

THE ROLES OF FOOD AND PREDATION IN SHAPING ADAPTIVE
AND MALADAPTIVE BEHAVIORS IN POSTFIRE BIRD SPECIES

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`But by far the most important consideration is that the chief part of the organization of every being is simply due to inheritance; and consequently, though each being assuredly is well fitted for its place in nature, many structures now have no direct relation to the habits of life of each species'.

--Origin of Species: The Preservation of Favored Races in the Struggle for Life

Charles Darwin, 1859

The roles of food and predation in shaping adaptive and maladaptive behaviors in postfire bird species

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Abstract:

Most animals live in rapidly changing environments, and within-individual phenotypic plasticity can allow populations to track sources of selection that often vary dramatically in time and space. However, if conditions change too rapidly, the cues animals use to track environmental changes may become uncoupled from the ultimately important factors with which they have been historically correlated. Animals relying upon proximal cues to guide their behaviors may, in novel environments, consistently make errors. When these errors occur within the context of choosing a habitat, the organism is said to be caught in an ‘ecological trap’.

Herein, I develop a conceptual model to explain how an ecological trap might work, outline the specific criteria that are necessary for demonstrating the existence of an ecological trap, and provide tools for researchers to use in detecting ecological traps. I then review the existing literature and summarize the state of empirical evidence for the existence of traps. My conceptual model suggests that there are two basic kinds of ecological traps and three mechanisms by which traps may be created. To this point in time, there are still only a few solid empirical examples of ecological traps in the published literature, although those examples suggest that both types of traps and all three of the predicted mechanisms do exist in nature. Next I examine habitat selection behavior and nest success of Olive-sided Flycatchers (*Contopus cooperi*) in naturally occurring burned forest and in an anthropogenically created habitat type—a selectively harvested forest. I show that Olive-sided Flycatchers preferred to settle in the selectively harvested forest despite the fact that estimated nest success in that habitat was roughly half that found in naturally burned forest. These results are consistent with the hypothesis that selectively harvested forest can act as an “ecological trap” by attracting Olive-sided Flycatchers to a poor-quality habitat type.

Natural disturbances, such as wildfire, are important ecological processes in that they alter habitat structure and resource availability. I used the dramatic temporal and spatial variation in microclimatic conditions generated by variation in wildfire severity to examine the microclimatic consequences of nest site preferences and the fitness costs to parents and offspring in the Dark-eyed Junco (*Junco hyemalis*). Adults preferred to select nest sites with the most moderate microclimates. Nestlings reared in colder nest sites gained mass more slowly and experienced retarded skeletal growth while parents suffered costs associated with hot microclimates; incubating females reduced their nest attentiveness and doubled their nestling provisioning rate at hot nest sites. Nest site preference in junco appear to be an adaptive consequence of the costs of hot nest sites to parents and the costs of overly cool climates to developing young.

Resource levels have been widely recognized to change over time as organisms recover from fire damage or recolonize a site after a wildfire. I report on the importance

of food limitation versus nest predation on the expression of plastic life-history traits in Dark-eyed Junco (*Junco hyemalis*). Junco clutch size was primarily determined by habitat-specific and seasonal changes in food availability, while nest predation risk shaped egg laying decisions when food was extremely limited. Conversely, nestling growth rates were primarily determined by habitat-specific, seasonal changes in nest predation risk, but were mediated by food availability. Results illustrate that food is more important than environmental risk of nest predation in shaping the expression of clutch size. Overall, results demonstrate the birds assess and respond to variation in nest predation risk and food availability at fine temporal and spatial scales, and that that both factors play an important role in the expression of avian reproductive strategies.

PREFACE

My years at The University of Montana have been years of tremendous personal and professional growth. In some ways, a more profound understanding of one's arc of discovery can only come after years of personal reflection. Still, it is clear that learning to think rigorously has been fundamentally formative to who I have become. In a sense, the most important lesson that I have learned is that doggedly pursuing a personal goal is among the most difficult and frustrating, yet rewarding of experiences one can have.

Many brilliant and generous people have given their time to help me throughout my years here at the University. First of all, I am grateful to my advisor, Dick Hutto for giving me a chance. He saw something in me that I hadn't yet seen in myself. Perhaps the most fundamental idea he imparted was an appreciation of the role of creativity in science. In teaching me to think through complex scientific problems Dick has had a fundamental influence on my development as a scientist, for which I am deeply grateful. His steady and patient personality was centering.

I don't even know how to begin to thank all of my fellow graduate students. They challenged me scientifically, exposed me to new and interesting ideas, yanked me away to far away places when school consumed me, and became friends without whom I could never have survived. Rob Fletcher, T.J. Fontaine, Christine Miller, Anna Chalfoun, Dan Barton, Brian Schwartz, Jose Hierro, Kristina Ramstad, Andrea Thorpe, and Karen Short all had a strong influence on my scientific development. Your comments and suggestions at my practice talks saved me from public embarrassment at scientific meetings and your genuine fascination for nature inspired creativity and fueled my persistence. You are the most fascinating and extraordinary people I have ever met. Learning to escape the rigors

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Finally, I would like to thank my family. I am humbled by your generosity. Thank you to Ron and Kathy Nomura who gifted me your love of the wild. Most importantly, I want to thank my parents for taking me hiking and camping as a kid, for making sure I always watched “Nature” and “Nova” and for providing the kind of love and support that allowed me the precious chance to follow my dreams.

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INTRODUCTION

The study of phenotypic adaptation and its genetic basis is a central theme of evolutionary biology. The term “adaptation” has accumulated myriad definitions (reviewed in Reeve & Sherman, 1993) but it is uniformly accepted that adaptations are traits that are always construed to be the result of natural selection. However, the fit of traits to environments implied in the term adaptation can never be perfect, in part because organisms are always adapted to at least one generation in the past. Thus, some degree of deviation from the maximal possible degree of adaptation is always expected even in the most evolutionarily labile of traits (e.g., behavior). Rapid environmental change, in particular, has the strong potential to reduce the fitness of organisms within their environment (Levins 1968). Yet, most animals live in rapidly changing environments (Endler 1986) and within-individual phenotypic plasticity can allow populations to track sources of selection that often vary dramatically in time and space via (Via 1993).

The broad goal of the chapters herein is to explore these contrasting perspectives by examining the adaptive and maladaptive nature of organismal responses to natural and anthropogenic disturbances of native habitats. The first paper (Chapter 1) entitled “A framework for understanding ecological traps and an evaluation of existing evidence” examines the phenomenon of maladaptive habitat selection from first principles by: (1) developing a conceptual framework for understanding the mechanistic basis for ecological traps, and (2) examining the empirical evidence for the existence of ecological traps. The second paper (Chapter 2) entitled “Is selectively harvested forest an ecological trap for Olive-sided Flycatcher” documents the existence of an ecological trap for a migratory bird species triggered by a novel forest management technique.

The third paper (Chapter 3) entitled “Avian nest preference and fitness consequences of nest microclimate” examines how the dramatic spatial and temporal variation in forest structure influences ground temperatures and, in turn, microclimatic conditions surrounding bird nests. Physiological costs to parents and young associated with microclimatic variation can shape the evolution of preferences for nest sites with favourable microclimates. The final paper (Chapter 4) entitled “Plastic expression of avian reproductive life-history traits: the importance of food vs. predation” uses a natural experiment generated by the passage of wildfire to ask whether food availability or nest predation risk is more important in shaping plastic reproductive life-history traits. It should be noted that these chapters are loosely linked by broad conceptual ideas in ecology and evolution and by the biological system in which they are tested, and not as much by their attempt to answer closely related questions. Consequently, they are best evaluated independently and on the merits of their ability to answer the specific questions they pose¹.

¹ references cited in the Introduction are included in the Literature Cited section of Chapter I

CHAPTER I

A FRAMEWORK FOR UNDERSTANDING ECOLOGICAL TRAPS AND AN EVALUATION OF EXISTING EVIDENCE

ABSTRACT

When an animal settles preferentially in a habitat within which it does poorly relative to other available habitats, it is said to have been caught in an “ecological trap.” Although the theoretical possibility that animals may be so trapped is widely recognized, the absence of a clear mechanistic understanding of what constitutes a trap means that much of the literature cited as support for the idea may be weak at best. Here, we develop a conceptual model to explain how an ecological trap might work, outline the specific criteria that are necessary for demonstrating the existence of an ecological trap, and provide tools for researchers to use in detecting ecological traps. We then review the existing literature and summarize the state of empirical evidence for the existence of traps. Our conceptual model suggests that there are two basic kinds of ecological traps and three mechanisms by which traps may be created. To this point in time, there are still only a few solid empirical examples of ecological traps in the published literature, although those examples suggest that both types of traps and all three of the predicted mechanisms do exist in nature. Therefore, ecological traps are either rare in nature, are difficult to detect, or both. An improved library of empirical studies will be essential if we are to develop a more synthetic understanding of the mechanisms that can trigger maladaptive behavior in general and the specific conditions under which ecological traps might occur.

INTRODUCTION

Animals choose (consciously or not) among options related to all aspects of their lives (e.g., food types, mates, territory locations). Habitat choice is a consequence of natural selection having favored individuals that recognize, are attracted to, and preferentially settle in, the best available habitat (Fretwell and Lucas 1970). Cues used as a basis for choice (e.g., tail length, tree density) are usually at least one step removed from the ultimate reason that the choice has been favored by natural selection (Tinbergen 1963, Sherman 1988). This is because an animal cannot always know the consequences of a choice at the time a choice needs to be made. In terms of habitat selection behavior, where an animal makes a choice about where to live, that choice may affect the individual's survival and reproductive success at some later point in time but, again, the ultimate factors that determine success may not be evident at the time the choice has to be made (Hutto 1985).

Because animals must assess the suitability of habitats indirectly, it is possible for the attractiveness of a habitat to become uncoupled from its suitability for survival and reproduction, such that lower quality habitats may be as attractive as, or even more attractive (i.e., more likely to elicit settling and reproduction) than, higher quality habitats. This can happen when animals whose behaviors have been shaped by exposure to one set of conditions are suddenly confronted by novel or very different conditions (Levins 1968). For example, sea turtle hatchlings normally rely on light cues from the open horizon to orient and migrate toward the ocean after emerging from the nest at night. However, light pollution from beachfront structures can cue hatchlings to migrate inland instead, where their survival is unlikely (Witherington 1997).

The most extreme situation, where a poor habitat becomes relatively attractive, thus “baiting” individuals to settle, has been termed an “ecological trap” (Dwernychuk and Boag 1972, Gates and Gysel 1978). An ecological trap is a scenario that occurs when sudden environmental change (e.g., brood parasitism, predation, pesticide use, human disturbance) acts to uncouple the cues that individuals use to assess habitat quality from the true quality of the environment (Dwernychuk and Boag 1972, Gates and Gysel 1978). An animal’s preference remains unchanged, but the positive outcome normally associated with a given cue is now a negative outcome (Misenhelter and Rotenberry 2000). The potential for being deceived is precisely why mimicry, brood parasitism, and a host of other behavioral phenomena are possible.

The mechanism that underlies an ecological trap is more broadly applicable. Organisms rely on environmental cues to make a variety of behavioral and life-history ‘decisions,’ such as when to migrate, when to reproduce, with whom to mate, how many young to bear, and what to eat. Schlaepfer et al. (2002) coin the term “evolutionary trap” to describe this broader set of situations in which use of a formerly reliable behavioral cue has become maladaptive because of a sudden anthropogenic disruption. Note that all evolutionary traps, including ecological traps, involve the behaviors of individual organisms. Thus, in contrast with some definitions of ecological traps (e.g., Battin 2004), we wish to emphasize here that an ecological trap is a behavioral, not a population phenomenon.

Now widely recognized as a theoretical possibility within academic circles, the concept of an ecological trap represents a bridging of the disciplines of evolutionary biology and cognitive ecology. As a potentially new mechanism explaining widespread

population declines of native species, the ecological trap concept has also garnered a great deal of attention from conservation interests. Even so, and even though the concept of an ecological trap was first described more than a quarter-century ago (Gates and Gysel 1978), the extent to which ecological traps operate in the world is still unclear. In addition, the current mechanistic framework developed to elucidate the possible processes that might create ecological traps (Schlaepfer et al. 2002) is not sufficient to describe the full range of interactions between cue sets and ultimately important factors that can trigger ecological traps.

The purpose of this paper is to (1) develop a conceptual framework within which the concept of an ecological trap can be better understood, (2) present the criteria that are essential if one is to demonstrate the existence of an ecological trap, (3) use existing literature to evaluate the empirical evidence for the existence of ecological traps, and (4) discuss the implications of our literature review.

A conceptual model for an ecological trap

An ecological trap is likely to arise for one of three reasons, which differ slightly from the two avenues described by Schlaepfer et al. (2002). Each results from decoupling the attractiveness of, and the suitability in, the altered habitat. First, an ecological trap will arise if the settlement cues normally used by an individual change in intensity, type, or number such that the habitat becomes more attractive while habitat suitability remains unchanged (the settlement cues have changed, but not the ultimate factors). The second way in which a trap is likely to arise is if the environment of the organism is altered in such a way that, although the original cue(s) that elicits a settling response is unaltered,

the quality of the habitat has decreased (the ultimate factors have changed, but the settling cues have not). Thirdly, alterations to a habitat may alter the settlement cues, causing an increase in the attractiveness of the habitat, while reducing the suitability of the habitat for survival and/or reproduction (both settlement cues and ultimately important factors change). Thus, habitat alteration capable of creating an ecological trap must (1) alter the cue set (increasing its attractiveness), (2) decrease the suitability of a habitat, or (3) do both simultaneously.

To illustrate these alternatives more fully, consider four scenarios: in scenario A, suppose that the density of shrubs is the primary cue an organism uses to assess habitat quality, and that shrub density in an area of sparse shrub cover is artificially increased to normal levels through a restoration planting program. If the perceived value of this habitat (Habitat A) is now greater than its actual suitability, and if the cue stimulus value is now similar to that of a second habitat (Habitat B), which is normally of higher quality, both habitats would appear equally attractive to the animal, and, unable to distinguish a difference in suitability between Habitat A and B, the animal would be equally likely to settle in each despite the fact that Habitat A is of lower quality. This kind of scenario would lead to what we call an equal-preference trap.

In scenario B, suppose the primary cue (shrub density) is artificially increased in value to a supernormal level (so that it serves, in effect, as a “supernormal releaser”). Habitat A would now appear to be even more attractive than Habitat B, and an animal choosing between Habitat A and B would select Habitat A. Thus, it would prefer (be more likely to settle in) the lower quality habitat. At a population level, scenario B would probably have more severe demographic consequences than the equal-preference trap

represented by scenario A because animals would actually be drawn away from the higher quality habitat (Habitat B) as a result of their preference for the lower quality habitat (Habitat A). This kind of scenario, in which animals actively prefer the lower quality habitat, would lead to what we call a “severe trap.”

In scenario C, suppose a portion of Habitat A is altered such that the inherent suitability is reduced, while the settlement cues remain unaltered. For example, suppose that an insectivorous bird species chooses to settle on the basis of the appearance of fresh green vegetation. Next, suppose that forest managers spray an area for insects so that two options exist for an insectivorous bird—one where insect densities available later in the season are well correlated the amount of fresh green vegetation (unaltered Habitat A) and another where that correspondence has been severed due to spraying (altered Habitat A). An animal choosing between the two habitats would be equally likely to settle in both, illustrating how a change in the suitability of a patch of highly attractive habitat in the absence of a change in settling cues can result in an equal-preference trap.

Scenario D is similar to scenario C in that a portion of Habitat A is reduced in suitability, but in this scenario, there is also a simultaneous increase in the value of a settlement cue. Hypothetically, suppose that the particular chemical spray used by forest managers also makes the vegetation glisten so that it appears to be fresher and greener than normal. Habitat A is now perceived as having a “very high” attractiveness even though it has a “low” suitability. An animal choosing between unaltered Habitats A and altered Habitat A would prefer the altered habitat despite the fact that it is poorer in quality. The simultaneous reduction in suitability and increase in attractiveness results in

the creation of a severe trap where animals will be actively drawn away from high-quality habitat by the strong attractiveness of the low-quality habitat.

Two important results emerge from this conceptual model. First, there are two quantitatively different types of ecological traps—severe and equal-preference traps. Second, traps can occur via three mechanisms: (1) an increase in the attractiveness of a habitat in the absence of a change in its suitability, (2) a reduction in habitat suitability without a loss in attractiveness, or (3) a simultaneous increase in the attractiveness and reduction in suitability of a habitat.

The model also suggests that to demonstrate an ecological trap actually exists, the following lines of evidence are required: (1) individuals should have exhibited a preference for one habitat over another (in a severe trap) or an equal-preference for both habitats (in an equal-preference trap); (2) a reasonable surrogate measure of individual fitness should have differed among habitats; and (3) the fitness outcome for individuals settling in the preferred habitat or equally-preferred habitat (depending on the kind of trap, as described in the conceptual model above) must have been lower than the fitness attained in other available habitats. In other words, individuals cannot experience the greatest fitness consequences from settling in the preferred habitat. While, a study illustrating that changes in a particular cue(s) and/or ultimate factor(s) are causal in triggering an ecological trap are more compelling in that they provide a mechanistic explanation for the trap, simply fulfilling the three criteria is sufficient to illustrate the existence of an ecological trap. Using a strict application of these three criteria, we examine the empirical evidence for the existence of ecological traps and attempt to understand which mechanisms are most likely to result in ecological traps.

METHODS

We examined peer-reviewed articles in which there was supporting evidence for the existence of an ecological trap. A search of the literature was conducted using the Ingenta, BIOSIS, Biological Abstracts, AGRICOLA, and Wildlife and Ecology Studies Worldwide databases from 1969 to 2005. We initially confined our search to the terms “ecological trap,” “evolutionary trap,” and “maladaptive.” The bibliographies of published papers captured in this search were also examined for the identification of other relevant studies. Therefore, many references were initially located because they had been cited as examples of ecological traps by other authors.

We evaluated all references to determine if they met the three criteria necessary to demonstrate the existence of an ecological trap. With respect to the first criterion, it is important to note that the demonstration of habitat preference is not the same thing as the demonstration of nonrandom habitat use or of differences in density among habitats (Van Horne 1983). While relatively high densities of individuals in a habitat may suggest a preference for that habitat, such a pattern may result, for example, when individuals are displaced from preferred habitat by dominant individuals (Sherry and Holmes 1988). There are a multitude of situations in which density of individuals in a habitat might not be positively correlated with a preference for that habitat (summarized in Railsback et al. 2003). As such, we do not consider density to be a reliable surrogate measure of habitat preference. Furthermore, the term “habitat preference” is not a synonym for “habitat use” or “habitat selection.” These terms have very different meanings even though they are frequently used interchangeably. We define preference here as “the likelihood of a

resource being chosen if offered as an option, on an equal basis, with others (Johnson 1980).” In other words, individuals must not be physically impeded in selecting a particular option or it cannot be concluded that the option that is more likely to be selected is the preferred one. Moreover, the presence of conspecifics or predators in a habitat are factors that may contribute to the evolution of habitat preference, but don’t necessarily prevent individuals from making choices. Because habitat selection is defined as the process of choosing a habitat in which to settle, presumably based on innate or learned preferences, preference cannot be demonstrated without observing the process of habitat selection by individuals directly or by observing some necessary consequence of that process.

Based on the formal definition above, preference can be measured most reliably by observing the behavioral decisions of individuals or by inferring preference from patterns in time and space that necessarily result from this behavior. We can envision five possible ways to assess whether an organism actually prefers one habitat over another, and we suggest that multiple lines of evidence would provide the clearest case for the existence of habitat preference:

1. Settlement patterns—Migratory taxa, such as many insects and birds, make excellent study species to test the ecological trap hypothesis because they colonize breeding habitat anew each year, making it possible to observe the behavioral process of habitat selection and to infer preference from settlement patterns (Krebs 1971). Thus, arrival time should be an accurate index of preference and, assuming that numerous individuals respond similarly to a given set of environmental cues, the average arrival

date among males within one habitat type should represent a preference ranking relative to other habitat types (e.g. Székely 1992, Remeš 2003, Sergio and Newton 2003).

2. *Distribution of dominant individuals*—In some species there may be a clear dominance hierarchy. Under conditions in which there is competition for resources within a habitat, preference may also be inferred from the distribution of dominant individuals among habitat types (e.g., Davies 1992). Whatever settlement model applies to a species, the most dominant individuals should be found disproportionately often within the preferred habitat type.

