (Reznick and Endler 1982; Martin 1988, 1996; Begon et al. 1996; Pianka 2000). Understanding causes of variation in predation rates therefore is necessary to advancing our understanding of phenotypic traits. Predation risk is influenced by predator abundance, habitat structure, and predator and prey behavior (Lima and Dill 1990, Begon et al. 1996, Soderstrom et al. 1998, Chalfoun et al. 2002). While predation risk is influenced by prey behavior, it also shapes the evolution of prey behavior. This complex dynamic between predation risk and prey behavior makes the generalization of predation processes across different habitats or different species complicated, because causes of predation risk are difficult to isolate from changes in prey behavior. Understanding ecological sources of variation in predation risk, independent from prey behavior, is imperative to understanding the evolutionary pressures that have shaped predator-prey dynamics.

Nest predation, for example, can impose major limitations on individual fitness and demographics in birds (Martin 1988, 1992, 1998, 2001; Donovan et al. 1995; Chalfoun et al. 2002; Fletcher and Koford 2004; Lloyd et al. 2005; Fletcher et al. 2006). Therefore, understanding causes of variation in nest predation rates is important to understanding the evolution of phenotypic attributes of bird species. Still, despite evidence that both habitat features and parental care behaviors can influence nest predation outcomes (Skutch 1949; Martin 1995, 1996; Martin et al. 2000a, b), we do not know their relative importance in determining nest predation rates. The issue remains unclear because parental care behaviors can change across habitats or among nest types

that differ in inherent predation risk and thereby alter measured rates of nest predation and mask the ecological sources of predation risk (Martin and Ghalambor 1999, Ghalambor and Martin 2000, Martin et al. 2000b, Ferretti et al. 2005, Chapter 1). Here we attempt to separate how parental care behaviors, background predator abundance, and nest type independently influence nest predation risk. We did this by conducting two artificial nest experiments.

Researchers have long assumed that nest type (i.e. cavity versus open-cup) is the major ecological factor driving differences in nest predation rates among species nesting in different nesting guilds (Lack 1948, Nice 1957, Martin 1995, Owens and Bennett 1995, Martin and Ghalambor 1999). Patterns of increasing nest site safety from open-cup to secondary cavity to primary cavity are well established, and generally explained by differences in predation risk inherent to each nest type (Lack 1948, Nice 1957, Martin 1995). However, species occupying different nesting guilds also differ in parental care behaviors that can influence predation risk (Skutch 1949, Marzluff 1985, Montgomerie and Weatherhead 1988, Martin 1992, Kleindorfer and Hoi 1997, Martin and Ghalambor 1999, Martin et al. 2000a, Tewksbury et al. 2002). In particular, mate-feeding rates are higher at safer nests, and are associated with higher nest attentiveness (Martin and Ghalambor 1999). This relationship could suggest that safe nest sites allow high rates of mate-feeding, which facilitates high nest attentiveness (Skutch 1949, Martin and Ghalambor 1999, Martin et al. 2000a); or, conversely, the causal arrows could be reversed where increased nest attentiveness reduces predation risk but requires higher mate-feeding rates (Marzluff 1985, Montgomerie and Weatherhead 1988, Martin 1992, Kleindorfer and Hoi 1997, Tewksbury et al. 2002). In the latter case, nest types with low

nest predation risk may result from parents exhibiting high nest attentiveness rather than from some inherent influence of the nest type. Direct tests of these alternative directions of causality and the assumption that different nest types have inherent differences in risk are lacking because no tests have separated the influence of parental care behaviors from the influence of nest type. Here, we tested for inherent differences in nest site safety across four nest types known to differ in predation rates by using artificial nests to remove the potentially confounding effects of parental care behaviors.

Differences in predator abundance are also often assumed to explain differences in nest predation rates, particularly between different habitats or among years (Skutch 1949, Chalfoun et al. 2002). However, direct tests of the influence of predator abundance on predation risk independent of habitat structure and parental behavior are lacking. Parental care behaviors can change with predator abundance (Chapter 1) and may affect predation risk and confuse the influence of predator abundance on predation rates. Recent experimental manipulation of a predator community demonstrates that predator abundance alone cannot predict predation outcomes (Chapter 1, 2). Nest predation rates on predator treatment plots only decreased by 30-50 percent across a diverse suite of breeding birds (Chapter 2), despite a 90-95 percent decrease in predator abundance (Chapter 1). This contrast raises the question of why we fail to see similar changes in actual nest predation rates despite apparent changes in environmental risk of nest predation as reflected by predator abundance?

An increase in mate-feeding rate and a decrease in nest attentiveness coincided with a decrease in predator abundance (Chapter 1), and may have increased nest predation rates beyond that predicted by predator abundance alone. In other words,

predation rates were inflated on removal plots because those predators that remained were more successful at finding and depredating nests because parent birds expressed more risky behaviors. Alternatively, other predators may have switched to this food resource because of increased nest density (Chapter 2). To separate between these alternatives we conducted another artificial nest experiment overlaid on a predator removal experiment to examine how changes in predator abundance affect predation outcomes independent of the influences of parental care.

We used artificial nests to test: 1) if the pattern of increasing nest predation rates from primary cavity < secondary cavity < ground < shrub nests observed in real nests (see Martin 1995) existed independent of parental behaviors, and 2) if predator abundance determined nest predation risk independent of parental behaviors or if the expression of risky parental behaviors changed nest predation risk.

Methods

Study area and species

We studied nest predation in a community of birds breeding in a series of snowmelt drainages located along the Mogollon Rim in central Arizona from 1998-2004. This system is particularly appropriate for examining the effects of nest predation on breeding birds because nest predation accounts for 98% of nest failure (Martin 1998) and is known to influence both population trends and individual behaviors (Martin and Ghalambor 1999, Martin 2000a, Chapter 1). The vegetation and climate are typical of western mixed conifer forests (Martin 1998). Study species included thirteen species of

passerine birds representing a diverse continuum of ecological and behavioral characteristics and known to differ in nest predation risk and nest type (Table 1).

From video and photo documentation as well as personal observation we have determined that the primary nest predators in this system include: red squirrel (*Tamaiasciurus hudsonicus*), gray-neck chipmunk (*Eutamias cinereicollis*), deer mouse (*Peromyscus maniculatus*), white-footed mouse (*P. leucopus*), and Steller's Jay (*Cyanocitta stelleri*) (Martin 1998). Additional nest predators exist within the community but have been documented depredating nests in this system so rarely (Martin 1998, pers obs) that their effect on nesting productivity is likely minimal under normal conditions.

Nest Type Experiment

From May to July of 1998 and 1999, we created four nest types known to differ in nest predation rates: primary cavity, secondary cavity, ground, and shrub (see Martin 1995). We chose all artificial nest sites based on characteristics typical of the species they represented (from Martin 1998). To begin we established sampling points for artificial nests by locating naturally occurring secondary cavities typically preferred by House Wrens. To control for spatial and temporal variation in predation risk we placed nests representing all other nest types within 25 m of these natural secondary cavities and baited (see below) all the nests at the same time. We modeled primary cavities after Red-breasted Nuthatches created in a different tree of the same species and at the same height as our artificial House Wren nest. Using a power drill, we excavated cavities to a depth and width of approximately 7-15 cm, with an entrance diameter of 2.5 cm. We

created shrub nests modeled after Hermit Thrushes from small wicker baskets covered with lichen and placed at a height of 0.5-2.5m. Finally, we modeled ground nests after Orange-crowned Warblers by creating a depression at the base of a stem and lining it with dried grasses.

Twenty replicate nests representing each nest type were set out in the last week of May of each year. Due to high variation in nest predation within open-cup nests, an additional forty pairs of ground and shrub nests were set out in the second week of June 1999 in the same series of drainages. We baited each nest with one Zebra Finch (*Poephila gullata*), and one Buttonquail (*Turnix sp.*) egg. We checked nests every 2 days for a period of 13 days, a typical incubation period for these species (Martin 2002), to determine nest fate. Nests in which any of the eggs were disturbed or removed were considered depredated and monitoring was discontinued.

