2003

Avian life-history evolution: Explaining variation among species populations and individuals

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AVIAN LIFE HISTORY EVOLUTION: EXPLAINING VARIATION AMONG SPECIES, POPULATIONS, AND INDIVIDUALS

by

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presented in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

The University of Montana

May 2003

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Date

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Lloyd, John D. Ph. D. May 2003 Wildlife Biology

Avian Life History Evolution: Explaining Variation Among Species, Populations, and Individuals.

Directors: I. J. Ball and Thomas. E. Martin

Explaining the diversity of life history strategies adopted by organisms is a central goal in evolutionary ecology. However, the goal of understanding life history evolution is complicated by the fact that variation exists at many different levels of organization, and the sources of variation at one level often fail to explain variation at another. I explored this problem by examining the causes of life history variation at three levels: among species, populations, and individuals.

First, I used a comparative analysis of 70 bird species to test the hypothesis that sibling competition favors the evolution of rapid development. All three measures of sibling competition (extra-pair paternity, brood parasitism, and hatching asynchrony) covaried with incubation period in the direction expected under the sibling competition hypothesis, but only extra-pair paternity explained significant variation in incubation period after controlling for phylogeny. This suggests that interspecific variation in development may be an adaptive response to the evolutionary pressure of sibling competition.

Life history variation also can arise as a consequence of environmental constraints and hence need not be adaptive. To explore these potential roles of constraint and adaptation, I collected data on life history traits of Chestnut-collared Longspurs (*Calcarius ornatus*) breeding in habitats that differed in nest predation risk. Contrary to the expectations of life history theory, nestlings in the high-risk habitat, which consisted of monocultures of an introduced grass, grew more slowly and had longer post-natal developmental periods than did nestlings in the low-risk, native habitat. In this case, life history variation is not adaptive but instead reflects constraints imposed by the environment, most likely reduced food availability in the exotic habitat.

Averaging life history traits across habitats may mask smaller-scale variation. In particular, variation in nest site choice within a habitat may be an important source of life history variation among individuals. Indeed, I found that Longspurs choose nest sites that created an amenable radiative environment for offspring, and by experimentally manipulating nest orientation I found that the direction a nest faces, by modulating insolation, has a significant effect on growth and development of nestlings.

ACKNOWLEDGMENTS

I have been humbled in the course of completing my doctorate, but I am far wiser now then when I first began at the University of Montana. In this regard, my dissertation must be viewed as a success and I am grateful to all who helped me in this process. For teaching me to think critically about my own work, I thank Tom Martin. Tom has taught me much of what I know about science, and has been a mentor throughout my time in Missoula. Joe Ball has patiently supported my work from the beginning, through all the fits and starts, and has helped me to learn from my mistakes. Joe has worked relentlessly to improve my writing, and for that I am forever in his debt. None of the work described in my dissertation would have been possible without the help of both Tom and Joe, and so throughout the chapters that follow I use the pronoun "we", rather than "I", when describing any actions taken. However, I was the final arbiter of what was left out of and what was included in these chapters, and so any shortcomings or errors are my fault alone.

My friends and labmates Josh Tewksbury, Cameron Ghalambor, Paul Martin, and Alex Badyaev revealed to me the possibilities of ecology and evolutionary biology. I sincerely doubt that a finer and more talented group of graduate students has ever been assembled, and I thank them for tolerating my parasitism. But most of all I thank them for their friendship.

Thank you also to the rest of my graduate committee: Dan Pletscher, Ray Callaway, and Jeff Marks. I know for a fact that they all had better things to do then give me advice and read my proposals, but nonetheless each was generous with time and constructive support.

Victoria Adamski provided support and love at a time when I needed it most, and has been a steadfast partner through it all. I thank her for her patience, and for her unwavering commitment through the many nights and weekends during which I was consumed with writing.

I am not certain if my family ever understood exactly what I was doing as a graduate student, but they always supported me and, at the very least, feigned interest when I told them about my latest results. My parents worked especially hard so that I might have the opportunity to pursue my goals, and for this I dedicate my dissertation to my father, Alex, and to the memory of my late mother, Jacqueline.

PREFACE

On first glance, the chapters presented here appear to focus on somewhat disparate topics. However, they all reflect my attempt to understand the causes of life history variation, albeit at a several different levels of explanation. Chapter I examines the evolution of developmental rates, in particular the role of sibling competition as an agent of selection on avian incubation periods. Chapter II addresses the problem of separating adaptive life history variation from variation induced by proximate constraints by comparing life history traits of populations of Chestnut-collared Longspurs breeding in habitats that differ in predation risk. Chapter III focuses on how individual decisions by female Longspurs about nest placement can produce variation in nestling growth. Together, these chapters address variation in growth and development at three scales of observation; however, each chapter has been written as a separate publication and thus they do not always follow the conceptual framework I have laid out above. The format of each chapter is somewhat different and in some cases information is repeated, especially when discussing methods and study site.

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CHAPTER 1

SIBLING COMPETITION AND THE EVOLUTION OF PRE-NATAL DEVELOPMENT RATES

INTRODUCTION

Developmental rates are an integral component of life history strategies and vary tremendously among species. For example, incubation period can vary more than three-fold among birds with similarly sized eggs (Rahn and Ar 1974). Such extensive variation in the time required to complete development is somewhat of a paradox, because most selection pressures are presumed to favor rapid development (Ricklefs 1993). Williams (1966) suggested that the length of development might vary because of variation in age-specific mortality, and a number of studies have found that species with high juvenile predation rates have more rapid development (Lack 1968; Case 1978; Crowl and Covich 1990, Promislow and Harvey 1990; Bosque and Bosque 1995; Martin 1995, 2002; Remeš and Martin, in press). In contrast, Ricklefs (1968, 1982, 1983, 1993; Ricklefs et al. 1998; see also Werschkul and Jackson 1979) argued that nest predation is not related to developmental rate among birds and that competition among siblings instead is the primary agent of selection on development rate; greater sibling competition favors faster pre-natal development because earlier hatching can provide a competitive advantage over siblings.

Although many studies in a variety of taxa support a role for mortality in the evolution of developmental rate (see above), an influence of mortality does not necessarily negate a potential role of other factors, such as sibling competition. Indeed, Royle et al. (1999) showed that post-natal growth rates of birds were positively related to rates of extra-pair paternity, which should influence sibling competition. Yet, pre- and post-natal developmental rates are genetically independent of one another (Siegel et al. 1968; Ricklefs 1984, 1987; *contra* Lack 1968) and therefore the potential influence of sibling competition on pre-natal development remains unclear. Avian pre-natal development (incubation) should be an ideal period to look for a role of sibling competition because nestling survival hinges upon position in the hatching order in many species; when brood reduction occurs, the last hatched nestling is almost invariably the victim (Mock et al. 1990, Stoleson and Beissinger 1995). Thus, sibling competition should strongly favor shorter incubation periods (Ricklefs 1993).

Here, we use comparative analyses of 70 species of birds to test the potential role of sibling competition on pre-natal developmental period. First, we use a kin-selection approach and compare the length of incubation among species in which siblings are expected to differ in their average genetic relatedness. Theory predicts that the cost of competition to inclusive fitness decreases as the average relatedness of the interacting individuals decreases, and therefore competition among siblings is expected to be more intense when relatedness is low (Hamilton 1964). Briskie et al. (1994) provide empirical support for the connection between competition and relatedness, showing that begging intensity of nestling birds, a measure of sibling competition, increases as the average genetic relatedness among nest-mates declines. Thus, we predict that the length of incubation will be negatively correlated with relatedness if sibling competition is important. We use two indices of average relatedness: the proportion of broods sired by multiple males (extra-pair paternity) and the proportion of broods containing parasitic young (e.g., the result of con- or inter-specific females laying eggs in nests of other females).

We also examine the importance of sibling competition by testing for a relationship between the length of incubation and the degree to which offspring hatch asynchronously. Ricklefs (1993) suggested that parents create asynchronous hatching patterns to minimize sibling competition and thereby allow longer incubation periods that presumably enhance fitness. According to this hypothesis, sibling competition is determined by parental control of offspring hierarchies based on hatching order. Thus, we also test Ricklefs' (1993) hypothesis that the length of incubation increases with increasing hatching asynchrony.

METHODS

We gathered published data on length of incubation, extra-pair paternity, brood parasitism, and hatching asynchrony for as many bird species as we could find in the literature, resulting in a total of 70 species (Appendix A). We also collected data on two potentially confounding variables: egg size and egg predation. We considered only species with a modal clutch size greater than one, as individuals in species laying a single egg per clutch will not experience intrabrood sibling competition. In no case were estimates for all variables available from the same population. When estimates of a variable were available from multiple populations we used the unweighted mean in analyses.

Most studies of avian parentage report the percentage of nestlings in a population that are the product of extra-pair fertilizations, but for this analysis the relevant variable is the likelihood that an individual will be raised among nestmates that are less than full siblings. Thus, using the extensive summaries of avian paternity rates in Schwagmeyer et al. (1999) and Moller and Cuervo (2000) as a starting point, we gathered published data on the percentage of broods containing extra-pair young (e.g., young in a brood sired by a male other than the social mate of the female). Three of the species included in this analysis have social systems in which multiple males and females form stable breeding groups, and for these species estimates of extra-pair paternity will overestimate the average relatedness among siblings within a nest. Thus, for polygynandrous species (*Calcarius pictus*, *Prunella* spp.), we considered the percentage of multiply sired broods rather than the percentage of extra-pair broods. However, for the sake of brevity we refer to this variable as "extra-pair paternity" throughout the text. We excluded estimates of parentage that came from electrophoretic analyses unless the authors corrected estimates as in Westneat et al. (1987), and thus most of the paternity data reported here come from DNA fingerprinting studies.

Brood parasitism, in which con- or co-specific females lay their eggs in nests of other females, may also favor rapid pre-natal development. In fact, because in most cases parasitic eggs are completely unrelated to their nestmates, brood parasitism should exert even stronger selection on incubation periods. To test the possible importance of variation in parasitism rates among species, we included inter- and intraspecific parasitism rates as a single variable in all analyses. We did not separate the two rates because, for the species included in this analysis, species that had significant intraspecific parasitism were not reported to be susceptible to interspecific parasitism (e.g., *Progne subis*). Significant and systematic intraspecific brood parasitism was also relatively rare across the species included in this analysis, and thus most estimates of brood parasitism reflect interspecific parasitism by Brown-headed Cowbirds (*Molothrus ater*) and Common Cuckoos (*Cuculus canorus*). None of the species in this analysis from the orders Galliformes, Anseriformes, Strigiformes, and Ciconiiformes are known to be hosts for obligate interspecific brood parasites (although some are subject to intraspecific parasitism), and thus when no mention could be found of brood parasitism for these species (either in general species accounts or in the parasitism reviews of Friedmann et al. (1977) and Davies (2000)), we assumed that parasitism is infrequent and assigned a zero value for those species. Species known to be susceptible to parasitism (e.g., from general species accounts; most Passeriformes), but for which no estimate was available, were excluded from analysis.

Hatching asynchrony, if it results in dominance hierarchies that cannot be overcome by individual selection for more rapid development, may eliminate sibling competition. We considered three levels of asynchrony: synchronous (all young hatch within 24 hours of one another), partially asynchronous (hatching interval between first and last young is greater than 24 hours, but not completely asynchronous), and asynchronous (one young hatches per day). We chose to use three categories rather than a synchronous/asynchronous dichotomy because many species in our sample were neither completely synchronous nor asynchronous (see also Clark and Wilson 1981). Even a three-tier categorical approach may obscure some meaningful variation, but insufficient data are available to consider asynchrony as a continuous variable.

Incubation period has a strong positive relationship with egg size (e.g., Worth 1940, Rahn and Ar 1974). Thus, to control for this allometric effect, we included egg volume (calculated as in Ricklefs 1993) as an independent variable in all analyses.

For most bird species, nest predation is the primary source of mortality for eggs (Ricklefs 1969, Martin 1992) and may favor shorter incubation periods (Lack 1968; Bosque and Bosque 1995; Martin 1995, 2002). Thus, we included the percentage of nests lost to predators as an independent variable in our analyses. We assume that interspecific differences in the total number of nests lost to predation reflect similar differences in egg mortality (e.g., Ricklefs 1969). Predation typically results in the loss of all eggs in a nest, so for most species the percentage of nests lost to predators should provide a reasonable index of time-dependent mortality. However, for some of the larger precocial species (e.g., *Chen* spp.), predation apparently rarely results in the loss of the entire nest and for these species rates of nest predation will underestimate mortality of individual eggs. Thus, when partial predation of nests was reported to be frequent, we used the percentage of eggs lost to predators as an estimate of time-dependent mortality.

Although a correlation exists between the developmental stage of the neonate and the length of incubation (e.g., Boersma 1982, Ricklefs 1984), we did not include developmental mode as a predictor because this correlation is due to allometric effects of egg size rather than a difference between altricial and precocial young in developmental rate (Ricklefs and Starck 1998). Nonetheless, to be certain, we tested and confirmed the lack of relationship between the precocity of the neonate and the length of incubation in our sample ($P = 0.62$) and thus we do not consider developmental mode further.

To control for possible phylogenetic effects, we analyzed independent contrasts (Felsenstein 1985) generated by the CRUNCH option of program CAIC (Purvis and Rambaut 1995). We also present results of analyses on uncorrected species means. We generally followed the phylogeny of Sibley and Ahlquist (1990) to infer evolutionary relationships among the species in this analysis, but included more recent information from Sheldon et al. (1992; for the genera *Parus* and *Poecile*), Sheldon and Winkler (1993; for the subfamily Hirundidae), Patten and Fugate (1998; for the New World sparrows and buntings in Emberizidae), and Ohta et al. (2000; for the placement of *Panurus biarmicus*) to increase the resolution of the phylogeny. The phylogeny used in this analysis is available from the authors upon request.

We evaluated two models for determining the length of branches in the phylogeny, which are used to standardize the independent contrasts: a punctuational model of evolution in which all branches are of equal length, and the method suggested by Grafen (1989) in which the length of a branch is proportional to the number of taxa it supports. The punctuational model produced contrasts that met the assumptions of the statistical model (Purvis and Rambaut 1995), whereas Grafen's approach did not, and therefore we present only the results obtained from contrasts generated assuming equal branch lengths.

For all analyses, we used a regression approach to examine the relationship between extra-pair paternity and incubation length. We forced all independent variables into the model to analyze the effect of sibling competition on the length of incubation independent of any effect of egg size or nest predation. Following Harvey and Pagel (1991), the regression on independent contrasts was forced through the origin. All variables were transformed prior to analysis to achieve normality: egg size and incubation period were log-transformed, and extra-pair paternity, predation rate, and brood parasitism were arcsin-transformed. The residuals from all regressions were normally distributed.

RESULTS

Analysis of species means showed that length of incubation increased strongly with egg size (*b* = 0.763, P < 0.001), but was not related to nest predation (*b* =-0.015, P = 0.786). Length of incubation was negatively related to extra-pair paternity after controlling for the effect of the other independent variables (Fig. 1a; n = 70, *b* = -0.178, P = 0.007). Brood parasitism also was negatively related to length of incubation (Fig. 1b, *b* = -0.119, P = 0.04), whereas hatching asynchrony was positively related to the length of incubation (Fig. 1c; *b* = 0.095, P = 0.021).

The pattern that emerged from the analysis on independent contrasts was somewhat different. The length of incubation was still negatively related to extra-pair paternity (Fig. 2a; n = 67, *b* = -0.239, P = 0.029) and positively related to egg volume (*b* = 0.474, P < 0.001). However, after controlling for phylogeny, neither brood parasitism (Fig. 2b; *b* = -0.051, P = 0.643) nor hatching asynchrony (Fig. 2c; *b* = 0.125, P = 0.248) was significantly associated with length of incubation. Nest predation (*b* = 0.155, P = 0.156) remained insignificant in explaining variation in the length of incubation.

The results of comparative analyses can be influenced by the taxonomic scale of the study, even if phylogeny is controlled with independent contrasts. To test the consistency of our results, we repeated our analysis on the raw data for species in the order Passeriformes, the most well-represented group in our data set. Within this subset of data, only extra-pair paternity was significantly related to length of incubation (n = 46, *b* = -0.386, P = 0.007). Egg volume, which explains significant variation in the length of incubation across orders, was only marginally related to variation among passerines (*b* = 0.248, P = 0.077). Brood parasitism (*b* = -0.103, P = 0.461), hatching asynchrony (*b* =

0.162, P = 0.243), and predation (b = -0.192, P = 0.164) did not explain variation in incubation period.

DISCUSSION

Based largely on theoretical considerations, sibling competition has been proposed as a key evolutionary pressure driving interspecific variation in developmental rates (Ricklefs 1982, 1993; Ricklefs and Starck 1998). Testing this hypothesis depends on quantifying variation in sibling competition. Variation in the genetic relatedness of siblings seems one reasonable way to estimate sibling competition; as the average relatedness among nest-mates decreases, siblings can afford to compete more fiercely because the cost to inclusive fitness decreases, and the benefits of developing faster can be large when it yields a position atop the dominance hierarchy. We used two measures that should reflect broad differences among species in the average relatedness of nest-mates: extra-pair paternity and brood parasitism. Royle et al. (1999) showed that post-natal growth rates of birds were correlated with rates of extra-pair paternity. We show here for the first time that extra-pair paternity, as a proxy for sibling competition, is also related to more rapid pre-natal development.