3. *Site fidelity*—Habitat selection theory predicts, and empirical evidence illustrates (e.g., Sergio and Newton 2003), that individuals claiming territories in a preferred habitat will have the greatest site fidelity and the lowest rates of emigration. Conversely, individuals in less-preferred habitats will relocate to claim territories in the preferred habitat when they become available (e.g. Weldon and Haddad 2005). Habitats can be ranked in order of preference, where more preferred habitats should be occupied by individuals with higher site-fidelity and lower emigration rates.

4. *Temporal variance in population size*—There should be large year-to-year changes in animal numbers in sites perceived as poor-quality habitats, but only small changes in those perceived as high-quality habitats. Hence, population density in good sites should be “buffered” by population density variation in poor sites (Kluwer and Tinbergen 1953, Brown 1969). Hence, less preferred habitats will be occupied only during years or time periods when populations are high and individuals are forced to settle in habitats they perceive as poor quality; conversely, population densities in preferred habitat types should be relatively stable (O’Connor 1981, Gill et al. 2001).

Researchers can rank the relative preference with the more preferred habitats having the least variance in use among years and the less preferred habitats having the greatest variance.

5. *Choice experiments*—Cues that animals use for habitat choice, and their relative preference for different cue sets, can be determined using an experimental approach in a laboratory or semi-natural setting (e.g., Roberts and Weigl 1984, Kriska et al. 1998). However, because individuals normally face multiple constraints (e.g., competition from other individuals) laboratory settings may not recreate the full range of cue types and strengths an individual would experience in a natural setting (but see Brown 1988).

The first four methods of measuring preference are field-based and, alone, may not unequivocally establish preference due to potential confounding factors. For example, early arrival may not be correlated with habitat preference if there are alternative habitat selection strategies in a population (for example among age-classes or morphs). Moreover, changes in territory use from one year to the next could conceivably reflect changing physiological needs rather than preference. Still, several correlated lines of evidence for habitat preference can provide greater certainty that preference is being accurately assessed. Experimental (lab or field-based) approaches to measuring preference are suggested where they are feasible.

To better assess the strength of evidence provided by authors, we also looked at whether the experimental units were replicated and whether treatments were randomly assigned. We considered individual animals or their territories to be samples within each habitat type. Comparative or experimental studies in which there was only one study plot

per habitat type were considered unreplicated. Among studies that met all 3 criteria, replicated studies were considered to provide “strong” evidence for the existence of an ecological trap while unreplicated studies were considered to provide “weak” evidence. \

RESULTS AND DISCUSSION

Empirical evidence for the existence of ecological traps

We found 45 peer-reviewed papers (Table 1) in which the authors claimed that their research constituted evidence of an ecological trap or in which other papers were cited as presenting such evidence. Because many of the studies were not designed to test for the existence of an ecological trap, a failure to satisfy our three criteria for demonstrating the presence of an ecological trap does not necessarily reflect a lack of quality in the study. Of the papers we reviewed, 27 (60%) were replicated, but only two included randomization (Horváth et al. 1998, Kriska et al. 1998). In a few instances replication was impossible due to the nature of the experiment, but overall it is unclear why many researchers did not choose to replicate.

Criterion 1: Measuring Preference.—The authors of only 8 (18%) of the 45 studies we reviewed provided at least one reasonable measure of preference. Three used the mean arrival date of migratory birds in different habitat types to rank habitats in terms of perceived quality (Székely 1992, Remeš 2003, Lloyd and Martin 2005). Four studies used experimental methods to account for the availability of resources and then showed that one resource was chosen preferentially over another when both resources were equally available (Chew 1980, Horváth et al. 1998, Kriska et al. 1998, Pöysä et al. 1999). Finally, Weldon and Haddad (2005) used the relative age-class distribution and site-

fidelity of territorial males to rank habitats in terms of perceived quality. Among studies that failed to meet the first criterion, the density of nests, breeding territories or individuals was relied upon or inferred to be an appropriate index of preference in 18 (40%) of the reviewed studies. In addition, a total of 6 (13%) of the 45 studies that we considered relied upon use-availability models to infer habitat preference based on non-random use (Mundy 1983, Johnson and Temple 1986, Boal and Mannan 1988, Crabtree et al. 1989, Misenhelter and Rotenberry 2000, Kolbe and Janzen 2002).

Five studies employing artificial nest experiments were designed to test the ecological trap hypothesis or were cited as doing so (Yahner and Wright 1985, Angelstam 1986, Ratti and Reese 1988, Pasitschniak-Arts and Messier 1995 Carignan and Villard 2002). These studies were primarily designed to assess the potential reproductive outcome of nest placement through the estimation of predation rates on artificial bird nests. Even if the placement of artificial nests were a good estimate of the placement of natural nests, and even if predation rates upon these nests were similar to those of natural nests, there is no way of knowing which locations a hypothetical bird might have perceived as superior or inferior. In the absence of an individual, the adaptive value of a behavior cannot be evaluated because there can be no measure of individual preference. For this reason alone, an artificial nest experiment cannot demonstrate the existence of an ecological trap.

Criterion 2: Fitness of individuals varies by habitat.—In terms of fitness, only one study obtained estimates of both adult survival and reproductive success (Thomas et al. 1996). Most authors opted to estimate either survival only (6 of 45, or 13%) or reproductive success only (27 of 45, or 60%). Six papers provided no estimates of

survival or reproduction. It is unclear to what extent artificial nest experiments reflect actual nest survival rates (Paton 1994).

Criterion 3: The animal has equal or lower fitness in the preferred habitat.—

Only five of the reviewed papers contained the data necessary to meet this criterion (Horváth et al. 1998, Kriska et al. 1998, Remeš 2003, Lloyd and Martin 2005, Weldon and Haddad 2005).

In summary, according to the criteria that we propose, only five studies have yet established existence of an ecological trap. Evidence is considered “strong” in the three replicated studies (Horváth et al. 1998, Kriska et al. 1998, Weldon and Haddad 2005) and “weak” in the 2 unreplicated studies (Remeš 2003, Lloyd and Martin 2005).

The strongest support comes from two experimental studies of habitat selection in insects belonging to the order Odonata. Orientation to polarized sources of light (polarotaxis) is the most important mechanism that guides dragonflies and mayflies during in their search for a suitable habitat or site for oviposition (Kriska et al. 1998, Horváth and Zeil 1996). Kriska et al. (1998) used experimental methods in the field to show that some types of asphalt also polarize light horizontally and that because of the relatively homogenous distribution of the degree and direction of polarization reflected from asphalt roads, roads can actually be much more attractive to mayflies than the surface of a pond or stream. In this way, Kriska et al. (1998) demonstrate that some types of asphalt act as a supernormal stimulus for water-seeking mayflies in comparison with the light reflected from water. In this instance, natural habitat is not altered, but a novel element is introduced, and it happens to mimic a traditional cue for habitat choice. As a result, mayflies lay their eggs on an inappropriate substrate where they are unable to

hatch successfully; therefore, complete mortality of the clutch results. There is little question that asphalt is an ecological trap for mayflies. Kriska et al. (1998) appear to document a severe trap of the type described in scenario B—a supernormal cue has emerged from asphalt blacktop, which is an otherwise inappropriate, low-quality habitat.

Similarly, dragonflies (Anisoptera) and damselflies (Zygoptera) are highly attracted to the horizontally polarized light given off by crude oil slicks such as the lakes of oil that resulted from the destruction of oil pipelines during the Gulf War (Horváth and Zeil 1996). Dragonflies are preferentially attracted to crude and waste oil even when suitable sources of water are available nearby. Once insects land on the surface of the oil they are caught and eventually die (Horváth et al. 1998). Thus, waste oil slicks also act as supernormal stimuli for habitat selection behavior in water-seeking insects and appear to fit our description of a severe trap of the type described in scenario B.

Weldon and Haddad (2005) provide strong evidence that artificial forest edges can act as ecological traps for Indigo Buntings (*Passerina cyanea*). Buntings are highly attracted forest edges and have historically relied upon natural disturbance to create suitable early-successional habitat that was frequently disturbed and supported relatively low predator populations (Suarez et al. 1997). Weldon and Haddad (2005) show that experimentally created habitat patches with greater amounts of forest edge attracted older territorial males that exhibit greater interannual site-fidelity compared to patches with less forest edge. In addition, birds that nested closer to edges and in patches with more edge had lower annual reproductive success, presumably because anthropogenic edges are highly attractive to nest predators. Highly edgy patches of the convoluted shape created to attract buntings in this experiment are probably an evolutionary novelty and

appear to act as a supernormal habitat selection cue. Weldon and Haddad (2005) appear to document a severe trap of the type described in scenario D—experimental cutting has produced a supernormal cue that simultaneously attracts buntings and their nest predators.

The remaining two studies were neither replicated nor randomized in design and, therefore, must be considered in that light. Nonetheless, Lloyd and Martin (2005) demonstrated that the Chestnut-collared Longspur (*Calcarius ornatus*) settled in patches of native and exotic habitat, but reproductive success was lower in monocultures of a non-native plant due to elevated rates of nest predation. In addition, nestlings in the exotic habitat gained mass at a slower rate, took longer to fledge, and left the nest at a lower mass than nestlings in the native habitat, suggesting food limitation as a mechanism contributing to poor reproductive success in this habitat type. Because there was no significant difference in the mean arrival date of male longspurs or in the laying date of females settling in native and exotic habitats, it appears that longspurs regard both habitat types as equally attractive, which would make this an example of an ‘equal-preference’ trap. Patches of exotic habitat appear to be ecological traps that may function as population sinks due to low annual reproductive success (Lloyd and Martin 2005). The introduction of a non-native plant may or may not have caused a change in the cue set, but the overall attractiveness ended up the same as that in the native habitat while success there was less, so this case would fit under the mechanism described in scenario C.

Finally, Remeš (2003) found that arriving blackcaps (*Sylvia atricapilla*) settled first in (preferred) a plantation of exotic black locust (*Robinia pseudoacacia*) relative to natural floodplain forest, but suffered lower nesting success there due to predation. The

settlement cues used by individuals are unclear but are probably the earlier leafing of shrubs and/or food supply. This would represent the type of severe trap depicted in scenario B because a novel, super attractive habitat has been created.

While there are currently an insufficient number of empirical studies available to determine which mechanism is more likely to trigger an ecological trap, it is interesting to note that the four studies we cite as the clearest examples of ecological traps illustrate the operation of all three of the possible mechanisms: two of type B (change in cue, but not ultimate factors, Horváth et al. 1998, Kriska et al. 1998), one of type C (change in ultimate factors, but not cues, Lloyd and Martin 2005), one of type D (change in both cues and ultimate factors, Weldon and Haddad 2005) and one of either type B or D (Remeš 2003). In addition, there is evidence for the existence of both equal preference (Lloyd and Martin 2005) and severe (Horváth et al. 1998, Kriska et al. 1999, Remeš 2003, Weldon and Haddad 2005) traps.

Even if a study demonstrates a negative relationship between a fitness component and an estimate of habitat preference, some caution is required before one can infer that the existence of a trap will result in a long-term population decline. In particular, a behavioral strategy that reduces survival or reproduction in the short term is not necessarily maladaptive if it enhances longer-term reproductive success. For example, characteristics of successful nest sites can vary over time and space (van Riper 1984), and nest-site selection may reflect long-term optima that are neutral or maladaptive in the short term (Clark and Shutler 1999). In this way, temporal and spatial variation in selection could invalidate presumed differences between high- and low-quality habitats. Theoretically, the entire life-cycle of an organism must be taken into account because a

novel environment could have compensating effects on the survival and reproductive output of different life stages. At the very least, we can and should demonstrate that at least one aspect of, or one time period within, the life-cycle of an organism has become compromised because of the existence of an ecological trap.

Why is there such a paucity of empirical evidence for the existence of ecological traps? One possibility is that ecological traps are quite rare. Alternatively, researchers may simply fail to detect them. Detecting an ecological trap requires a great deal of data, especially if a study is well replicated. Not only do researchers have to estimate habitat-specific survival and/or reproductive success among habitat types and replicate experimental plots, but they must obtain concurrent estimates of habitat preference. The rarity of studies adequately measuring preference should be highlighted because it probably reflects the inherent difficulty of demonstrating individual habitat preference. Nevertheless, demonstrating habitat preference is an important component of studies designed to detect the existence of ecological traps.

Conclusion

Results from this review and synthesis suggest that we have not been careful enough to correctly identify ecological traps on a case-by-case basis. In general, the literature on ecological and evolutionary traps has been dominated by demographic approaches that seek to understand the factors that shape population-level evolutionary responses to traps. However, progress in understanding the mechanisms by which traps are triggered and in identifying factors that predispose animals to responding to deceptive stimuli will need to embrace a behavioral approach that considers the conditions under which habitat

selection behavior evolved, variation in habitat selection behavior among individuals in a population, and the importance of learning.

A close examination of the mechanisms that create the traps associated with specific kinds of habitat alteration (or even with specific kinds of restoration activity) will be an important step toward mitigating the negative effects of traps. Further research into this interesting phenomenon should lead us toward an ability to identify, correct, and potentially even prevent the occurrence of traps in the future where they threaten the persistence of native species. If a more holistic and synthetic theory of the ecological trap is to be developed it will be essential to have a library of empirical studies illustrating not only the breadth of impacts that cause ecological traps and the range of species that are susceptible to them, but also a depth of understanding that examines the mechanisms that can trigger maladaptive behavior in general.

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Table 1. A summary of our evaluation of the presence of each of three criteria (see text) needed to demonstrate an ecological trap for each of 45 papers that we reviewed. Where the existence of a trap is supported by evidence, the possible mechanisms that could have triggered the trap are indicated. Studies are listed hierarchically by the criteria they satisfy, then alphabetically by author.

Journal Article	Criterion 1		Criterion 2		Criterion 3	
	Preference index	Reasonable preference measure?	Habitat -Specific reproduction or survival estimated?	Lower quality habitat preferred?	Mechanism type	
Angelstam 1986	none	no	no	N/A	N/A	
Basore et al. (1986)	density (nest)	no	yes	N/A	N/A	
Best (1986)	none	no	no	N/A	N/A	
Black et al. (1991)	none	no	no	N/A	N/A	
Boal (1997), Boal and Mannan (1998)	non-random use	no	yes	N/A	N/A	
Bollinger et al. (1990)	density (territory)	no	yes	N/A	N/A	
Carignan and Villard (2002)	none	no	no	N/A	N/A	
Chasko and Gates (1982)	density (nest)	no	yes	N/A	N/A	
Crabtree et al. (1989)	non-random use	no	yes	N/A	N/A	
Dwernychuk and Boag (1972)	none	no	yes	N/A	N/A	
Eadie et al. (1998), Semel and Sherman (2001)	none	no	yes	N/A	N/A	
Easton and Martin 1998	density (territory)	no	yes	N/A	N/A	
Ferreras and MacDonald (1999)	density (individual)	no	yes	N/A	N/A	
Flaspohler et al. (2001a,b)	density (nest)	no	yes	N/A	N/A	
Galbraith (1988)	density (territory)	no	no	N/A	N/A	
Ganter and Cooke (1998)	none	no	yes	N/A	N/A	
Gates and Gysel (1978)	density (nest)	no	yes	N/A	N/A	
Johnson and Temple (1986)	non-random use	no	yes	N/A	N/A	
Kershner and Bollinger (1996)	density (individual)	no	yes	N/A	N/A	
Kolbe and Janzen (2002)	non-random use	no	yes	N/A	N/A	

Journal Article	Criterion 1	Criterion 2		Criterion 3	
	Preference index	Reasonable preference measure?	Habitat -Specific reproduction or survival estimated?	Lower quality habitat preferred?	Mechanism type
Loery et al. (1997)	none	no	yes	N/A	N/A
Misenhelter and Rotenberry (2000)	non-random use	no	yes	N/A	N/A
Mundy (1983)	non-random use	no	yes	N/A	N/A
Packard et al. (1989)	density (individual)	no	no	N/A	N/A
Pasitschniak-Arts and Messier (1995)	none	no	no	N/A	N/A
Pidgeon et al. 2003	density (nest)	no	yes	N/A	N/A
Purcell and Verner (1998)	density (territory)	no	yes	N/A	N/A
Ratti and Reese (1988)	none	no	no	N/A	N/A
Reed et al. (1985)	none	no	yes	N/A	N/A
Ries and Fagan 2003	density (egg case)	no	yes	N/A	N/A
Rodenhouse and Best (1983)	density (territory)	no	yes	N/A	N/A
Schmidt and Whelan 1999	none	no	yes	N/A	N/A
Shane, S.H. 1984	density (individuals)	no	no	N/A	N/A
Stallman and Best (1996)	density (nest)	no	yes	N/A	N/A
Thomas et al. (1996)	density (individual)	no	yes	N/A	N/A
Woodward et al. (2001)	density (nest)	no	yes	N/A	N/A
Yahner and Wright (1985)	none	no	no	N/A	N/A
Chew (1980)	choice experiment	yes	no	N/A	N/A
Pöysä et al. (1999)	choice experiment	yes	yes	no	N/A
Székely, T. (1992)	arrival date	yes	yes	no	N/A
Horváth et al. (1988)	choice experiment	yes	yes	yes	B
Kriska et al. (1998)	choice experiment	yes	yes	yes	B
Lloyd and Martin (2005)	arrival date	yes	yes	yes	C
Remeš (2003)	arrival date	yes	yes	yes	B or D
Weldon and Haddad (2005)	Age-class distribution / Site-fidelity	yes	Yes	yes	D

CHAPTER II

IS SELECTIVELY HARVESTED FOREST AN ECOLOGICAL TRAP FOR OLIVE-SIDED FLYCATCHER?

ABSTRACT

Disturbance-dependent species are assumed to benefit from forestry practices that mimic the appearance of post-disturbance landscapes. However, human activities that closely mimic the appearance of natural habitats could attract animals to settle whether or not these habitats are suitable for their survival or reproduction. I examined habitat selection behavior and nest success of Olive-sided Flycatchers (*Contopus cooperi*) in naturally occurring burned forest and in an anthropogenically created habitat type—a selectively harvested forest. Olive-sided Flycatcher density and nestling provisioning rates were greater in the selectively harvested landscape whereas estimated nest success in selectively harvested forest was roughly half that found in naturally burned forest. Reduced nest success was probably a result of the relatively high abundance of nest predators found in the artificially disturbed forest. These results are consistent with the hypothesis that selectively harvested forest can act as an “ecological trap” by attracting Olive-sided Flycatchers to a relatively poor-quality habitat type. Such scenarios further highlight the importance of considering animal behavior in biodiversity conservation.

INTRODUCTION

When selecting a place to settle, animals must choose among potential habitats based on environmental and structural cues which, over evolutionary time, have become reliably correlated with components of habitat quality (Hutto 1985). However, if animals whose habitat selection behavior has been shaped by exposure to one set of conditions are rapidly confronted by novel or very different conditions, formerly reliable cues may trigger maladaptive settlement behavior (Tinbergen 1951, Levins 1968). This situation, where a poor habitat becomes more attractive, thus “baiting” individuals to settle has been termed an “ecological trap” (Dwernychuk & Boag 1972, Schlaepfer et al. 2002). An ecological trap is a scenario that occurs when sudden environmental change (e.g., brood parasitism, predation, pesticide use, human disturbance) acts to uncouple the cues that individuals use to assess habitat quality from the true quality of the environment (Schlaepfer et al. 2002, Robertson & Hutto 2006). An animal’s preference remains unchanged, but the positive outcome normally associated with a given cue is now a negative outcome (Misenhelter & Rotenberry 2000). Importantly, ecological traps are predicted to have significant, often dramatic, negative effects upon the persistence of populations of wild animals (Delibes et al. 2001, Donovan & Thompson 2001, Kokko & Sutherland 2001).

When humans attempt to mimic the effects of natural disturbances (e.g., fire, flood events, windstorm) or other natural processes through their land-management practices, those managed lands may provide all the evolved stimuli that promote settling by an organism, but may not provide the ultimately important food resources or relief from predation normally associated with a naturally occurring habitat (Weldon & Haddad 2005). Historically, large-scale natural disturbances, especially fires, have played a major role in determining the structure of Rocky Mountain landscapes (Habeck & Mutch 1973, Frost 1998). Recently, however, timber

harvesting has replaced wildfire as the dominant disturbance process shaping the landscape pattern of forest age classes (DeLong & Tanner 1996). Consequently, land managers are now encouraged to use green-tree retention techniques to mimic natural disturbance patterns (e.g., Hejl et al. 1995, Arno & Fiedler 2005). Although forest management may show some similarities with natural disturbances (fire and insect outbreaks) to which organisms are adapted (Hutto 1995), there are important differences between these two types of disturbances.