Artificial nests may not adequately replicate real nests, and their utility for examining questions relative to nest predation is unclear (Major and Kendal 1996, Moore and Robinson 2004). However, when artificial nests are coupled with studies of real nests, as we do here, they can be a useful experimental tool, but care must be paid to design and assumptions. The nests we used were specifically designed to replicate actual nests in size, shape, substrate, and material (Martin 1987). Although we likely did not choose nesting locations as well as real birds, we based our decisions on more than 35 years of combined experience searching for these nests, and any biases were likely systematic across all nest types allowing us to eliminate this error when comparing among types. The nest predator community in this system is simple (see below), limiting potential differences between nest predators of real and artificial nests (Moore and

Robinson 2004). Additionally, our nests included eggs typical of eggs found in real nests and therefore did not limit our predator community (Major and Kendal 1996). Finally, we are not suggesting that artificial nests represent real nests (Sievings and Willson 1998). Indeed, we specifically used artificial nests to remove many of the confounding factors present at real nests, particularly parental behaviors, to test general patterns of predation risk across environmental gradients.

We located and monitored real nests (see Martin and Guepel 1993) in drainages adjacent to experimental sites for use in comparing relative nest predation rates. Only nests monitored during incubation are considered here. We grouped all nests by nest type to compare to artificial nests (Table 1).

Daily nest predation rates were calculated for both real and artificial nests using the Mayfield method (Mayfield 1961, Mayfield 1975, Hensler and Nichols 1981). We pooled data across years because both years showed a similar pattern of nest predation. We compared the patterns of nest predation among nest types between real and artificial nests using a Kendall's Tau signed ranks test to determine if nest type could explain known differences in nest predation rates among types (Martin 1995).

Behavioral Correlations

We measured parental care behaviors at real nests of all four nest types to determine whether parental care behaviors could explain additional variation in nest predation risk among nest types. We assessed parental behaviors by videotaping nests for approximately six hours starting within 30 minutes of sunrise (Martin and Ghalambor 1999, Martin et al. 2000a, Martin 2002). Whenever possible we video recorded nests

once in early incubation and once in late incubation and averaged these samples to determine incubation behaviors. We scored tapes for both nest attentiveness and mate-feeding rates (Martin and Ghalambor 1999, Martin et al. 2000a). Behavioral data gathered in the study years did not differ from a much broader sample gathered from 1987 to 2004 ($F = 0.698$, $p = 0.404$). Consequently, we used behavioral data pooled from all years because we were interested in the most robust estimates of behaviors for the nest types examined here. We tested if patterns of behavioral data were explained by nest type using a standard ANOVA with a LSD Post Hoc test.

Predator Removal and Artificial Nest Experiment

We created artificial nests in sites typical of Orange-Crowned Warblers (see above for details) on plots undergoing predator removals (removal plots) and plots with intact predator communities (control plots) from May to July of 2002, 2003, and 2004, (see Chapter 1 for a detailed description of predator removal experiment). Twenty nests were set out on a series of four removal and four control plots in the last week of May of each year, for a total of 240 nests for each treatment. Again, we baited each nest with one Zebra Finch, one Buttonquail egg and checked nests every 2 days for a period of 13 days to determine their fate. Nests in which any of the eggs were broken or removed were considered depredated and monitoring was discontinued. We also monitored real nests on these plots (see above) to compare relative nest predation rates.

We predicted that if changes in parental care behaviors lead to elevated nest predation rates on removal plots then the difference in predation rates on artificial nests between treatments would be significantly greater than the difference in predation rates of

real nest between treatments. Alternatively, if the difference in predation rates of artificial nests between treatments resembles that of real nests then it is unlikely that parental care behaviors can explain the slight decline in predation rates on removal plots considering the decline in predator numbers. Instead, prey switching by alternative predators may have limited nest success on removal plots. To determine which hypothesis was best supported, we calculated daily nest predation rates for real Orange-crowned Warbler nests and artificial nests that simulated this species on both treatments (see above for detailed descriptions). We then used these data to calculate the percent difference between the two treatments [((removal – control)/control)*100] for both nest types in each year on each plot. We compared the yearly percent difference between real and artificial nests for each plot using a paired t-test.

Results

Real nests of all species in each guild, real nests of the representative species of each guild, and the artificial nests meant to simulate the nests of those species all showed correlated patterns of nest predation across the four nest types (Fig. 1a, $p = 0.021$). However, artificial nests had higher predation rates than representative real nests ($t_3 = -3.379$, $p = 0.043$) or combined nests for the entire guild ($t_3 = -4.250$, $p = 0.024$). Mate-feeding rate and nest attentiveness increased across species with increasing nest site safety (Fig. 1b; $F_{3, 12} > 6.146$, $p < 0.015$).

For both predator treatments nest predation rates were again higher for artificial nests (Fig. 2a, $t_3 = -6.762$, $p < 0.001$). The percent change between nest predation treatments did not differ for real and artificial nests (Fig. 2b, $t = 0.144$, $p = 0.888$).

Discussion

Predation is a major ecological force influencing biological systems at a multitude of levels. Yet, our understanding of how inherent differences in predation risk influences the phenotypic expression of complex sets of traits and how these traits can feedback to influence predation risk remains unclear. Here we attempted to distinguish between sources of predation risk inherent to the environment (i.e. predator density and nest type) and sources of predation risk imposed by prey behavior (i.e. mate-feeding rate and nest attentiveness).

Our data clearly demonstrate that inherent differences in nesting environments can readily influence nest predation risk. Real and artificial nests experienced similar patterns of nest predation risk across nest types (Fig 1a), and between predator treatments (Fig 2). These data support the common but previously untested assumptions that predation risk is strongly determined by nest type and predator abundance, independent of parental behaviors. Understanding differences in environmental sources of nest predation risk is important, because nest predation plays a critical role in the evolution of phenotypic expression (Martin 1992, 1995; Martin and Ghalambor 1999; Martin et al. 2000a, b; Ghalambor and Martin 2001, 2002). Indeed, the differences in parental care behaviors observed among nest types (Fig. 1b, 1c) potentially reflect responses to these inherent differences in nest site vulnerability (Martin and Ghalambor 1999, Martin et al. 2000a).

Differences in nest predation between real and artificial nests suggest the possibility that other factors beyond nest type or predator abundance may influence nest predation risk (Fig. 1a, Fig. 2a). This difference could simply reflect our inability to

adequately simulate nest sites chosen by real birds, and certainly nest placement played some role. At the same time, differences in nest predation between real and artificial nests were greater for cavity-nesters than for open-cup nesters (Fig. 1a). These differences suggest that at least some of the increase in predation risk for artificial nests may be due to factors beyond our ability to choose appropriate nest sites. These factors may include parental care behavior, particularly behaviors that can directly influence nest predation risk such as mate-feeding rates and nest attentiveness (Skutch 1949; Montgomery and Weatherhead 1988; Martin 1992; Martin et al. 2000a, b; Tewksbury et al. 2002). If these parental care behaviors covary with the differences we detected between real nests and artificial nest by either increasing risk at open-cup nests or decreasing risk at cavity nests, than they may be an important cause of additional variation in nest predation risk between these nest types.

We failed to find any influence of parental behavior on nest predation risk between our predator treatments. Parents on removal plots clearly altered their parental care behaviors (Chapter 1), but our artificial nest study suggests that these changes did not lead to a significant increase in nest predation risk (Fig. 2b). Instead, prey switching by alternative predators may more easily explain the limited influence of the predator reduction on nest predation rates (Chapter 1, 2). While individuals nesting in safer nests, either due to nest type or predator abundance, express more risky parental care behaviors, these behaviors appear appropriate and do not appear to exaggerate their risk.

In summary, our experiments showed that inherent differences in nest site vulnerability, independent of parental behaviors, do exist among nest types and between habitats with different predator community assemblages. Individuals or species with

inherently safe nests are afforded the luxury of expressing behaviors that would be costly if expressed in unsafe nests (Martin and Ghalambor 1999; Martin et al. 2000a, b; Chapter 1). The extent to which parental care behaviors further influence nest predation rates still remains unclear, however, and deserves further experimental study. Ultimately, consideration of both inherent differences in nest site safety and parental care strategies is critical to understanding variation in nest predation and life-history traits in birds.