The effect of brood parasitism was mixed. Based on the analysis of the raw data, our results suggested that brood parasitism may exert some influence on the length of incubation, but the effect was not significant after controlling for phylogeny nor was it significant when considering only Passeriformes. The lack of relationship within Passeriformes also suggests caution is needed in interpreting the significant relationship in the complete set of raw data; this relationship must depend in part upon differences among higher-level taxa that may not reflect sibling competition. Nonetheless, given the consistently strong relationship between extra-pair paternity and incubation, it is somewhat surprising that no effect of brood parasitism was evident, especially when analysis was restricted to passerines. Based on our kin-selection approach, the effect of brood parasitism on developmental rate should be stronger than that of extra-pair paternity because, in general, brood parasitism results in the introduction of genetically unrelated individuals into a nest. Thus, the inclusive fitness costs that are presumed to restrain competition among siblings are absent. On the other hand, estimates of brood parasitism vary extensively among populations of a single species, such that determination of the level of selection on a species over its range and over evolutionary time may be difficult. This problem is compounded by the fact that much variation in parasitism may arise from recent changes in habitat that have either allowed brood parasites to expand their range to exploit new hosts or that have made old hosts more susceptible.

Our third approach to quantifying sibling competition followed Ricklefs (1993), who proposed that parents create asynchronous hatching patterns in their offspring to blunt the selective force of sibling competition and allow longer incubation periods. Hatching asynchrony was indeed positively related to incubation period in the raw data, but not among the independent contrasts. Moreover, hatching asynchrony was not significant in the analysis restricted to Passeriformes. This suggests that the significant relationship seen in the complete set of raw data is a result of differences among higher-level taxa. Thus, within our sample, hatching synchrony seems relatively unimportant in explaining variation in incubation period.

Nest predation is expected to favor more rapid embryonic development (Lack 1968, Ricklefs 1993, Bosque and Bosque 1995). We found that nest predation did not explain variation in incubation period in our sample. Several factors may have confounded our analyses, however. First, some of the estimates of nest predation are based on small samples gathered over a short period of time. Second, the estimates of nest predation used in this study may reflect current ecological conditions that differ from those present over evolutionary time because of changes in habitat quality or abundance and composition of the predator community. Finally, when comparisons are made across geographic regions, or among distantly related species, the relationship between predation and incubation becomes more difficult to isolate (Ricklefs 1993, Martin et al. 2000, Martin 2002). Nonetheless, we find no evidence for a role of nest predation in lengths of the incubation periods for species examined here.

Ultimately, all three of our measures of sibling competition were related to length of the incubation period in the predicted directions, although two of the measures (brood parasitism and hatching asynchrony) showed no relationship once phylogenetic effects were removed. On the one hand, that all three tests vary in the directions predicted by sibling competition provides some support for this hypothesis. On the other hand, the weak and mixed nature of the results for two of the measures raises questions. The relationship between incubation period and extra-pair paternity was strongest and clearest, and may reflect effects of sibling competition. However, rather than being a cause-and-effect relationship, the relationship between extra-pair paternity and the length of incubation may arise indirectly from correlated selection on both traits.

Variation in extrinsic mortality can drive the evolution of life history strategies (e.g., Gadgil and Bossert 1970, Michod 1979, Reznick 1982, Reznick et al. 1990), and longer incubation periods are associated with low adult mortality (Ricklefs 1993, Martin 2002). Extra-pair mating activity is a form of investment in current reproduction and may thus also be influenced by adult mortality, especially if garnering extra-pair copulations incurs a cost to future survival or reproduction (e.g., Westneat and Rambo 2000; see also Wink and Dyrcz 1999). Consequently, incubation period and extra-pair paternity may be correlated with each other as an indirect consequence of adult mortality acting on both traits, rather than representing the effect of sibling competition. Thus, the importance of sibling competition on incubation period remains unclear, although our results suggest that it may play a role. At the same time, the strength of correlations observed here between extra-pair paternity and incubation suggest at the very least that life history strategies represent linkages among a larger suite of traits than previously recognized and argue for a broad approach to considerations of the evolution of life histories.

ACKNOWLEDGMENTS

We thank 3 anonymous referees for helpful comments on the manuscript. Thanks also to V. Adamski for help during the preparation of the manuscript. This work was supported by grants from the National Science Foundation (DEB-9707598, DEB-9981527). The Wildlife Biology Program at the University of Montana and the United States Fish and Wildlife Service provided additional support.

APPENDIX A. Raw data used in the analysis, ordered following Monroe and Sibley (1993; this taxonomy departs from our phylogeny because we incorporated additional sources to create the phylogeny used in this study). Values are: length of incubation (days) and degree of synchrony (S = synchronous, PA = partially asynchronous, A = completely asynchronous; see text for details), percent of multiply-sired broods, percent nest predation, percent brood parasitism (inter- or intraspecific), and egg volume (calculated from linear dimensions; mm^3). References follow each value in parentheses. For some species, when no mention of brood parasitism was found in any reference, we assumed the value was zero and entered a question mark in lieu of a reference (see Methods in text for details).

Galliformes

Phasianidae. *Lagopus lagopus*: 22.1, S (Cramp and Simmons 1980), 7.4 (Freeland et al. 1995), 24 (Cramp and Simmons 1980), 0 (?), 226 (Cramp and Simmons 1980). *Lagopus leucurus*: 24.9, S (Braun et al. 1993), 17 (Benson 2002), 54 (Braun et al. 1993), 0 (Braun et al. 1993), 201 (Braun et al. 1993).

Anseriformes

Anatidae. *Chen caerulescens*: 23.6, S (Mowbray et al. 2000), 13 (Dunn et al. 1999), 8 (Cooke et al. 1995), 5.5 (Mowbray et al. 2000), 1116 (Mowbray et al. 2000). *Chen rossi*: 21.9, S (Ryder and Alisauskas 1995), 8.3 (Dunn et al. 1999), 2.4 (Ryder and Alisauskas 1995), 2.7 (Ryder and Alisauskas 1995), 873 (Ryder and Alisauskas 1995). *Branta leucopsis*: 24.5, S (Cramp and Simmons 1977), 0 (Larsson et al. 1995), 19 (Tombre and Erikstad 1996), 0 (?), 1007 (Cramp and Simmons 1977).

Piciformes

Picidae. *Picoides borealis*: 10.5, S (Jackson 1994), 2.2 (Haig et al. 1994), 22 (LaBranche and Walters 1994; this estimate includes predation as well as mortality caused by competitors for nest cavities), 0 (Jackson 1994), 38 (Jackson 1994).

Apodiformes

Apodidae. *Apus apus*: 19.6, A (Cramp 1985), 9.5 (Owens and Hartley 1998), 9.1 (Cramp 1985), 0 (?), 33.5 (Cramp 1985).

Strigiformes

Strigidae. *Otus asio*: 30, PA (Gehlbach 1995), 0 (Lawless et al. 1997), 50 (Gehlbach 1995), 0 (Gehlbach 1995), 167 (Gehlbach 1995). *Otus flammeolus*: 22.7, PA (McCallum 1994), 0 (Arsenault et al. 2002), 0 (?), 12 (McCallum 1994), 102 (McCallum 1994).

Ciconiiformes

Scolopacidae. *Calidris mauri*: 21, S (Wilson 1994), 8 (Blomqvist et al. 2002), 31 (Wilson 1994), 0 (Wilson 1994), 80 (Wilson 1994). *Phalaropus fulicarius*: 19, S (Cramp and Simmons 1983), 25.4 (Dale et al. 1999), 46 (Mayfield 1978), 0 (Cramp and Simmons 1983), 76 (Cramp and Simmons 1983).

Charadriidae. *Haemotopus ostralegus*: 25.5, S (Cramp and Simmons 1983), 3.8 (Heg et al. 1993), 30 (Harris 1967), 0 (?), 180 (Cramp and Simmons 1993). *Charadrius morinellus*: 26.1, S (Owens et al. 1994), 9.1 (Owens et al. 1995), 47 (Byrkjedal 1987), 0 (?), 180 (Cramp and Simmons 1983).

Laridae. *Catharacta maccormicki*: 29.7, A (Higgins and Davies 1996), 7.7 (Millar et al. 1997), 2 (Young 1963), 0 (?), 925 (Higgins and Davies 1996). *Larus canus*:

25.25, PA (Cramp and Simmons 1983), 8.3 (Bukacinska et al. 1998), 58 (Cramp and Simmons 1983), 0 (?), 510 (Cramp and Simmons 1983). *Larus occidentalis*: 30, PA (Pierotti and Annett 1995), 0 (Gilbert et al. 1998), 55 (Pierotti and Annett 1995), 0(?), 880 (Pierotti and Annett 1995).

Falconidae. *Falco naumanni*: 28.5, S (Cramp and Simmons 1980), 3.8 (Negro et al. 1996), 11 (Tella et al. 1996), 0 (?), 154 (Cramp and Simmons 1980). *Falco tinnunculus*: 28, A (Cramp and Simmons 1980), 2.6 (Korpimaki et al. 1996), 18 (Cramp and Simmons 1980), 0 (?), 196 (Cramp and Simmons 1980). *Falco eleonorae*: 28, S (Cramp and Simmons 1980), 0 (Swatschek et al. 1993), 6 (Walter 1979), 0 (Cramp and Simmons 1980), 239 (Cramp and Simmons 1980).

Phalacrocoracidae. *Phalacrocorax aristotelis*: 30.5, PA (Cramp and Simmons 1983), 20 (Graves et al. 1992), 38 (Cramp and Simmons 1983), 0 (?), 501 (Cramp and Simmons 1983).

Ciconiidae. *Coragyps atratus*: 38.5, S (Buckley 1999), 0 (Decker et al. 1993), 17 (Buckley 1999), 0 (?), 1005 (Buckley 1999).

Spheniscidae. *Pygoscelis adeliae*: 35.4, A (Lishman 1985), 11.1 (Pilastro et al. 2001), 18 (Marchant and Higgins 1990), 0 (?), 1066 (Lishman 1985).

Gaviidae. *Gavia immer*: 28, S (McIntyre and Barr 1997), 0 (Piper et al. 1997), 16 (Belant and Anderson 1991), 0 (?), 1393 (McIntyre and Barr 1997).

Passeriformes

Tyrannidae. *Sayornis phoebe*: 16, S (Weeks 1994), 20 (Conrad et al. 1998), 37 (Weeks 1994), 11 (Weeks 1994), 21.6 (Weeks 1994).

Corvidae. *Corvus monedula*: 17.6, PA (Cramp and Perrins 1994), 0 (Henderson et al. 2000), 25 (Johnsson 1994, Soler and Soler 1996), 2 (Davies 2000), 114.5 (Cramp and Perrins 1994). *Aphelocoma coerulescens*: 17.8, S (Woolfenden and Fitzpatrick 1996), 0 (Quinn et al. 1999), 51 (Woolfenden and Fitzpatrick 1996), 0 (Woolfenden and Fitzpatrick 1996), 57.7 (Woolfenden and Fitzpatrick 1996).

Sturnidae. *Sturnus vulgaris*: 12.1, S (Cabe 1993), 28.6 (Pinxten et al. 1993), 35 (Cabe 1993), 28 (Evans 1988, Power et al. 1989), 69.5 (Cabe 1993).

Muscicapidae. *Sialia sialis*: 15.7, S (Gowaty and Plissner 1998), 24 (Meek et al. 1994), 23 (Radunzel et al. 1997), 0.5 (Gowaty and Plissner 1998), 29.8 (Gowaty and Plissner 1998). *Turdus grayi*: 12.3, PA (Dyrcz 1983), 53 (Stutchbury et al. 1998), 47 (Dyrcz 1983), 0 (Friedmann et al. 1977), 61.6 (Wetmore et al. 1984). *Oenanthe oenanthe*: 13.26, PA (Kren and Zoerb 1997), 29 (Currie et al. 1998), 26 (Kren and Zoerb 1997), 0 (Kren and Zoerb 1997), 27.4 (Kren and Zoerb 1997). *Ficedula hypoleuca*: 14.1, S (Cramp and Perrins 1993), 15 (Lifjeld et al. 1991), 11 (Huhta et al. 1998), 0 (Soler et al. 1999), 16.4 (Cramp and Perrins 1993). *Ficedula albicollis*: 12.8, S (Cramp and Perrins 1993), 32.9 (Sheldon and Ellegren 1999), 56 (Walankiewicz 1991), 0 (Davies 2000), 15.7 (Cramp and Perrins 1993).

Certhiidae. *Troglodytes aedon*: 12.5, PA (Johnson and Kermott 1993), 26.7 (Soukup and Thompson 1997), 31 (Johnson 1998), 0 (Johnson 1998), 13.9 (Johnson 1998).

Paridae. *Remiz pendulinus*: 14, PA (Schleicher et al. 1997), 17.3 (Schleicher et al. 1997), 4 (Cramp and Perrins 1993), 0 (Cramp and Perrins 1993), 9.7 (Cramp and Perrins 1993). *Parus montanus*: 14.1, PA (Orell and Ojanen 1983), 4 (Orell et al. 1997), 21

(Orell and Ojanen 1983), 0 (Soler et al. 1999), 13.0 (Cramp and Perrins 1993). *Poecile atricapillus*: 12.5, S (Smith 1993), 37.5 (Otter et al. 1994), 40 (Christman and Dhondt 1997), 0 (Smith 1993), 11.8 (Smith 1993). *Parus major*: 14, PA (Cramp and Perrins 1993), 25.1 (Gullberg et al. 1992, Blakey 1994, Verboven and Mateman 1997), 17.7 (Cramp and Perrins 1993), 0 (Soler et al. 1999), 17.4 (Cramp and Perrins 1993). *Parus caeruleus*: 14.2, PA (Cramp and Perrins 1993), 30 (Gullberg et al. 1992, Kempenaers et al. 1992), 19.9 (Dunn 1977, Nilsson 1984), 0 (Soler et al. 1999), 11.5 (Cramp and Perrins 1993).

Aegithelidae. *Psaltiparus minimus*: 12.5, S (Sloane 2001), 0 (Bruce et al. 1996), 47 (Sloane 2001), 0 (Sloane 2001), 7.1 (Sloane 2001).

Hirundidae. *Tachycineta bicolor*: 14.5, PA (Robertson et al. 1992), 71 (Lifjeld et al. 1993, Dunn et al. 1994), 22 (Robertson et al. 1992), 0 (Robertson et al. 1992), 17.1 (Robertson et al. 1992). *Tachycineta albilinea*: 17, PA (Dyrcz 1984), 26 (Moore et al. 1999), 37 (Dyrcz 1984), 0 (Moore et al. 1999), 14.8 (Dyrcz 1984). *Progne subis*: 16.5, PA (Brown 1997), 50 (Morton et al. 1990), 22 (Morton and Derrickson 1990), 36 (Brown 1997), 38.2 (Brown 1997). *Riparia riparia*: 14.25, PA (Garrison 1999), 36 (Alves and Bryant 1998), 45 (Hjertass et al. 1988), 0 (Garrison 1999), 14.4 (Garrison 1999). *Hirundo rustica*: 14.2, S (Brown and Brown 1999), 33 (Moller and Tegelstrom 1997), 1 (Shields and Crook 1987), 16.5 (Moller 1987), 19.1 (Brown and Brown 1999). *Delichon urbica*: 14.9, S (Cramp 1988), 46 (Whittingham and Lifjeld 1995, Riley et al. 1995), 13 (Cramp 1988), 0 (Soler et al. 1999), 16.7 (Cramp 1988).

Sylviidae. *Acrocephalus arundinaceus*: 14, S (Cramp 1992), 8.3 (Hasselquist et al. 1995, Leisler et al. 2000), 45 (Hansson et al. 2000), 29 (Mosknes et al. 1993, Moskat and Honza 1999), 32.2 (Cramp 1992). *Phylloscopus sibilatrix*: 13, S (Cramp 1992), 0 (Gyllensten et al. 1990), 38 (Cramp 1992), 0.09 (Soler et al. 1999), 13.5 (Cramp 1992). *Phylloscopus trochilus*: 13.2, PA (Cramp 1992), 0 (Gyllensten et al. 1990), 49 (Tiainen 1983, Bjornstad and Lifjeld 1996), 0.06 (Soler et al. 1999), 12.1 (Cramp 1992). *Panurus biarmicus*: 11.5, S (Hoi and Hoi-Leitner 1997), 29.5 (Hoi and Hoi-Leitner 1997), 47 (Stepniewski 1995), 0 (Soler et al. 1999), 18.0 (Cramp and Perrins 1993).

Passeridae. *Passer domesticus*: 11, S (Lowther and Cink 1992), 26.1 (Wetton and Parkin 1991), 20 (Anderson 1978, Moller 1991), 0 (Lowther and Cink 1992), 27.4 (Lowther and Cink 1992). *Prunella collaris*: 11.35, S (Davies et al. 1995), 50 (Hartley et al. 1995), 18 (Davies et al. 1995), 0 (Davies et al. 1995), 34.0 (Cramp 1988). *Prunella modularis*: 12.5, S (Cramp 1988), 40 (Burke et al. 1989), 34 (Tuomenpuro 1991), 1.94 (Davies 1992), 21.7 (Cramp 1988). *Taeniopygia guttata*: 14.5, PA (El-Wailly 1966), 8 (Birkhead et al. 1990), 66 (Zann 1994), 0 (Zann 1996), 9.4 (Zann 1996).