Timber management can modify the structure and composition of forest mosaics in an unnatural fashion (Spies et al. 1994) by altering age-class distribution (Hejl et al. 1995, DeLong & Tanner 1996), disturbing soil, leaving coarse woody debris and live trees (Spies et al. 1994), and removing standing dead trees (Hutto 1995). Unlike the situation following a typical, naturally occurring stand-replacement fire where blackened trees remain after disturbance, post-harvest forests are dominated by green trees. As such, harvested forests are “unnatural” in that their structure consists of combinations of elements (e.g., widely, or evenly spaced live trees) that simply do not exist in natural successional seres. Burned-forest insect communities are also fundamentally different from those that occur in harvested forests (Short & Negron 2003), as is the community of potential nest predators—particularly corvids and squirrels (Hutto & Young 1999, Stuart-Smith & Hayes 2003). Thus, harvested forests may act as ecological traps if they elicit settling responses by species that are “programmed” to respond to superficially similar, but fundamentally different, early successional forest types (Hutto & Young 1999), and if they also provide poor suitability (in terms of reproductive success or adult survival) due to altered food resources or due to unnaturally high predation rates (Stuart-Smith & Hayes 2003).

The Olive-sided Flycatcher (*Contopus cooperi*) makes an ideal subject for a comparison of nest success between artificially and naturally created early post-disturbance habitats because

it is not only relatively abundant in naturally disturbed, early post-fire forests in the northern Rocky Mountains, but it is equally or more abundant in variously harvested forest types, specifically seed-tree, shelterwood, and clearcut forest types (Hutto & Young 1999). Thus, based on abundance data alone, this species appears to be a specialist on artificially or naturally created early post-disturbance environments. Within burned forest, this single-brooded species (Wright 1997) is most abundant in patches that have burned at high severity in the northern Rockies (Smucker et al. 2005). Thus, it could be considered a fairly narrow post-fire specialist species, except for the fact that it also frequents artificially disturbed forests.

In order to demonstrate the existence of a ‘severe’ ecological trap (Robertson & Hutto 2006), three general criteria must be met: (1) individuals must exhibit a behavioral preference for one habitat over another; (2) a reasonable surrogate measure of individual fitness should differ among habitats; and (3) the fitness outcome for individuals settling in the preferred habitat must be lower than the fitness attained in other available habitats. To date, empirical evidence for the existence of ecological traps is limited to only a half-dozen examples, and this is primarily because of the difficulty of demonstrating the existence and direction of habitat preference (Robertson & Hutto 2006). Despite the difficulties associated with assessing habitat preference, we nonetheless tested several predictions that follow necessarily from the hypothesis that selectively harvested forests serve as ecological traps for the Olive-sided Flycatcher in the northern Rockies.

METHODS

Study site and species

I used an impact-reference design with the reference site being a previously unharvested forest that burned at high severity, and the impact site being a green-tree forest affected by various selective harvesting techniques. The study was conducted in 2002 within two sites, one located within the 29000-ha Moose Fire that burned through Glacier National Park and the Flathead National Forest in 2001, and the other within neighboring Plum Creek Timber Company land that was harvested in 1999-2001. Within the Flathead National Forest portion of the Moose Fire, we selected the 4000-ha Big Creek Basin as a study area. Burn severity was heterogeneous throughout the burned study area and the minimum distance to the burn perimeter was greater than 1 km. I located a physiognomically similar study area of similar size within nearby Plum Creek Timber Company land. The forest structure consisted of patches of thinned forest interspersed with unharvested patches. Harvested and burned sites were of similar age-class, forest type, elevation, and latitude. Both study areas were mid-elevation sites dominated by mixed-coniferous forest stands of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*).

Territory and nest site selection

Habitat features associated with territories were characterized to enable comparisons between (a) successful and failed nests, and (b) areas surrounding nest sites and randomly located but unoccupied sites. I measured floristic and structural habitat components thought to be important to Olive-sided Flycatchers at four spatial scales: nest, nest tree, and two plots centered on the nest tree—one an 11.3-m-radius intensive plot, and the other a 36-m-radius (one acre) extensive plot. Information from within additional 11.5- and 36-m-radius plots were also collected at

randomly located unoccupied points. I estimated nest and tree heights by triangulation using a clinometer and measuring tape, and estimated the distance from each nest to the tree trunk. Nest concealment was visually estimated as the percentage of vegetation cover within 1 m above, and within a square m centered on, the nest. I tallied the total number trees and suitable nest trees in the understory (1.5-9m tall) and at canopy height (>9 m tall) in both the 11.5- and 36-m-radius plots and recorded whether individual trees were alive (some green vegetation) or dead (all leaves are brown). Suitable nest trees were defined as living or dead Engelmann spruce or subalpine fir that still retained some intact foliage (green or brown needles) within the top meter of trunk. I estimated the percentage of canopy cover surrounding the nest tree as the mean of five readings at 2-m intervals along transects in four cardinal directions made with an ocular estimation tube. At these same measurement intervals, I estimated the percentage of bare ground surrounding the nest tree as the percentage of ground occluded from above by live vegetation. We also estimated the heterogeneity of the forest canopy by using the Shannon diversity index (Shannon & Weaver 1963) for canopy-height trees (>9 m). I estimated ground slope within a 36-m radius surrounding nests and random points using a clinometer. I visually estimated the distance (in meters) of a nest from the tree trunk. Because vegetation characteristics did not differ significantly between the 11.5-m and 36-m-radius plots within sites, I report only vegetation estimates collected at the 36-m-radius scale.

Vegetation characteristics associated with nests were quantified within two weeks of fledging. I compared all nest habitat variables associated with occupied and unoccupied sites to determine which habitat components were likely to serve as habitat selection cues and we also compared variables associated with successful and depredated nests. Fire severity surrounding nests was estimated within a 100-m radius using standardized severity criteria (USDI 2001).

Habitat preference

While not necessarily true (Robertson and Hutto 2006), most researchers assume that relative density is a reasonable surrogate measure of habitat preference. Here, I make the same assumption, but also add information on flycatcher settlement patterns in the two habitat types as a second measure of habitat preference. Specifically, I assumed that the males that arrive earliest on breeding grounds will select territories that they perceive as being of the highest quality (Ketterson and Nolan 1983, Bensch & Hasselquist 1991, Cristol 1995, Aebischer et al. 1996, Fransson and Jakobsson 1998, Verboven and Visser 1998; Kokko 1999, Currie et al. 2000). Thus, I systematically surveyed each study area daily for territorial males, and the mean arrival time for a site was used as a measure of preference for that site relative to the other site.

I began surveying for territorial males beginning in mid-May (before the arrival of any male). Singing males were detected from point count locations that were evenly spaced along tertiary roads throughout the study areas (burn: $n = 41$, cut: $n = 56$). A conservative estimate of the detection distance for Olive-sided Flycatcher is 250 m (Brandy 2001), so count locations were spaced at 500-m intervals. Each station was surveyed daily for 10 min prior to and throughout the arrival period (20 days after the arrival of the first male). Surveys began at a randomly selected station each day, but were executed in a consistent order until all points were complete. I assumed that a male was defending a territory if it was detected for at least three consecutive days during the arrival period and if it was observed defending a territory at that location for at least five consecutive visits during nest searching activities. Arrival date was estimated as the number of days after arrival of the first male in the respective year of study. Habitat specific pairing success was estimated as the percentage of territorial males that were

observed in association with a female on at least three separate occasions. Density estimates were calculated for each study area based on the number of territorial males.

Reproductive success

Full-time field technicians attempted to locate and monitor all Olive-sided Flycatcher nesting attempts using standard techniques (Ralph et al. 1993), monitoring active nests a minimum of every four days. To avoid observer bias, two technicians searched for nests as a team, alternating between study areas on successive days. I searched for nests daily from the onset of nesting until late June when birds no longer renested after failure (Robertson, unpublished data). Because Olive-sided Flycatchers may nest as high as 34 m (Altman & Sallabanks 2000), intensive nest monitoring would have required a telescoping nest pole, which may have disrupted nesting and attracted predators. Technicians, therefore, monitored nests only to obtain estimates of nest success. I did not estimate clutch size or seasonal fecundity; rather, a nest was considered successful if at least one young fledged. I confirmed fledging by resighting fledglings, listening for fledgling begging calls, or sighting parents carrying food or scolding near the nest. A nest was considered unsuccessful if either no fledglings were located, adults did not scold when I was close to the nest site, the nest was empty before the expected fledge date, or if a renesting attempt was located with the territory shortly after completion of a previous nesting attempt.

Food availability and nest predator abundance

Based on the well-studied functional responses of animals to prey density (Holling 1965, 1966), feeding rate of a predator should be proportional to food density until it can increase no further because of satiation or handling limitations. Nestling provisioning rates in aerial foragers are

positively correlated with food density (Blancher & Robertson 1987) and the relationship seems consistent among studies (Hutto 1990). If food supply is a factor limiting Olive-sided Flycatcher reproductive success, food provisioning of young should differ between the two habitat types. The number of chick feedings per chick per hour was estimated for each nest during the late nesting period (> 10 days after hatching), for two 30-min periods during fair weather. Late nestling period was chosen to observe nestling feeding behavior because growth rates of nestlings are generally highest (Pereyra & Morton 2001); therefore, food demands on parents are the greatest during that period (Walsberg 1978) and should best reflect food limitation (Hutto 1990). Because flycatchers exhibit a bimodal distribution of foraging activity throughout the day (Fitzpatrick 1981), two 30-min foraging bouts were observed for each nest on any given sample day: one during midmorning (10:00-11:00) and one during mid-afternoon (15:00-17:00). The observation period began immediately after the first feeding to reduce bias due to unequal disturbance caused by observers. Differences in average nestling provisioning rates between treatments were tested using an independent samples t-test.

To determine if differences in potential nest predator abundance differed between the burned and harvested habitat types, I compared the habitat-specific relative abundance of known nest predators of Olive-sided Flycatchers occurring in the study area—red squirrel (*Tamiasciurus hudsonicus*), Gray Jay (*Perisoreus canadensis*), and Common Raven (*Corvus corax*)—using point count data. Other potential nest predators include deer mouse (*Peromyscus maniculatus*), and yellow pine chipmunk (*Eutamias amoenus*), but given the typical height of Olive-sided Flycatcher nests in this study (mean = 12.06 m \pm 1.26) we assumed that these generally terrestrial mammals were unlikely to be significant predators. Point counts were conducted concurrently with surveys for Olive-sided Flycatchers during the arrival period and involved the

use of standard techniques (Ralph et al. 1993) including all individuals detected within a 50-m radius. Locations were randomly selected points within the burned ($n = 71$) and selectively harvested ($n = 80$) study areas. I attempted to adjust for any source of detection bias due to habitat structure by using fixed-radius data for our analyses and we also explored the possibility that animals were detected more readily in open, burned habitat than unburned habitat by examining detection profiles at burned and unburned points. Detection profiles were similar between burned and unburned points within 50 m, suggesting that any differences in detection rates were unlikely to have been a result of differences in lateral detection probabilities. The relative abundance of predators within each site was computed as the average number of detections per point for that site.

Statistical analyses

I estimated daily nest survival (the probability that a nest survives a given day) and tested hypotheses about the causes of variation in daily nest survival using the generalized linear modeling approach of Shaffer (2004). I fit logistic-exposure models using PROC GENMOD (SAS Institute 1999), a binomial response distribution, and the link function defined by Shaffer (2004). I developed a set of *a priori* candidate models that reflected our assessment of likely causes of variation in nest survival. Candidate models were built using the following variables that we considered potentially important in explaining variation in nest success: (1) *Habitat*—habitat was defined as either burned or harvested forest; (2) *Stage*—predators may use parental activity as a cue for locating nests. As a result, daily nest survival may decline from incubation to fledging as parents make more trips to the nest to provide food for their young (Skutch 1949, Martin et al. 2000). I modeled a daily nest survival as a binomial response to the variable stage;

(3) *Percent Canopy Cover*—canopy cover influences the abundance of known nest predator species and the likelihood of predation of artificial songbird nests in selectively harvested and burned forests in the northern Rockies (Stuart-Smith & Hayes 2003). Because canopy cover is also predicted to delineate treatments in this study we considered a linear effect of canopy cover on nest success in the model set; (4) *Trunk distance*—Olive-sided Flycatcher nests are typically quite conspicuous (Wright 1997, Altman and Sallabanks 2000, see RESULTS). However, nests located more distant from the tree trunk may be more conspicuous than those located closer to the tree trunk. I examined whether the horizontal distance of a nest from the trunk of its supporting tree was linearly related to nest survival probability; (5) *Snag Density*—tall, emergent snags are frequently used by Olive-sided Flycatchers as foraging perches (Wright 1997) and may be essential habitat components providing unobstructed air space that facilitates prey detection, so we included a linear density trend in daily nest survival in our model set; (6) *Slope*—Because even relatively short perch trees and snags may provide high open-sky visibility for flycatchers if they are located on steep slopes I examined a linear effect of slope on nest survival.

Based on combinations of the above variables, I evaluated a candidate set of 14 *a priori* models that we believed could reasonably explain variation in nest survival. Given the relatively small sample size of nests available for analysis and relatively large number of parameters evaluated, I included no interaction terms in our models. Using the output from PROC GENMOD, we evaluated the degree of support for each model using goodness-of-fit tests (Hosmer & Lemeshow 1989) and a second-order Akaike's Information Criterion (AIC_c ; Akaike 1973) which is a small-sample bias adjustment. The goodness-of-fit test of the global model was performed to determine whether this model provided an adequate description of the data. The best model was selected by judging the degree of support as measured by AIC_c and normalized

Akaike weights. Models with $\Delta AIC_c \leq 2$ were considered to have substantial support whereas models with $\Delta AIC_c \geq 4$ were considered to have little to no empirical support (Burnham & Anderson 2001).

I interpreted the strength of each variable by using odds ratios calculated from model-averaged coefficients and 95% confidence intervals based on unconditional standard errors (Burnham & Anderson 1998). The use of model-averaged estimates incorporates model-selection uncertainty and provides a more robust indication of the effect of each variable on daily nest survival (Anderson et al. 2000). I selected odds ratios to evaluate the strength of each variable because they are widely used in logistic regression and reflect effect size. I calculated the percentage change in the odds of nest survival for each one-unit change in an independent variable by subtracting 1 from the odds ratio and multiplying this value by 100. I interpret odds ratios with confidence intervals that overlap 1 as indicating no effect.

Estimates and their confidence limits were back transformed from the logit scale for presentation (proportion = $e^{\text{estimate}} / [1 + e^{\text{estimate}}]$). Estimates of daily nest survival probability were compared using a chi-square goodness-of-fit test. Vegetation height, density, cover, and arrival date were not normally distributed, and no transformation improved their distribution, so we tested for differences between the two plots through the use of Mann-Whitney *U*-tests. I compared the mean abundance of predators between burned and harvested sites using an independent samples *t*-test (two-tailed). Values for daily nest survival probability and odds ratios are reported with 95% upper and lower confidence limits because errors are asymmetrical about the mean. All other values reported are means \pm SE and we used $\alpha = .05$ as the level of statistical significance.

RESULTS

Vegetation differences between habitats

Burned and harvested plots were similar in the density of canopy-height (>9 m) tree trunks, density of canopy-height spruce/fir trunks, and in tree height diversity, suggesting that the two plots were similar in pre-fire forest structure and species composition (TABLE 1). The burned study plot had a greater snag density, a greater percentage of bare ground and a lower density of live understory trees than the selectively harvested plot. Conversely, the harvested plot had a greater density of live trees and percentage of canopy cover. The density of suitable nest trees was greater in the harvested plot, as was the density of both suitable spruce and subalpine fir.

Male flycatchers selected territories on steeper slopes than were randomly available in both the burned and harvested study plots (TABLE 2). Male flycatchers settling in the burned study plot selected territories with ten times higher density of suitable nest trees compared to random plots, and territories in burned forest also contained significantly greater densities of snags than did randomly located plots.

We located 36 Olive-sided Flycatcher nests in burned and harvested forest. Most nest sites were located in high-severity burn patches (16/18, 88%); two nests were placed in mixed-severity patches. Nests were placed primarily in subalpine fir (24/36, 66%) and Engelmann spruce (10/36, 28%). One nest each was built in western hemlock and western larch. In the burned study plot, most nests (17/18, 94%) were placed in a dead subalpine fir in which the only remaining vegetation was a small cap of brown needles at the top of the tree. Nest placement in the harvested plot was more variable, but all nests in the harvested plot were placed in live trees. Nests placed in burned trees were located closer to the top of the nest tree, closer to the trunk and were less concealed than nests in the harvested plot (TABLE 3). In general, Olive-sided

Flycatcher nests were poorly concealed—concealment was less than 40% for all nests regardless of treatment.

Habitat preference

Male flycatchers were first detected on both study plots on 25 May. However, settling male Olive-sided Flycatchers began defending territories, on average, 7.4 days earlier in the harvested plot (mean = day 8.0 ± 1.3) than in the burned plot (mean = day 15.4 ± 0.9 ; $U = 27.5$, $P < .001$) indicating a preference for the harvested plot. Pairing success in the harvested plot ($76\% \pm 7\%$) was higher than in the burned plot ($62\% \pm 9\%$), but not significantly so ($t_{35} = 1.2$, $P = 0.25$). Olive-sided Flycatcher territories were well spaced and were only rarely observed to abut one another, yet territory density was more than two times higher in the harvested study area (0.81 territories km^{-2} , $n = 29$) than in the burned study area (0.38 territories km^{-2} , $n = 28$).

Reproductive success

Estimated nest success in the burned plot (61%) was twice that in the harvested plot (30%). Daily nest survival rate in the selectively harvested plot was lower than that in the burned forest plot (harvest: 0.97, 0.941, 0.982; burn: 0.99, 0.970, 0.995; $\chi^2_{1} = 3.1$, $P = 0.07$). This overall lower survival rate in the harvested plot was driven by the lower daily nest survival rate during the nestling period (harvest: 0.97, 0.931, 0.986; burn: 0.99, 0.969, 0.996; $\chi^2_{1} = 3.0$, $P = 0.08$). There was no difference in daily nest survival rate between treatments during the incubation period. We were unable to determine whether predation was responsible for all nest failures, but no failures were associated with extreme weather events. The outcome of two nests was unknown and these nests were not included in analysis.

The global model of nest survival showed no evidence of lack of fit ($\chi^2_8 = 1.9, P = .99$). Three related models received the greatest support in explaining variability in daily nest survival probability (TABLE 4). The best-fitting model contained variables describing forest canopy cover surrounding the nest and the distance of the nest from the tree trunk (cm). The two next best models were single-parameter models containing these same variables. The Akaike weights suggest (summed weights = 0.61) that one of these three models is the best model for the data. The weight of support for the best-fitting models is strong relative to other models. Ultimately, selecting between the top two or three models is relatively unimportant as they produce nearly identical parameter estimates (β from the three models are within 0.001 of one another). However, for the purpose of estimating daily nest survival, we accepted $S_{canopy + trunkdistance}$ as the best-fitting model because it had the lowest AIC_c value, it received support from Akaike weights, and it was more parsimonious despite the penalty for increased numbers of parameters in the model. The logistic regression equation for the best model was:

$$\text{Logit}(\hat{S}_i) = 4.40 - 0.05 (\% \text{ canopy}) - 0.02 (\text{trunk distance}).$$

By incorporating values for the selected covariates to solve this equation, we found a decreased daily survival for nests surrounded by denser canopy and for nests placed farther away from the trunk of the nest tree.

Although the estimates of β and associated standard errors reveal the relative strength and direction of each effect, converting these values to odds ratios and 95% confidence intervals allows additional interpretation of size effects. Canopy cover had the strongest effect on nest success, with a 1% increase in canopy cover producing a 0.5% decrease in the odds of a nest surviving a given day (odds ratio = 0.95, 0.98, 0.94). This means that a 50% increase in canopy cover produces a 25% decrease in the odds of a nest surviving a given day. Each centimeter a

nest was located farther from the trunk increased the probability of nest failure by 2% (odds ratio = 0.98, 0.96, 0.99). This is equivalent to a 20% decrease in the odds of daily nest survival for each 10 cm distant a nest is from the nest tree trunk.

Nest predator abundance and food availability

Known nest predator species were estimated to be more than twice as abundant in the harvested plot than in the burned forest plot (red squirrel: $t_{132} = 3.5$, $P = 0.001$; Common Raven: $t_{88} = 2.3$, $P = 0.02$; Gray Jay: $t_{87} = 2.4$, $P = 0.02$; FIGURE 1). Mean chick provisioning rates (feedings per chick per hour) were higher for adult flycatchers in harvested than in burned forest habitat (harvest: $5.4, \pm 0.41$; burn: $4.0, \pm 0.40$, $t_{32} = 2.5$, $P = 0.02$). Allocation rates did not differ between morning and afternoon sampling sessions.