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Table 1 | Species occupy different nest types.

Nest Type	Common Name	Scientific Name
Primary Cavity	Red-breasted Nuthatch	*Sitta canadensis*
Primary Cavity	Pygmy Nuthatch	*Sitta pygmaea*
Secondary Cavity	White-breasted Nuthatch	*Sitta carolinensis*
Secondary Cavity	Mountain Chickadee	*Parus gambeli*
Secondary Cavity	House Wren	*Troglodytes aedon*
Secondary Cavity	Western Bluebird	*Sialia mexicana*
Ground	Orange-crowned Warbler	*Vermivora celata*
Ground	Virginia's Warbler	*Vermivora*
Ground	Red-faced Warbler	*Cardellina*
Ground	Gray-headed Junco	*Junco hyemalis*
Shrub	Green-tailed Towhee	*Pipilo chlorurus*
Shrub	MacGillivray's Warbler	*Oporornis tolmiei*
Shrub	Hermit thrush	*Catharus guttatus*

Figure Legends

Figure 1 | Nest success of real and artificial nests predicted parental care behaviors across nest types. (a) Real nests for the entire guild and a representative species from 1998-1999, as well as the artificial nests showed the same pattern of nest predation rates across the four nest types: primary cavity (primary, n = 841 real, 64 rbnu, 20 artificial), secondary cavity (secondary, n = 1784 real, 82 howr, 20 artificial), ground (n = 2327 real, 25 ocwa, 60 artificial), and shrub (n = 903 real, 40 heth, 60 artificial). This pattern corresponded with differences in **(b)** mate-feeding rate (rate at which males feed incubating females on the nest) **(c)** and nest attentiveness (percentage of time female is on the nest) across the four nest types: primary cavity (primary, n = 56), secondary cavity (secondary, n = 90), ground (n = 444), and shrub (n = 54). Columns denoted by the same letter are not significantly different. Columns denoted by different letters are significantly different at the 0.05 level according to an LSD Post Hoc test. All data are means ± s.e.m.

Figure 2 | Predator reductions lead to consistent changes in nest success for real and artificial nests. (a) Artificial nests experienced greater nest predation rates than real nests in both treatment groups (n = 103 real, 240 artificial), but **(b)** the percent change in nest predation rates between the treatment groups did not differ between real and artificial nests. All data are means ± SE.

Figure 1

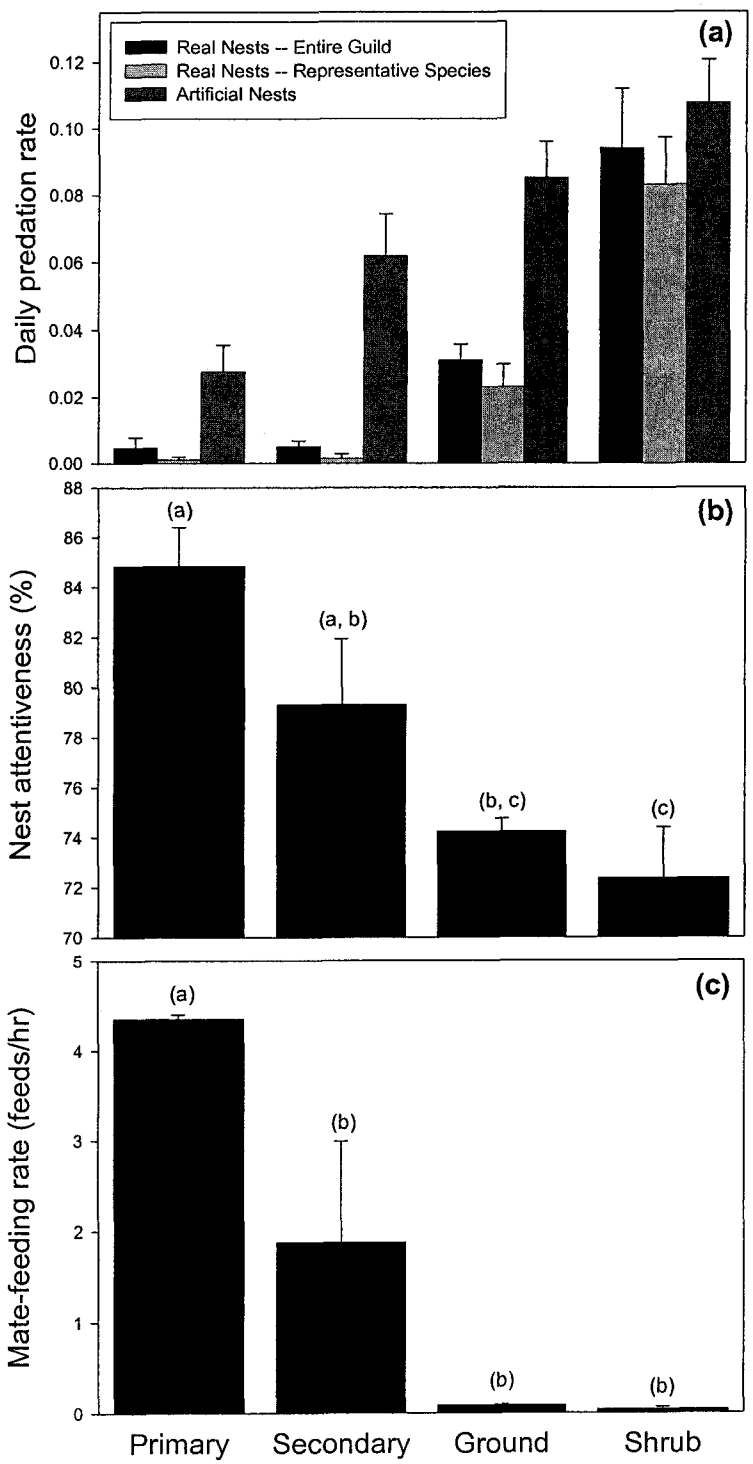
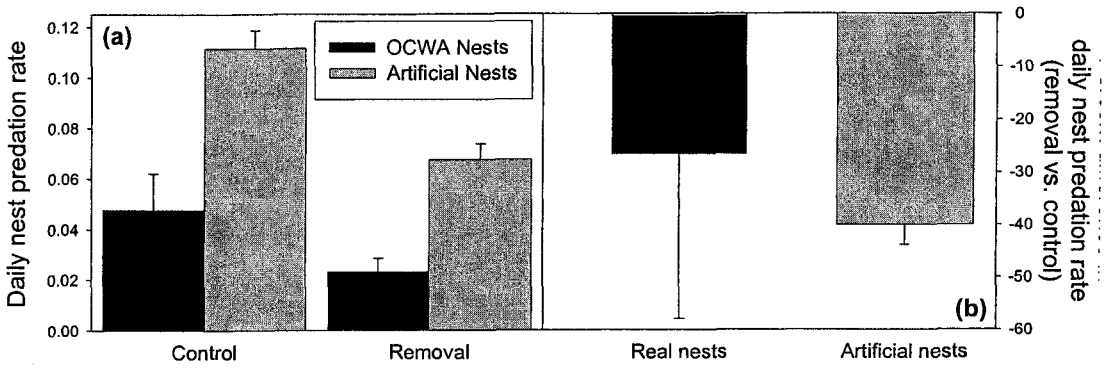


Figure 2



CHAPTER 4

CORTICOSTERONE RESPONSES OF INCUBATING FEMALES TO SEASONAL CHANGES AND EXPERIMENTALLY REDUCED NEST PREDATION RISK

Abstract

Risk of predation to offspring can influence the expression of reproductive strategies, both within and among species. Appropriate expression of reproductive strategies in environments that differ in predation risk can have clear fitness advantages. Although adult predation risk appears to influence corticosteroid levels leading to changes in behavioral and life history strategies, the influence of offspring predation risk on adult corticosteroids remains unclear. We compared baseline corticosterone levels of adults of six species of passerine birds nesting on plots with and without experimentally reduced risk of nest predation. Despite clear differences between treatments in nest predation risk that lead to differences in reproductive strategies, we failed to find any differences in baseline corticosterone between treatments or among species that differed in nest predation risk. Corticosterone did increase across the breeding season consistent with other studies, but we show that these increases are independent of changes in nesting stage. Nest predation can impose strong selection on the expression of reproductive strategies, and birds can assess and respond to differences in nest predation risk, but corticosterone does not appear to be a key physiological mechanism regulating these changes.