Fringillidae. *Fringilla coelebs*: 12.6, S (Cramp and Perrins 1994), 23 (Sheldon and Burke 1994), 48 (Hanski and Laurila 1993, Moller 1991), 0.01 (Soler et al. 1999), 22.5 (Cramp and Perrins 1994). *Serinus serinus*: 12.8, S (Cramp and Perrins 1994), 14.9 (Hoi-Leitner et al. 1999), 37 (Cramp and Perrins 1994), 0 (Mosknes and Roskraft 1995), 12.1 (Cramp and Perrins 1994). *Carduelis tristis*: 13 (Middleton 1993), 26.7 (Gissing et al. 1998), 22 (Middleton 1993), 4.9 (Middleton 1993), 13.2 (Middleton 1993). *Carpodacus mexicanus*: 13.5, PA (Hill 1993), 14.3 (Hill et al. 1994), 45.8 (Martin and Badyaev 1996), 0 (Hill 1993), 20.0 (Hill 1993). *Emberiza citrinella*: 13, S (Sundberg and Larsson 1994), 69 (Sundberg and Dixon 1996), 28.9 (Moller 1991), 0.01 (Soler et al. 1999), 30.6 (Cramp and Perrins 1994). *Emberiza schoeniclus*: 13, S (Cramp and Perrins 1994), 86 (Dixon et al. 1994), 58 (Cramp and Perrins 1994), 0.15 (Soler et al. 1999), 21.8 (Cramp and Perrins 1994). *Calcarius pictus*: 11.6, S (Briskie 1993), 77 (Briskie et al. 1998), 33 (Briskie 1993), 0 (Briskie 1993), 25.1 (Briskie 1993). *Passerculus sandwichensis*: 12.2, PA (Wheelwright and Rising 1993), 43 (Freeman-Gallant 1996), 25 (Wheelwright and Rising 1993), 1 (Wheelwright and Rising 1993), 23.8 (Wheelwright and Rising 1993). *Dendroica petechia*: 11.5, PA (Lowther et al. 1999), 53.8 (Yezerinac et al. 1996), 34 (Martin 1992), 36 (Lowther et al. 1999), 14.0 (Lowther et al. 1999). *Dendroica caerulescens*: 12, S (Holmes 1994), 43.6 (Chuang et al. 1999), 42.8 (Martin 1992), 0.3 (Holmes 1994), 14.6 (Holmes 1994). *Setophaga ruticilla*: 11, S (Sherry and Holmes 1997), 60 (Perreault et al. 1997), 48 (Sherry and Holmes 1997), 23 (Sherry and Holmes 1997), 13.3 (Sherry and Holmes 1997). *Wilsonia citrina*: 12, PA (Evans-Ogden and Stutchbury 1994), 35.3 (Stutchbury et al. 1997), 38 (Evans-Ogden and Stutchbury 1994), 41 (Evans-Ogden and Stutchbury 1994), 17.8 (Evans-Ogden and Stutchbury 1994). *Geothlypis trichas*: 12, S (Guzy and Ritchison 1999), 49 (Thusius et al. 2001), 37.5 (Spautz 1999), 27 (Guzy and Ritchison 1999), 16.2 (Guzy and Ritchison 1999). *Cardinalis cardinalis*: 12.6, S (Halkin and Linville 1999), 16 (Ritchison et al. 1994), 54 (Martin 1992), 82 (Halkin and Linville 1999), 44.8 (Halkin and Linville 1999). *Passerina cyanea*: 12.5, S (Payne 1992), 48 (Westneat 1990), 53 (Martin 1992), 19.0 (Payne 1992), 19.7 (Payne 1992). *Agelaius phoeniceus*: 12, PA (Yasukawa and Searcy 1995), 47.7 (Gibbs et al. 1990, Westneat 1993, Gray 1997), 41 (Yasukawa and Searcy 1995), 4.3 (Friedmann et al. 1977), 39.9 (Yasukawa and Searcy 1995). *Dolichonyx oryzivorous*: 12.4, PA (Martin and Gavin 1995), 38 (Bollinger and Gavin 1991), 29.8 (Martin 1995), 4 (Martin and Gavin 1995), 29.8 (Martin and Gavin 1995).

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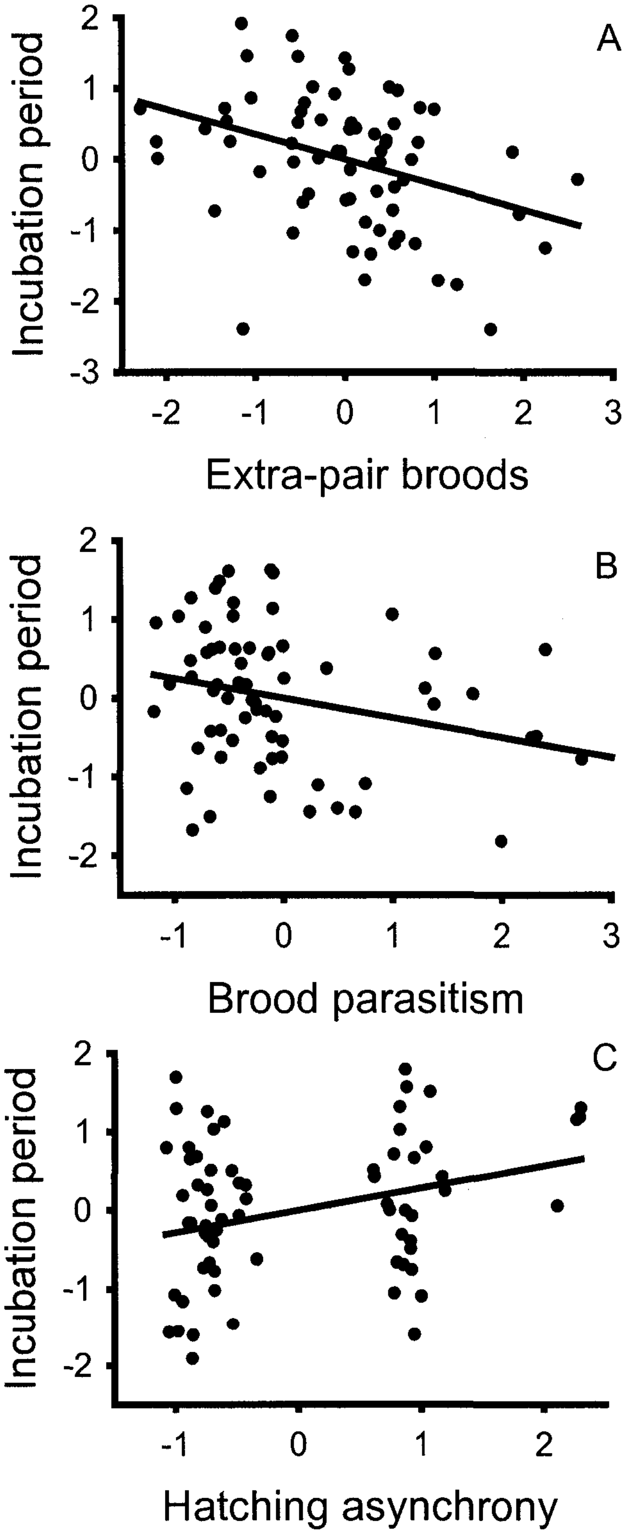
FIGURE LEGENDS

Figure 1. Partial regression plots of residual values showing interspecific variation (n = 70 species) in incubation period relative to extra-pair paternity, brood parasitism, and degree of hatching asynchrony after controlling for effect of other independent variables in a multiple regression. (*a*) Incubation period is shorter in species with high rates of extra-pair paternity ($b = -0.178$, P = 0.007). (*b*) Incubation period is shorter in species with high rates of brood parasitism ($b = -0.119$, P = 0.04). (*c*) Incubation period is positively associated with degree of hatching asynchrony ($b = 0.095$, P = 0.021).

Figure 2. Partial regression plots of residuals of phylogenetically independent contrasts (n = 67 contrasts) in incubation period relative to residuals of contrasts in extra-pair paternity, brood parasitism, and degree of hatching asynchrony. Residuals produced by multiple regression including all independent variables. (*a*) Incubation period decreases with increasing extra-pair paternity ($b = -0.239$, P = 0.029). There is no relationship between incubation contrasts and (*b*) brood parasitism contrasts ($b = -0.051$, P = 0.643) or (*c*) hatching asynchrony contrasts ($b = 0.155$, P = 0.156).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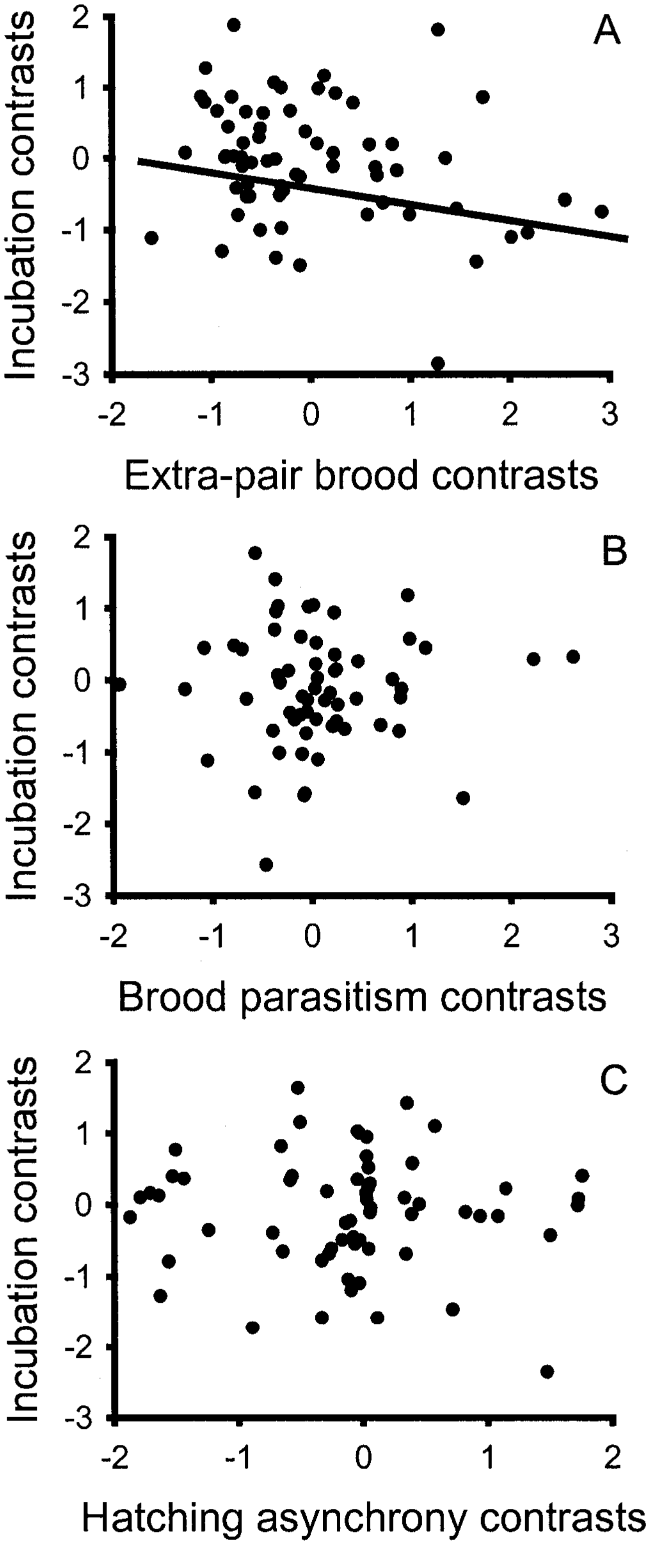
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Brood parasitism contrasts
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Incubation contrasts
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Hatching asynchrony contrasts

CHAPTER II

ADAPTIVE HABITAT SELECTION IN CHESTNUT-COLLARED LONGSPURS: EXOTIC VERSUS NATIVE HABITAT

INTRODUCTION

Most organisms occur in a variety of distinct habitats that are often of varying quality (May & Southwood 1990). As a consequence, understanding the distribution of individuals among habitat patches, and the fitness consequences of these distributions, is necessary for understanding population dynamics and regulation (Brown 1969; Pulliam 1988) and for assessing the conservation value of different habitats and the ramifications of habitat loss (Bernstein, Krebs & Kacelnik 1991). The most prominent model for explaining the distribution of individuals among habitats is the ideal-free distribution (Fretwell & Lucas 1970; Fretwell 1972; Petit & Petit 1996), in which individuals are unconstrained by competitors and settle in the habitat that maximizes their fitness. Thus, in an ideal-free distribution, fitness is equivalent in all habitats. In nature, however, vital rates often are habitat specific (Lundberg *et al.* 1981; Holmes, Marra & Sherry 1996; Murphy 2001; Remes *in press*). Therefore, an important alternative to the ideal-free model is the ideal-despotic distribution model (Fretwell & Lucas 1970; Fretwell 1972) in which dominant or early arriving individuals occupy the best habitat and relegate other individuals to habitats of lower quality. In contrast to the ideal-free distribution, ideal-despotic distributions result in higher fitness for individuals that settle in habitats with a higher inherent suitability.

A critical assumption of both models is that individuals have complete information about the suitability of all patches of habitat and make decisions accordingly (e.g., individuals behave ideally). Settling individuals often must rely on indirect cues to assess the expected quality of a habitat patch (Hilden 1965; Chew 1980; Knopf & Sedgwick 1992), and presumably over evolutionary time such cues have been reliable predictors of survival or reproductive success. However, the proximate factors that promote settling do not always reflect habitat quality; in particular, anthropogenic changes to the environment may confound the cues used in habitat selection and can result in individuals settling preferentially in low-quality habitats in which survival or reproduction is low. The creation of attractive habitats that function as ecological traps has been associated with a variety of human activities, including changes in vegetation structure that increase predation risk (Gates & Gysel 1978; Purcell & Verner 1998) and changes in disturbance regime that increase mortality (Best 1986; Bollinger & Gavin 1992).

Testing competing models of habitat selection is increasingly important as human-modified habitat patches come to dominate most landscapes. For example, if habitat selection patterns commonly follow an ideal free distribution, we can expect that populations will persist despite the creation of patches of poor-quality habitat. In contrast, under the ecological trap scenario, even landscapes with abundant, high-quality habitat may not support viable populations (Donovan & Thompson 2001). Clearly, understanding the relationship between habitat selection and fitness is essential in conserving populations of native plants and animals.

Here, we examine patterns of habitat selection in Chestnut-collared Longspurs (*Calcarius ornatus* Townsend; hereafter, Longspurs), a grassland songbird endemic to the northern Great Plains of North America. Across much of this region, native mixed-grass prairie has been replaced by monocultures of the introduced grass *Agropyron cristatum*. *Agropyron cristatum* excludes native plants and thus has significant effects on community structure and composition, and also changes ecosystem functioning in areas that it dominates (Christian & Wilson 1999). Fields of *A. cristatum* differ from native prairie both phenologically, beginning growth much earlier in the spring, and physiognomically, producing significantly more aboveground biomass than native prairie (Christian & Wilson 1999). The replacement of native prairie by *A. cristatum* can also have cascading effects on insect populations (Lattin *et al.* 1994). However, Longspurs, like species in many other systems (Chew 1980; Wilson & Belcher 1989; Schmidt & Whelan 1999; Remes *in press*), readily use patches of exotic habitat in addition to native habitat, making this a useful system for testing models of habitat selection in perturbed landscapes. Although the consequences of settling in exotic habitats for native animals are largely unknown, determining the suitability of *A. cristatum* as habitat for native birds is critical, for it is one of the most widespread exotic species in western North America and covers at least 6-10 million hectares (Lesica & DeLuca 1996).

Using information on settlement patterns, nesting density, and seasonal fecundity, the predictions generated by the three models of habitat selection are tested. Predictions of the ideal-free distribution model are similar settlement times in both habitats, higher density of nesting birds in the native habitat, and no difference in reproductive success. Under the ideal-despotic distribution model, habitat-specific variation in reproductive success is expected and Longspurs should settle first, and at higher density, in the high-quality habitat. Finally, the ecological trap hypothesis also predicts differences in reproductive success between habitats. However, unlike the ideal-despotic distribution, under the ecological trap hypothesis individuals are not relegated to low-quality habitat through competitive interactions but instead choose to settle in habitats with low fitness payoffs. Thus, the ecological trap hypothesis predicts no relationship between habitat preference, as measured by settlement time and nesting density, and reproductive success.

METHODS

Work was conducted at Medicine Lake National Wildlife Refuge, located on the glaciated plains north of the Missouri River in eastern Montana. The 8100 ha refuge consists of native mixed-grass prairie (dominant species include *Stipa spp.*, *Agropyron smithii*, *Koeleria cristata*, and *Bouteloua gracilis*), monocultures of *Agropyron cristatum*, hayfields, small agricultural fields, and a variety of seasonal and permanent wetlands surrounding a large (c.a. 3200 ha) freshwater lake.

In 2000, study plots were established in 3 monocultures of *A. cristatum* and 3 patches of native prairie. Individual study plots ranged in size from 12-25 ha, but the total area of the 3 plots in each habitat was the same. In 2001, 2 plots in each habitat on which few Longspur nests were found were replaced with new plots of equal size. Thus, over the course of the study 4 plots in each habitat were sampled, but only 3 plots in each habitat were sampled for more than one year. All of the *A. cristatum* fields that contained study plots were planted in the 1940's and 1950's to revegetate abandoned agricultural fields, and have been stable monocultures since then. All of the plots, both native and exotic, had been grazed or burned in the 10 years prior to this study, but to minimize the confounding effects of these disturbances plots were chosen that had not been disturbed for at least 2 years. Each plot was overlain with a 50m x 50m grid of flags to facilitate territory mapping and nest relocation.

In 2002, settlement patterns were examined by systematically surveying each plot for territorial Longspur males. Male Longspurs began arriving at the study site on 9 April, but remained in migratory flocks for several weeks as females arrived (see also Hill & Gould 1993). Beginning on 24 April, when migratory flocks began to break up, a single observer walked slowly along the flagged grid lines covering each plot and counted the number of singing males. Males that were fighting but not singing were also assumed to be defending territories. Each plot was surveyed every 3 days until 9 May, at which point most birds appeared to have settled on a territory and were beginning to nest. Because Longspurs sing during conspicuous flight displays, and because of the flat and open nature of the terrain, counting the same individual multiple times was not a concern.

Nests were located and monitored throughout the 2000-2002 breeding seasons to examine patterns of reproductive success. Nests were located using both systematic searches and behavioral observations of adult Longspurs. During systematic searches, adults were flushed off of the nest by dragging a weighted rope across the plot. Each plot was searched systematically 3 times between early May and late June of each year, but nests continued to be found until late July using behavioral observations. The total search effort was similar in both habitats. By combining behavioral observations, which allowed us to locate nests early in the nesting cycle (e.g., during building) and follow pairs throughout the season, and systematic searches, which allowed us to search large areas in a short amount of time, we are confident that we located nearly all of the nests on each study plot. Behavioral observations suggest that very few territorial males remained unpaired, and thus the density of nests (excluding re-nests) was used to reflect overall density in each habitat.