DISCUSSION

Results from this study are consistent with the hypothesis that, relative to burned forests, selectively harvested forests serve as ecological traps for Olive-sided Flycatchers. Birds arriving on the breeding grounds appear to have preferentially selected reproductively inferior breeding habitat. This scenario may represent what we have labeled elsewhere (Robertson & Hutto 2006) as a severe trap, in which the introduction of habitat selection cues makes a relatively poor-quality habitat more attractive than a higher quality habitat.

Why might Olive-sided Flycatchers prefer the harvested forest over the burned forest?

One possibility is a greater availability of suitable nest trees in a harvested forest. The significantly greater density of spruce/fir trees in burned territories compared to random post-fire locations suggest that nest tree availability is an important habitat selection cue for this species,

while the relatively high availability of suitable nest trees in the selectively harvested landscape provides a mechanism by which the attractiveness of this habitat supersedes that of the burned landscape. The strong preference for spruce/fir trees as nesting substrates (94% of nests) in this study parallels use patterns observed in other studies (reviewed in Altman and Sallabanks 2000) and is attributed to a branching and leafing structure suitable for the woven nest types used by Olive-sided Flycatchers (Altman and Sallabanks 2000). It is unclear if the observed differences in nest site characteristics between treatments (Table 3) are adaptive responses to differences in predation pressure or microclimate between habitat types, or are a consequence of unmeasured factors. Another possible reason why flycatchers preferred the harvested forest is a greater early-season abundance of food relative to the burned forest. Chicks received food at a greater rate in harvested patches in both this study and in another study in California (Brandy 2001).

Moreover, food availability and peak foraging rates for Olive-sided Flycatchers are tightly correlated and significantly higher in harvested forest than in burned forest, and that pattern holds across breeding seasons and years (Meehan & George 2003). Aerial insectivores grow more slowly than do similar-sized species of perching insectivores in both temperate and tropical regions (Ricklefs 1976) because young store lipids as “insurance fat” against temporary food shortages that can cause starvation (Lack & Lack 1951). For this reason, habitat characteristics that increase foraging efficiency are likely to be important. That territories with steep slopes were preferred may also be attributed to the fact that perches on steep slopes provide a greater open field of clear sky, which could facilitate prey capture (Fitzpatrick 1981).

The difference in daily nest survival rate between treatments was only marginally significant in a statistical sense, but may be biologically significant nonetheless. Olive-sided Flycatchers have the longest reproductive period of any North American passerine bird (~38

days [incubation + nestling periods]; Altman & Sallabanks 2000). Based on this long reproductive period, total nest success in the burned plot (61%) was twice that of the harvested plot (30%). These results closely match published estimates of reproductive success in these habitat types taken across a slightly broader range of harvested age classes and post-fire years (Altman & Sallabanks 2000).

While I present no data on the population consequences of this trap, such a discrepancy in overall nest success is likely to exert pressure on habitat selection behavior. Poor reproductive success in the harvested site was probably a result of the relatively high abundance of nest predators in that habitat. That most nest failures in the harvested area took place during the nestling phase where food provisioning rates were relatively high suggests the activity of nest predators as the causal agent. The likelihood of nest predation by visually-oriented predators increases during the nestling phase because the high level of parental activity around the nest can cue predators to its location (Martin et al. 2000). Furthermore, it appears that lower nest predator abundance (avian and mammalian) in post-fire landscapes relative to green and harvested landscapes is emerging as a general ecological pattern (Stuart-Smith & Hayes 2003, Smucker et al. 2005). Consequently, early successional post-fire habitat may represent relatively enemy-free space for many songbirds that have evolved to breed in recently burned landscapes.

Because severe ecological traps result from the inappropriate stimulation of an innate or learned settling response of an organism by one or more environmental stimuli, it may be relatively easy to remove the “bait” from such a trap by managing the cues that attract a species into the trap. Results from this study suggest at least two potential habitat selection cues that could be managed to reduce the attractiveness of selectively harvested habitat to Olive-sided Flycatchers: (1) snag density and (2) spruce/fir density. Snags are thought to be important

foraging resources for flycatchers in that they provide unobstructed views and flight paths for pursuing insects (Altman and Sallbanks 2000) and flycatchers settling in the harvested landscape in this study appeared to prefer patches with a greater snag density. If snag abundance and suitable nest tree density do, in fact, act as habitat selection cues for this species, removal or reduction of these elements should reduce the attractiveness of harvested forest types to Olive-sided Flycatcher. But even if the removal of snags and certain tree species from harvest units were economically and logistically feasible, such activity might conflict with habitat management guidelines for other species—notably snag-dependent bird species (e.g., woodpeckers and secondary cavity nesters). Moreover, studies examining settling responses of Olive-sided Flycatchers to experimental manipulations of potential habitat selection cues are needed before management implications are fully understood.

It is important that I address several issues that might emerge from the results of this study. First, I acknowledge that a behavioral strategy that reduces survival or reproduction in the short term is not necessarily maladaptive if it enhances longer-term reproductive success. For example, characteristics of successful nest sites can vary over time and space (van Riper 1984), and nest-site selection may reflect a long-term optimum that is, at times, neutral or maladaptive in the short term (Clark & Shutler 1999). Furthermore, I wish to emphasize that an ecological trap is a behavioral, not a population phenomenon (Robertson and Hutto 2006). Traps are defined by the mismatch between an individual's perception of habitat quality (proximal cues) and the actual habitat quality itself (ultimate factors) rather than on habitat-specific population growth rates. Thus, while the presence of an ecological trap may indeed reduce the likelihood of population persistence, absolute or relative population growth rates are not diagnostic characteristics of ecological traps (Robertson and Hutto 2006).

Another issue that emerges from our approach to assess habitat preference is whether relative abundance or arrival time are reasonable surrogates for preference. It is possible, for example, that average arrival time is influenced by site fidelity, and that because the harvested sites were occupied by birds the year before and burned sites probably not, this may have biased the arrival time estimate to be earlier in the harvested site. However, although males in this study began defending territories within the harvested habitat first, males began arriving on (and possibly assessing habitat quality in) both study sites at the same time. Thus, coupled with the difference in relative abundance between sites, the difference in average arrival time probably reflects a true preference by the birds, as discussed more fully elsewhere (Robertson & Hutto 2006).

With no treatment-level replication, I acknowledge that it is difficult to attribute differences in reproductive success between plots to the more general effects of either timber harvesting or fire. It is also relevant to consider which naturally occurring vegetation should serve as a “control” to test for the existence of an ecological trap. What if unburned forest edges are the “natural” environment to which the flycatchers are best adapted? The answer does not matter. Just as adaptive traits can be identified only through comparisons among selective regimes (Reeve & Sherman 1993), maladaptive habitat selection behavior can be demonstrated only through comparisons of the fitness consequences of a particular behavior in different habitat types. Thus, independent of whatever habitat might be “optimal” habitat for this species, it appears that the selectively harvested site in this study acted as an ecological trap relative to the early post-fire site.

Because my study suffers from a lack of treatment-level replication, it will only be after a number of similar studies are published that the generality of these results can be evaluated.

Nonetheless, these results are important not so much because they are definitive, but because they underscore the potential danger of altering or even “restoring” vegetation conditions if those conditions resemble a naturally occurring vegetation type only superficially. Indeed, recent evidence suggests that similar mechanism may be operating to generate ecological traps in other habitat types. Shochat et al. (2005) found that habitat preferences in grassland birds were affected by arthropod availability while nesting success was determined by nest predator abundance. One other study (Meehan and George 2003) has examined reproductive success of Olive-sided Flycatchers in burned and harvested forest, but with no estimate of habitat preference and with differences in methodology and study design, it is difficult to make a meaningful comparison. With greater and greater interest in mimicking nature through management (e.g., Arno & Fiedler 2005), we must be careful to consider whether the ultimately important features of a habitat (e.g., food, shelter, predators) are appropriately coupled with the environmental cues that are created through management action. The creation of an ecological trap may be an unintended consequence of attempting to more closely mimic the effects of natural disturbance, and such a consequence reveals the complexity of managing artificial landscapes for native biodiversity. Our results also suggest that animal behavior is a critical component in management effects studies (Caro 1998). The possibility that we might be creating ecological traps through our land management activity compels conservation biologists to examine more closely not just habitat quality, but habitat attractiveness as well.

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Figure Legends.

FIGURE 1. Mean (\pm SE) detections per survey point of Red Squirrel (n = 132), Common Raven (n = 88) and Gray Jay (n = 87) in burned and selectively harvested study areas. Nest predator species were detected less frequently in burned areas.

FIGURE 1.

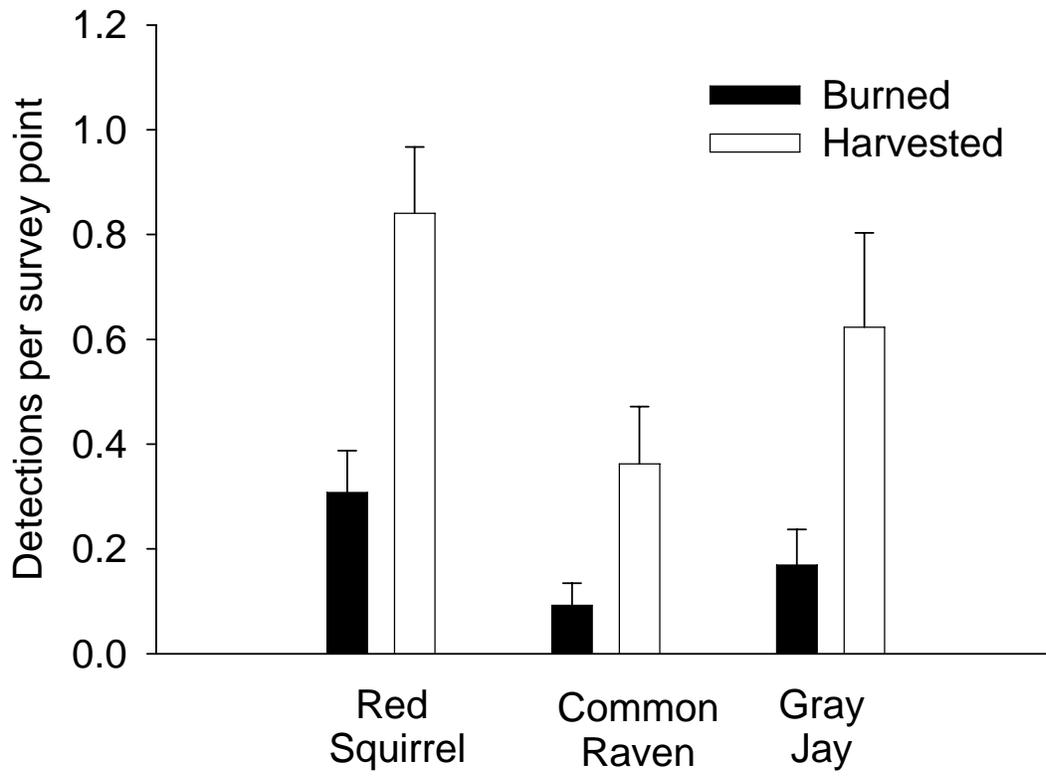


TABLE 1. Vegetation characteristics of the burned and selectively harvested study areas (mean \pm SE). Tree (understory height = 1.5-9.0 m; canopy height = >9.0 m) densities are estimated as trees per hectare. Suitable nest trees are defined as spruce or fir trees with some attached foliage within the top meter of the tree. Higher values of tree height diversity indicate a greater heterogeneity in total height of canopy trees (see Methods). The density of understory, living canopy and suitable nest trees was greater in the selectively harvested landscape, whereas snag density was greater in the burned landscape.

Variable	Burned Forest ($n = 18$)	Selective Harvest ($n = 18$)
Canopy tree density	152.4 \pm 31.0	118.0 \pm 22.6
Live canopy tree density *	20.3 \pm 8.9	112.7 \pm 21.6
Live understory tree density *	6.2 \pm 5.1	26.6 \pm 7.7
Spruce/fir tree density	22.0 \pm 5.4	29.1 \pm 9.6
Suitable nest tree density *	2.1 \pm 1.1	27.3 \pm 8.9
Spruce density *	0.0 \pm 0.0	22.8 \pm 5.3
Subalpine fir density*	2.1 \pm 1.1	13.1 \pm 6.6
Tree height diversity	1.5 \pm 0.2	1.8 \pm 0.2
Canopy Cover (% cover) *	0.8 \pm 0.3	8.2 \pm 2.5
Snag density *	21.2 \pm 6.5	0.6 \pm 0.2
Bare ground (%)*	56.1 \pm 8.2	21.7 \pm 4.3

* *Treatment means significantly different at $p \leq 0.02$. All other variables not significant (Mann-Whitney U-tests).*

TABLE 2. Comparisons of vegetation structure characteristics at nest site ($n = 17$) and random ($n = 18$) study plots in burned and harvested forest (mean \pm SE). P -values for territories vs. random Mann-Whitney U -tests are in parentheses. Densities are reported as tree per hectare (see Table 1 and METHODS for variable definitions). The density of suitable nest trees was greater in flycatcher territories than in random plots within the burned study area.

Variable	Burned forest			Harvested forest		
	Territories	P	Random plots	Territories	P	Random plots
Slope (degrees)	33.8 \pm 2.9	0.01	15.9 \pm 5.1	15.5 \pm 2.4	<.001	7.2 \pm 0.9
Spruce/fir density	34.3 \pm 9.1	<.001	2.9 \pm 1.4	53.2 \pm 15.0	0.78	58.9 \pm 13.3
Suitable nest tree density	30.5 \pm 8.3	<.001	2.1 \pm 1.1	32.3 \pm 11.0	0.64	27.3 \pm 8.9
Snag density	66.7 \pm 14.0	0.14	132.1 \pm 32.0	15.8 \pm 3.3	0.02	5.9 \pm 2.0

TABLE 3. Comparisons of Olive-sided Flycatcher nest-site characteristics in burned ($n = 18$) and selectively harvested ($n = 17$) study areas (mean \pm SE). P -values are listed for Mann-Whitney U-tests. Olive-sided Flycatcher nests were located closer to tree trunks and treetops and further from concealing foliage within the burned study area.

Variable	Burned forest	P	Harvested forest
Distance of nest from tree top (meters)	1.2 \pm 0.2	<.001	5.6 \pm 1.6
Distance from trunk to nest (cm)	7.0 \pm 3.4	<.001	67.2 \pm 10.4
Distance from nest to outer foliage (cm)	17.6 \pm 2.9	0.02	31.2 \pm 6.0
Distance from nest to foliage above (cm)	21.0 \pm 2.4	0.002	42 \pm 6.1

TABLE 4. Candidate set of *a priori* models used to examine the effects of habitat type, canopy cover, nesting stage (incubation vs. nestling), snag density, distance of nests from tree trunks and ground slope on the daily survival of Olive-sided Flycatcher nests. Models were ranked using Akaike’s information criterion corrected for small sample size (AIC_c); Deviance is a measure of model fit, K is the number of parameters estimated by the model, ΔAIC_c is the difference between a given model and the model with the lowest AIC_c score^a, and AIC_c weight reflects the relative support for each model. Note that two of the three best models contain the variable canopy cover.

Model	k	Deviance	ΔAIC_c	AIC _c Weight
Canopy + Habitat	3	117.01	0	0.31
Canopy	2	120.44	1.41	0.15
Trunkdistance	2	120.46	1.43	0.15
Canopy + Habitat	3	119.18	2.17	0.11
Trunkdistance + Habitat	3	120.26	3.25	0.06
Stage + Canopy	3	120.17	3.43	0.06
Stage + Trunkdistance	3	119.80	3.44	0.06
Habitat	2	123.50	4.46	0.03
Constant ^b	1	126.84	5.79	0.02
Slope	2	125.12	6.1	0.01
Stage + Habitat	3	126.50	6.37	0.01
Global ^c	7	126.54	6.8	0.01
Snag	2	126.54	7.52	0.01
Stage	2	126.32	7.59	0.01

^a The lowest AIC_c score was 130.651

^b Constant model contains no parameters

^c Global model contains all parameters

CHAPTER III

AVIAN NEST PREFERENCE AND FITNESS CONSEQUENCES OF NEST MICROCLIMATE

ABSTRACT

Maternal preference for nest sites is predicted to be an adaptive consequence of selection pressures acting on parents and young at the nest site. Nest microclimate has the potential to impose fitness costs upon both adults and young, yet evidence supporting microclimate as a selective factor shaping the evolution of avian nest site preference is lacking. I used the dramatic temporal and spatial variation in microclimatic conditions generated by variation in wildfire severity to examine the microclimatic consequences of nest site preferences and the fitness costs to parents and offspring in the Dark-eyed Junco (*Junco hyemalis*), a facultative cavity nesting bird. Adults preferred to select non-cavity nests oriented toward the north and preferred sites that consistently had the most moderate thermal regimes. Nestlings reared in colder cavity-type nests gained mass more slowly and experienced retarded skeletal growth, while nestlings reared in open south-facing nests that experienced the hottest mid-day temperatures grew more rapidly. Results suggest that parents suffer costs associated with hot microclimates; incubating females reduced their nest attentiveness and doubled their nestling provisioning rate at hot nest sites. Nest site preferences in junco appear to be an adaptive consequence of the costs of hot nest sites to parents and the costs of overly cool climates to developing young. Results of this study suggest that the generally slow growth rates exhibited by cavity nesting birds may be a direct consequence of microclimatic costs to nestlings associated with cool temperatures. Thus, as in other taxa, it appears that temperature has the ability to act as a selective force shaping nest site preferences in birds.

INTRODUCTION

Because all organisms have a finite number of opportunities to breed during a lifetime maternal preference for suitable oviposition sites is assumed to be under strong natural selection such that choice of preferred sites results in high offspring fitness (Jaenike and Holt, 1991, Martin, 1998). Indeed, oviposition behavior can have dramatic effects on survival rate and development of offspring (e.g., Sinervo and Doughty 1996, Mousseau and Fox, 1998, Brown and Shine 2004). Yet, nest site preferences can also influence the costs of reproduction experienced by the parent (Madsen and Shine 1999).

The adaptive significance of breeding site preference has been extensively studied in birds, but investigations have focused almost exclusively on predator avoidance (Martin 1998, Weibe and Martin 1998, Clark and Shutler 1999). Importantly, many abiotic factors in the environment have the potential to shape the evolution of nest site preference (Lima and Dill 1990, Martin, 2001, Goldsbrough et al. 2004). Nest placement in birds has been associated with microclimatic conditions (Walsberg 1981, Clark et al. 1990, With and Webb 1993, Gloutney and Clark 1997) and both parents and developing young are known to be sensitive to moisture and thermal conditions at the nest (Haftorn and Reinertsen 1982, Webb and King 1983, Dawson and O'Connor 1996). Consequently, as in other taxa, features of nest sites that shape nest microclimate may impose significant constraints on nest-site choice in birds (Ricklefs and Hainsworth 1969, With and Webb 1993, Gloutney and Clark 1997, Madsen and Shine 1999, Conway and Martin 2000Am, Lloyd and Martin, 2004;).

Nest temperature, in particular, can have a major influence on energy and water budgets of both parents and developing young (Ricklefs and Hainsworth 1969, Wolf and

Walsberg 1996, Stokes and Boersma 1998, Dawson et al. 2005). Incubating parents must regulate the nest environment while meeting their own energetic and hydric needs by leaving the nest to forage (Vleck 1981, Conway and Martin 2000a). Overly hot or cool nest sites are predicted to increase thermoregulatory costs to incubating parents while simultaneously requiring parents to meet the increased energy and/or water requirements of developing young (Conway and Martin 2000a). Selection should favor individuals with preferences for nest sites with microclimatic features that maximize offspring fitness and minimize the costs of parental care that can reduce energy available for subsequent nesting attempts (Reid et al. 2000, Milonoff et al. 2004, Hanssen et al. 2005). However, evidence that avian nest site preferences are an adaptive response to costs imposed by nest microclimate is lacking. A single test of the hypothesis that microclimate influences maternal nest site preference found the behavior to be maladaptive; nest sites in more moderate microclimates resulted in reduced offspring growth rates (Lloyd and Martin 2004).