Introduction

The extent to which individuals invest in current reproductive attempts is influenced by a variety of extrinsic and intrinsic sources of selection. In particular, sources of mortality, either to the offspring or the parents, are known to influence the relative effort of parents in current reproduction (Roff 1992, Ghalambor and Martin 2001, Fontaine and Martin 2006). Yet the physiological mechanisms underlying these patterns are less well known (Sinervo and Svensson 1998, Ketterson and Nolan 1999). Understanding the physiological processes underlying adjustments in parental effort are paramount to understanding the evolution of life histories and parental care as well as the management and conservation of species (Clutton-Brock 1991, Sinervo & Svensson 1998, Ketterson and Nolan 1999, Martin 2002; Ricklefs and Wikelski 2002; Barnes and Patridge 2003, Wikelski and Cooke 2006). The hypothalamic-pituitary-adrenal (HPA) axis is suggested as a potential physiological mechanism that may mediate tradeoffs between risk or mortality and reproductive effort (Salmon et al. 2001, Ricklefs and Wikelski 2002, Wingfield and Sapolsky 2003). However, broad experimental studies of its influence on reproductive traits in alternative predation environments are conspicuously lacking (Clinchy et al. 2004).

Nest predation is the primary cause of reproductive failure in avian systems (Ricklefs 1969, Martin 1987) and, thus, represents an important source of selection acting on the expression of reproductive strategies. Indeed, correlative studies (Lack 1948, Slagsvold 1982, Martin 1995, Martin et al. 2000, Ferretti et al. 2005), as well as recent experimental tests (Fontaine and Martin 2006), have shown that parents adjust reproductive strategies in response to risk of nest predation. Yet the physiological

mechanism mediating these responses remains conspicuously untested. Exposure to adult predators can elevate baseline levels of corticosterone (Silverin 1998, Wingfield et al. 1998), and short-term increases in corticosterone can alter behaviors (Wingfield et al. 1998). Indeed recent work on stonechats (*Saxicola torquata axillaries*) and song sparrows (*Melospiza melodia*) have demonstrated correlations between baseline corticosterone, predator abundance, reproductive success and parental effort (Scheuerlein et al. 2001, Zanette et al. 2003, Clinchy et al. 2004). Although risk of nest predation differed between treatments in these studies, treatments also differed in adult predation risk. Thus elevated corticosterone levels in high predation environments may result from either adult or offspring predation risk. Given the ubiquity of nest predation and its influence on reproductive strategies, the question remains whether corticosterone can mediate this response.

To answer this question we experimentally altered the risk of nest predation, which lead to clear changes in reproductive strategies (Chapter 1). Here we examine whether baseline corticosterone levels could explain these changes in reproductive strategies in a community of six passerine birds. Specifically, we tested whether circulating corticosterone levels were reduced in safer nesting environments, and whether differences in baseline corticosterone were associated with differences in egg mass, clutch size, nest attentiveness (percentage of time females are on the nest incubating), and mate-feeding rate (rate males feed incubating females at the nest) both within and among species.

Methods

Study area and species

We studied birds breeding in 20 snowmelt drainages located along the Mogollon Rim in central Arizona, from 2001-2004. Vegetation at the study site is typical of a western mixed conifer forest (Martin 1998). This system is particularly appropriate for examining these questions because nest predation accounts for 98% of nest failure (Martin 1998), and therefore should impose direct selection on the expression of reproductive strategies and the proximate mechanisms that regulate them.

We examined baseline corticosterone levels for incubating females from six neotropical migrants that returned after nest predators were experimentally reduced in portions of the landscape (see next). We also compared baseline corticosterone levels for males from one species (GHJU) that was particularly abundant. These species represent a diverse continuum of ecological and behavioral characteristics and differ in nest predation risk (Martin 1995, 1998; Fontaine and Martin 2006). In all figures species are referenced by their four letter American Ornithological Union code: OCWA – Orange-crowned warbler (*Vermivora celata*), RFWA – Red-faced Warbler (*Cardellina rubrifrons*), GHJU – Gray-Headed Junco (*Junco hyemalis caniceps*), HETH – Hermit Thrush (*Catharus guttatus*), COFL – Cordilleran Flycatcher (*Empidonax occidentalis*), and HOWR – House Wren (*Troglodytes aedon*).

Nest predator removals

We conducted a predator removal experiment to alter nest predation risk across the landscape (see Fontaine and Martin 2006 for detailed description). We removed

predators from 10 removal plots to compare with 10 neighboring control plots with intact predator communities. Each plot is an individual drainage with similar vegetation composition and structure and separated from other drainages by ridges of different habitat (Martin 1998). We paired plots based on 20 years of prior data that suggested similar bird, predator, and plant assemblages. We removed predators from ten, 5-10 hectare drainages. Control and removal plots were spatially paired to minimize possible spatial influences, but separated by at least one intervening drainage to buffer against possible carryover effects of removals on control plots. We removed predators from the same plots each year to maximize effect size.

Removals began before the arrival of any female migrant birds to the study site and continued throughout the breeding season. The primary nest predators we removed included: red squirrel (*Tamaiasciurus hudsonicus*), gray-neck chipmunk (*Eutamias cinereicollis*), deer mouse (*Peromyscus maniculatus*), white-footed mouse (*P. leucopus*), and Steller's Jay (*Cyanocitta stelleri*) (Martin 1998). These predators significantly influence nest predation rates, but represent no threat to adult birds; therefore, any changes in adult corticosterone levels reflect risk to offspring and not adult mortality.

Nest finding and monitoring

Nests were located based on parental behaviors using long-standing techniques (Martin and Guepel 1993). When checking nests, we did not flush incubating females from nests to limit human disturbance, which birds may perceive as a predation threat. Instead, nests were either checked from afar by observing parental behavior or nest contents were checked when females were off during normal foraging bouts. Hormone

levels are known to vary with stage of breeding; therefore we determined the exact initiation dates for all nests found prior to clutch completion. Incubation periods are well established for all study species (Martin 2002), allowing us to increase our sample size by backdating known incubation periods from nests for which exact hatch date was observed.

Life history and parental care behaviors

We measured egg mass for nests located during nest building or egg-laying, and measured all eggs within two days of clutch completion using a calibrated digital scale accurate to 0.001 g. Clutch size was taken from all nests found prior to hatching because partial losses are virtually never observed in this system.

We assessed parental behaviors by videotaping nests for approximately six hours starting within 30 minutes of sunrise (Martin et al. 2000). Whenever possible we recorded nests once in early incubation and once in late incubation and averaged to determine incubation behaviors. Tapes were scored for behaviors including: percentage of time females spent on the nest (nest attentiveness) and the rate that males visited the nest to feed incubating females (mate-feeding rate) (Martin et al. 2000).

Capture and handling techniques

We captured all individuals by setting a 6m-net within 2m of nests. Females were flushed from the nests while incubating or captured while returning to incubate. Males were captured while returning to the nest to feed nestlings. All samples included here were collected within three minutes of capture. We obtained blood samples (~50 μl)

from the brachial vein and using heparinized microcapillary tubes. The blood was centrifuged and seperated, and the plasma was removed and frozen for future analysis.

Measurement of baseline corticosterone

We measured plasma corticosterone in plasma samples ranging from 10-20 μl (average 13 μl) by radioimmuneassay, with a sensitivity of 1.1ng/ml plasma (intra-assay coefficient of variation 5.7%). For the assay, tritiated corticosterone (2000 cpm) was added to each plasma sample for estimation of recoveries (mean 76%), and samples were allowed to equilibrate overnight at 4° C. Steroids were extracted with 2 X 4 ml of petroleum ether and diethylether (3:7 by volume) using minicolumns, and extracts were dried at 37° C over a stream of N2. The assay was performed following standardized protocol developed by Schwabl (1995) using corticosterone antibody B3-163 (Esoterix Endocrinology Inc.).