The location of each nest was marked with 1 or 2 small pieces of flagging placed 1-2 m from the nest cup. Flagging does not appear to increase the risk of nest predation (Hein & Hein 1996) and was necessary to allow relocation of nests. The fate of nests was determined by visits every 2-3 days, except when hatching or fledging was expected, at which point nests were visited daily. Nests were considered successful if at least 1 young fledged. If the nest was empty prior to the expected fledging date, the territory was searched for adults to determine if they were feeding fledglings. Parents continue to feed and defend fledglings on the territory for several weeks after the young leave the nest, and thus predation was assumed to have occurred if no adults could be found feeding fledglings. In 2001 and 2002 nestling growth rate was measured (see below), which provided a third way to assess the fate of nests. Among nestlings of known fate, in no case did individuals with a body mass of less than 10 g on or after day 7 of the nestling period fledge, and thus mass of nestlings at the last nest check was used to test the determination of nest fate. Rates of nest success and daily mortality were calculated using the Mayfield method (Mayfield 1961; Hensler & Nichols 1981), and the chi-square approach of Sauer and Williams (1989), as implemented by Program CONTRAST (Hines & Sauer 1989), was used to compare rates of nest predation.

Adults were monitored after the completion of a nesting attempt in order to locate re-nests and estimate seasonal fecundity. Although most birds were not banded, many of the males in the study area were individually identifiable based on variation in the extent, shape, and color of the plumage forming the ventral bib, and some of the females were identifiable by their aberrant plumage (intermediate between male and typical female plumage). All of the identifiable birds remained on the same territory throughout the breeding season, as has been reported elsewhere for this species (Hill & Gould 1993). Furthermore, within-season divorce is exceedingly rare in Chestnut-collared Longspurs; in a study of a large, banded population, only 1 possible case of pair-bond dissolution was noted (Hill & Gould 1993). Thus, although birds were not individually marked, we feel that our estimate of seasonal fecundity is accurate. Estimates of fecundity were used in a single-sex, two-stage population model to examine what levels of adult and juvenile survival are necessary to achieve a stable population (lambda = 1) in each habitat. For the purposes of calculating the mean number of female offspring/female/year, an equal sex ratio among offspring was assumed.

Nestling growth rate was measured during 2001-2002 as an additional component of reproductive success. Growth rate is an important component of fitness in altricial birds because it affects the duration of the nestling period, and thus the probability that young survive to fledge, as well as future prospects for survival and reproduction (reviewed in Gebhardt-Henrich & Richner 1998). In 2001, nestlings were individually marked with a felt-tipped pen as they hatched, and mass was estimated every 2 days using a portable electronic balance. A similar procedure was used in 2002 except that in addition to body mass the length of both tarsi was measured as well. Mass was estimated to the nearest 0.1 g and tarsus length to the nearest 0.1 mm. Nestling growth rates for each trait were analyzed by using non-linear regression to fit a logistic growth curve to the entire data set. For both mass and tarsus growth, the logistic curve provided an excellent fit (mass $r^2 = 0.85$, tarsus $r^2 = 0.81$; both P's < 0.001). Differences in growth between habitats were examined by comparing residuals from the non-linear regression using ANOVA (Ricklefs 1983). To avoid artificially inflating error degrees of freedom, residuals from the growth curve were first pooled among nestlings within a nest, then among nests within a plot, and finally among plots within a habitat. Basing the analysis on residuals allowed us to include all measured individuals in the analysis; had we attempted to estimate growth parameters separately for each individual or each nest we would have been forced to exclude samples with fewer than three measurements.

Nest microhabitat can be an important determinant of predation risk (Martin 1993; 1998), so data on nest-site selection was collected to examine the potential causes of any between-habitat differences in reproductive success. All vegetation sampling was conducted within 2 weeks of the day that the nesting attempt terminated, using the standardized BBIRD methodology (Martin et al. 1997). At 4 points, 1 cm from the edge of the nest in each cardinal direction, the volume of vegetation was estimated by measuring the visual obstruction of vegetation (Robel *et al.* 1970). Overhead concealment of the nest was also measured (percentage of a 5 cm radius cardboard disc that was occluded when viewed from directly above). To examine which features of the environment Longspurs select when choosing a nest site, the same vegetation variables (excepting nest concealment) were measured at a randomly located point within the same territory but at least 10 m from the nest. The same protocol was used at 10 random points within each plot to quantify vegetation differences between habitats. Finally, to examine the classification of plots as either exotic or native, the percent cover of different plant species was estimated within the 5 m radius sampling plot surrounding each nest and each random point.

RESULTS

As expected, *A. cristatum* dominated plots in the exotic habitat with a mean cover of 98.9%. *Artmesia frigida* was the only other species recorded at more than one point, and accounted for 1.1% cover in the exotic habitat. In contrast, plots in the native habitat were dominated by a mix of species including: *Stipa spp.* (38.3%), *Koeleria cristata* (19.6%), *Selaginella sp.* (9.9%), *Agropyron smithii* (9.6%), *Bouteloua gracilis* (6.2%), *A. frigida* (5.0%), and *Carex spp.* (4.4%). Along with greatly reduced plant species diversity, MANOVA indicated that plots in the exotic habitat also differed structurally ($F_{3,6} = 13.753$, $P = 0.004$). This difference was due to significantly greater vegetation volume in the exotic habitat (one-way ANOVA; $F_{1,6} = 22.474$, $P = 0.001$).

In 2002, the number of territorial male Longspurs recorded increased between 24 April and 9 May (repeated-measures ANOVA; $F_{4,16} = 59.35$, $P < 0.001$), but settlement patterns did not differ between habitats (habitat X time: $F_{1,4} = 0.229$, $P = 0.657$). Furthermore, a two-way ANOVA indicated that the date that egg laying began in first nests did not differ between habitats ($F_{1,12} = 0.034$, $P = 0.857$) although there was significant yearly variation in the onset of egg laying (year: $F_{2,2} = 266.611$, $P = 0.004$; year * habitat: $F_{2,10} = 0.027$, $P = 0.973$). The density of Longspurs was similar in both habitats (native: 1.4/ha, 95% CI = 0.93 - 1.87; exotic: 1.1/ha, 95% CI = 0.75 - 1.45; $F_{1,4} = 0.853$, $P = 0.401$).

During the three years of this study, 352 Longspur nests were located and monitored (54% on native habitat plots, 46% on exotic habitat plots). Predation was the main source of mortality, causing 86% (n = 163) of all nest failures. Parasitism by Brown-headed Cowbirds (*Molothrus ater*) was relatively infrequent (14.2% (n = 50) of nests were parasitized) and of little consequence: only five nests fledged cowbirds, and cowbird parasitism accounted for only 3.1% (n = 6) of nest failures. Inclement weather was also a negligible source of mortality, accounting for 2.6% (n = 5) of nest failures. Total daily survival rates were significantly lower for nests in the exotic habitat (native: 0.9548; exotic: 0.9315; $\chi^2 = 3.1947$, df = 1, P = 0.07; Fig. 1). Over the 24-day nesting cycle typical of Chestnut-collared Longspurs, these daily survival rates amount to an average nest success of 32.9% in the native habitat and only 18.2% in the exotic habitat. Survival during the nestling stage was lower than during incubation, and although daily survival rates did not differ statistically between habitats in either the incubation ($\chi^2 = 1.85$, df = 1, P = 0.174) or nestling ($\chi^2 = 0.8019$, df = 1, P = 0.371) stage, nestling survival was very low in the exotic habitat (Fig. 1).

There was no evidence that maladaptive nest-site selection within a habitat contributed to differences in predation rates. Vegetation was sampled at 71 nests in native habitat and 75 nests in exotic habitat, and nest sites in exotic habitat were marginally different in structure from those in native habitat (MANOVA; $F_{3,4} = 4.468$, P = 0.091). One-way ANOVAs indicated that this difference was a result primarily of denser vegetation surrounding nests in the exotic habitat ($F_{1,6} = 15.268$, P = 0.008) and greater overhead concealment of nests in the exotic habitat ($F_{1,6} = 13.35$, P = 0.011). However, within a habitat nest sites did not differ significantly from random points within the territory (MANOVA; exotic: $F_{2,5} = 0.785$, P = 0.505; native: $F_{2,5} = 2.070$, P= 0.221) nor were there differences between successful and depredated nests (MANOVA; exotic: $F_{3,4} = 2.22$, P = 0.228; native: $F_{2,3} = 1.875$, P = 0.296). Thus, between-habitat differences in nest sites appear to arise as a consequence of large-scale settling decisions (e.g., native or exotic habitat) rather than differences in nest-site selection within each habitat.

Neither clutch size nor average number of young fledged from successful nests varied among years (all P's > 0.20) and thus data were pooled across years for use in one-way ANOVA. Clutch size was similar in both habitats ($F_{1,6} = 0.090$, $P = 0.775$; Fig. 2). The number of young fledged from successful nests was also equivalent ($F_{1,5} = 0.530$, $P = 0.499$; Fig. 2), although attrition was common and in both habitats the number fledged was smaller than the clutch size. Hatching success was high in both habitats (exotic: 94.2%; native: 93.7%), and much of the difference between clutch size and the number of young fledged reflects unknown losses that are assumed to be due to partial predation. Starvation of nestlings was rare, and in only 17 nests did we document the death of a nestling due to starvation (none of which contained nestling Brown-headed Cowbirds). Nestling starvation was more common in the exotic habitat although the difference was only marginally significant (exotic: 12 nests with at least one nestling dead from starvation; native: 5 nests; $\chi^2 = 2.428$, df = 1, $P = 0.118$).

Seasonal fecundity did not differ significantly between habitats (native: 1.8 offspring/year; exotic: 1.1 offspring/year; $t_3 = 1.089$, $P = 0.337$). Females in the exotic habitat took nearly 3 days longer to re-nest following failure (mean time between failure and egg laying; native: 7.2 days; exotic: 9.8 days), but this difference is only marginally significant ($t_3 = -2.316$, $P = 0.103$). Females re-nested at similar rates in both habitats; most pairs that we followed made at least 2 nesting attempts and several pairs attempted 3 nests (exotic: 1.5 broods/year; native: 1.7 broods/year).

Given the above estimates of seasonal fecundity, population models indicated that very high adult and juvenile survival rates are necessary to maintain a stable population in the exotic habitat (Fig. 3). In general, absent immigration, both adult and juvenile survival would have to exceed 70% in the exotic habitat for lambda > 1. The situation is only slightly better in the native habitat; here, adult survival rates as low as 60% could produce a stable population, but only with high (70%) juvenile survival rates. The only published estimate of annual adult survival for Chestnut-collared Longspurs, based on return rates of banded birds, is 66.7% (Hill & Gould 1993). Adult survival for a congener, Lapland Longspur (*Calcarius lapponicus*), has been estimated at 67.7% (Custer & Pitelka 1977). Although estimates of survival based on return rates are biased unless re-sighting probabilities are high (Lebreton *et al.* 1982); (Martin, Clobert & Anderson 1995), they can at least provide guidance for heuristic analyses such as ours (e.g., Martin 1993). Juvenile survival estimates are lacking for Longspurs; however, Ricklefs (2000) has shown that juvenile survival tends to be a relatively invariant function of adult survival. Using the function presented in Ricklefs (2000), we can estimate that juvenile survival of Longspurs is unlikely to be greater than 40-50%. Thus, barring adult survival greater than 70%, our estimates of fecundity suggest that lambda < 1 is likely, and that populations in both habitats are sustained by immigration.

Nestling Longspurs grew at a similar rate in 2001 and 2002 (all P's > 0.28 for year effect on growth), and therefore data were pooled among years for subsequent ANOVAs. Nestlings in the exotic habitat gained mass at a slower rate ($F_{1,5} = 12.726$, $P = 0.016$; Fig. 4) and fledged at a smaller mass (native: 14.15 g; exotic: 12.87 g; $F_{1,5} = 9.062$, $P = 0.03$). In addition, nestlings in the exotic habitat took significantly longer to fledge (native: 8.7 days; exotic: 9.8 days; $F_{1,9} = 5.952$, $P = 0.032$). Growth rates of tarsi ($F_{1,5} = 0.344$, $P = 0.583$) and the outermost primary feather ($F_{1,5} = 1.072$, $P = 0.348$) were similar in both habitats.

DISCUSSION

For mobile organisms that occupy heterogeneous landscapes, the choice of where to settle among the mosaic of different habitats available generally will have strong fitness consequences (Krebs 1971; Grant 1975; Lundberg *et al.* 1981; Blondel *et al.* 1993; Petit & Petit 1996; Blondel *et al.* 1999; Remes *in press*). Models that seek to explain the distribution of individuals among habitat patches therefore are useful not only in understanding population dynamics, but also are essential in determining the value of different habitats for a species. Assessing the quality of different habitats is important when choices must be made about which patches to protect and when considering whether restoration of human-modified habitats is necessary. In this study, predictions from three models of habitat selection were tested using data on the distribution of Chestnut-collared Longspurs in a mosaic of native and exotic habitat patches.

Little evidence was found that Longspurs were distributed in an ideal-free fashion. In contrast to the predictions of the ideal-free distribution, evidence of habitat-specific variation was found in several components of fitness. Nest success was higher in the native habitat as a consequence of lower predation rates. Furthermore, nestlings in the exotic habitat grew more slowly and took longer to fledge, which may have increased their susceptibility to predators. Starvation, although rare, was more common among nestlings in the exotic habitat. Nestlings in the exotic habitat also had lower body mass at fledging, which can reduce post-fledging survival (Krebs 1971; Magrath 1991). Finally, the population model suggests that productivity in the exotic habitat is too low to support stable populations; only with unrealistically high juvenile and adult survival rates did lambda approach 1.

Habitat-specific variation in fitness is predicted by the ideal-despotic distribution; however, this model also predicts that density should co-vary with habitat quality and that the higher quality habitat will be settled first. In 2002, settlement patterns were examined and no difference was found between habitats in the temporal progress of territory establishment. In support of the settlement data, no difference was found between habitats in the date that egg laying began. Nesting density tended to be slightly higher in the native habitat, but the difference was small and not statistically significant. Thus, the ideal-despotic model does not adequately explain the habitat distribution of Longspurs in this system.

The ecological-trap hypothesis offers an alternative explanation for habitat-specific variation in fitness. In environments that have been modified by humans, the indirect cues used by animals to assess the expected quality of a habitat may become decoupled from the actual quality of the habitat. The introduction of exotic plants into native communities may frequently generate the conditions necessary for ecological traps; for example, both Schmidt & Whelan (1999) and Remes (*in press*) have shown that breeding birds are attracted by the earlier leafing phenology of exotic plants but that nest predation rates are higher in exotic habitats. Similarly, the habitat created by the introduction of *A. cristatum* was of lower quality yet settling Longspurs did not avoid the exotic habitat. In fact, based on settlement times and nest densities, Longspurs exhibited no preference for the higher quality native habitat.

Thus, the exotic habitat appears to act as an ecological trap because upon arrival in the spring Longspurs do not perceive that the exotic habitat is of lower quality. Birds can use a variety of cues when selecting breeding habitat (Hilden 1965; Boulinier *et al.* 1996; Forsman *et al.* 1998), but may often rely on vegetation conditions at the time of settling to predict habitat quality (e.g., Badyaev 1995). Although fields of *A. cristatum* differ from patches of native prairie in a number of ways, the two habitats are broadly similar in structure and appearance and thus differentiating exotic from native habitat may be difficult for settling individuals. Furthermore, *A. cristatum* begins growing earlier in the year than most of the native grasses, and may be attractive to Longspurs prospecting for a nesting site (e.g., Schmidt and Whelan 1998; Remes *in press*).

Individuals may also be hindered by a lack of direct cues that would allow them to assess their breeding prospects in both habitats. For example, prey species appear to be able to assess predation risk in an area by recognizing the presence of predators, and can modify their habitat use accordingly (Werner *et al.* 1983; Turner & Mittlebach 1990; Nordahl & Korpimaki 1998). In this system, the causes of high nest predation in the exotic habitat are unknown but are unlikely to be driven by differences in predator abundance that could be assessed by settling Longspurs. Our study plots are in close proximity to one another and thus larger predators (e.g., Northern Harriers, *Circus cyaneus*) will have ranges that encompass multiple patches of habitat. At a smaller scale, a predator trapping study conducted near our study plots showed no significant differences between native and exotic habitats in the composition of the predator community (Elizabeth Madden, unpublished data). Poor choice of nest sites within the exotic habitat may play a role, as historically appropriate patterns of nest site selection do not always confer safety in a changed environment (e.g., Misenhelter & Rotenberry 2000). However, statistically non-random nest placement within a habitat could not be detected and thus the contribution of maladaptive nest site selection to the pattern of high nest predation in the exotic habitat remains unclear.

Trade-offs between food availability and predation risk are often important in shaping habitat selection (Grubb & Greenwald 1982; Werner *et al.* 1983; Lima & Dill 1990); however, in this case, Longspurs apparently did not choose to breed in the high-predation exotic habitat because of increased food availability. Nestling starvation was more common in the exotic habitat, females had longer intervals between nesting attempts, and nestlings grew more slowly, took longer to fledge, and left the nest at a smaller size, all of which are expected if food is limiting (reviewed in Martin 1987). Slow growth and long nestling periods caused by food limitation should increase predation mortality in the exotic habitat independent of any differences in the predator community, although the observed one day difference in the length of the nestling period cannot explain the entire difference in nest predation rate. However, food and predation may interact in a number of other ways to influence reproductive success. Limited food may force adults to increase their foraging effort and decrease the time they spend guarding the nest, which can increase the risk of predation (Martin 1992; Komdeur & Kats 1999). For example, Lynn et al. (2002) found that predation rates increased when male Chestnut-collared Longspurs reduced the amount of time they spent perched near the nest.