Here, I seek to address this information gap first by documenting nest site preferences and the microclimatic consequences of those preferences in Dark-eyed Junco (*Junco hyemalis*) nesting in postfire forest habitat in the northern Rockies. Wildfire has dramatic effects on forest structure when fire severity and extent vary over space (Platt and Connell 2003; Turner et al. 2003) and creates dramatic gradients in canopy and ground cover which are known to affect the thermal regime of nest sites (Walsburg 1981, With and Webb 1993, Lloyd and Martin 2004). The Dark-eyed Junco (*Junco hyemalis*) is a primarily ground and open-cup nesting songbird, abundantly found across a range of fire severities in this region (Smucker et al. 2005), and so is likely to have evolved

strategies for dealing with the dramatic temporal and spatial heterogeneity found in postfire environments. Furthermore, juncos are facultative cavity nesters (Nolan et al. 2002) that select nest sites on open ground under vegetation (Martin, 1998), and in other locations that are effectively underground. Thus, in postfire environments, juncos may be faced with dramatic thermal gradients, but also with a wide range of nest site options that are likely to differ in their thermal properties. I focus on nest orientation and nest type (cavity vs. non-cavity) as components of nest site choice because the direction of the nest opening and the overall concealment of a nest site determines the duration, timing and extent of exposure to direct sun.

Next I relate variation in nest microclimate arising from nest site preference to a component of offspring fitness (nestling growth rate) and two components of parental investment (nestling provisioning and incubation nest attentiveness). Nestling growth rate is an important component of fitness (Gebhardt-Henrich and Richner 1998) and is thought to be sensitive to temperature variation at nest sites (Dawson et al. 1995, Wolf and Walsburg 1996), but in altricial species is ultimately limited by the ability of parents to provide food to fuel growth. Parent birds experience similar thermoregulatory costs associated with microclimate (Haftorn and Reinertsen 1985, Schmidt-Nielson 1994) that may reduce their ability to provide parental care (Conway and Martin 2000b). Consequently, thermally stressful nest sites are likely to impose energetic demands on both parents and young that can shape the evolution of nest site preferences through parental decisions regarding the allocation of energy to self-maintenance and parental care.

METHODS

Study site and study organism

This study was conducted in 2004-2005 within the boundaries of the 7,062-acre Black Mountain fire of 2003 in the Lolo National Forest near Missoula, Montana. The study area is a low- to moderate-elevation site dominated by mixed-conifer forest stands of ponderosa pine and (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*) and western larch (*Larix occidentalis*). I established a 300-ha subplot as the focal study area based upon its narrow elevation range (1280-1340 meters) and the presence of forest patches that burned at different severities. Female juncos select nest sites and perform nearly all of the construction of open cup type nests (B. Robertson, personal observation, Nolan et al. 2002). Only females incubate (Wolf et al. 1991) but both sexes assist in feeding nestlings (Ketterson et al. 1992).

Nest-site selection and nest temperature

Field assistants monitored each junco territory for the entire breeding season and searched daily for all junco nesting attempts from late April to early-August each year using behavioral cues to locate nests initially. To examine patterns of nest-site selection, I measured the following variables immediately after the termination of a nesting attempt: nest concealment, nest orientation, percent canopy and ground cover, and burn severity. Nest concealment was defined as a visual estimate of the percentage of the bowl of each nest that was visible from a distance of 1 m from each of the four cardinal directions and from directly above. All five measurements were averaged, yielding a single index of concealment for each nest. In post-fire landscapes juncos frequently nest in carbonized

holes in the ground created by the incineration of tree roots (Robertson, personal observation). Nests were categorized as cavity type nests if > 50% of the nest bowl was visually occluded from directly above by a roof of rock or soil. Only 2 nests out of 70 categorized as cavity nests had an above concealment of < 80% and these were excluded from analysis.

Nest orientation was defined as the compass direction from which the greatest percentage of the nest bowl was visible, relative to magnetic north, as the azimuth bisecting the direction of greatest exposure. I categorized nests as having one of four possible orientations: northeast ($1^{\circ} - 90^{\circ}$), southeast ($91^{\circ} - 180^{\circ}$), southwest ($181^{\circ} - 270^{\circ}$), and northwest ($271^{\circ} - 360^{\circ}$). These categories reflect four distinct temperature regimes shaped by the azimuth angle of the sun (Lloyd and Martin 2004): northeastern orientations receive direct sun only immediately after sunrise, when ambient temperatures are low; southeast orientations experience direct sunlight during the morning as temperatures rise; southwestern orientations experience direct afternoon sun as hot afternoon temperatures decline; and northwest orientations experience direct sun immediately prior to sunset when ambient temperatures have fallen. These categories, then, reflect biologically relevant physical conditions that parent birds could use in selecting a nest orientation and have been causally linked to variation in nest microclimate (Lloyd and Martin 2004)

I measured vegetation structural components associated with nest sites and randomly selected locations within 75 m of the nest site. At each nest site and random point I laid two measuring tapes crosswise to delineate nested, 5- and 11-m-radius subplots. Canopy cover from woody plants and trees > 3 m was estimated by tallying the

proportion of the 45 meter markings along the tapes with target vegetation directly overhead in the 11-m-radius plot. Similarly, by looking down while standing over each meter mark, I estimated ground cover as the proportion of the 45 meter marks along the tapes with target vegetation intersecting the tape at a height of <1 m. Ground cavity availability was estimated by systematically searching 5-m-radius plots for ground cavities that had openings 5-10 cm in diameter at their widest point and were 10-30 cm deep. These represented the range of dimensions of actual ground cavity nest sites within the study site (Robertson, unpublished data).

Burn severity of forest patches (estimated at a 75m radius) was defined based on a modified version of the composite burn index (CBI, Ryan & Noste 1985, Key & Benson 2001): (1) *Low severity*—Light charring with up to moderate consumption of downed fuels including litter and duff. Regenerated herbs and grass dominate understory. Shrubs and saplings show little mortality. Overstory not scorched or blackened, and tree charring remains < 2m; (2) *Intermediate severity*—Deep char, largely consumed small fuels litter and duff. Increased densities of new serals (fireweed, lodgepole pine), but some pre-fire herbs and shrubs persist. Most tree crowns blackened or largely scorched, a few green crowns remain; (3) *High severity*—Major portions of large downed fuels litter and duff consumed, substantial amounts of exposed mineral soil. Pre-fire herbs and shrubs essentially absent, low-density patches of seral species occupy understory. Significant portions of overstory consumed including most fine branching in crowns.

I quantified the microclimatic characteristics of each nest by measuring temperature within the nest cup continuously for 24 hours immediately following each nesting attempt. Because nest temperatures were measured before any structural changes

could occur to the vegetation surrounding nest sites, measurements of nest-site microclimate likely provided an unbiased index of conditions experienced by eggs, nestlings, and adults. Moreover, while nest temperatures may vary over a nesting cycle, relative nest temperature provides an unbiased method of comparing nest microclimate among nests differing in nest orientations and structural types (ground cavities vs. exposed nests). I simultaneously measured ambient air temperature at a point 5 m from the nest in order to control for variation in ambient temperature that could have influenced estimates of nest temperature. Nest and ambient temperatures were measured using ThermoChron® ibutton data loggers (Maxim Integrated Products, Sunnyvale, CA). Ibuttons were placed on a plastic support stand with a rubber insulator anchored at base of the bowl of each nest such that the sensor was approximately 1 cm above the base of the nest. While nest temperatures obtained from thermocouples are not identical to the operative environmental temperature experienced by birds at nest sites (Bakken 1992, Walsberg and Weathers 1986), sensors do provide unbiased estimates of thermal conditions at the nest (Stoutjesdijk 2002). Ambient temperatures were measured by ibuttons placed on insulated supports approximately 3 cm above the ground and shielded from direct sunlight with a round plastic shade 15 cm in diameter.

I determined whether juncos preferred to orient their nests in particular directions using a one-sample Rao's U test, in which the observed distribution of directions was compared against the null hypothesis that the distribution of nest orientations was uniform (Zar 1999). To determine if orientation changed seasonally, I used a multisample Watson-Williams test (Zar 1999).

I used logistic regression to determine if juncos preferred cavities or exposed nest sites and to compare vegetation structure at nest sites and paired, randomly-located, non-nest sites, using nest initiation date as a covariate to test for seasonal changes in nest site preferences. Although the availability of exposed (non-cavity) nest sites cannot meaningfully be measured at random points, I did assess the availability of cavity nests across seasons, burn severities and post-fire years. I analyzed the relationship between nest orientation and nest temperature using a repeated-measures ANCOVA. Because I measured nest temperatures over the length of the breeding season, ambient air temperature varied and so was included as a covariate. Because nest orientation is likely to have little effect on nest temperature when the sun is down or low in the sky, I limited the comparisons of maximum and mean nest temperatures to the hours of 1200–2000.

Nestling growth and survival

Most nests (68% of 168) were located during nest building, egg laying, or incubation periods. Nests were monitored regularly (minimum of every 3–4 days) and noted as active, failed, or fledged. Nests were visited every day during the laying, incubation and nestling periods, if necessary, in order to determine the exact day of clutch initiation, hatching, and fledging. Fledging was confirmed if fledglings were sighted or begging calls were heard or if I observed parents with food. A nest was considered successful if at least one young was observed as a fledgling or if the final nest-feeding visit suggested a fledging event. A nest was considered unsuccessful if no nestlings were located, adults did not scold when we were close to the nest site, the nest was empty before the expected

fledge date, or if a renesting attempt was located within the territory within 5 days of completion of a previous nesting attempt.

To estimate nestling growth rate, I individually marked nestlings immediately after hatching using a permanent marker, returning every 2 days to remark nestlings and to measure body mass, total length of the outermost primary on each wing (shaft, and feather when pinfeathers broke), and length of both tarsi. I used the mean of the right and left measurements for tarsus and primary length in analysis of growth rates. I estimated mass to the nearest 0.01 g using a portable electronic balance, and measured primary and tarsus length to the nearest 0.1 mm using digital calipers.

Growth rates of all nestling traits were estimated by using nonlinear regression to fit a logistic growth curve to the entire data set for each trait (Ricklefs 1983, Remeš and Martin 2002). Residuals from the growth curve were pooled among nestlings within a nest before analysis (Ricklefs 1983) to avoid inflating degrees of freedom. Consequently, growth rates for each nest were represented as a single residual that reflected the average growth of nestlings in a nest relative to all other nests in the sample. To compare growth rates of nestling traits among orientations, I analyzed pooled residuals from the nonlinear regression using MANCOVA, including brood size and hatching date as covariates (Ricklefs 1983).

I tested for year effects on partial brood loss by estimating individual egg and nestling survival rates within nests using a modified Mayfield model that accounts for a lack of independence among nestlings within a nest by considering each nest as a clustered sampling unit (Flint et al. 1995). I right-censored data when nests terminated, either from fledging or failing, to focus on nestling mortality in the absence of predation

pressure and I tested for treatment effects using the program CONTRAST (Hines and Sauer 1989, Flint et al. 1995). I examined potential factors influencing nest predation risk using the methods recommended by Shaffer (2004). Daily nest predation rate (the probability a nest will be predated on a single day) was estimated with a logistic-exposure model using PROC GENMOD (SAS Institute 1999), a binomial response distribution, and the link function defined by Shaffer (2004). I tested for differences in daily predation probability among years, burn severities, nest types, nest orientations and nests differing in concealment using chi-square goodness-of-fit tests and included nest attentiveness and feeding rates as possible factors influencing nest predation probability.

Effect of microclimate on parental behavior

High nest attentiveness (percent of time that parent sits on the nest) is favored during incubation to prevent the increased mortality and reduced developmental rate of embryos associated with increased nest absence (White and Kinney 1974, Lyon and Montgomerie 1985). Yet, if high nest temperatures overwhelm parents' thermoregulatory capabilities, then placing nests in thermally stressful sites may constrain nest attendance, which may then reduce nesting success or offspring fitness (Grant 1982, Jehl and Mahoney 1987, Wiebe and Martin 1998, Conway and Martin 2000a). Thermally stressful nest sites may also impose high energetic costs on nestling that parent birds must mitigate in the form of increased food allocation or other behavioral compensation. I examined how two elements of parental behavior, female nest attentiveness (% of time females were incubating) and parental feeding rate, varied in response to microclimate. By monitoring feeding and incubation behavior at all nests during the same developmental stage, I

controlled for natural variation in incubation and feeding that could occur during the nesting cycle. On day three of the incubation period (day of hatching = 0) an ibutton was placed beneath the lining of each nest equidistant from the base and rim of the nest bowl. Thermocouples were programmed to record temperature every minute and I inferred incubation patterns from temperature patterns in thermocouples (Badyaev et al. 2003, Lloyd and Martin 2004), estimating total nest attentiveness. In order to control for differences in weather conditions among nests at the time of observation, I also recorded ambient air temperature during foraging observations and incubation monitoring. Ambient air temperature was recorded with a shaded temperature probe attached to a data logger and placed 5 m from the nest. To examine how parents respond to changes in microclimate, I compared percentage of time spent incubating among treatments using ANCOVA, with ambient temperature and brood size as covariates.

I quantified nestling feeding rates by observing parental feeding during the late nesting period (day 7 of the nestling period), for two 30-min observation periods. The number of chick feeds/chick/hour was estimated for each nest. The observation period began immediately after the first feeding to reduce bias due to unequal disturbance caused by observers. I used ANCOVA to test for differences in parental allocation of food to young among nest types and nest orientations, while controlling for year and burn severity; Julian date and nest concealment were included in the model as covariates.

RESULTS

Climate and habitat structure at the study site

Successional patterns in herbaceous ground cover were an interacting function of date, postfire year and burn severity (year x severity: $F_{2,317} = 5.66$, $P = .004$; year x date: $F_{2,317} = 14.91$, $P < .001$). Percent herbaceous ground cover was highest at lower severities during the first postfire year, but increased to become similar among burn severities during the second postfire year (Figure 1). Herbaceous ground cover increased seasonally across the first postfire breeding season (slope = 3.8 %/day, SE = .09) but remained relatively constant across the second postfire breeding season (slope = -.09 % day, SE = .08). Canopy cover was consistently lowest in high-severity patches while low severity patches had the highest mean canopy cover (severity: $F_{2,323} = 76.26$, $P < .001$; year: $F_{1, 323} = 2.56$, $P = .08$, Figure 1).

Nest-site selection and nest temperature

Overall, juncos preferred to orient their nests towards the north ($n = 163$, mean = 36 °, Rao's $U = 2.20$, $p = .02$, Figure 2). Preference for north-facing nests did not change seasonally and the distribution of nest orientation was similar when comparing early (initiated before 9 June, $n = 99$, mean = 24.6°) and late (initiated after 9 June, $n = 64$, mean = 45.5°) breeding attempts ($F_{1,161} = 1.24$, $p = .27$, two-sample Watson-William's test). Juncos did not select nest patches that differed from random patches in percent ground cover, litter/duff burn severity, mid-story burn severity, or canopy cover (all $P > .30$).

The global model for the multinomial logistic regression fit the data well ($\chi^2_6 = 108.5$, $P = 0.001$). Nest types selected by females differed by year and across burn severities (year: $\chi^2_1 = 64.16$, $P < 0.001$; severity: $\chi^2_2 = 12.78$, $P < 0.002$). Females

preferentially selected cavities as nest sites within high-severity patches (Wald $\chi^2_1 = 10.17, P = 0.001$), and were more likely to locate nests in exposed locations during the second postfire year (Wald $\chi^2_1 = 38.32, P < .001$) when ground cover was significantly higher. Female nest type preference was related to ground cover in both postfire years (% ground cover: Wald $\chi^2_1 = 6.75, P = .009$). Females preferred to select cavity nests in patches with sparser vegetative ground cover (cavity: $\bar{x} = 34.6\%$, SE = 5.9) while females preferred exposed nests in patches with high ground cover (exposed: $\bar{x} = 47.5\%$, SE = 3.0). Yet, ground cavity availability did not differ among years or burn severities ($p > .20$). Cavity nests were more concealed than exposed nests ($F_{1,156} = 4.22, P = .042$) but concealment did not differ by severity or among orientations (severity: $F_{2,156} = 0.12, P = .88$; orientation: $F_{3,156} = 0.07, P = .97$). Nest initiation date did not explain significant variability in nest types selected by females ($\chi^2_2 = 3.99, P = 0.14$) so it was removed from the model.

Average mid-day nest temperatures varied among orientations and nest types (orientation: $F_{1,46} = 5.46, P < .02$; nest type: $F_{1,46} = 8.77, P = .005$; ambient temperature: $F_{1,52} = 7.03, P = .02$). Nests with the preferred northerly orientations (northeast and northwest) had cooler mean temperatures than either southeast or southwest-facing nests (mean difference = 8.0°C , $p = .04$, figure 3A) and cavity nests were consistently cooler than exposed nest types (mean difference = -11.3°C , $P = .005$, Figure 3B). Mean early mid-day (10:00-15:00) temperatures were highest for southeast-facing nests (orientation: $F_{3,52} = 11.96, P < .001$; nest type: $F_{1,52} = 11.71, P = .001$; ambient temperature: $F_{1,52} = 5.91, P = .02$, Figure 3B). Late mid-day temperatures differed among orientations (15:00-20:00) temperatures (orientation: $F_{3,45} = 2.89, P = .04$; nest type: $F_{1,45} = 2.10, P = .15$;

ambient temperature: $F_{1,45} = 10.87$, $P = .002$, Figure 3A) with southeast-facing nests reaching the hottest temperatures (mean difference = 6.7°C , $p = .05$)

Ambient temperature did not differ among severities ($F_{2,48} = .64$, $p = .53$), and was unrelated to % canopy cover, mid-story density, or fire severity (all $p > .20$). Ground cover was important in shaping ambient temperatures near the ground as patches with greater proportions of bare ground reached higher maximum temperatures during mid-day ($F_{1,55} = 7.15$, $P = .01$).

Offspring survival and growth

Rate of mass gain was greater for nestlings reared in exposed nests compared to those raised in cavity nests (nest type: $F_{1,86} = 3.91$, $P = .05$; concealment: $F_{1,86} = 3.13$, $P = .08$; brood size: $F_{1,86} = 4.69$, $P = .03$; orientation: $F_{3,86} = 0.48$, $P = .70$, Figure 4). Similarly, wing feather growth was more rapid for chicks in exposed nests and growth rate was positively related to nest exposure (nest type: $F_{1,86} = 5.30$, $P = .02$; concealment: $F_{1,86} = 8.72$, $P = .004$, brood size: $F_{1,86} = 10.64$; $P = .002$, orientation: $F_{3,86} = 1.92$, $P = .13$; Figure 4). The rate of tarsus growth was also slower for chicks nesting in cavities but the effect of exposure on tarsus growth was only marginally significant (nest type: $F_{1,86} = 5.65$, $P = .02$; concealment: $F_{1,86} = 2.85$, $P = .09$; brood size: $F_{1,86} = 2.91$, $P = .09$; orientation: $F_{3,86} = 0.61$, $P = .61$; Figure 4). Hatching date was insignificant in predicting nestling growth rates and was removed from the model. Clutch size, fledgling number, and length of the incubation and nestling periods were similar among orientations, nest types and severities (all $p > .20$).

As is common among passerine birds, nestling and egg mortality was almost entirely the result of predation, and starvation was rare. Daily nest predation probability was not affected by nest orientation ($\chi^2_1 = 0.59, P = 0.89$), nest type ($\chi^2_1 = 3.12, P = .21$) or nest concealment ($\chi^2_1 = .92, P = .34$), but was related to burn severity ($\chi^2_1 = 8.92, P = .011$). Nests initiated in intermediate severity patches had a significantly lower daily probability of nest predation than those in low or high severity patches ($\chi^2_1 = 10.78, P = .001$). Daily nest predation probability did not differ between low and high severity patches ($\chi^2_1 = .07, P = .79$) or between years ($\chi^2_1 = 2.99, P = 0.08$). Partial brood loss from nestling mortality did not differ among nest types, orientations or burn severities (all $P > .8$). Similarly, hatching success was unrelated to nest orientation, nest type, or severity (all $P > .70$).

Effect of microclimate on parental behavior

Females selecting southeast or southwest facing nests had reduced nest attentiveness (orientation: $F_{3,71} = 8.293, P < .001$; nest type: $F_{1,83} = 0.164, P = .68$; concealment: $F_{1,83} = .094, P = 0.76$, Figure 5) during incubation compared to northeast or northwest facing nests. Burn severity was unrelated to nest attentiveness ($p > .2$) so this factor was removed from the model. Nest attentiveness was unrelated to nest predation risk (attentiveness: $\chi^2_1 = 0.03, P = 0.87$; severity: $\chi^2_2 = 2.93, P = 0.087$; date: $\chi^2_1 = 12.58, P < .001$).