Analysis

We compared corticosterone levels between treatments and across species using analysis of covariance to test for overall differences between treatments and across species that differ in risk of nest predation, while controlling for date as a covariate. We excluded non-significant variables or interactions from final models. We then tested for correlations between corticosterone and life history and parental care traits using a multivariate analysis.

Results

Sampling date had a significant effect on baseline corticosterone levels for incubating females independent of treatment (Fig. 1). This was not related to the day within the incubation period when samples were taken (Date: $F_{1, 41} = 11.291$, $p = 0.002$; Day of Incubation: $F_{1, 41} = 0.632$, $p = 0.432$; Species: $F_{5, 41} = 1.529$, $p = 0.208$). Thus, we included date in subsequent analyses.

Although experimental nest predator removals led to changes in avian reproductive strategies (Fontaine and Martin 2006), baseline corticosterone levels did not differ between treatments for incubating females (Fig. 2a; Treatment: $F_{1, 41} = 0.766$, $p = 0.389$; Date: $F_{1, 41} = 10.786$, $p = 0.003$; Species: $F_{5, 41} = 1.196$, $p = 0.337$; Treatment by Species: $F_{5, 41} = 0.329$, $p = 0.891$), or for male GHJU's feeding nestlings (Fig. 2b; Treatment: $F_{1, 9} = 0.363$, $p = 0.703$). Differences among species in nest predation risk also did not correspond to differences in baseline corticosterone during incubation (Fig. 3; Species: $F_{5, 41} = 1.419$, $p = 0.243$; Date: $F_{1, 41} = 11.462$, $p = 0.002$). Baseline corticosterone levels were not associated with any variation in life history or behavioral traits among individuals (Life history and behavioral traits: $F < 0.292$, $p > 0.592$; Species: $F < 0.735$, $p > 0.589$) although nest initiation date was weakly correlated (Trait: $F_{1, 70} = 3.323$, $p = 0.073$; Species: $F_{5, 70} = 0.544$, $p = 0.742$).

Discussion

Predation is a major ecological and evolutionary force that can clearly shape the expression of behavioral and life history traits both within and among species (Roff 1992; Martin 1986, 1996; Begon et al. 1996; Pianka 2000). Moreover, behavioral and life

history traits shift in response to changes in nest predation risk (Fontaine and Martin 2006), and corticosteroids are a potential physiological mechanism mediating these responses However, we found no discernable effect of nest predation risk on baseline corticosterone levels between treatments (Fig. 2) or among species that differed in nest predation risk (Fig. 3). Furthermore, we failed to find any relationship between baseline corticosterone and the expression of any of the reproductive traits that we measured. Thus, baseline levels of corticosterone do not appear to be the physiological mechanism regulating life history and behavioral modifications in response to nest predation risk.

This result is particularly surprising, not only because previous studies have found correlations between nest predation risk and baseline corticosterone levels (Scheuerlein et al. 2001, Clinchy et al. 2004, but see above), but also because of apparent differences in food stress. The rate that males supplied females with additional food at the nest and the percentage of time females spent off the nest foraging for themselves both increased on removal plots (Fontaine and Martin 2006). Consequently, females on removal plots were significantly less food limited, which should decrease baseline corticosterone levels (Wingfield 2003, Clinchy et al. 2004). The lack of difference in corticosterone levels between treatments may suggest that the costs of elevated levels of corticosterone (Sapolsky et al. 2000 Romero 2004) favors alternative physiological mechanisms for regulating reproductive responses to nest predation risk.

Selection against elevated corticosterone may be particularly high during the reproductive period not only because corticosteroids may suppress reproduction (Wingfield and Sapolsky 2003), but also because these costs may be transferred to offspring. Recent work demonstrates the transfer of corticosterone from females to eggs

(Hayword and Wingfield 2004, Saino et al. 2005), and eggs with elevated levels of corticosterone can have reduced hatching success, take longer to hatch and produce smaller, lower quality offspring (Eriksen et al. 2003, Hayword and Wingfield 2004, Rubolini et al. 2005, Saino et al. 2005). These effects, while always bad, are further compounded in environments with high nest predation rates. For example, increasing hatching time increases risk of nest predation because nest predation risk compounds daily, but this risk is particularly elevated in high nest predation environments. Poor offspring quality is also exaggerated in high nest predation environments because parents tend to feed less in these environments (Fontaine and Martin 2006) and attempts to compensate for poor offspring quality by increasing feeding rate can lead to increased nest predation risk (Skutch 1949, Martin et al. 2000). Thus, the high costs of elevated corticosterone to offspring may favor alternative physiological mechanisms for regulating reproductive strategies in environments that differ in nest predation risk, independent of the costs to parents.

Baseline corticosterone levels did not vary with nest predation risk, but consistently increased across the breeding season for all species (Fig. 1). Seasonal changes in baseline corticosteroid levels are well known, and for birds corticosterone levels are generally elevated during the breeding season (see Romero 2002 for a review). Furthermore, both corticosterone responses and baseline corticosterone levels can vary within a breeding season across breeding stages (Holberton and Wingfield 2003, Adams et al. 2005, Raouf et al. 2006), but whether these differences are due to time of year effects or stage effects remains unclear. Here we control for stage and show a clear

pattern of increasing baseline corticosterone levels across a breeding season for incubating females representing a diverse continuum of reproductive ecology (Fig. 1).

Why baseline corticosterone levels would increase across a breeding season independent of nesting stage is unclear, but here we discuss some possible explanations. First, seasonal increases in competition, predation risk, food limitation, or parasite prevalence could lead to increased chronic stress and thus elevate baseline corticosterone levels across the breeding season. In this case, date is simply a correlate of these ecological factors. Second, date itself may be of primary importance. As the breeding season progresses and timing for alternative life stages such as molt or migration approach, baseline corticosterone may be elevated either as preemptive or reactionary response. For example, elevated corticosterone levels may act preemptively to suppress the initiation of alternative life stages despite external cues (i.e. photoperiod) and thus allow females to continue incubation behaviors. Alternatively, corticosterone levels may rise to prepare individuals for a future life stage, particularly molt or migration that require increased fat deposition. Finally, baseline corticosterone may increase as a reaction to a diminishing window to successfully fledge offspring and may aid in a female's ability to assimilate energy and therefore increase her reproductive effort and ultimately her chances of successfully rearing young.

Corticosteroids play an important role in regulating behaviors, particularly when environmental conditions impose a major threat to an individual (Wingfield et al. 1998). However the production and mobilization of corticosteroids to mediate external costs must be balanced against potential internal costs, and this may be particularly important when an individual is breeding (Wingfield and Sapolsky 2003). These data suggest such

a balance, as corticosterone levels do not respond to nest predation risk, but do respond to the changing season. Ultimately, the reproductive value of the offspring and the life history strategy of the species may dictate this balance as in both cases the physiological responses of the parents may have been in the best interest of the offspring.

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Figure Legends

Figure 1 | Baseline corticosterone levels increased with date. Across all six species incubating females sampled later in the breeding season had higher baseline corticosterone levels.

Figure 2 | Baseline corticosterone levels did not differ between nest predator treatments. Birds nesting on control and removal plots did not differ in circulating corticosterone levels for **(a)** incubating females and **(b)** males feeding nestlings. Data presented are marginal means evaluated for sampling date ± s.e.m.

Figure 3 | Baseline corticosterone levels were not predicted by nest predation risk across species. Incubating females for species differing by more than an order of magnitude in daily nest predation risk showed no clear pattern of baseline corticosterone expression. Data presented are marginal means evaluated for sampling date ± s.e.m.