In conclusion, Chestnut-collared Longspurs were distributed evenly among patches of native and exotic habitat but reproductive success was lower in monocultures of *A. cristatum* due to elevated rates of nest predation. The exotic habitat appears to be an ecological trap and our population model suggests that it is likely a sink. Although Longspurs performed better in their native habitat, our estimates of seasonal fecundity suggest that patches of native habitat may also be incapable of supporting stable populations at present. This suggests that larger-scale processes, affecting individuals in all habitats within a landscape, may be more important in determining population stability than habitat-based differences in reproductive success. Thus, although restoring native prairie will likely benefit Longspurs, the importance of habitat-specific demographics may be limited in highly fragmented and modified landscapes such as those of the North American Great Plains.

ACKNOWLEDGMENTS

Thanks to D. H. Johnson, E. Madden, and R. Callaway for constructive comments on earlier drafts. Thanks to V. Adamski for help during manuscript preparation. Thanks also to the staff of Medicine Lake NWR for help at all phases of the project, and to the many people who provided field assistance over the years.

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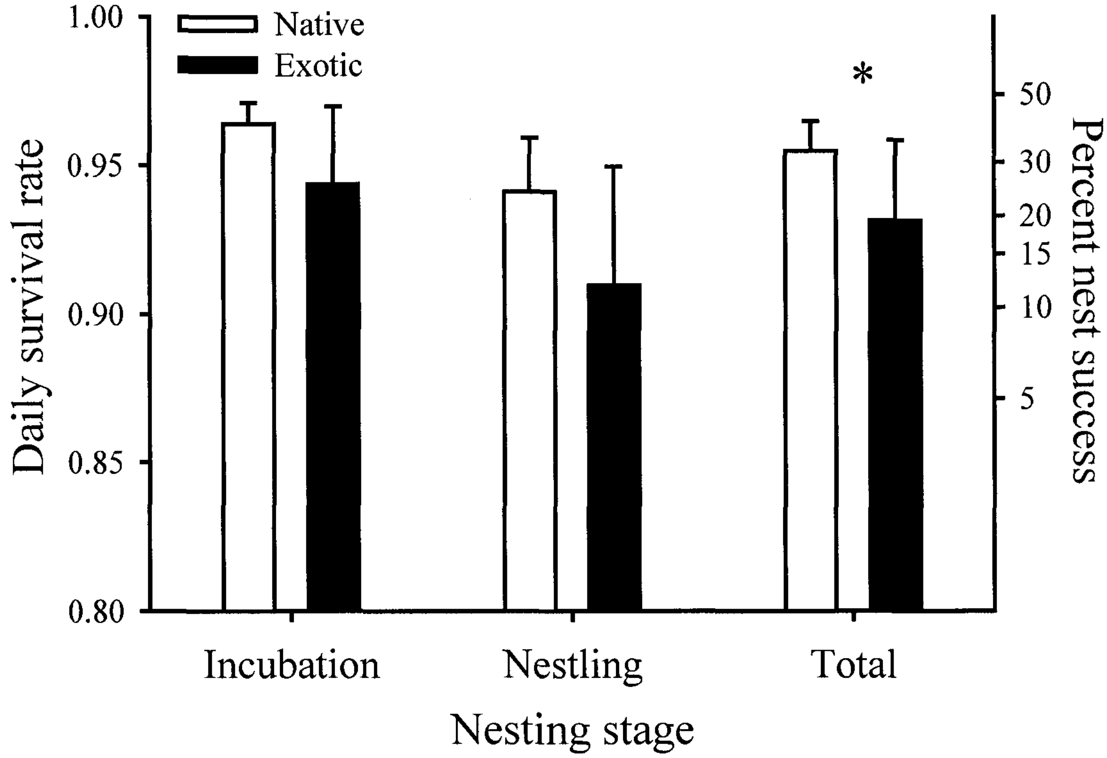
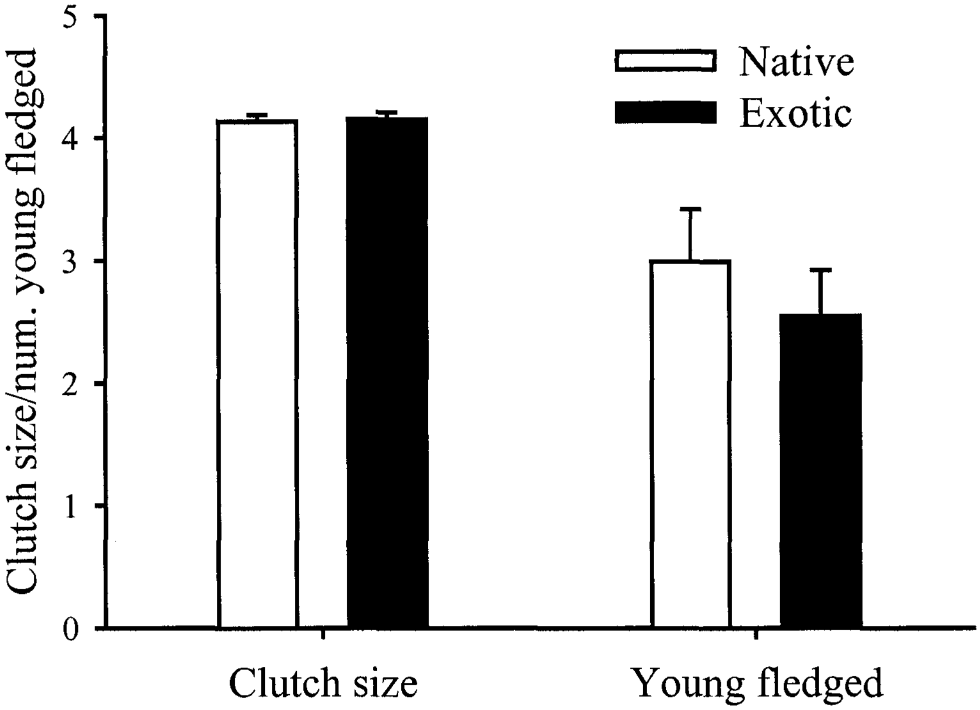
Figure 1. Daily nest survival rates (± s.e.) for Chestnut-collared Longspurs, calculated using the Mayfield method, in plots in exotic habitat (n = 4) and plots in native habitat (n = 4). *P = 0.07.

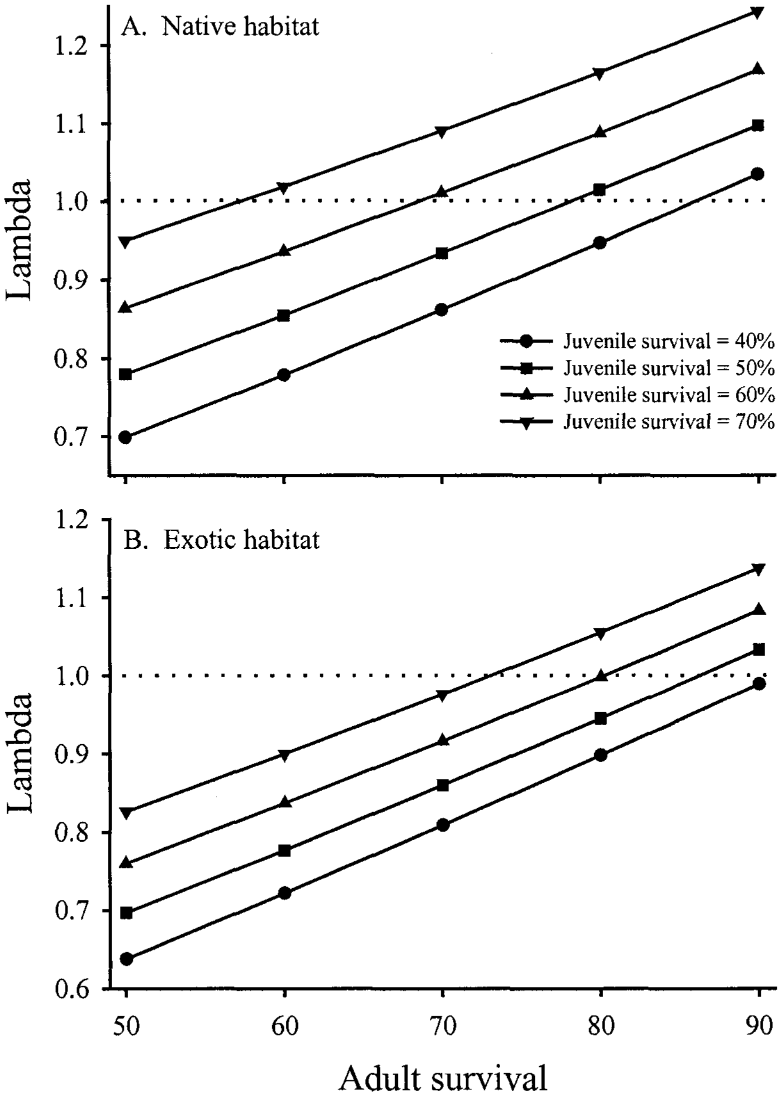
Figure 2. Clutch size and the number of young fledged from successful nests for Chestnut-collared Longspurs breeding in plots of native (n = 4) and exotic (n = 4) habitat.

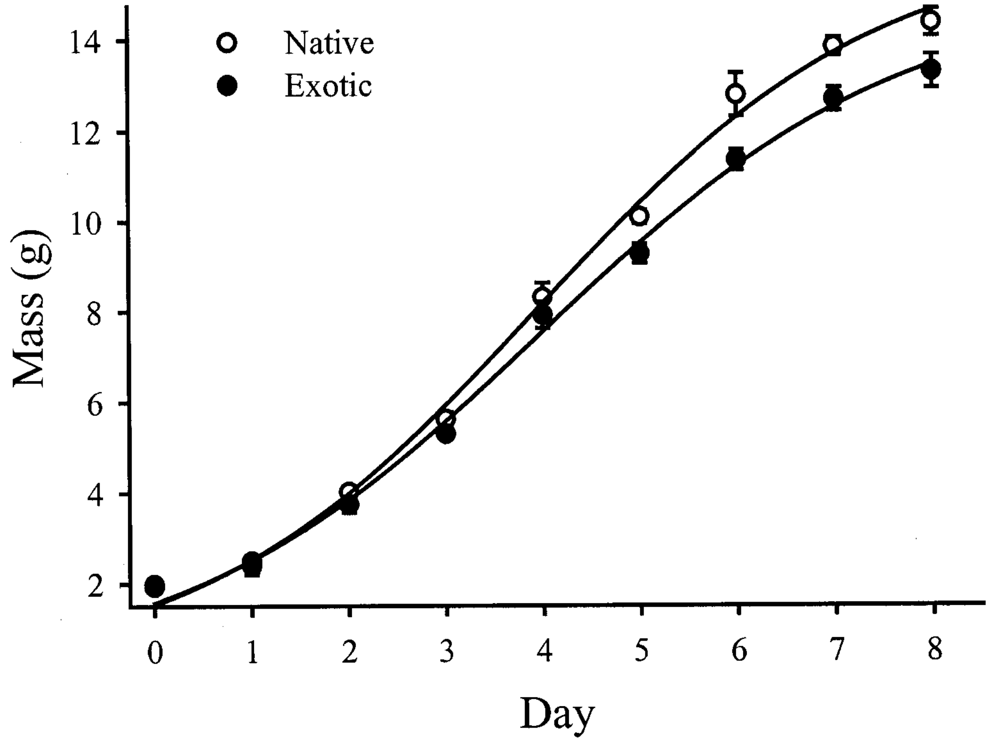
Figure 3. Model estimates of annual adult and juvenile survival rates necessary to maintain stable populations based on field estimates of seasonal fecundity for Chestnut-collared Longspurs. (**a**) model estimates for populations in native habitat and (**b**) model estimates for populations in exotic habitat.

Figure 4. Logistic mass growth curve for Chestnut-collared Longspur nestlings in plots of native habitat (n = 3) and plots of exotic habitat (n = 3).


Native
Exotic
1.00
0.95
0.90
0.85
0.80
Daily survival rate
50
30
20
15
10
5
Percent nest success
*
Incubation
Nestling
Total
Nesting stage


Clutch size/num. young fledged
0
1
2
3
4
5
Native
Exotic
Clutch size
Young fledged


A. Native habitat
B. Exotic habitat
Lambda
1.2
1.1
1.0
0.9
0.8
0.7
0.6
Juvenile survival = 40%
Juvenile survival = 50%
Juvenile survival = 60%
Juvenile survival = 70%
50
60
70
80
90
Adult survival


○ Native
● Exotic
Mass (g)
2
4
6
8
10
12
14
0
1
2
3
4
5
6
7
8
Day

CHAPTER III

NEST SITE SELECTION AND MATERNAL EFFECTS ON OFFSPRING GROWTH

INTRODUCTION

Non-genetic maternal effects on offspring phenotype appear to be widespread and often of profound importance (Kirkpatrick and Lande 1989, Etges 1998, Agrawal 2001). For example, many studies have shown that females can adjust the size or composition of propagules in order to produce adaptive shifts in offspring phenotype (Fox et al. 1997, Agrawal 2002, Gasparini et al. 2002). Far less is known about how maternal behavior, rather than maternal allocation decisions, influences offspring phenotype and fitness (Bernardo 1996). The choice of an oviposition site may be a particularly important source of maternal effects because it will in part determine the early environment that offspring experience, which can have profound and long-lasting effects on phenotype (e.g., Boag 1987, Bernardo 1993, Fox et al. 1994, Sinervo and Doughty 1996, Roitberg 1998, Mousseau and Fox 1998). Maternal oviposition decisions may commonly influence offspring fitness and phenotype and therefore may be important both for understanding population dynamics and predicting evolutionary change (Kirkpatrick and Lande 1989, Roitberg 1998).

Among insects and reptiles, choice of an oviposition site can influence offspring traits such as sex, size, growth and development rates, and locomotor performance (Fox et al. 1994, Shine and Harlow 1996, Qualls and Shine 1998, Kolbe and Janzen 2002). Nest-site selection has also been widely studied in birds, but almost exclusively in the context of understanding how predator avoidance has shaped the evolution of nest microhabitat preferences (Martin 1998, Clark and Shutler 1999). As a consequence, most studies of avian nest-site selection consider only the immediate survival consequences of variation in nest placement. However, maternal nest-site preference may have a variety of non-lethal effects on offspring phenotype as well. Most importantly, as with reptiles, nest-site preference may influence offspring phenotype through the effect of microclimate on developing embryos and nestlings (Webb and King 1983, Haftorn 1988, With and Webb 1993, Conway and Martin 2000).

A number of studies have shown correlations between nest-site choice and aspects of microclimate (Ricklefs and Hainsworth 1969, Walsberg 1981, Korol and Hutto 1984, With and Webb 1993, Gloutney and Clark 1997, Martin 2001) and several studies have shown correlations between some measure of fitness and nest-site features presumed to influence microclimate (Austin 1974, Yanes et al. 1996). However, clear demonstrations of fitness consequences arising from microclimate differences associated with nest-site choice are lacking. Although most studies of nest-site selection consider only the role of predation, habitat preferences ultimately reflect trade-offs between a variety of conflicting selection pressures (Werner et al. 1983, Lima and Dill 1990) and thus examining alternative selection pressures, such as nest microclimate, may provide a better understanding of the evolution of nest-site preferences. Integrating nest microclimate into our understanding of nest-site selection may also be important from a conservation standpoint. For example, if offspring are adapted to particular conditions at the nest site (Davis et al. 1984), then environmental changes that decouple nest-site preferences from microclimatic conditions, such as the spread of exotic plants or global climate change, may have detrimental effects on individual fitness and subsequent population growth.

Nestling growth rate is an important component of fitness (Gebhardt-Henrich and Richner 1998) that is likely to be sensitive to variation in nest microclimate (Bryant 1975, Ernst et al. 1984, Petersen et al. 1986, Konarzewski and Taylor 1989, McCarty and Winkler 1999). Temperature in particular can have a major influence on growth through its effect on energy and water budgets (Ernst et al. 1984, Sullivan and Weathers 1992, Wolf and Walsberg 1996). Temperatures at the nest-site are largely a consequence of the orientation of the nest opening because the directionality of the nest determines when, and for how long, the nest is exposed to direct insolation (Walsberg and King 1978, Walsberg 1981). Nest orientation can also influence the convective environment by changing wind velocity around the nest site, but solar radiation generally has a much greater effect on heat balance than does wind (Wolf and Walsberg 2000, Wolf et al. 2000). Although effects of nest orientation on microclimate have been shown in many species, the fitness consequences have not been measured.

Here, we examine how nest orientation influences nestling growth rate in Chestnut-collared Longspurs (*Calcarius ornatus*; hereafter, longspurs), a songbird of the northern Great Plains of North America. An important difficulty in assessing the relationship between nest orientation and offspring phenotype is that microclimate effects may be confounded with individual quality if low quality individuals tend to choose non-preferred orientations. To counter this problem, we experimentally shifted the orientation of nests and examined the effect on nestling growth. By randomly re-assigning a new orientation to a nest, we equalized sample sizes among orientations and experimentally separated the effects of individual quality and nest-site microclimate.

METHODS

Study site

Work was conducted at Medicine Lake National Wildlife Refuge, which is located on the glaciated plains north of the Missouri River in eastern Montana. The 8100 ha refuge consists of native mixed-grass prairie (dominant species include *Stipa spp.*, *Agropyron smithii*, *Koeleria cristata*, and *Bouteloua gracilis*), monocultures of the introduced grass *Agropyron cristatum*, hayfields, small agricultural fields, and a variety of seasonal and permanent wetlands surrounding a large (c.a. 3200 ha) freshwater lake. Data for the descriptive portion of this study were gathered between 2000-2002 and our experiment was conducted in 2002.