Adults at the hot southeast and southwest facing nests fed nestlings more often than parents with northerly oriented nests (orientation: $F_{3,90} = 8.75, P < .001$; date: $F_{1,90} = 9.15, P = .003$; nest type: $F_{1,90} = 0.67, P = .41$; year: $F_{1,90} = 1.23, P = .27$, concealment:

$F_{1,90} = 1.66$, $P = .201$, Figure 6). Parents also increased their feeding rates during periods of higher ambient temperatures (ambient temperature: $F_{1,90} = 3.84$, $P = .05$). The rate at which chicks received food in nests of different orientations were a function of similar responses in female feeding rates (orientation: $F_{3,93} = 7.27$, $P < .001$; date: $F_{1,93} = 11.94$, $P = .001$; nest type: $F_{1,93} = 0.91$, $P = .34$; year: $F_{1,93} = 0.50$, $P = .48$; ambient temperature: $F_{1,93} = 4.39$, $P = .04$; concealment: $F_{1,93} = 9.68$, $P = .33$, Figure 6), and male feeding rates (orientation: $F_{3,93} = 8.24$, $P < .001$; date: $F_{1,93} = 12.53$, $P = .001$; nest type: $F_{1,93} = 0.28$, $P = .60$; concealment: $F_{3,93} = 3.64$, $P = .05$; ambient temperature: $F_{1,93} = 9.23$, $P = .003$, Figure 6). Parental feeding rate was not related to nest predation risk (feeding rate: $\chi^2_1 = 0.25$, $P = 0.61$; severity: $\chi^2_2 = .001$, $P < 0.99$; date: $\chi^2_1 = 1.62$, $P < 0.20$). Nestling feeding rates were not related to year, burn severity or nest exposure (all $p > .2$) and so these were removed from all models.

DISCUSSION

One of the most important choices any animal makes is where to breed, as it affects many of an individual's subsequent reproductive choices (Orians and Wittenberger 1991). Natural selection should lead to the evolution of nest-site preference when there are fitness consequences associated with nest sites and a genetic basis for nest site preference (Levins 1968, Jaenike and Holt 1991). In this study I found preferences for nest types and orientations that resulted in parents minimizing their parental care and thermoregulatory costs, while maximizing the growth rate of offspring. Nest site preference should evolve in response to selection conferred by nest microclimate and, at equilibrium, preferences

should reflect adaptive decisions assuming that there is a genetic basis for nest site preference.

Studies using doubly labeled water have shown that parents spend as much energy incubating as when feeding nestlings (Mertens 1980, reviewed in Williams 1996) and that metabolic costs are strongly dependent on temperature (Tinbergen and Williams 2002). High nest temperatures are known to increase water loss and metabolic costs to incubating parents (Haftorn and Reinertsen 1985, Dawson and O'Connor 1996) requiring more frequent forays from the nest in search of food and water (Conway and Martin 2000a). As predicted, female juncos selecting hot south-facing nests appear have been forced to reduce nest-attentiveness as a consequence of thermal stress associated with direct insolation of south-facing nest sites.

Low nest attentiveness increases the exposure of eggs to high radiant heat loads that can result in rapid overheating and embryonic death (Barrett 1980, Bennett et al. 1981) and while altricial nestlings thermoregulate effectively at temperatures as high as 40° C (Olson 1991, Visser 1998), nestlings can withstand only relatively short periods of heat stress without becoming dehydrated (Visser 1998). Yet, reduced nest attentiveness by juncos at hot nest sites did not result in increased mortality of embryos and nestlings, nor did young raised in the hot, south-facing nest sites experience reduced growth rates. While nestlings may have suffered unmeasured costs associated with hot, south-facing nests (e.g. reduced immune function, developmental anomalies) parent juncos appear to have offset increased thermoregulatory costs and/or water loss to offspring by increasing nestling provisioning rates (see Hoset et al. 2004). Increased energetic demands on parents during incubation are known to lead to delayed reproductive costs such as lower

adult survival (Visser and Lessells 2001, de Heij et al. 2006) and depressed parental performance later in the same and subsequent breeding attempts (Reid et al. 2000, Hanssen et al. 2005, Parejo and Danchin 2006). Increased brood-rearing costs can also result in reduced adult survival or future fecundity (Dijkstra et al. 1990, Golet et al. 1998, Milonoff et al. 2004). Nest microclimate, then, can have important fitness consequences for parent juncos and selection should favor preference for nest sites that minimize fitness costs to parents.

While nest orientation did not affect nestling growth rates, junco young raised in colder cavity-type nests did experience retarded feather and skeletal growth as well as slower rates of mass gain. Nestling birds are faced with a tradeoff between devoting energy to growth or to thermoregulation (Dawson et al. 2005), and in altricial species it is likely that the thermal environment of the nest site influences the nature of this trade-off. Overly cold or hot nest microclimates may force offspring to invest more energy in thermoregulation, at a cost to the development of other traits that will affect fitness such as body size or immunocompetence (Schew and Ricklefs, 1998, Conway and Martin 2000b). Such costs may be especially important in retarding nestling growth during the early nestling period when young are unable to thermoregulate. Relatively warm nest sites likely reduce thermoregulatory costs allowing more rapid growth (see Visser 1998). Indeed, experimental heating of nest cavities increases nestling growth rates in Tree Swallow (*Tachycineta bicolor*, Dawson et al. 2005), an obligate cavity nesting species.

Growing evidence suggests that conditions during nestling development influence the subsequent performance of the bird as an adult, such as its clutch size (Haywood and Perrins 1992) and subcutaneous fat accumulation prior to autumn migration (Merilä and

Svensson 1997). The condition of passerine birds at fledging is also positively related to their probability of recruitment (Gebhardt-Henrich and Richner 1998) and yearly survival (Tinbergen and Boerlijst 1990, Gebhardt-Henrich and Richner 1998, McCarty 2001). Faster development is also an advantage for offspring because it reduces the period of exposure to nest predators (Lack 1968, Keller and van Noordwijk 1994, Conway and Martin 2000a). Collectively, these findings suggest that the thermal regime of nest sites can have important fitness consequences for nestling juncos.

As a group, cavity-nesting passerines have been observed to have slower growth rates than open-cup nesting species (Case 1978, Robertson, 1988). It has been posited that reduced nestling growth rates in cavities could have evolved as a covariate of larger clutch sizes permitted by lower predation rates (Martin and Li 1992). In this study, however, there was no difference in nest predation rate, clutch size, nest attentiveness or parental feeding rates between cavity and exposed nest types and among nest orientations. Furthermore, nest predation risk was unrelated to nest concealment or nest visitation rate that have previously been linked to increase nest predation risk (Martin et al. 2000a,b, Ferretti et al. 2005). These results support the hypothesis that the generally slower growth rates observed in cavity-nesting birds relative to open-cup nesters may not be an adaptive strategy that minimizes parental care costs in the presence of relaxed predation pressure, but rather an energetic constraint imposed on young as a result of nest microclimate.

Results of this study demonstrate that variation in nest-site selection (choice of nest orientation and nest type) lead to variation in nest microclimate and that relatively hot and cold nest sites were associated with costs to parents and offspring, respectively.

While co-variation of the putative selection pressure (direct insolation) with the predicted responses in nestling growth rates and parental care strengthen inference, the correlative nature of these results cannot allow definitive conclusions about the effect of nest microclimate in shaping parental investment and nestling growth rates. Preference by juncos for exposed, north-facing nest sites is likely to have evolved because the thermal environment at these sites minimizes costs associated with parental care (nest attentiveness and chick feeding) while maximizing nestling growth rates. It appears that nest microclimate can exert selective pressure upon nest-site preferences and so shape the evolution of nest site preferences in birds.

Much of the work on the effect of temperature on avian growth and parental care has come from studies on precocial birds nesting in cold climates (Dawson et al. 2005), yet nests eggs and chicks of ground-nesting birds are highly susceptible to hyperthermia because they are located within the boundary layer (With and Webb 1993). Results of this study illustrate that both temperature extremes are relevant to thermoregulation as predicted by theory (Conway and Martin 2000b). Behavioral solutions to mitigating the effects of harsh nest microclimates (e.g. shading, feather wetting and shivering) may be sufficient in some habitats, but temperature extremes may create microclimates too severe to be ameliorated by parental behavior. Future research on the adaptive significance of nest site preference will benefit by recognizing that nest-site selection can respond to multiple agents of selection (Lloyd and Martin 2004) and result from microclimatic costs to both parents and offspring that occur during different developmental stages.

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FIGURE LEGENDS

Figure 1. Estimated marginal means of percent ground cover and estimated mean percent canopy cover (\pm SE) across burn severities and two postfire years. Yearly means for canopy cover were pooled for presentation. Canopy cover was inversely related to burn severity in both postfire years. Herbaceous ground cover was inversely related to burn severity in the first postfire year but similar across severities during the second postfire year.

Figure 2. Nest orientations of Dark-eyed Junco nests monitored during 2004-2005.

Figure 3. (A) Estimated hourly marginal means of operative environmental temperature at Dark-eyed Junco nests as a function of nest orientation. (B) Estimated hourly marginal means of operative environmental temperature recorded at Dark-eyed Junco nests as a function of nest type (cavity vs. exposed).

Figure 4. Growth rate of nestling Dark-eyed Juncos as a function of nest type. Points represent the marginal means (\pm SE) of residuals from a logistic curve fit to the entire data set, averaged among nestlings within a nest and within cavity and non-cavity nests.

Figure 5. Female incubation behavior of Dark-eyed Juncos as a function of nest orientation. Data represent estimated marginal means \pm SE. Nest attentiveness (% of mid-day female is sitting on the nest) is greater for females incubating north-facing nests.

Figure 6. Chick feeding rates (feeding trips per chick per hour) as a function of nest orientation. Bars represent estimated marginal means \pm SE. Parents fed chicks in south-facing nests with greatest frequency.

Figure 1.

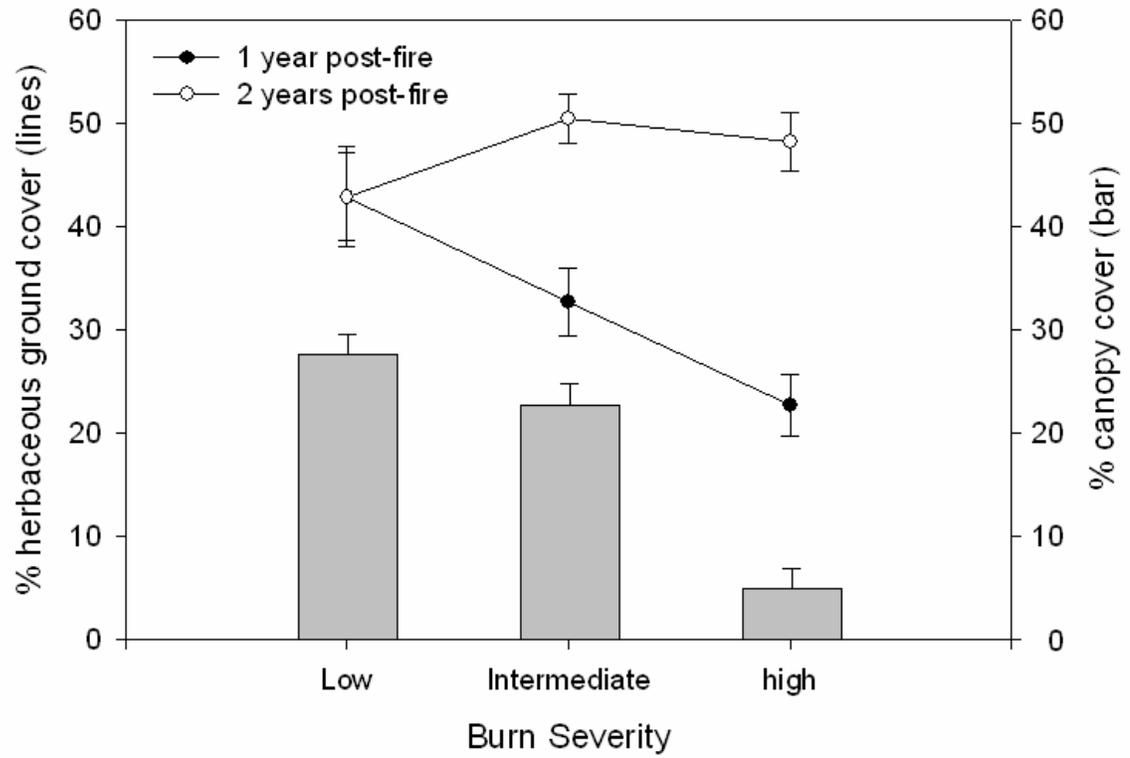


Figure 2.

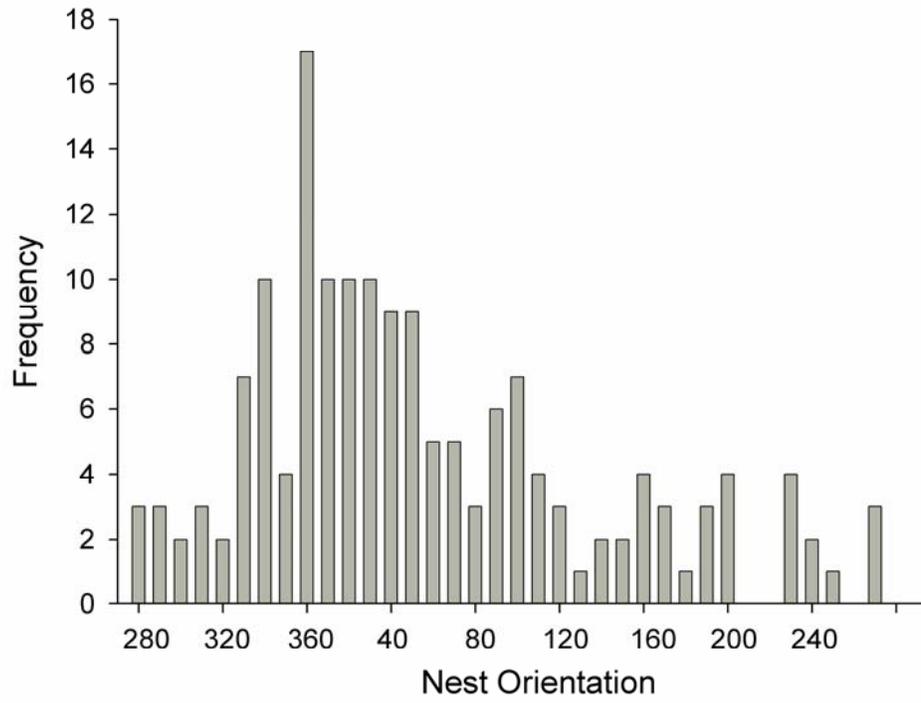
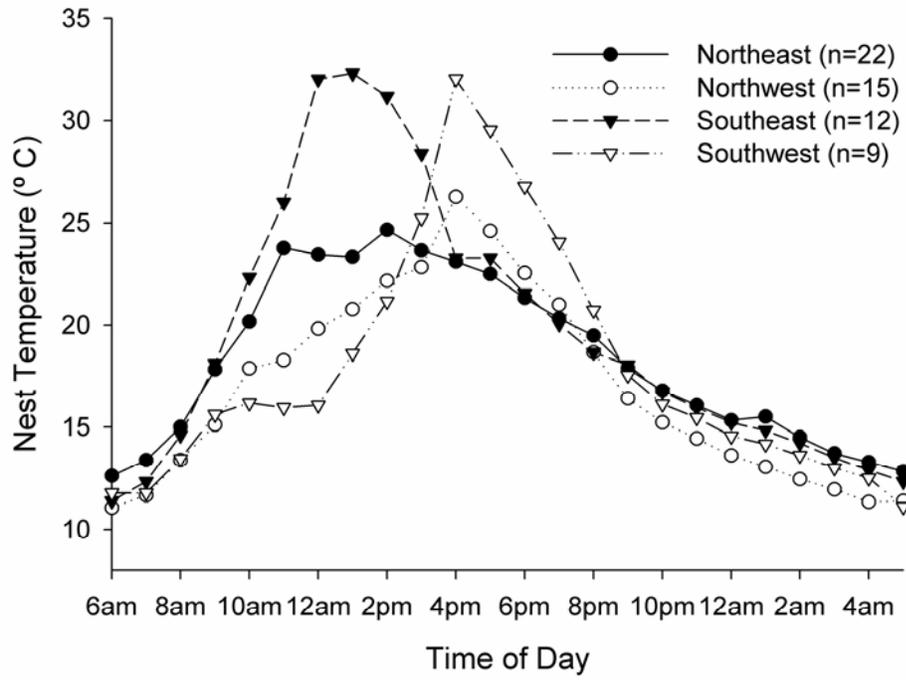


Figure 3.

A)



B)

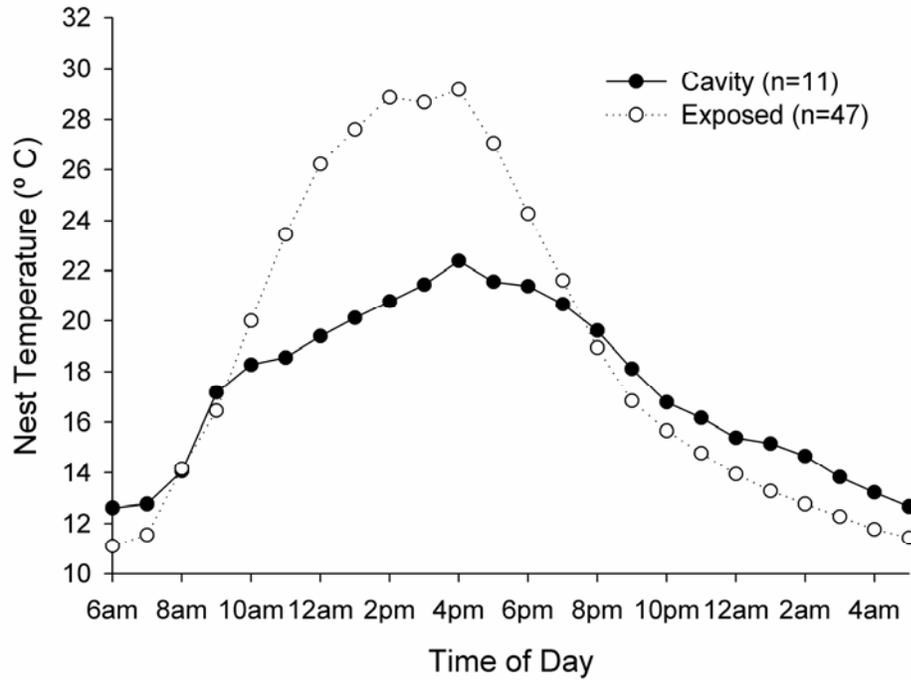


Figure 4.

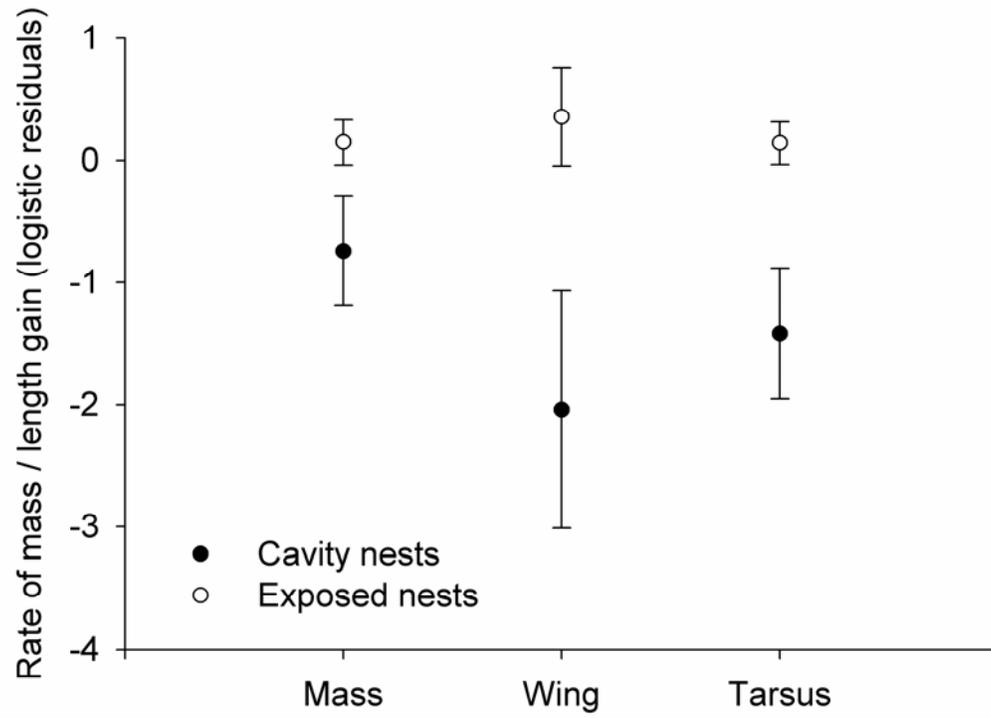


Figure 5.