Figure 1

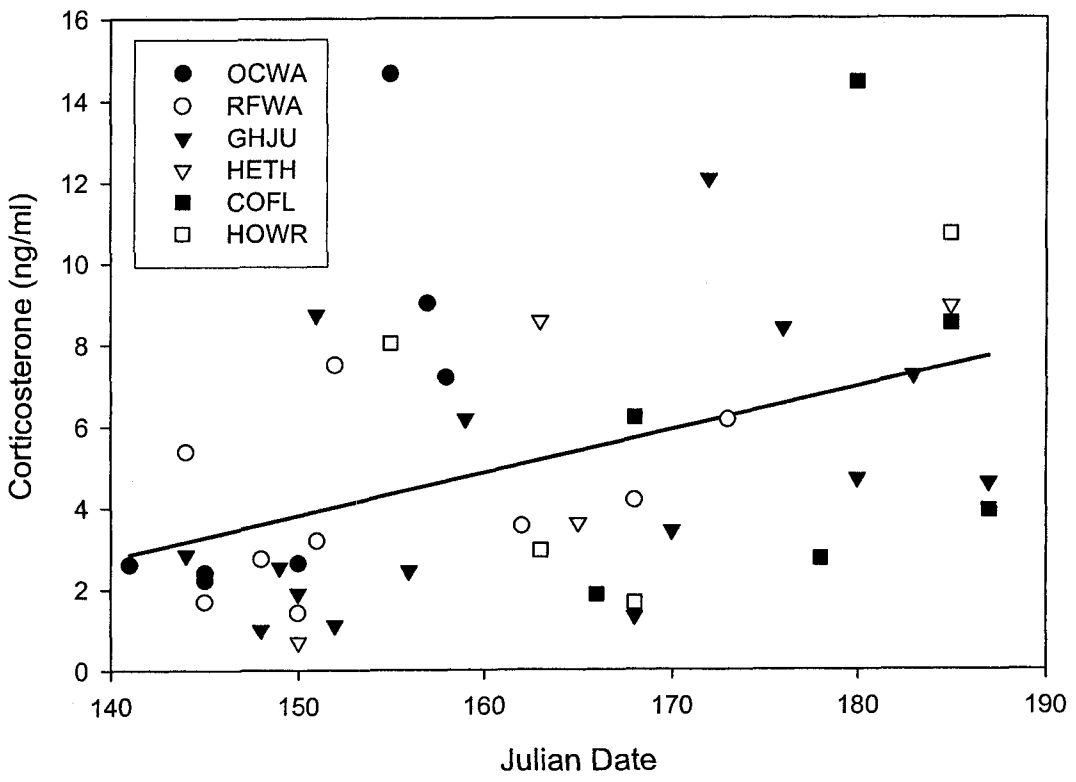


Figure 2

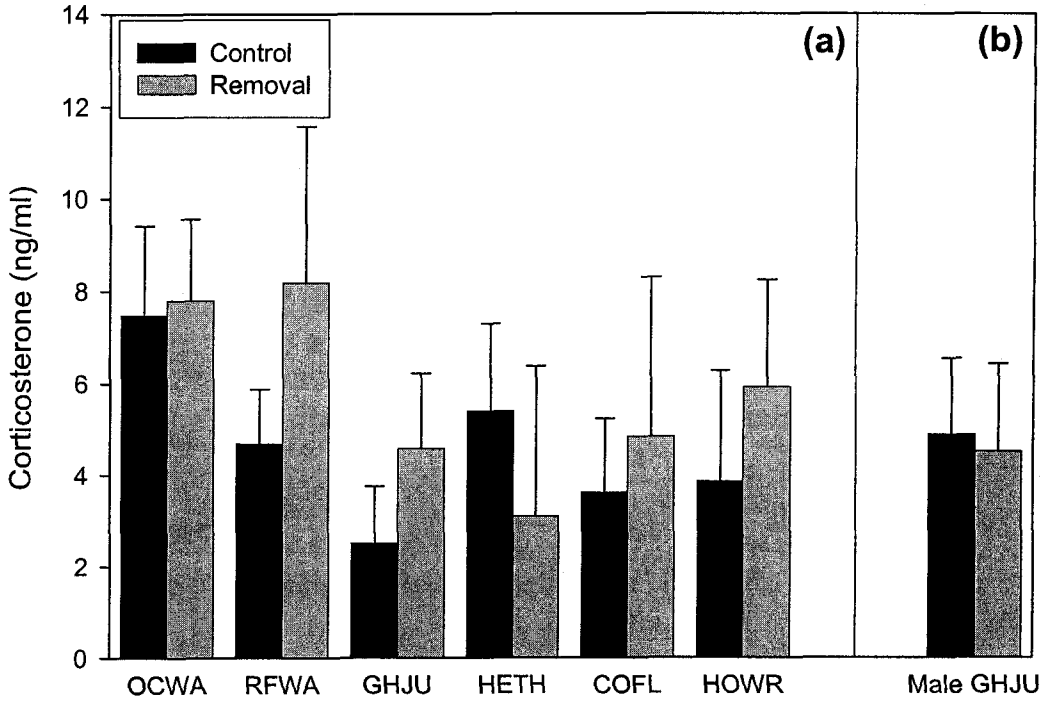
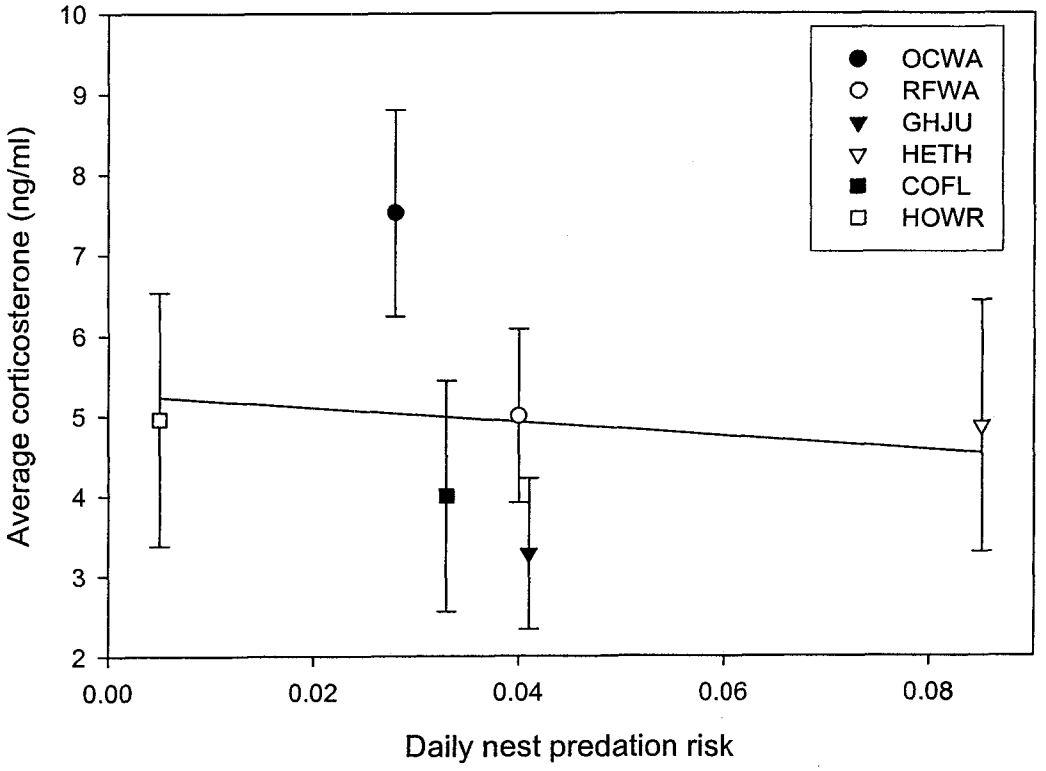


Figure 3



CHAPTER 5

USING MICROCLIMATE TO PREDICT PLANT DISTRIBUTION IN THE OUTDOOR CLASSROOM

Introduction

Subtle differences in temperature, humidity, or light often have profound effects on plant and animal communities (Begon et al. 1996). Although geographic variation the availability of light and water are used to explain broad patterns in the distribution of animals and plants (Pianka 2000), we often fail to recognize the importance of these same ecological factors in shaping local communities. This is particularly true for plants, because they are unable to move and thus often limited by local environmental conditions. For students to understand the structure and function of their local environments they must gain an appreciation for the potential impacts of small changes in local microclimate on plant distribution.