Study organism and nesting biology

Chestnut-collared Longspurs build open-cup nests on the ground. The female appears to choose the site and performs nearly all of the construction. Construction begins with the female digging a 4-5 cm deep hole in the ground, which is subsequently lined with grasses such that the rim of the nest is approximately level with the surface of the ground. Nests are usually placed next to a clump of grass but have little overhead cover; in 4 years of study at this site the percent of the nest obscured from overhead by vegetation averaged only 27% (n = 161).

Nest-site selection and nest temperature

We located nests from April-July of each year using both systematic searches and behavioral observations of adult longspurs. During systematic searches, we flushed adults from nests by dragging a weighted rope across the plot. After a nest was located, we marked its position with 1 or 2 small pieces of flagging placed 1-2 m from the nest cup. Flagging does not appear to increase the risk of nest predation (Hein and Hein 1996) and was necessary to allow us to relocate nests.

To examine patterns of nest-site selection, we measured the following variables immediately following the termination of a nesting attempt: orientation, side cover, and the volume of vegetation immediately surrounding the nest. We measured nest orientation by first locating the opening in the vegetation used by adults to access the nest. Nest orientation was then recorded, relative to magnetic north, as the azimuth bisecting the nest opening. We assessed side cover by placing a 5 cm radius cardboard disc in the nest and then estimating the percentage of the disc that was occluded when viewed from 1 m away in each of the cardinal directions. At 4 points, 1 cm outside the edge of the nest in each cardinal direction, we estimated the volume of vegetation by measuring the visual obstruction of vegetation against a wooden pole marked in 25 cm increments (Robel et al. 1970). We measured vegetation volume in the same fashion at a random point within the same territory, allowing us to determine the importance of this feature in nest-site selection. Directional patterns in side cover and the height and density of vegetation surrounding the nest determine the orientation of the nest, and thus we included these measures to shed light on how females shape the exposure of their nest to the sun.

We quantified nest microclimate at each nest by measuring temperature within the nest cup for 24 continuous hours as soon as the nesting attempt ended. We simultaneously measured ambient air temperature at a point 5 m from the nest. For both temperature measures we used Stow-Away data loggers (Onset Computer Corporation, Bourne, MA) equipped with external, black-bulb thermistor sensors that were sensitive between -39°C and 122°C. For nest temperature measurements, we used a piece of wire to position the sensor approximately 1 cm above the center of the base of the nest, such that the sensor was suspended horizontally above and parallel to the base of the nest. Nest temperatures obtained from our sensors are not the same as the operative environmental temperature experienced by birds at the nest (Walsberg and Weathers 1986), but they do provide an unbiased way of characterizing thermal conditions at the nest (Stoutjesdijk 2002). To measure ambient air temperature we positioned the sensor approximately 5 cm above the ground and shielded the thermistor from direct sunlight with a plastic shade.

We determined if longspurs preferred to orient their nests in particular directions lusing a one-sample Kolmogorov-Smirnov test, in which the observed distribution of directions was compared against the null hypothesis that the distribution of nest orientations was uniform (Bergin 1991). MANOVA was used to compare vegetation volume (square-root transformed for normality) at nest sites and random, non-nest sites. Because side cover is a unique characteristic of nest-sites, it can not be meaningfully measured at random points and therefore we were unable to determine whether longspurs select nest sites with more or less cover than is generally available in the environment. Thus, we only present descriptive statistics for side cover. We used repeated-measures ANCOVA to analyze the relationship between nest orientation and nest temperature. Because we measured nest temperatures over the length of the breeding season, ambient air temperature varied greatly and was thus included as a covariate. Orientation has little effect on temperature during the evening, early morning, and late afternoon, so to achieve reasonable power in our repeated-measures test we limited our comparison of nest temperatures to the hours of 1000-1600. For comparisons among unmanipulated nests, we treated orientation as a categorical variable with four levels: northeast (0-90°), southeast (91-180°), southwest (181-270°), and northwest (271-360°).

Nestling growth and survival

To determine the fate of nestlings we returned every 2 days to inspect the contents except when fledging was expected, at which point we visited daily. If the nest was empty prior to the expected fledging date, we searched the territory for adults to determine if they were feeding fledglings. Adult longspurs continue to feed and defend fledglings on the territory for several weeks after the young leave the nest, and thus we assumed that predation had occurred if we were unable to locate adults feeding fledglings. To estimate nestling growth rate, we individually marked nestlings as they hatched using a felt-tipped pen, and returned every 2 days to measure body mass, total length of the outermost primary on each wing (shaft, and feather when applicable), and length of both tarsi. For analysis, we used the mean of the right and left measurements for tarsus and primary length. Mass was estimated to the nearest 0.1 g using a portable electronic balance, and primary and tarsus length were both measured to the nearest 0.1mm using calipers.

We estimated growth rates of all nestling traits by using non-linear regression to fit a logistic growth curve to the entire data set for each trait. The logistic curve provided an excellent fit for all measured traits (mass $r^2 = 0.85$, tarsus $r^2 = 0.81$, primary feather r^2

= 0.86; all P's < 0.001). To compare growth among orientations, we analyzed residuals from the non-linear regression using ANCOVA with brood size and hatching date as covariates (Ricklefs 1983). To avoid artificially inflating error degrees of freedom, residuals from the growth curve were pooled among nestlings within a nest before analysis. This approach allowed us to include all measured individuals in the analysis; had we attempted to estimate growth parameters separately for each individual or each nest we would have been forced to exclude samples with fewer than three measurements. For successful nests, we compared the final mass of nestlings using ANCOVA using the same covariates. We also used ANOVA to compare treatment effects on survival, expressed as the percentage of eggs that fledged young (arcsin transformed); the number of young fledged; and the length of the nestling period.

Because microclimate effects on nestling growth may be mediated through indirect effects on parental behavior we used video cameras to examine how two elements of parental behavior, feeding rate and time spent brooding young, varied in response to microclimate. On day three of the nestling period (day of hatching = 0) we placed a Hi-8 video camera at each nest and recorded activity from 0700-1400 hours. By taping all nests at the same developmental stage, we were able to control for natural variation in feeding and brooding rates that occur as nestlings age. To control for differences among nests in weather conditions at the time of taping, we also recorded ambient air temperature during videotaping. 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, we compared percent of time spent brooding (arcsin transformed) and the number of feeds per hour (natural log transformed) among treatments using ANCOVA, with ambient temperature and brood size as covariates. In all cases, *post-hoc* comparisons among treatments were adjusted for multiple comparisons using the Bonferroni method. Unless otherwise noted, variables were normally distributed and thus not transformed for analysis.

Experimental manipulation of microclimate

We experimentally manipulated nest orientation to examine the causative relationship between maternal choices about nest-site placement and offspring phenotype and fitness. By removing vegetation and adding artificial shade, we experimentally altered nest orientations to manipulate the radiative environment experienced by nestling and adult longspurs. We manipulated nests to create three experimental orientations: northeast (40-50°), southeast (130-140°), and southwest (220-230°). We chose these orientations to represent the three general radiative conditions a nest might experience: no direct sun, morning sun, and afternoon sun. We applied the treatment with the constraint that the experimental orientation must be in a different quadrant than the natural orientation; for example, nests that faced between 0-90° were assigned to either a southeast or southwest orientation but never a northeast orientation. Otherwise, treatments were assigned randomly and nests not selected were left unmanipulated for comparison. All treatments were applied on the day of hatching. We created artificial orientations by clipping vegetation to expose the nest in the desired direction while simultaneously using an artificial shade to eliminate the natural nest opening. We standardized the size of the artificial nest openings by clipping vegetation until the disc used to measure concealment was completely unobscured by vegetation when viewed from 1 m away at the desired orientation. Artificial shade was created by placing a 15 x 15 cm square piece of fine-mesh (1 mm) metal window screen, stretched between two metal pins, in front of the nest opening. We placed the screens immediately adjacent to the nest and at a slight angle such that the top of the screen was in the same plane as the edge of the nest cup. Thus, by shading the natural opening and clipping vegetation to create a new opening, we were able to artificially manipulate realized nest orientation.

After clipping and shading a nest, an observer hid 150 m from the nest and recorded the time that elapsed until parents returned either to feed the nestlings or to brood them. Using ANOVA, time to return at experimental nests was compared with data gathered in a similar fashion at unmanipulated nests of the same age that were visited for routine nest checks (e.g., parents flushed off of the nest and contents recorded). Comparing return times allowed us to assess the extent to which the application of our treatments disrupted normal behavioral patterns.

Predictions

A southeast nest orientation should help minimize morning cold stress while avoiding the potential for heat stress caused by direct exposure to the sun during the afternoon, the period of highest ambient air temperatures. Thus, we expect that growth and survival should be highest in southeast-facing nests (morning sun) and lowest in southwest-facing nests (afternoon sun), and intermediate in northeast-facing nests (no direct sun). Predation has been shown to influence many features of avian nest sites, and thus is an important alternative to consider. We do so in two ways. First, we compare the distribution of nest orientations at successful and depredated nests. Second, we compare predation rates among our experimental treatments. If orientation is related to the risk of predation, we expect differences in the distribution of nest orientations between successful and depredated nests, and differences in predation rates among our treatments.

RESULTS

Climate at the study site

Average maximum air temperatures during the course of our study were similar to the long-term average (Fig. 1a). During 2002, when we conducted our experiment, temperatures in May, June, and August were slightly cooler than the long-term average and nearly identical to the long-term average during July.

Weather station data from out site, average across the breeding season, show that minimum temperatures occur just prior to and just following sunrise, and that maximum daily temperatures are generally achieved between 1400-1700 hours (Fig. 1b). During the coldest daylight hours (0500-0800), the solar azimuth ranges between 55-90°; during the time of maximum daily temperatures (1300-1700) the solar azimuth is between 185-265°. Prevailing winds come from the east-northeast and the west-southwest (Fig. 2).

Nest-site selection and nest temperature

Longspurs preferred to orient their nests towards the southeast ($n = 313$, Kolmogorov-Smirnov $Z = 4.417$, $P < 0.001$; Fig. 3). Preference for southeast-facing nests did not change seasonally. The distribution of nest orientation was similar when comparing early (initiated before 1 June, n = 155, median = 141°) and late (initiated after 1 June, n = 121, median = 145°) breeding attempts (Kolmogorov-Smirnov Z = 0.880, P = 0.480). The distribution of vegetation around nest sites differed from random points ($F_{4, 204} = 2.280$, P = 0.05); in particular, nest sites had significantly lower volume of vegetation on the south ($F_{1, 207} = 4.957$, P = 0.027) and east ($F_{1, 207} = 4.912$, P = 0.028) sides. Similarly, the percent of the nest obscured by vegetation was lower on the south (mean = 40.9%) and east (mean = 39.2%) sides than on the north (mean = 64.5%) or west (mean = 64.0) sides. Thus, as predicted, female longspurs appear to position nests so as to create a favorable radiative environment for themselves and their young. Given the pattern of prevailing winds (Fig. 2), a southeast orientation may also help reduce wind velocity at the nest. Nest orientation was not related to the risk of predation; the distribution of nest orientations was similar in successful (n = 116) and depredated nests (n = 130; Kolmogorov-Smirnov Z = 0.931, P = 0.351).

Orientation has a strong effect on nest temperature, especially during midday (Fig. 4a). A repeated-measures ANCOVA on nest temperatures between 1000-1600 hours indicates a significant difference among orientations after controlling for the effect of ambient air temperature at the time when nest temperature was measured (ambient temperature: $F_{1, 49} = 116.02$, $P < 0.001$; nest orientation: $F_{3, 49} = 5.887$, P = 0.002). Nests facing southeast are significantly hotter during this period than nests oriented towards either the northeast (mean difference = 8.7°C, P = 0.04) or the northwest (mean difference = 10.3°C, P = 0.007). Temperatures at nests facing southeast were not significantly different than nests facing southwest (mean difference = 3.6° C, P = 0.644). Nests oriented to the southwest were marginally warmer than northeast-facing nests (mean difference = 7.2°C, $P = 0.101$). Thus, contrary to expectations, a southeast orientation does not appear to provide a consistent buffer against afternoon heat stress.

Operative temperatures at nests with experimentally altered orientations were similar to unmanipulated nests with the same orientation, and more importantly strong differences emerged among treatments during midday (Fig. 4b). After controlling for ambient temperature, nest temperatures between 1000-1600 differed significantly among treatments (ambient temperature: $F_{1, 22} = 16.337$, $P = 0.001$; treatment: $F_{2, 22} = 20.334$, $P < 0.001$). As at unmanipulated nests, experimental nests with a southeast orientation ($n = 17$) experienced significantly greater temperatures between 1000-1600 than did experimental nests with a northeast orientation ($n = 22$; mean difference = 10.2°C, $P < 0.001$). Nests facing southwest ($n = 22$) had higher temperatures than did nests facing northeast (mean difference = 9.5°C, $P < 0.001$) but were not significantly different than nests facing southeast (mean difference = 2.2°C, $P = 0.701$). Thus, our experimental nests were largely successful in recreating the radiative environment experienced at natural nests.

Despite the effect of treatment on nest temperature, the disturbance associated with applying treatments did not have an immediate effect on adult behavior. Adults took an average of 15.1 minutes to begin feeding nestlings after application of the treatment; adults took an average of 12.3 minutes to return to unmanipulated nests following routine nest checks, a non-significant difference ($F_{1, 23} = 0.932$, $P = 0.408$). None of the nests in the experiment were abandoned following treatment.

Nestling growth and survival

The rate of mass gain varied significantly among orientations (orientation: $F_{3, 116} = 3.083$, $P = 0.03$; hatching date: $F_{1, 116} = 1.102$, $P = 0.296$; brood size: $F_{1, 116} = 16.94$, $P < 0.001$), but paradoxically growth was slowest among nests facing the preferred direction (Fig. 5a). Rate of mass gain was significantly greater for nestlings in northeast-facing nests than in nests with a southeast orientation ($P = 0.023$), but none of the other means differed significantly. Tarsus growth, feather growth, length of the nestling period, survival, and number of nestlings fledged were similar among orientations (all P's > 0.20).

Similar results were obtained by experimentally changing nest orientation; in no case did nestlings perform better in nests that had been shifted to face the preferred direction. First, experimentally changing the orientation of a nest had a significant effect on the rate of mass gain among nestlings after controlling for hatching date and brood size (orientation: $F_{2, 54} = 2.773$, $P = 0.012$; hatching date: $F_{1, 54} = 12.52$, $P = 0.001$; brood size: $F_{1, 54} = 0.055$, $P = 0.816$; Fig. 5b). As in natural nests, nestlings in nests shifted to face southeast grew significantly slower than nestlings in northeast-facing nests ($P = 0.01$). Growth in southwest-facing nests was similar to growth in nests shifted to face southeast ($P = 0.901$) and northeast ($P = 0.201$). The length of the nestling period was similar among treatments (northeast: 8.4 days; southeast: 8.9 days; southwest: 8.2 days; $F_{2, 23} = 0.886$, $P = 0.426$) and similar to that of unmanipulated nests (over the course of 4 years at this site, mean length of nestling period = 9.1 days; $n = 112$).

Mass at fledging varied among treatments (orientation: $F_{2,26} = 3.864$, $P = 0.034$; hatching date: $F_{1,26} = 2.770$, $P = 0.108$; brood size: $F_{1,26} = 2.888$, $P = 0.101$; Fig. 5c) and was also lowest in nests with the preferred orientation. Mass at fledging in southeast-facing nests was significantly lower than in nests with a northeast orientation ($P = 0.034$). As with growth rate, fledging mass was intermediate in nests shifted to face southwest (both P's > 0.30).

Tarsus growth also varied by treatment (orientation: $F_{2,54} = 4.881$, $P = 0.01$; hatching date: $F_{1,54} = 8.395$, $P = 0.001$; brood size: $F_{1,54} = 0.771$, $P = 0.273$; Fig. 6). Nestlings in nests with the preferred orientation did not have more rapid tarsus growth; instead tarsus growth in southeast-facing nests was significantly slower than in northeast-facing nests ($P = 0.013$). Once again, tarsus growth in southwest-facing nests was intermediate to growth at southeast ($P = 1.0$) and northeast ($P = 0.12$) orientations. Length of the tarsus at fledging did not vary among treatments (orientation: $F_{2,29} = 0.051$, $P = 0.951$; hatching date: $F_{1,29} = 11.988$, $P = 0.055$; brood size: $F_{1,29} = 0.772$, $P = 0.387$), nor did feather growth (orientation: $F_{2,54} = 1.583$, $P = 0.215$; hatching date: $F_{1,54} = 12.312$, $P = 0.001$; brood size: $F_{2,54} = 0.231$, $P = 0.633$). However, the trend was the same as for mass and tarsus growth; rate of feather growth was greatest in northeast-facing nests, intermediate in southwest-facing nests, and lowest in nests oriented to the southeast.

The percent of young that survived to fledge did not vary among treatments (orientation: $F_{2,58} = 0.215$, $P = 0.807$; hatching date: $F_{1,28} = 0.644$, $P = 0.015$) and mean percent survival at experimental nests (25.3%) was similar to that at unmanipulated nests (24.9%). As is typical of passerine birds, nearly all nestling mortality was the result of predation. Predation caused the complete loss of all nestlings at 44% of northeast-facing nests, 53.8% of southeast-facing nests, and 50% of southwest-facing nests. Partial predation of broods likely accounted for most of the other nestlings that disappeared during the course of the study. Starvation was rare, and accounted for the loss of 6 nestlings (in 3 nests) in northeast-facing nests, 8 nestlings (in 7 nests) in southeast-facing nests, and 7 nestlings (in 4 nests) in southwest-facing nests. Partial brood losses, whether by predation or starvation, were distributed equally among treatments: the number of young fledged from successful nests (e.g., at least one young fledged) did not vary among treatments (orientation: $F_{2, 32} = 0.817$, $P = 0.451$; hatching date: $F_{1, 32} = 0.009$, $P = 0.926$).