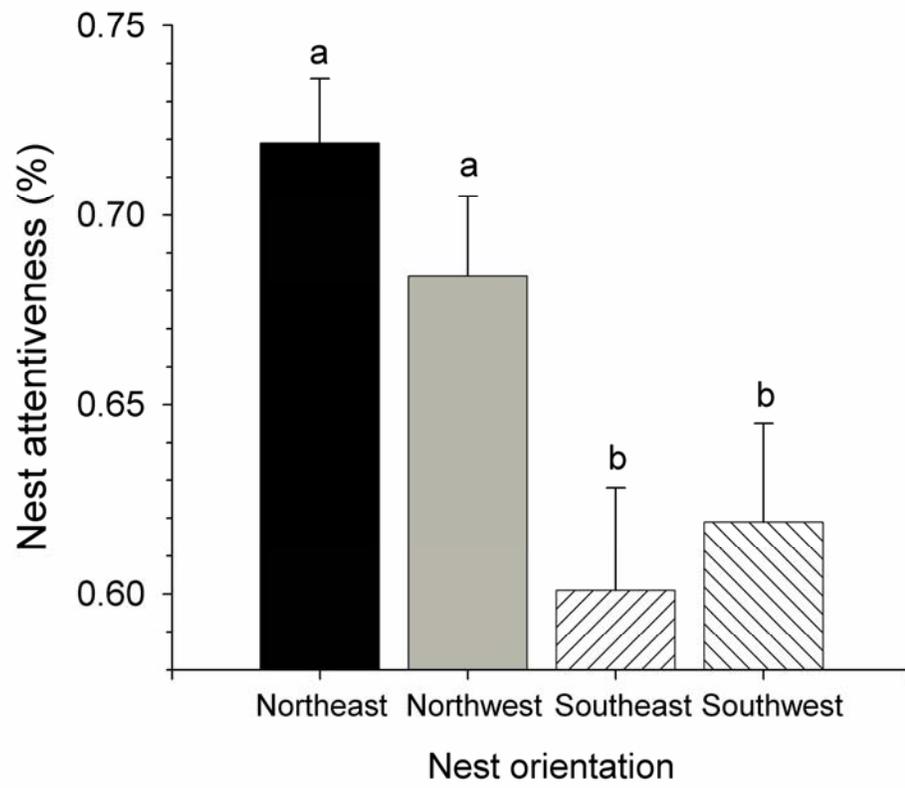
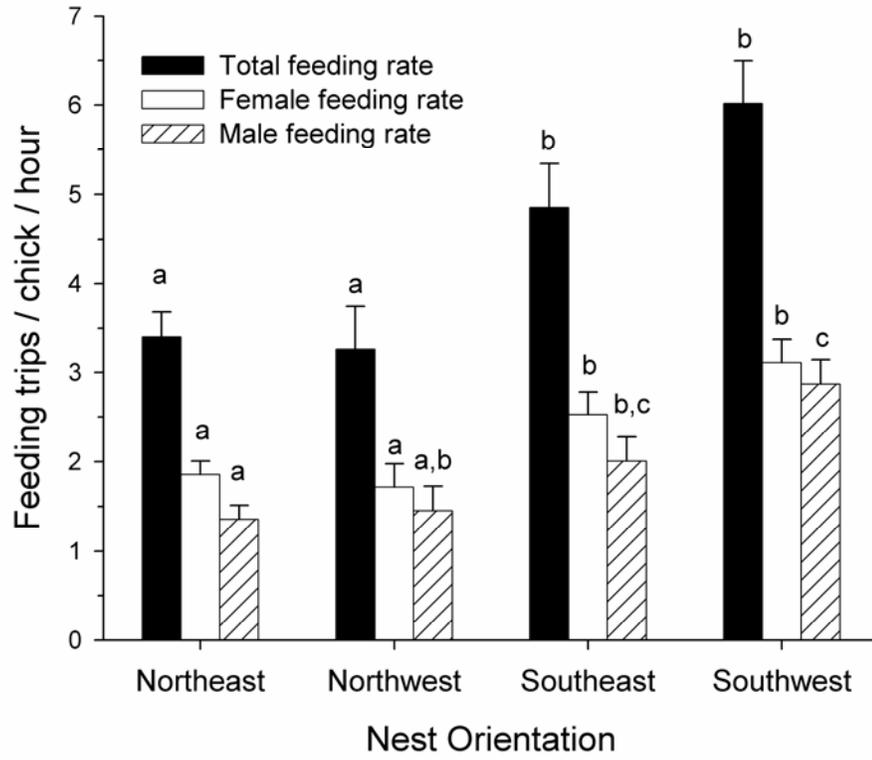


Figure 6.



CHAPTER 4

PLASTIC EXPRESSION OF AVIAN REPRODUCTIVE LIFE-HISTORY

TRAITS: THE IMPORTANCE OF FOOD VS. PREDATION

ABSTRACT

Food limitation and nest predation have garnered much attention in explaining observed variation in life-history traits in birds. Yet, single-factor experiments have been unable to determine the relative importance of food and predation in shaping the expression of life-history traits in birds. I report on the importance of food limitation versus nest predation on the expression of plastic life-history traits in Dark-eyed Junco (*Junco hyemalis*) using a natural experiment generated by the passage of wildfire. Junco clutch size was primarily determined by habitat-specific and seasonal changes in food availability, while nest predation risk shaped egg laying decisions when food was extremely limited. Conversely, nestling growth rates were primarily determined by habitat-specific, seasonal changes in nest predation risk, but were mediated by food availability. Results illustrate that food is more important than environmental risk of nest predation in shaping the expression of clutch size. This provides intraspecific evidence supporting Lack's original contention that, while growth rates are limited by food availability, predation is the primary selective factor shaping fast developmental rates in birds. These results also demonstrate that birds assess and respond to variation in nest predation risk and food availability at fine temporal and spatial scales, and that both factors play an important role in the expression of avian reproductive strategies.

INTRODUCTION

Life-history theory is crucial for how we view fitness and gain predictive power in biology (Searns 1992). Its central focus is in understanding the underlying causes of variation in clutch size and other life-history traits (Roff 1992, Stearns 1992). Food limitation has been used to explain observed variation in life-history traits in birds (Lack 1947, reviewed in Martin 1987). Where food is limited, parents may reduce the number of young they attempt to raise because of a greater risk of mortality from starvation or because of impaired growth that can affect survival after fledging (Lack 1947, Martin 1987, Saether 1994, Martin 1995). Another evolutionary force that has been considered to influence life-history evolution is nest predation, which is the primary source of reproductive mortality in birds (Ricklefs 1969a, Martin 1993). Greater risk of nest predation is predicted to favor smaller clutch size (Skutch 1949, 1976; Cody 1966, Ricklefs 1969a, Slagsvold 1982, 1984, Martin et al. 2006) allowing more energy for renesting attempts following failure (Foster 1974, Slatkin 1974, Slagsvold 1982, 1984, Bulmer 1984). If birds adjust their clutch size or other reproductive life-history traits to optimize the trade-off between food availability and nest predation, then both factors could interact to shape the expression of reproductive strategies (Martin 1995). Clear tests of the relative importance of food and predation in shaping the expression of reproductive life-history traits are lacking, however.

Population-scale experiments examining the effects of food limitation and predation on terrestrial vertebrates have focused on one limiting factor at a time and most experiments on birds have examined food (Newton 1998). These experiments have demonstrated that experimental increases in food supply (Martin 1987, Boutin 1990,

Newton 1998, Zanutte et al. 2003) or reductions in predator pressure (McCleery et al. 1996; Fontaine and Martin 2006) can each have an independent, positive influence on annual reproductive success in birds. Because most food supplementation experiments have been conducted on species that experience relatively low levels of nest predation, such as cavity nesters (Newton 1993, 1998), presumed responses to increased food may be overemphasized. Moreover, if reproductive effort is relatively fixed (e.g. Wilbur 1977, Sinervo and Licht 1991, Boggs and Ross 1993), natural food availability is already high, or the timing of food supplementation occurs after investment has already been decided by parents, then individuals may not increase effort with additional food (Martin 1987, Martin 1995). Food availability and nest predation risk may vary over short temporal and spatial scales within habitats and may have the potential to simultaneously shape the expression of individual life history traits if animals are capable of continuously assessing environmental variation in these factors. A compelling test of how food and predation shape the immediate expression of reproductive life-history traits should examine responses to dramatic but naturally occurring temporal and spatial variation in food and predation pressures to which species are known to have evolved.

Here, I report on the importance of food limitation versus nest predation on the expression of plastic life-history traits in Dark-eyed Junco (*Junco hyemalis*) using a dramatic natural experiment generated by the passage of wildfire. Wildfire is the primary disturbance that has shaped the evolution and dynamics of floral and faunal communities throughout western North America (Habeck and Mutch 1973, Agee 1993, Arno and Allison-Bunnell 2002). Fire has also shaped the local distributions of species by creating a mosaic of patch types when fire severity and extent vary over space (Brawn et al. 2001,

Platt and Connell 2003, Turner et al. 2003). The Dark-eyed Junco is primarily a ground feeding, open-cup nesting songbird that occurs in abundance across all fire severities (Smucker et al. 2005), and so is likely to have evolved plastic strategies for dealing with the dramatic temporal and spatial heterogeneity found in postfire environments. Data suggest that the abundance of potential junco nest predators such as chipmunks, squirrels and deer mice appear to be lowest at moderate severity (Kreftin & Ahlgren 1974, Stuart-smith and Hayes 2003, Robertson, unpublished data), so nest predation risk could differ across post-fire habitats. Given the dramatic effects of fire in removing living and decaying biomass and the spatial variability in fire severity, the vegetative and animal prey available for ground-feeding birds is likely to decrease with increasing fire severity during the first postfire year before vegetative succession has occurred and to recover with the succession of vegetation. Consequently, if food and predation gradients exhibit independent across-severity patterns, robust predictions can be made regarding the relative importance of food limitation and nest predation risk in shaping the expression of a suite of plastic life-history traits (Figure 1). In addition, seasonal patterns in nest predation risk and food availability have the potential to shape life-history traits.

I examined a suite of life history traits that included clutch size, incubation period, and nestling period. Greater food limitation is should favor smaller clutch sizes, but also shorter incubation and nestling periods resulting from constraints on parental food availability that subsequently limits nest attentiveness (Weathers and Sullivan 1989) and adult food allocation to young (Lack 1954, 1968, Walsberg 1983, Murphy and Haukioja 1986, Nur 1988, Lindén and Møller 1989, Daan et al. 1990, Williams 1996). Higher predation risk also favors smaller clutch sizes (Skutch 1949, Slagsvold 1982) as well as

shorter developmental periods which reduce accumulating daily risk of predation (Bosque and Bosque 1995, Remeš and Martin 2002). While reduced food availability and greater environmental nest predation risk predict identical responses in life-history traits, contrasting across-severity patterns in the expression of these life-history traits should be observed if food limitation or nest predation is the stronger selective force in shaping the plastic expression of an individual trait. Consequently, I examine across-severity and seasonal patterns in junco food availability and nest predation risk and then examine how the expression of life-history traits co-vary with the sources of selection predicted to favor the expression of those traits.

METHODS

Study area

This study was conducted in 2004-2005 within the boundaries of the 2,850-ha Black Mountain fire of 2003 in the Lolo National Forest near Missoula, Montana. The study area is a low- to moderate-elevation site dominated by mixed-conifer forest stands of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*) and western larch (*Larix occidentalis*). I established a 300-ha subplot to use as a focal study area based upon its narrow elevation range (~4200-4400 m) and the presence of patches that burned at different burn severities.

Burn severity of forest patches was defined based on a modified version of the composite burn index (CBI, Ryan and Noste 1985, Key & Benson 2001): (1) *Low severity*—Light charring with up to moderate consumption of downed fuels including litter and duff. Regenerated herbs and grass dominate understory. Shrubs and saplings

show little mortality. Overstory not scorched or blackened, and tree charring remains < 2m; (2) *Intermediate severity*—Deep char, largely consumed small fuels litter and duff. Increased densities of new serals (fireweed, lodgepole pine), but some pre-fire herbs and shrubs persist. Most tree crowns blackened or largely scorched, a few green crowns remain; (3) *High severity*—Major portions of large downed fuels litter and duff consumed, substantial amounts of exposed mineral soil. Pre-fire herbs and shrubs essentially absent, low-density patches of seral species occupy understory. Significant portions of overstory consumed including most fine branching in crowns.

Nest predation

Field assistants monitored each junco territory for the entire breeding season and searched full-time for all nesting attempts from late April to mid-August 2004 and 2005, using behavioral cues to locate nests initially. To avoid observer bias, technicians alternated searching for nests individually and in small teams and searched plots for nests by holding effort constant across burn severities. Most nests (68% of 168) were located during nest building, egg laying or incubation. Nests were monitored regularly (minimum of every 3–4 days) and noted as active, failed, or fledged. Nests were visited every day during the laying, incubation and nestling periods, if necessary, in order to determine the exact day of clutch initiation, hatching and fledging. Fledging was confirmed when we sighted fledglings or heard begging calls by fledglings and observed parents with food. A nest was considered successful if at least one young was observed as a fledgling or if the final nest-feeding visit suggested a fledging event. A nest was considered unsuccessful if no nestlings were located, adults did not scold when we were close to the nest site, the

nest was empty before the expected fledge date, or if a renesting attempt was located within the territory within 5 days of completion of a previous nesting attempt.

Characteristics of nest sites were measured within two weeks of the completion of a nesting attempt. To control for the effects of nest concealment on nest depredation, nest concealment was quantified by estimating the percentage of each nest that was visible from a distance of 1m from each of the four cardinal directions and from directly above. All five measurements were averaged, yielding a single index of concealment for each nest. Because the effect of fire severity on nest predator communities may depend on the scale at which severity is assessed, I estimated the dominant burn severity of nest-centered circular plots with 50- and 100-m radii.

Reproductive data were analyzed using the methods recommended by Shaffer (2004). I estimated daily nest predation rate (the probability a nest will be predated on a single day) with a logistic-exposure model using PROC GENMOD (SAS Institute 1999), a binomial response distribution, and the link function defined by Shaffer (2004). I tested for differences in daily predation probability among burn severities using a chi-square goodness-of-fit test. Birds in seasonal environments may exhibit within-season variation in nest success (Nilsson 1989, Hochachka 1990) attributable to food or predation and predation risk. Moreover, seasonal changes in predation risk may be related to nest concealment. Consequently, variables representing date and nest concealment were also included in the model examining variation in nest predation risk. Estimates and their confidence limits were back transformed from the logit scale for presentation ($\text{proportion} = e^{\text{estimate}} / [1 + e^{\text{estimate}}]$). I used $\alpha = .05$ as the level of statistical significance.

For each junco nest I determined clutch size, clutch completion date and nest initiation date using maximum clutch size and assuming one junco egg laid per day (Nolan et al. 2002). Clutch size was taken from all nests found prior to hatching because no partial nest losses were observed over the course of this study. Incubation periods were calculated as the number of days from the first day of incubation to the day on which all eggs hatch. Nestling period was calculated as the number of days after hatching until all chicks left the nest on their own. I tested for differences in clutch size, incubation and nestling periods between burn severities, within each breeding season, and between the first two post-fire years using ANCOVA. Year, severity and an interaction were included as fixed effects while nest initiation date was included in the model as a covariate. Clutch size was used as a covariate in analysis of nestling period.

Food availability

Because Dark-eyed Junco is a ground-foraging species (Nolan et al. 2002), I focused sampling efforts on the forest floor. Parents eat primarily seeds and arthropods, but young are fed exclusively arthropod prey, so availability of this resource is likely to shape developmental rates. In order to estimate how food availability differs across burn severities and within breeding seasons I sampled terrestrial arthropods during three sampling periods evenly spaced across the breeding season: 1) during early May when females were initiating their first clutch; 2) during late July, the peak of the breeding season after the typically wettest summer month of the summer; and 3) during late July when clutches were no longer initiated, but nestlings and fledglings were still being fed. I randomly selected points within the study area at which to collect arthropods in pitfall

traps, excluding any points that fell on rock outcrops, where it was impossible to bury the traps, or within 50 m of a road or trail, where the traps could be seen or disturbed by people. I continued sampling random points until I located 23 points that were categorized as low, moderate, and high-severity. At each sampling point I installed a crosswise array of five traps at 1-m intervals. Each trap consisted of a 10-oz, white, plastic cup buried in the soil so that the 8-cm opening was level with the ground surface. I filled each trap halfway with a killing solution of unscented castile soap and water and ran the traps during a sampling period of five days each on the same Julian dates: 1) first clutch initiation (days 121-125); 2) mid-season (days 171-175); and 3) end of breeding season (days 213-217). At the end of each sampling period, the contents of all five traps at each point were pooled, fine-sieved, and transferred to Whirl-Pak™ bags containing 95% ethanol. I always collected samples from arrays in the same order and time in which they were placed. Arthropods >3 mm in length were oven dried (60°C for 4 h) and weighed. Beetles > 2.0 cm were considered unlikely prey items for juncos due to their size and were excluded from analysis. Results were analyzed using simple descriptive statistics.

RESULTS

Nest predation risk and reproduction

Considering only first nesting attempts (initiated before 1 June of each year), the nest initiation date of pairs did not differ among patches of different burn severity (burn severity: $F_{2,58} = 1.83$, $P = 0.17$; year: $F_{1,58} = 2.08$, $P = 0.15$). Throughout the course of the study, juncos continued to reneest following failed and successful attempts until either two

broods were produced (individual pairs re-nested up to five times) or until mid-July, when nest initiations ceased.

We located 168 nests, which represented 1745 exposure days. Daily nest predation probability was significantly lower at intermediate severity plots than in the other two treatments at the 50-m scale ($\chi^2_1 = 10.78$, $P = 0.001$, Figure 2a), and was not significantly different between low- and high-severity patches ($\chi^2_1 = 0.001$, $P = 0.79$). Daily nest predation probability did not differ significantly among severities at the 100-m scale ($\chi^2_2 = 4.89$, $P = 0.09$), and so all severity data hereafter refers to the 50-m scale. There was no significant difference in daily nest predation probability between postfire years ($\chi^2_1 = 2.99$, $P = 0.083$). Daily nest predation probability increased as the breeding season progressed in both years ($\chi^2_1 = 3.81$, $P = 0.051$, Figure 2b), with no significant difference in slope between years ($\chi^2_1 = 1.04$, $P = 0.31$). Nest concealment did not explain significant variation in daily nest predation rate ($\chi^2_1 = 0.92$, $P = 0.34$).

Food availability

As predicted, terrestrial arthropod biomass was inversely related to burn severity during the first two sampling periods in the first postfire year while biomass was more similar among severities at the end of the breeding season (Figure 3a). In the first postfire year, arthropod biomass was low in early May when first nests were initiated, but rose dramatically to a peak in June. Arthropod biomass was generally higher during the second postfire year, especially during May (Figure 3b), but burn severity was not clearly related to arthropod biomass.

Clutch size and developmental rates

There was a significant interaction between year and nest initiation date in explaining clutch size ($F_{1,94} = 22.29$, $P < 0.001$) so each year was analyzed separately. Clutch size increased with nest initiation date during the first postfire breeding season ($F_{1,34} = 14.99$, $P = 0.001$), and was greater at intermediate severity than at low and high severity ($F_{2,34} = 5.20$, $P = 0.01$, Figure 4). Conversely, clutch size decreased with nest initiation date across the second postfire year ($F_{1,68} = 5.02$, $P = 0.03$) but did not differ among severities ($F_{2,68} = 0.27$, $P = 0.76$).

There was no interaction between year and initiation date in explaining nestling and incubation periods and so I removed the interaction from these models. Nestling periods decreased as the breeding season progressed during both the first and second postfire breeding seasons ($F_{1,45} = 11.59$, $P = 0.001$) and were longer at higher burn severities in the first postfire year (burn severity: $F_{2,45} = 6.79$, $P = 0.002$; year: $F_{1,45} = 0.42$, $P = 0.52$, year by burn severity: $F_{2,45} = 6.26$, $P = 0.004$, Figure 5). Incubation periods declined throughout both breeding seasons and did not differ among severities (Initiation date: $F_{1,16} = 4.575$, $P = 0.048$; year: $F_{1,16} = 0.051$, $P = 0.82$; burn severity: $F_{2,16} = 0.75$, $P = 0.49$; year by initiation date: $F_{1,16} = 0.66$, $P = 0.43$, Figure 6).

DISCUSSION

Because animals live and reproduce in changing environments (Endler 1986) within-individual phenotypic plasticity represents one important means by which populations can track sources of selection that often vary dramatically in time and space (Via 1993).