In this lesson, students measure natural variation in microclimate for different plant types (i.e. deciduous tree, shrub, grass, forb, coniferous tree) and use this information to make predictions about local plant distribution. The basis of the ideas presented here and the procedures described are adaptable to any natural location or plant community with reasonable diversity in plant types and microclimate.

Background

The natural world exhibits substantial variation in abiotic factors that influence the distribution, reproductive success, and survival of plants and animals. Variation in abiotic factors are often evoked to explain large-scale geographic patterns of plant and animal distribution (Pianka 2000), but even small differences in temperature, elevation, water availability, soil structure, or light intensity can limit local distributions of plants and animals (Begon et al. 1996). Microclimate, for example, can influence where birds

place their nests (Rauter et al. 2002, Hartman and Oring 2003, Lloyd and Martin 2004), where insects reside (Lorenzo and Lazzari 1999, Guarneri et al. 2002), and where plants successfully germinate (Hennenberg and Bruelheide 2003, Zaady et al. 2003, Tomimatsu and Ohara 2004). Thus, microclimate can have a profound effect on local community structure and biodiversity.

Students have an innate interest in understanding the natural world, but generally fail to recognize their own potential to comprehend why the world functions as it does. Microclimate is something that is easy for students to comprehend, easy to measure, and has important and tangible ecological implications. By teaching students about microclimate, we enrich their understanding of the natural world and empower students to comprehend why it appears as it does.

The Activity

Materials

•Students will require a map of the outdoor classroom. A simple hand drawn map will work, but ideally, all students should have the exact same map. Using the same map will make it easier when the students combine their data. (If GPS equipment and software is available, this could replace a hand drawn map and could possibly be a great extension to this inquiry.)

•Students need a data sheet that includes a column for plant type, temperature, relative humidity, wind speed, light availability, etc. The exact parameters will depend on the equipment available and the interest of the class.

•If students are interested in looking at the influence of microclimate on specific species, a book of local flora is necessary to help students identify plants.

•To measure microclimate conditions students will require specific equipment, such as a thermometer (temperature), hygrometer (relative humidity), anemometer (wind speed), or photometer (light intensity). Instruments that give instantaneous digital readings are the best because they take less time, and are easier for students to use. Any instrument that will measure relative humidity will also measure temperature and therefore, is ideal for this inquiry (i.e. Testo 625, by GmbH & Co.).

• Students will also require a clipboard, pencil, and set of colored pencils or markers.

Time Required

Successful completion of this inquiry requires roughly two 1-hour class periods. Teachers require time to establish the ecological foundation of this exercise and to introduce students to the vocabulary necessary to understand the inquiry. Students require time to gather measurements, compile data, make microclimate maps, and develop predictions about plant distributions.

Primary Learning Goals and Objectives

This lesson challenges students' understanding of weather and climate, specifically, how climate may influence the distribution of plants globally and locally. Although most students are aware of local weather, their understanding of climate is typically less clear, especially the notion that climate can vary at small spatial scales. Our goal is to educate students about the differences between weather and climate and

enlighten them on the degree of natural variation in climate that exists across spatial scales. Once students understand climate, and how it varies, they are going to explore the natural variation in microclimate throughout the outdoor classroom. By having students measure microclimate at different plant types, they can begin to see how microclimate may effect where plants grow.

This curriculum is designed to address National Science Standards A (Science as Inquiry) and C (Life Sciences) by examining how variation in abiotic factors can lead to variation in the distribution of the plants. Students will observe and measure variation in microclimate and plant distribution and use this information to identify correlations between the two. Ultimately, students will use this information to generate predictions about the distribution of different plant types beyond where they sampled.

Introduction to the Activity

Begin the lesson by introducing the basic concepts needed to successfully understand and measure microclimate. Introducing the vocabulary may represent a significant time investment for the educator (Table 1) because much of the vocabulary is new for many students. Because the interest of this lesson is in teaching students through inquiry introducing concepts through open questioning may be the best approach. Starting with concepts that students understand, such as weather can facilitate this process.

Introduce the concept of climate, by having students describe current weather conditions and what they think are the components of weather (i.e. temperature, rain, wind, snow, etc.). Then ask students to consider general trends in weather at different

locations around the world (i.e. tropics versus polar). Use this question to help students define climate and distinguish it from weather. Many students will have difficulty distinguishing between weather and climate. A sports team can be a useful analogy for helping students to understand the differences. For example, if a basketball team wins twelve games then loses a game, is the basketball team a poor team? In this analogy, each game is like a day's weather event, and the team's win-loss record is like an area's climate. So, in the same way that a good team can lose a game but still be a good team, rain can fall in a desert but a desert is still a dry place.

Once students have grasped the concept of climate have them talk about the different climates of the world and their associated plant types (i.e. cactus in a deserts, rainforests in the tropics). As a result, students are introduced to the notion that the climate of an area can determine the plants found in that area. To ensure that students fully understand this relationship, talk about local features that they have experienced. In particular, differences between plant communities on north versus south facing slopes, or on valley floors versus mountainsides, are tangible concepts for students to visualize. After students appear to understand that climate is highly variable and that it can explain variation in plant communities, ask them if there is variation in climate in their outdoor classroom or their backyard. If they fail to recognize different microclimates in their schoolyard, ask them questions that will help them understand what they surely already know. Where is the best place in the outdoor classroom to warm up on cold mornings? Is that the same place to cool off on a hot afternoon? After a few questions like these, students will soon realize that even in their outdoor classroom there are distinct areas with different climates. Finally, ask the students if they think the small differences in

climate that they have felt in the outdoor classroom could lead to areas having different plant assemblages. They will address this question in the following lesson.

Procedure

1. Break students into groups, and give each group a data sheet and the appropriate instruments to measure the microclimate variables of interest.
2. Have students consider where different plant types grow (i.e. deciduous tree, shrub, grass, forb, coniferous tree) and what the microclimate might be in those areas. Depending on the level of the class and their understanding of local plants, students can make predictions about the microclimates for different plant types.
3. Take students outside and instruct them to find 4-6 of each plant type and take microclimate measurements at the base of the plant. All groups should take measurements at nearly the same height for all samples because height can influence microclimate measurements. Students can inflate error if they are not consistent in where they take measurements and make patterns more difficult to assess.
4. Students should record microclimate readings on their data sheet, and they should record an associated numbered location on the map for each set of measurements.

Data Analysis

Once students have gathered all of the data, each group transfers their data to the blackboard or overhead along with the number signifying its location on their map. This enables the entire class to have access to all of the data and its associated location. Have students calculate a class average for each of the microclimate measurements as well as

averages for each plant type. Simultaneously, supply all members of the class with one map of the outdoor classroom for each microclimate variable measured. Have students record the positions of all the sampling points from each group on their individual maps. Now using the class data and these maps, students can create microclimate maps for the outdoor classroom. For example, if students are going to create a temperature map for the outdoor classroom they must first replace the sampling point numbers on their maps with the appropriate temperature measured at that position. To simplify, round measurements to the nearest whole number and in some cases to the nearest 5 or 10 place. Once all of the measurements are on the map, students can use these points to create their own isocline map of the outdoor classroom. An isocline map is similar to a topographic map, but shows patterns of temperature rather than elevation. To create an isocline map draw colored lines between points with the same temperature, each temperature receiving its own color. Ultimately, students will create a map consisting of a series of circles indicating different temperatures (Fig. 1), although some circles may be incomplete as part of the circle lies off the map. Importantly, no lines of different colors can cross, as this would indicate that a point had two different temperatures. There are, however, few additional rules to creating an isocline maps, though students should attempt to create the simplest map possible (i.e. fewest number of circles). Students should feel free to be creative in designing their maps; there is no 'right' answer.