The percentage of time adults spent brooding varied significantly among treatments (orientation: $F_{2, 10} = 10.38$, $P = 0.004$; ambient air temperature: $F_{1, 10} = 0.821$, $P = 0.386$; brood size: $F_{1, 10} = 0.624$, $P = 0.448$; Fig. 7a). At the cooler, northeast-facing nests adults spent significantly less time brooding than at southeast-facing nests ($P = 0.003$); percent of time brooding was intermediate at southwest-facing nests and did not differ significantly from other orientations (northeast, $P = 0.176$; southwest, $P = 0.356$). Time spent brooding may have constrained the amount of time adults spent foraging for young, and the rate at which adults fed young varied among orientations (orientation: $F_{2, 22} = 4.191$, $P = 0.029$; ambient air temperature: $F_{1, 22} = 0.808$, $P = 0.378$; brood size: $F_{1, 22} = 0.348$, $P = 0.561$; Fig. 7b). Adults at southeast-facing nests fed young significantly less often than adults at northeast-facing nests ($P = 0.026$); all other comparisons were not significantly different (all P's > 0.45).

DISCUSSION

The environmental conditions to which organisms are exposed early in life can have long-lasting effects on phenotype and fitness (Boag 1987, Metcalfe and Monaghan 2001). The early environment for many organisms is determined by maternal decisions about where to deposit propagules, and as a consequence oviposition behavior can be an important source of maternal effects (Fox et al. 1994, Shine and Harlow 1996, Roitberg 1998). Incorporating information on how maternal oviposition preferences generate maternal effects is necessary in understanding the evolution of oviposition behavior. Many studies show that nest-site choices are adaptive in reducing the risk of predation on offspring (Martin 1993, 1998; Clark and Shutler 1999; Madsen and Shine 1999), but nest-site selection may also mediate more subtle maternal effects. For example, growth, development, and other life history traits of pre- and post-natal birds are known to be affected by abiotic conditions such as temperature and humidity (Davis et al. 1984, Ernst et al. 1984, Lyon and Montgomerie 1987, Haftorn 1988), and nest sites often appear to be chosen so as to minimize adverse environmental conditions (Ricklefs and Hainsworth 1969, Walsberg 1981). However, little direct evidence has been gathered to show that nest placement, through its effect on microclimate, can influence offspring phenotype.

In our system, longspurs exhibited a strong preference for nest sites with a southeast orientation. A similar pattern has been described for other birds, and this preference has been interpreted as an adaptation to minimize cold stress during the morning and heat stress during the afternoon (Walsberg and King 1978). However, data from unmanipulated nests suggest that heat stress is most likely in nests with a southeast orientation, as they are significantly hotter than other orientations during midday (Fig. 4).

Nests facing southwest tend to be warmest during the afternoon, but operative temperature differences among orientations diminish rapidly after 1400 hours. Paradoxically, nestling mass gain was lowest in nests with the preferred orientation, and was highest in northeast-facing nests (Fig. 5). Sample size was small for southwest and northwest orientations, and growth rates for these orientations could not be distinguished statistically from other orientations.

The experimental data provide better evidence that nest-site selection, by influencing nest microclimate, can affect nestling growth. The experimental data also suggest that nest-site orientation preferences are not adaptive. Rate of mass growth and, ultimately, fledging mass were lowest among nests with the preferred southeast orientation. Nestlings from northeast-facing nests were more than 2 g heavier at the time of fledging than nestlings from southeast-facing nests, and more than 1 g heavier than nestlings from southwest-facing nests. These differences equate to approximately 9% and 18% reductions in body mass, respectively, which likely has a strong negative effect on future survival prospects (Martin 1987, Magrath 1991). Tarsus growth showed the same pattern.

Altricial nestlings such as longspurs generally do not achieve homeothermy until just prior to fledging and can only deal with relatively short periods of heat stress without becoming dehydrated (Visser 1998). Despite the extreme temperatures to which nestlings in the southeast and southwest orientations were exposed, survival did not vary significantly among treatments. We attribute this to the behavioral response of adults; adults at nests with a southeast orientation spent more than 70% of the time they were under observation brooding, which is 3 times greater than the percent of time adults at northeast-facing nests spent brooding. Adults shaded their young from direct solar radiation, an important source of heat gain (Webb and King 1983, Wolf and Walsberg 1996), by sitting on, or immediately above, the nestlings. Although adults at southeast-facing nests spent more time brooding, feeding rates did not vary among treatments. Thus, growth differences among treatments likely reflected the direct physiological costs of elevated temperature rather than an indirect effect of microclimate on parental behavior.

Maternal decisions about the orientation of the nest can have strong effects on offspring phenotype. We suggest that this is a result of the effect of orientation on the radiative environment experienced by nestlings, although we cannot rule out a role of convective heat transfer. However, wind generally has much less of an effect on heat balance than solar radiation (Wolf et al. 2000, Wolf and Walsberg 2000). Furthermore, for ground nesters such as longspurs most wind reduction is accomplished by virtue of being within the boundary layer of the ground (With and Webb 1993), and thus nest orientation may have a minimal effect on the convective environment at the nest. Nonetheless, the cooling effect of prevailing west-southwest winds may help explain the similar growth rate of nestlings in northeast- and southwest-facing nests.

Predation is an important selective pressure shaping preferences for microhabitat features at the nest site (Martin 1988, 1993; Clark and Shutler 1999). We found no difference in the distribution of orientations for successful and depredated nests, nor did we find any difference in predation rates among our experimental treatments. Thus, although predation may shape many of the preferences for microhabitat features at the nest site, preference for nest orientation more likely relates to the need to ameliorate environmental conditions.

A surprising result of this study was that the preferred orientation produced the harshest microclimatic conditions. Contrary to the expectation that a southeast orientation maximizes thermal benefits, we found that the most extreme nest temperatures occurred at southeast-facing nests and that nestling growth was slowest in both natural and experimental nests oriented towards the southeast. Given that predation does not appear to constrain nest orientation preferences, why do longspurs in this system prefer to orient nests towards the southeast when doing so exposes offspring and attending adults to a harsh radiative environment? Other species breeding in similar habitat prefer to orient nests towards the north (With and Webb 1993), and in other areas of their range Chestnut-collared Longspurs prefer northwest orientations (Hill and Gould 1993). One possibility is that we somehow underestimated the benefit of a southeast orientation, perhaps because benefits only accrue when ambient temperatures are low. However, temperatures during our study were slightly cooler than the long-term average and thus our results are not an artifact of conducting the study during an abnormally warm year. Another possibility is that individuals are physically or mechanically constrained in their ability to construct a nest with the preferred orientation. None of the study plots had been disturbed since prior to 1998, and hence large amounts of standing dead vegetation had accumulated. Dead vegetation from growth in previous years tends to fall to the south, presumably as a consequence of the winter storms that tend to move south through the region. Longspurs often build nests among mats of dead vegetation, and thus nest orientation may be constrained the direction in which standing dead vegetation becomes matted. Although speculative, this scenario could explain why patterns of nest-site preference appear to be maladaptive. In addition, it would provide an interesting example of how anthropogenic effects on the environment can have untoward and unpredicted effects on species; the accumulation of dead vegetation on the study area is a result of human-caused changes in disturbance regimes, particularly the reduction or elimination of native herbivores (grasshoppers and bison, *Bison bison*) and fire. Similar reductions in the frequency of disturbance have occurred throughout what remains of the North American prairie.

Although we do not have an explanation for the apparently maladaptive nest-site preferences exhibited by longspurs at our site, our results demonstrate that nest-site selection can have strong effects on offspring phenotype and can be an important source of maternal effects. In particular, nest-site selection appears to mediate maternal effects through the influence of nest orientation on the radiative environment. The importance of nest microclimate for offspring development is well known among reptiles (Shine and Harlow 1996, Qualls and Shine 1998, Madsen and Shine 1999, Kolbe and Janzen 2002), but far is less known for other vertebrates. Here we show that growth and development of nestling birds, like reptiles, are strongly influenced by abiotic conditions at the nest site, which in turn are determined by the nest orientation chosen by the female. Our results are significant not only because they expand our concept of the role of maternal behavior as a source of maternal effects, but also because they clearly demonstrate that the process of choosing a nest site involves more than just avoiding predators. Most theories of habitat selection recognize the importance of trade-offs among conflicting selection pressures, but among the many studies of avian nest-site selection, few have considered agents of selection other than predation. Hopefully, our results will encourage the recognition of nest-site selection for the multifarious process that it is.

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Fig. 1. (a) Average maximum air temperature at Medicine Lake, Montana by month during the years included in this study in relation to long-term (1911-2002) averages. (b) Hourly average air temperature and hourly absolute extreme air temperature between May-July 2002 at Medicine Lake National Wildlife Refuge.

Fig. 2. Histogram of prevailing wind directions recorded hourly between May-July 2002 at Medicine Lake National Wildlife Refuge.

Fig. 3. Nest orientations of Chestnut-collared Longspur nests monitored during 2000-2002.

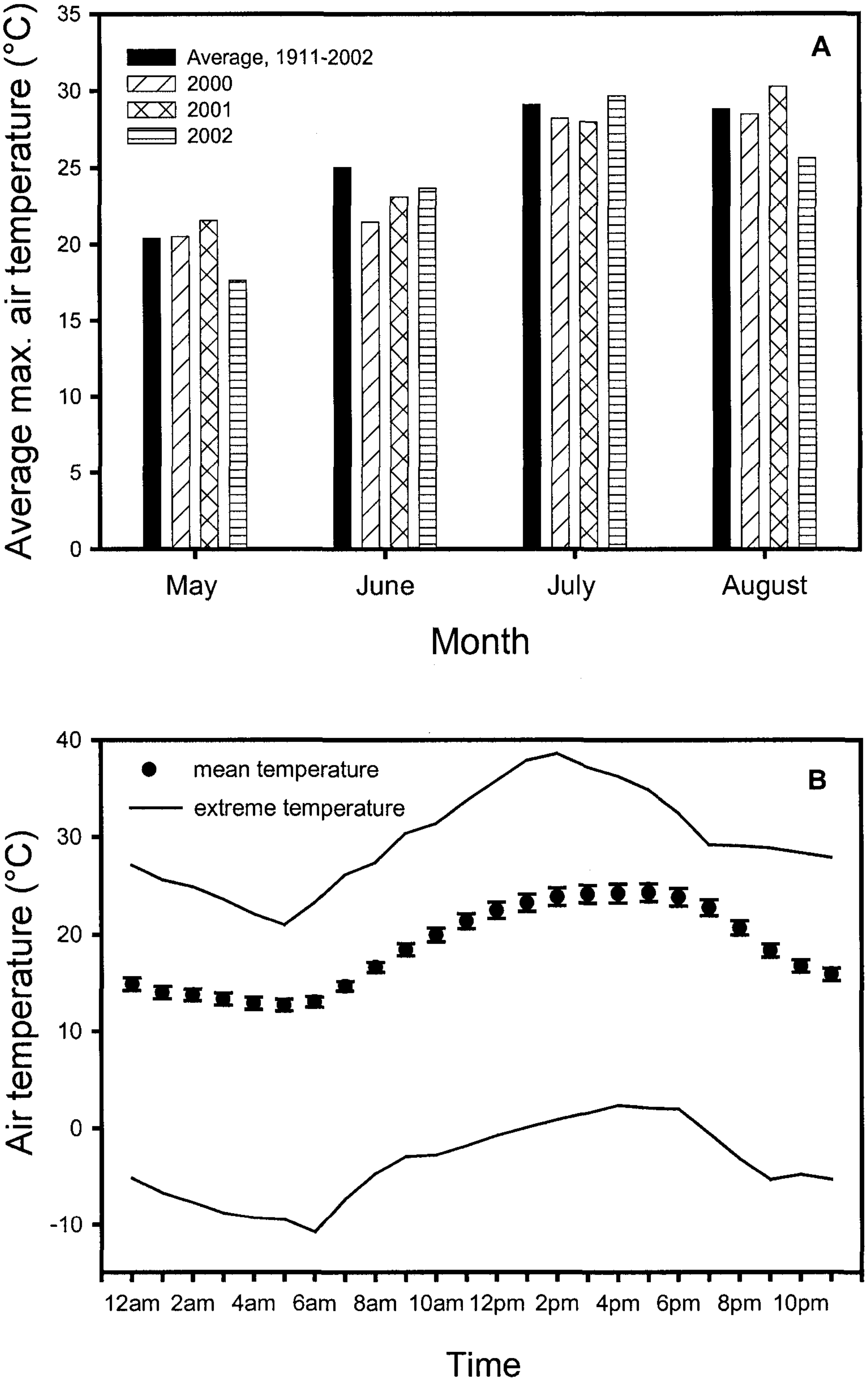
Fig. 4. (a) Operative environmental temperature at Chestnut-collared Longspur nests as a function of nest orientation. (b) Hourly marginal means (controlling for ambient air temperature at nest temperature recorded) of operative environmental temperature recorded at experimentally re-oriented Chestnut-collared Longspur nests.

Fig. 5. (a) Growth rate of nestling Chestnut-collared Longspurs as a function of nest orientation. Each point represents the marginal mean (± 1 s.e.) of residuals from a logistic curve fit to the entire data set, averaged among nestlings within a nest and among nests within each directional quadrant. Means with different letters are significantly different (see text for P-values). Data were collected from 2000-2002. (b) Growth rate and (c) mass at fledging of nestling Chestnut-collared Longspurs as a function of experimental shift in nest orientation. For growth, each point represents the marginal

mean (± 1 s.e.) of residuals from a logistic curve fit to the entire data set, averaged among nestlings within a nest and among nests within each treatment. Mass at fledging is the average mass of all nestlings in a nest on the last day before fledging. Means with different letters are significantly different (see text for P-values).

Fig. 6. Tarsus growth rate of nestling Chestnut-collared Longspurs as a function of experimental shift in nest orientation. Each point represents the marginal mean (± 1 s.e.) of residuals from a logistic curve fit to the entire data set, averaged among nestlings within a nest and among nests within each directional quadrant. Means with different letters are significantly different (see text for P-values).

Fig. 7. Percent of time adult Chestnut-collared Longspurs spent brooding nestlings (a) and hourly rate at which adults fed nestlings (b) as a function of experimental shift in nest orientation. Each point represents the marginal mean (± 1 s.e.) as estimated from 6-7 hours of video observation conducted on day 3 of the nestling period. Means with different letters are significantly different (see text for P-values).


A
Average, 1911-2002
2000
2001
2002
Average max. air temperature (°C)
0
5
10
15
20
25
30
35
May
June
July
August
Month
B
mean temperature
extreme temperature
Air temperature (°C)
-10
0
10
20
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8pm
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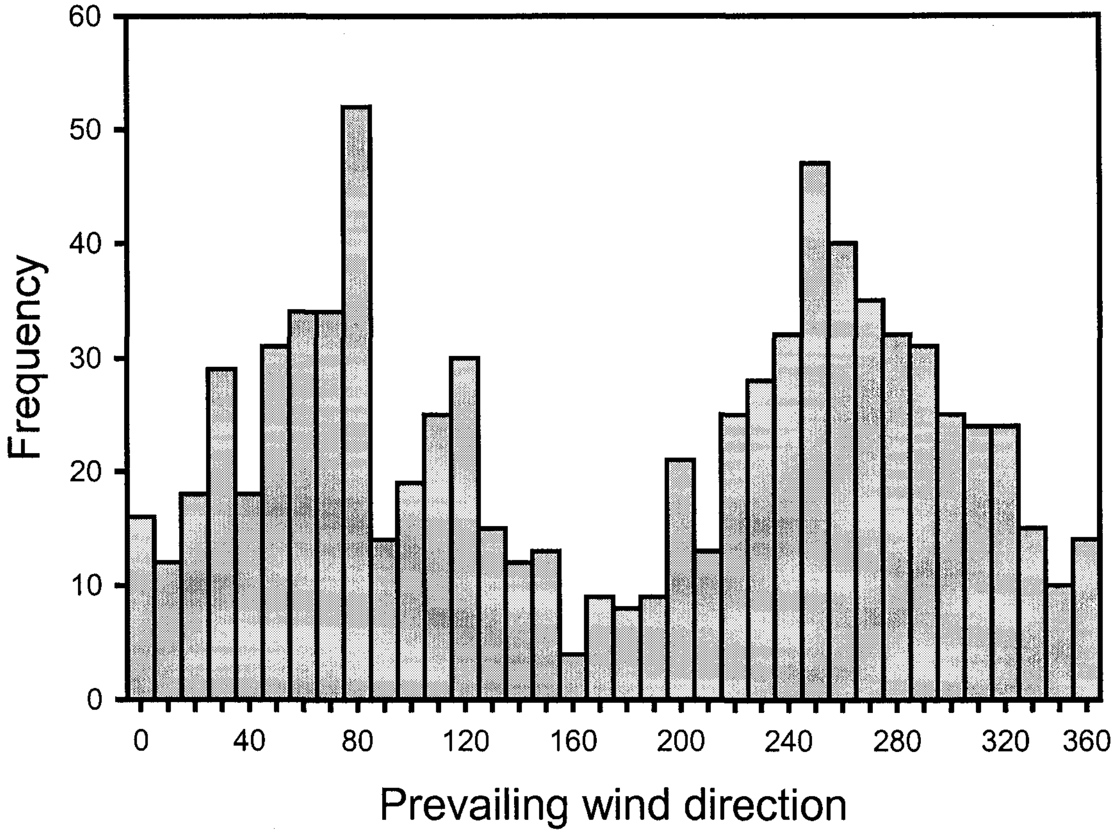
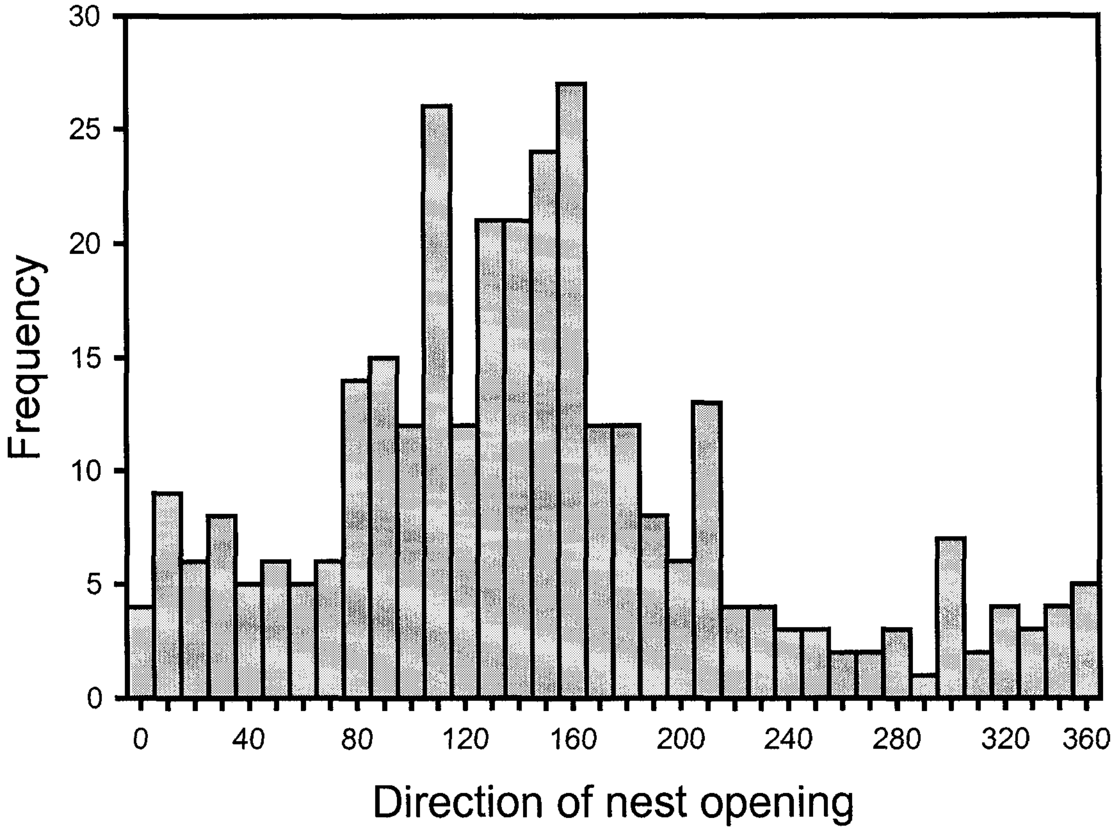
Time