If variable environmental conditions are rapid but predictable in ecological time, selection should favor the evolution of plasticity in life-history traits that maximize fitness in different environments (Schmalhausen 1949, Bradshaw 1965). Previous studies have shown that birds are capable of altering reproductive life history traits in response to (1) differences in nest predation risk across habitat gradients (Ferretti et al. 2005), (2) year of study (Julliard *et al.* 2005), (3) experimentally induced spatial variation in predator abundance (Fontaine and Martin 2006), and (4) spatial and temporal variation in food availability (reviewed in Martin 1987). Results of this study suggest that parent birds are capable of simultaneously assessing both spatial and temporal variation in predation risk and food availability and of altering their investment in reproductive components accordingly. Furthermore, it appears that the link between food availability and nest predation in shaping reproductive strategies is complex and trait-dependent.

Food limitation has widely been considered to be the major determinant of clutch size in birds (Lack 1947, reviewed in Martin 1987). Previous studies demonstrate that food supplementation increases clutch size (Arcese and Smith 1988, Hörnfeldt and Eklund 1990, Nager et al. 1997, Korpimäki and Wiehn 1998, Preston and Rotenberry 2006), and that the greatest effect of food on clutch size occurs during periods of low natural food availability (Boutin 1990, Svensson and Nilsson 1995, Nager et al. 1997). Results of this study show that only when food availability was at its minimum and females laid extremely small clutches did environmental risk of nest predation shape female decisions about how many eggs to produce. The dramatic seasonal increase in clutch size observed during the first postfire year paralleled dramatic seasonal increases in food availability and spanned the entire range of known clutch sizes in this species (2-

5, Nolan et al. 2002). Thus, while parental assessment of spatial variation in nest predation risk did appear to influence junco clutch size during the first postfire year, results suggest that food availability actually mediates female responses to perceived predation risk.

Seasonal declines in clutch size during the second postfire when food availability was relatively high are consistent with predicted responses by parents to the seasonally increasing nest predation rate (Cooke and Findlay 1982, Elridge and Krapu 1988). Yet, seasonal declines in clutch size have been documented for several bird species (e.g. Hochachka 1990, Crick et al. 1993, Christians et al. 2001), and have generally been attributed either to (1) individuals timing their breeding to match seasonally deteriorating food supplies that can reduce offspring survival, or (2) later breeding by individuals in poorer breeding condition (Brinkoff and Cavé 1997). Junco clutch size variation during the second postfire breeding season, however, is inconsistent with the predicted responses to the observed slight mid-season peak in food availability. Still, it is not possible to conclusively attribute seasonally declining clutch size during the second postfire year to the effects of increasing nest predation risk, and alternative mechanisms such as parasite loading may also play a role in shaping seasonal variation in clutch size (Møller 1994)

It is generally believed that predation is the most important selective factor in the evolution of fast growth rates in altricial birds (Lack 1968, Ricklefs 1969a, Skutch 1976, Case 1978, Bosque and Bosque 1995). Lack (1968) posited that while food supply limits growth, rapid growth rates might have evolved to minimize the length of time that eggs and nestlings are exposed to predators (see also, Ricklefs 1969a, Skutch 1976, Case 1978). Evidence that predation might be a significant factor in the evolution of growth

rates in birds is scant, however, and is limited to comparisons of developmental rates among species (Conway and Martin 2000, Remeš and Martin 2002).

Food availability is known to influence incubation behavior in female-only incubating species because hunger level dictates how long a female can remain on the nest before getting off to forage (Nice 1937, Kendeigh 1952, White and Kinney 1974, Haftorn 1988, Weathers and Sullivan 1989). Shorter off-bouts reduce incubation costs to the female by minimizing the need to rewarm the clutch (Drent 1975, Vleck 1981, Williams 1996) while longer off bouts are known to impair embryo development (Clark and Wilson 1981, Lyon and Montgomerie 1987, Haftorn 1988). Risk of nest predation can also shape nest attentiveness if common nest predators locate nests by observing adult activity near the nest. Juncos in this study exhibited similar seasonal declines in incubation periods in both postfire years, which is most consistent with the idea that they are responding to seasonal increases in predation risk, rather than food, and that predation risk is the primary selective agent shaping the expression of developmental rates. While it has been suggested that smaller clutch sizes may result in shorter developmental periods (Arnold et al. 1987, Martin 1995) due to more efficient incubation, bird species with smaller clutch sizes do not have shorter developmental periods (Martin 1995). Accordingly, the smallest junco clutches in this study actually had the slowest development. While results illustrate no effect of spatial variation of food availability and nest predation risk on incubation periods in this study, detection of any relationship may have been obscured by small sample size.

Juncos also exhibited seasonal declines in nestling periods in both postfire years consistent with responses to seasonal increases in predation risk as the selective agent

shaping the expression of developmental rates. There was no difference in the slope of seasonally declining nestling periods in the first two postfire years as would have been expected if food limitation was a factor constraining female juncos' ability to provision themselves and young. However, nestling periods during the food-limited first postfire year also exhibited a spatial, across-severity pattern consistent with the effects of food limiting the rate of nestling development, and that pattern was not present during the relatively food-rich second postfire breeding season. Consequently, this study provides the first intraspecific data to support the Lack's (1968) original contention that, while growth rates are limited by food availability, predation is the primary selective factor shaping developmental rates in birds.

Results suggest that perceived risk of nest predation can override the effects of food availability in shaping some life-history traits, but not others. While co-variation of the putative selection pressure (i.e., nest predation and food availability) with the predicted response in life-history traits increases inference, the correlative nature of these results cannot allow definitive conclusions about the importance of food limitation vs. predation. Nonetheless, the seasonal and across-severity patterns in clutch size and nestling periods follow predicted patterns based on habitat-specific and seasonal variation in risk of nest predation and of food limitation resulting from the effects of postfire succession and the differential effect of severity in limiting successional processes.

For adaptive phenotypic plasticity to evolve, reliable cues that can indicate the current or future state of the environment must exist (Dodson 1989). A recent predator reduction experiment illustrates that juncos are able to accurately assess their environmental risk of nest predation (Fontaine and Martin 2006), but the cues parent

birds use in this assessment remain unknown. Moreover, the species responsible for individual nest predation events in this study as well as their abundance and predation efficiency across fire-severities is unclear. Squirrels (*Tamiasciurus* spp.) and chipmunks (*Tamias* spp.) are known to be major predators of junco nests in the northern Rockies and are most abundantly found at lower fire severities (Stuart-smith and Hayes 2003). Deer mice are important nest predators to ground nesting birds (e.g. Bradley and Marzluff 2003) and are known to dramatically increase in abundance in the first several years after high-severity in mixed conifer forests (Krefting and Ahlgren 1974). If the relatively high abundance of these two groups of predators increase nest predation risk in low- and high-severity patches, respectively, the spatial distribution of these predators could explain the relatively safer nesting environment found in intermediate-severity patches.

The relative importance of “bottom-up” (resource limitation) and “top-down” (predation) influences in shaping reproductive strategies in birds has been debated for decades (e.g. Lack 1954, Martin 1987, Boutin 1990, Newton 1998, Zanette et al. 2003, Preston and Rotenberry 2006). Results associated with this natural experiment represent some of the most complex and dramatic responses in avian reproductive life history traits to spatial and temporal variation in food and nest predation risk seen to date, and illustrate the importance of both food availability and nest predation risk in shaping avian reproductive strategies. Previous studies have provided have provided insights into how food and predation shape the expression of life-history traits in birds through experimental supplementation of food and reduction of predation risk (Julliard et al. 1997, Doligez and Clobert 2003, Nagy and Holmes 2004, Fontaine and Martin 2006). However, it is unclear how such manipulations reflect natural variation in food or predation risk,

nor if these manipulations fail to concurrently alter the cues animals use to assess current and/or future food availability or predation risk. In fact, many authors have suggested this possibility as an explanation when animals fail to respond to experimental manipulations (e.g. Julliard et al. 1997, Nagy and Holmes 2005, Fontaine and Martin 2006, Preston and Rotenberry 2006). In addition, predation appeared to shape junco clutch size only when food availability was at its lowest level, a result which would be generally undetectable through the use of food supplementation. While controlled field experiments will continue to be an essential tool in understanding how variation in environmental conditions shape life history strategies, natural experiments will remain essential because the cues animals use to assess habitat quality will be less likely to be decoupled from the selective agents that have shaped the evolution of plasticity in reproductive strategies.

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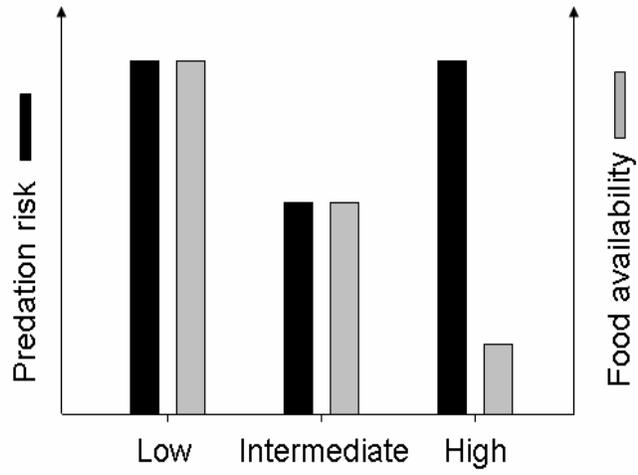
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Figure 1. Predicted nest predation risk and food availability for juncos nesting in patches of different burn severity during the first (A) and second (B) post-fire year.

A)



B)

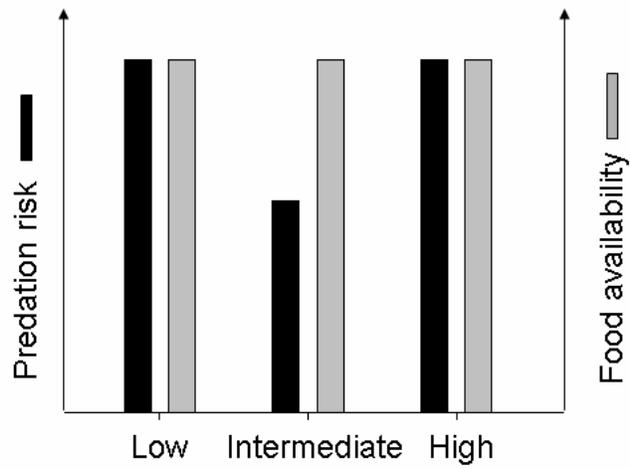
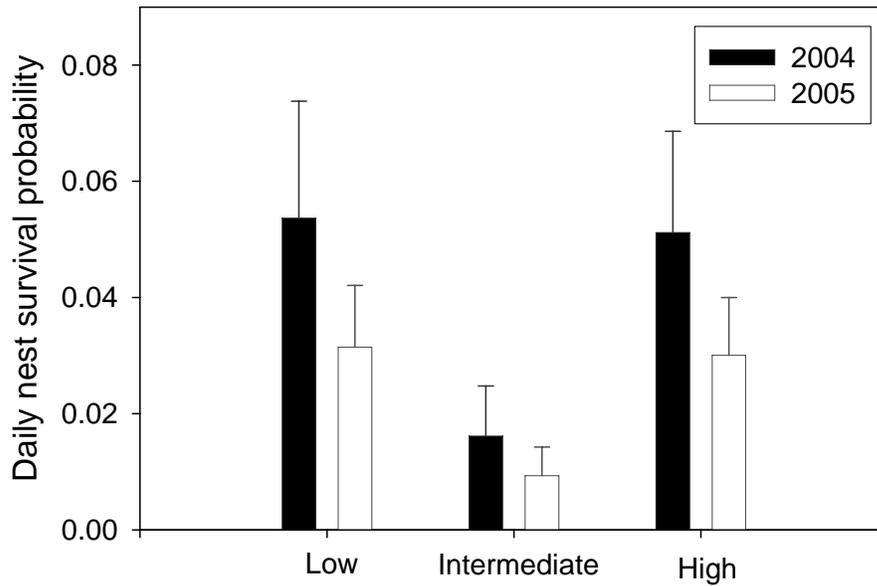


Figure 2. Daily nest predation probability for junco nests located in patches of differing burn severity. (A) Nests in intermediate severity patches experienced significantly lower probability of predation in both of the first two postfire years. Bars represent 95% confidence intervals. (B) Predicted rate of daily nest predation (calculated from the logistic exposure model, \pm SE) for junco nests in the first and second post-fire years.

A)



B)

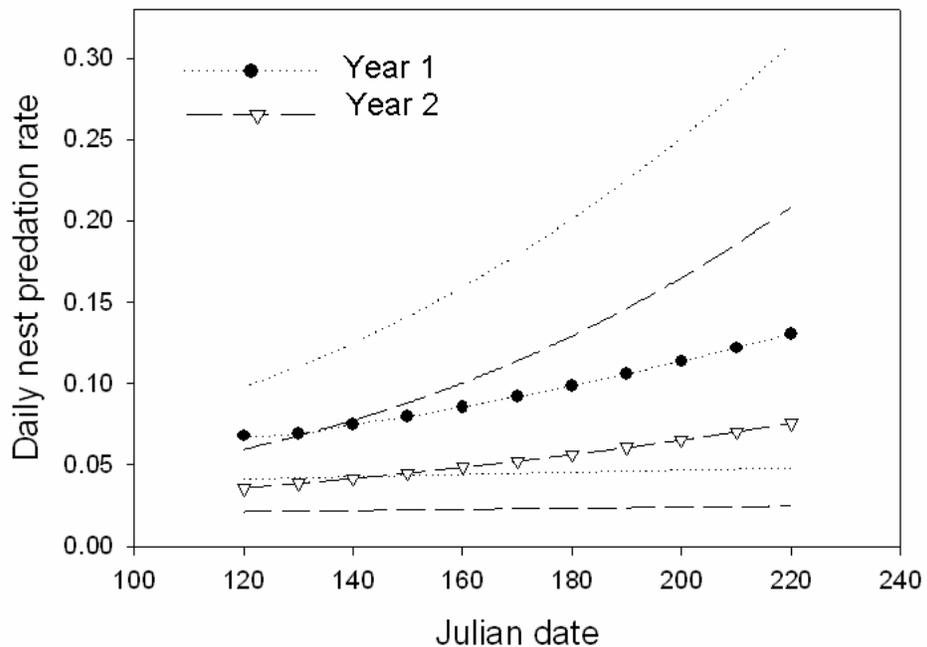
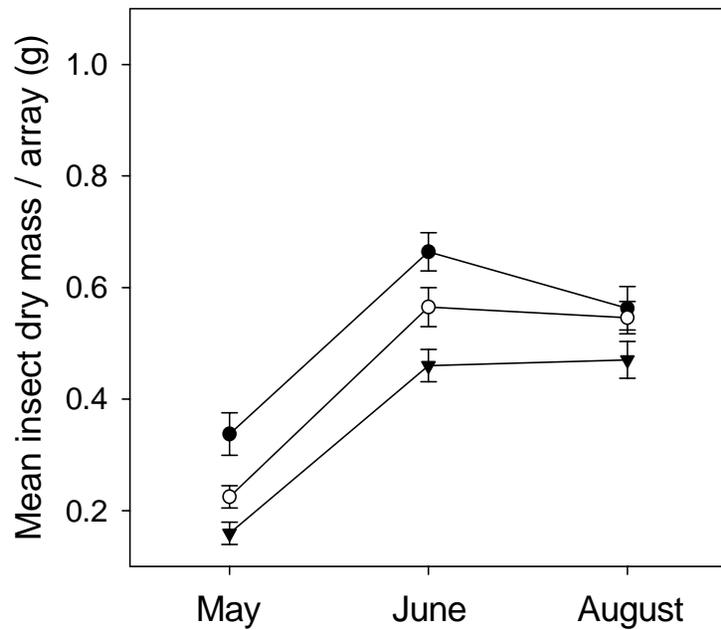


Figure 3. Average terrestrial arthropod biomass sampled at three periods during the junco breeding season in low (solid circles), intermediate (open circles) and high (filled triangles) severity patches (+/- SE). During the first postfire year (A) terrestrial arthropod biomass was inversely related to burn severity in May and June, but biomass was similar across severities throughout the season across the second postfire year (B).

A)



B)

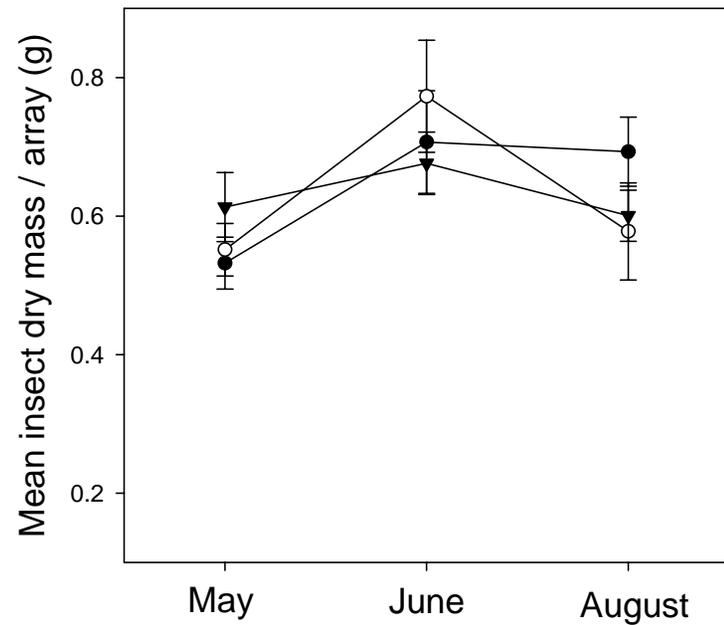


Figure 4. Partial regression of clutch size as a function of nest initiation date and burn severity. Predicted estimates are plotted with one standard error. Clutch sizes for nests built in low- and high-severity patches (year 1) and all burn severities (year 2) are pooled for presentation.

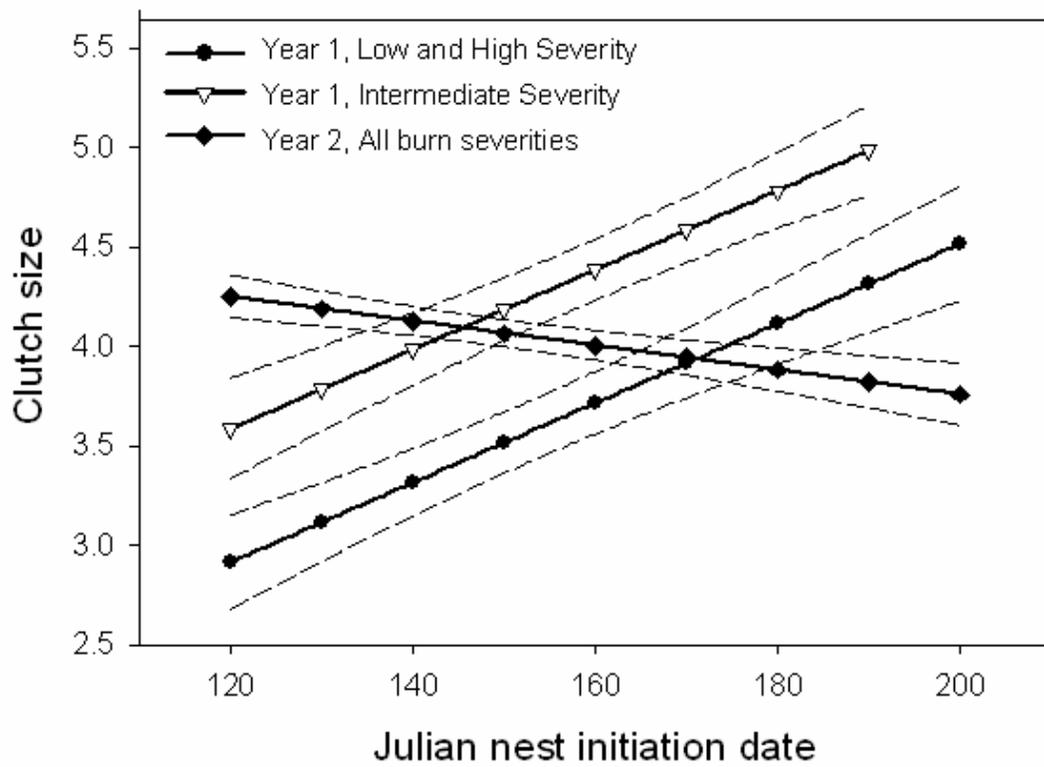


Figure 6. Partial regression of incubation period versus date of the onset of incubation pooled across postfire years. Predicted values are given with 95% confidence intervals for pooled years.