Discussion

One of the most difficult concepts for students to grasp is how much variation exists in the natural world, particularly for concepts they are unfamiliar with such as

climate. Students can fail to comprehend broad climatic differences because they have never experienced them, and they can overlook local variation because it is commonplace. By introducing climate at a global scale and ending by measuring small differences in microclimate, students become acutely aware of the degree of variation present in the natural world. To ensure that students understand how variable climate can be in a natural environment, have them consider the variation in temperature readings obtained by the class compared to the variation in the temperatures between their respective homes.

From this example, students can also see that the microclimate they occupy in their home is not readily available across the landscape, especially true on a cold winter day. Plants are also limited in the areas they can occupy based on the microclimates that exist across the landscape. Different plants have different requirements (i.e. water, light availability, etc.), which influences where they can effectively germinate and grow. Have the students consider the 'preferred' microclimates of the different plant types. Graphing the means and extremes for each plant type is an effective method of showing students the extent that different plants overlap in microclimate or if they 'prefer' different microclimates (Fig. 2). Depending on the area sampled, students may or may not find any differences among the different plant types in 'preferred' microclimate, but most likely, they will find that some plants differ from one another. Have the students consider why some plants occur in a variety of microclimates (generalists) while others appear more limited in where they occur (specialist).

Finally, once students have assessed the variation in microclimate and which microclimates different plants 'prefer', challenge students to use what they know to make

predictions about the distribution of different plant types beyond where they sampled (Table 2). Having students make predictions beyond where they sampled gives them the opportunity to assimilate all the information they have gathered and to use it in much the same way a research scientist might.

Assessment Strategy

Teachers should assess students based on their understanding of the content and the skills they developed to perform this lesson. Students must demonstrate a number of scientific skills (i.e. mathematical and graphical skills, attention to detail, and creativity) that educators can assess either formally or informally. A student's understanding of the content of this exercise can be evaluated by their ability to answer simple questions about the 'preferred' habitats of different plant types or the variation in microclimates. Ultimately, the student's ability to integrate all of the information they have gathered and make predictions beyond what they have see that will truly demonstrate their level of understanding.

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Table 1: Vocabulary

Weather	The state of the atmosphere at a given time and place, with respect to variables such as temperature, moisture, wind velocity, and barometric pressure
Climate	The weather conditions, including temperature, precipitation, and wind, that prevail in a particular region
Microclimate	The climate of a small, specific place within an area as contrasted with the climate of the entire area
Temperature	The degree of hotness or coldness of a body or environment
Relative Humidity	The ratio of water vapor in the air at a specific temperature to the maximum amount that the air could hold at that temperature, expressed as a percentage
Biodiversity	The number and variety of organisms found within a specified geographic region
Generalist	a species that can exploit a wide range of resources
Specialist	a species with specific resource requirements
Biotic	Produced or caused by living organisms
Abiotic	Factors affecting the environment produced or caused by nonliving influences, such as light, temperature, and wind

Table 2: Possible Discussion Questions

1. What were the highest and lowest temperatures (humidity, wind speed, light availability, etc.) for each plant type?

2. Which plant type, on average, lived in the coldest/warmest area (wettest, windiest, etc.)?

3. Do plants appear to differ in the microclimate they inhabit? If so, why do you think different plants might occur where they do (think about the biology of the plants)? If not, why not?

4. What are the potential sources of bias and/or error in the microclimate measurements that we measured?

5. We said that microclimate is an abiotic factor that can influence where a plant grows. Can biotic factors influence microclimate? For example, can plants or animals influence their local microclimate or the microclimate of other organisms (think about shade)?

6. Based on the graphs we made showing the mean and extreme microclimates for each plant type, which plant type do you think might be a generalist or a specialist?

7. Using the available data and the microclimate maps, how could you predict the distribution of plants in the outdoor classroom beyond where we measured?

8. Based on what we know about the different plant types and looking at your microclimate maps, which plant types would you expect to be the most common or rare?

Figure Legends

Figure 1 | Examples of two isocline maps based on the same data. Students should be encouraged to be creative when interpreting the data as there is no 'correct' answer. However, for these examples map **(b)** is more parsimonious than map **(a)** because it requires fewer separate circles. Students should consider this when developing their maps and attempt to make the simplest map possible.

Figure 2 | Example plot of temperature extremes for different plant types. By plotting the extreme values for the different plant types, students can quickly see the extent to which different plants are found in the same microclimate.

Figure 1

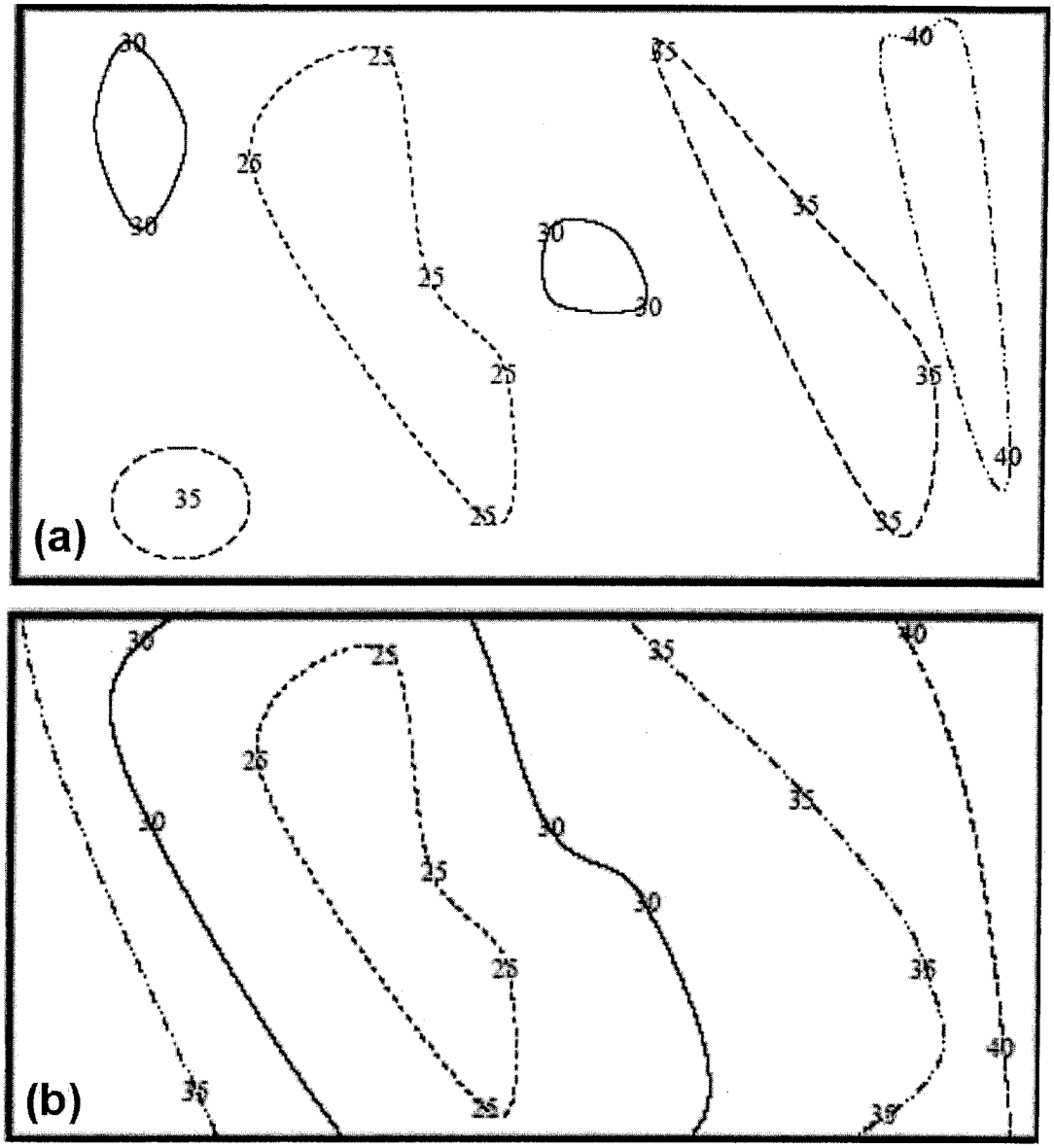

Figure 2