60
50
40
30
20
10
0
Frequency
0
40
80
120
160
200
240
280
320
360
Prevailing wind direction


Frequency
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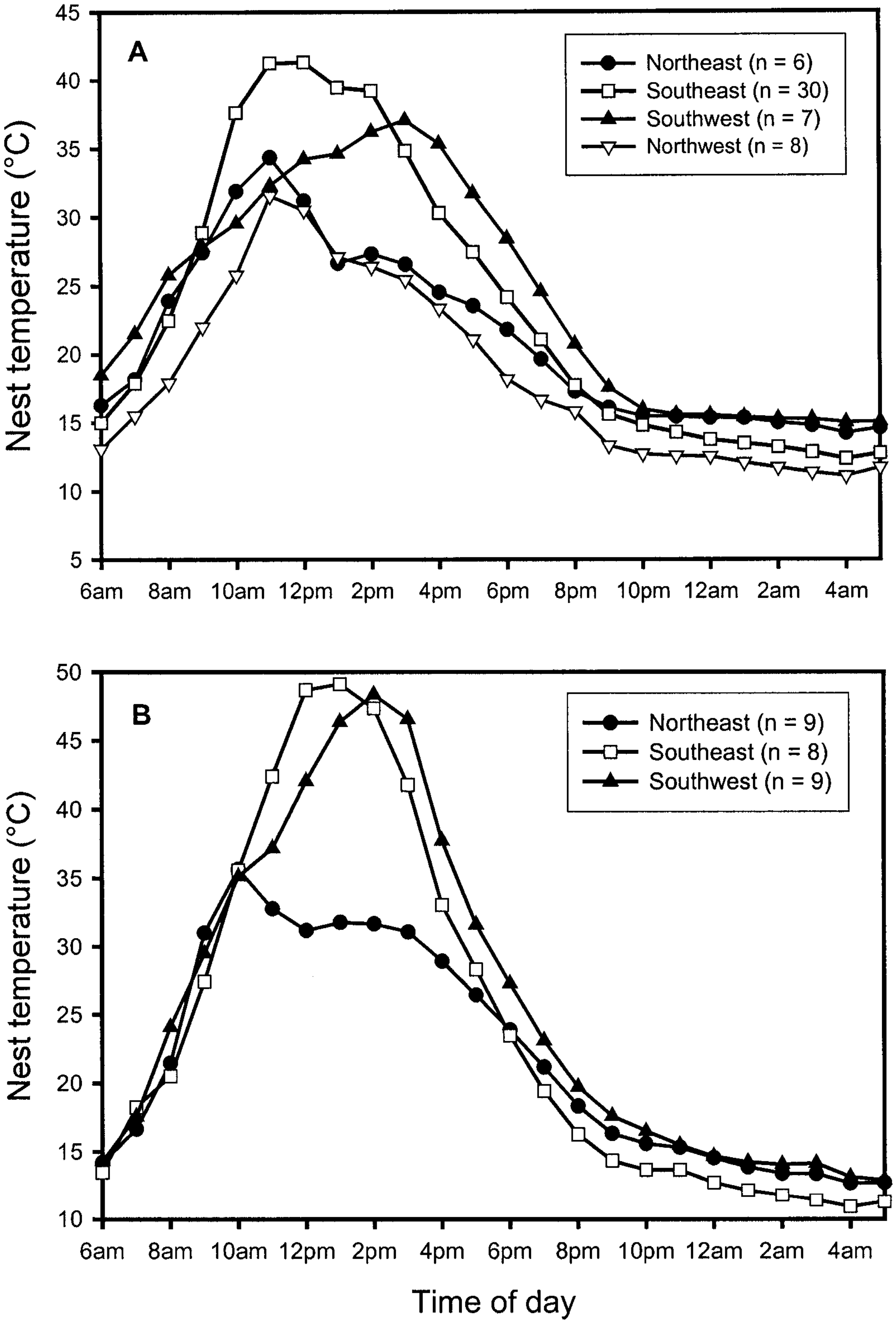
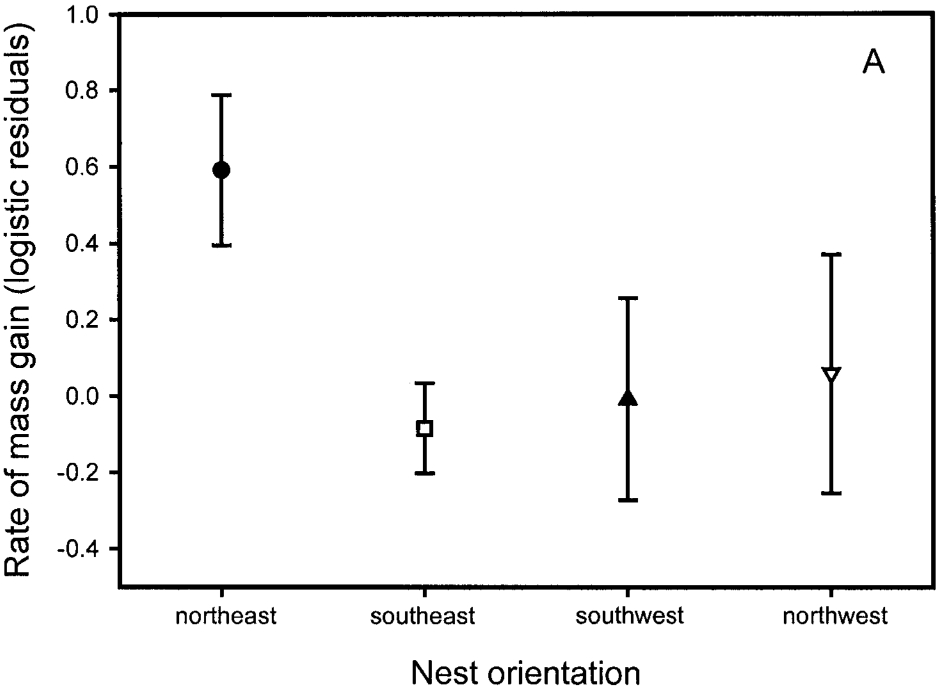
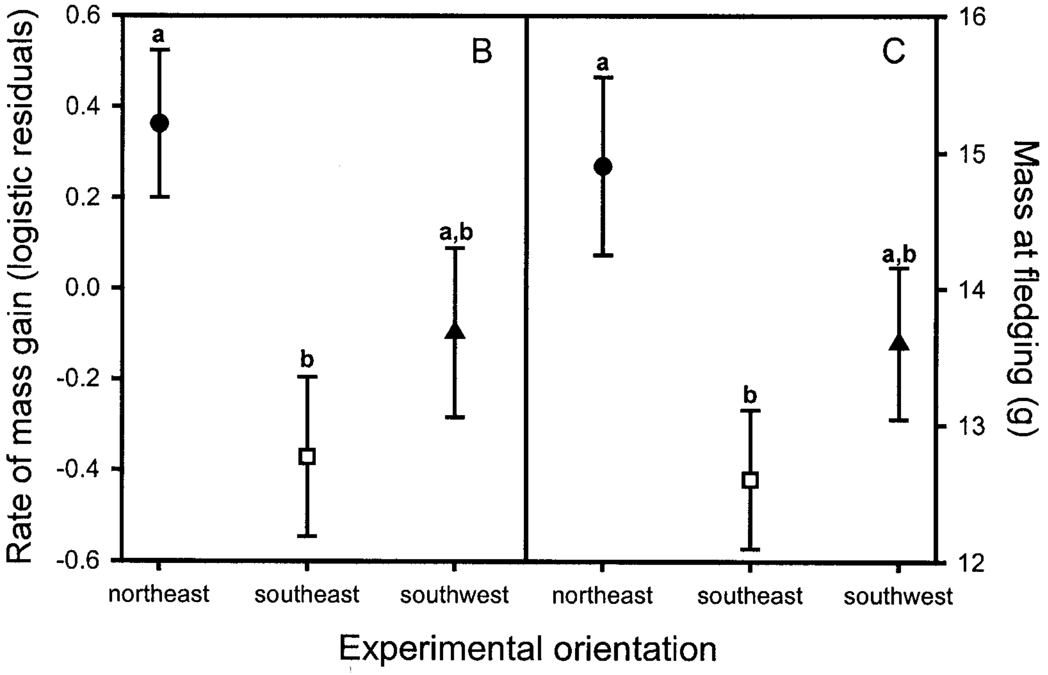
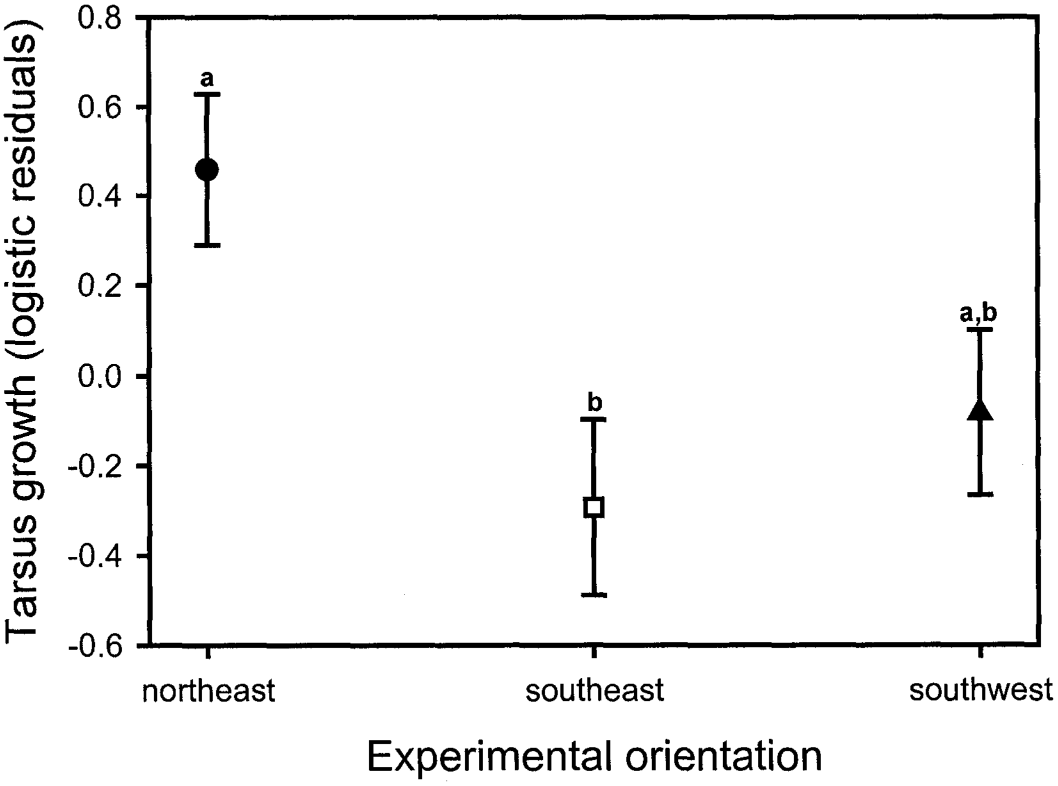
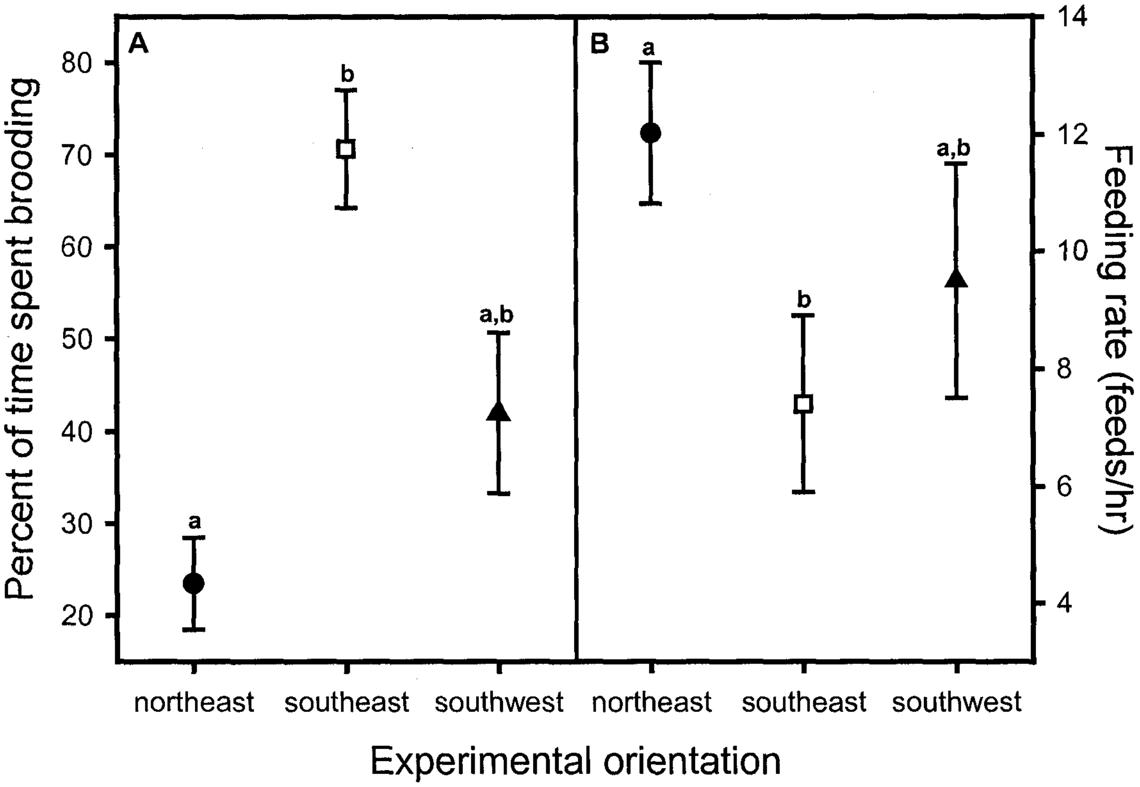
5
10
15
20
25
30
0
40
80
120
160
200
240
280
320
360
Direction of nest opening


A
Northeast (n = 6)
Southeast (n = 30)
Southwest (n = 7)
Northwest (n = 8)
Nest temperature (°C)
45
40
35
30
25
20
15
10
5
6am
8am
10am
12pm
2pm
4pm
6pm
8pm
10pm
12am
2am
4am
B
Northeast (n = 9)
Southeast (n = 8)
Southwest (n = 9)
Nest temperature (°C)
50
45
40
35
30
25
20
15
10
6am
8am
10am
12pm
2pm
4pm
6pm
8pm
10pm
12am
2am
4am
Time of day


A
Rate of mass gain (logistic residuals)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
northeast
southeast
southwest
northwest
Nest orientation


B
C
Rate of mass gain (logistic residuals)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
Mass at fledging (g)
16
15
14
13
12
a
b
a,b
a
b
a,b
northeast
southeast
southwest
northeast
southeast
southwest
Experimental orientation


Tarsus growth (logistic residuals)
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
a
b
a,b
northeast
southeast
southwest
Experimental orientation


A
B
Percent of time spent brooding
Feeding rate (feeds/hr)
Experimental orientation
northeast
southeast
southwest
northeast
southeast
southwest
a
b
a,b
a
b
a,b
20
30
40
50
60
70
80
4
6
8
10
12
14