

HABITAT SELECTION OF BAND-TAILED PIGEONS

by

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DEDICATION

This thesis is dedicated to my parents, Tim and Jean Hughes, and to Stephan Leimroth without whose support this project never would have been completed.

TABLE OF CONTENTS

LIST OF TABLES	7
LIST OF FIGURES	8
ABSTRACT	9
INTRODUCTION	12
PRESENT STUDY	13
REFERENCES	16
APPENDIX A.	
NESTING SUCCESS AND NEST-SITE SELECTION IN BAND-TAILED PIGEONS	18
ABSTRACT	18
INTRODUCTION	19
STUDY AREA	22
METHODS	23
Trapping and Radio-telemetry	23
Breeding Biology and Mortality Factors	24
Habitat Sampling	24
Analyses	25
RESULTS	27
Trapping and Radio-telemetry	27
Breeding Biology and Mortality Factors	27
Habitat Sampling	28
DISCUSSION	30
Movements	30
Breeding Biology and Mortality Factors	30
Nest-site Characteristics	32
MANAGEMENT IMPLICATIONS	34

TABLE OF CONTENTS - CONTINUED

ACKNOWLEDGMENTS	35
LITERATURE CITED	36
APPENDIX B.	
DOES RISK OF NEST PREDATION INFLUENCE NEST-SITE SELECTION IN BAND-TAILED PIGEONS?.....	45
ABSTRACT.....	45
INTRODUCTION	47
METHODS AND MATERIALS.....	51
Artificial Nest Experiment	52
Nest Predator Abundance and Distribution.....	54
Cone and Acorn Abundance.....	55
Analyses	56
RESULTS	59
Nest Predation in Mixed-Conifer Forest and Oak Woodlands.....	59
Artificial vs. Natural Band-Tailed Pigeon Nests.....	60
Abundance of Avian and Mammalian Nest Predators	61
Cone and Acorn Abundance on the Probability of Nest Predation.....	61
DISCUSSION	63
Conclusion.....	67
ACKNOWLEDGMENTS	68
LITERATURE CITED	69
APPENDIX C.	
THE INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE (IACUC).....	85

LIST OF TABLES

Table A.1. Vegetation and landscape features measured at 11 band-tailed pigeon nests and within a 25-m radius centered on nests in southeastern Arizona, 2002-2004 (the features measured within a 25-m radius of nests were also measured at 30 randomly selected points.	41
Table A.2. Nest-site characteristics at band-tailed pigeon nests in southeastern Arizona, 2002-2004 ($n = 11$).	42
Table A.3. Landscape and vegetation features of band-tailed pigeon nest sites and randomly selected points within a 25-m radius of nests or randomly selected points.	43
Table A.4. Logistic regression models for band-tailed pigeon nest sites vs. random sites in southeastern Arizona, 2002-2004. The model estimates are for the likelihood of nest sites vs. random sites. The full model for nest sites vs. random sites was significant (-log-likelihood = 2.1, $G^2 = 43.6$, $P < 0.0001$).	44
Table B.1. Number of artificial nests placed within each of 4 mountain ranges and 2 plant communities in southeastern Arizona during 2003 and 2004.	77
Table B.2. The risk of nest predation for artificial nests in southeastern Arizona varied among mountain ranges and plant communities, and was influenced by elevation, nest tree features, nest size, and abundance of potential nest predators. Results are based on 2-tailed t-tests, likelihood ratio chi-square tests, and simple linear regressions.	78
Table B.3. Results of two logistic regressions for binomial counts using stepwise variable selection ($P = 0.20$ to enter, $P = 0.10$ to remain). In each model, the risk of artificial nest depredation within forests in southeastern Arizona was the response variable. The two models were based on 1) nest clusters ($n = 136$) from 2003 and 2004 pooled, and 2) nest clusters ($n = 109$) from 2004 only.	79

LIST OF FIGURES

Figure B.1. Layout of an artificial nest cluster showing location of artificial nests, point-count survey stations, and food abundance transects. I sampled 136 of these nest clusters in 2003 and 2004, southeastern Arizona.	80
Figure B.2. The probability of artificial nest predation was positively related to nest concealment in 2004, but negatively related to nest concealment in 2003, southeastern Arizona.	81
Figure B.4. The relationship between the probability of artificial nest predation and nest concealment differed among mountain ranges, southeastern Arizona.	82
Figure B.3. The relationship between the probability of artificial nest predation and nest tree dbh differed among mountain ranges, southeastern Arizona.	83
Figure B.5. The probability of artificial nest predation was not related to cone and acorn abundance after accounting for other variables that explain nest predation risk, southeastern Arizona.	84

ABSTRACT

Band-tailed pigeons are migratory game birds whose populations have declined throughout their range. Understanding the habitat requirements and the underlying reasons for habitat choices of band-tailed pigeons, and identifying potential causes for declines will help management agencies develop plans to recover populations. My objectives in this study were to identify vegetation characteristics and landscape features that influence nest-site selection of band-tailed pigeons and determine whether these vegetation and landscape characteristics affect nesting success. Additionally, nest predation is a selective pressure thought to influence avian distribution and breeding habitat selection. I tested two predictions of the hypothesis that band-tailed pigeons nest more frequently in areas with a reduced risk of nest predation. Finally, variation in the abundance of main food resources for common nest predators has been implicated in affecting the probability of nest predation in forested systems. I tested one prediction of the alternative prey hypothesis.

INTRODUCTION

Nest-site selection has been studied extensively in birds (Cody 1985, Morrison et al. 1998, Hall and Mannan 1999) and recent efforts to document fitness consequences of nest placement (Martin 1998, Clark and Shutler 1999, Jones and Robertson 2001, Martin 2001) have provided wildlife managers with important metrics for assessing habitat quality (Conner et al. 1986, Pidgeon et al. 2003, Sara and Di Vittorio 2003, Borgmann and Rodewald 2004). When choosing where to breed, birds seem to make a series of choices at several spatial scales (Hilden 1965, Hutto 1985, Orians and Wittenberger 1991). Although birds likely use proximate cues to make these choices, ecological processes such as competition for nest sites and food (Nilsson 1984), predation (Martin 1993a), and climate (Martin 2001) can ultimately explain these choices. Identifying the proximate cues and ecological processes that birds use to select nest sites and the ensuing consequences of those choices is critical to managers for conservation planning (Caughley 1994), especially for species of conservation concern.

The band-tailed pigeon (*Patagioenas fasciata*) is a migratory game bird that breeds in two distinct regions within the western U.S. (Braun 1994). Information currently available suggests that populations in both regions are declining. Band-tailed pigeon populations have declined 1.8% annually throughout North America and 5.1% annually in the southwestern U.S. since 1966 (Sauer et al. 2005). Consequently, the band-tailed pigeon has been identified as a priority species of conservation concern at both the state (Latta et al. 1999) and national (National Audubon Society 2002) level.

Our knowledge of basic breeding biology and habitat requirements remains poor for the interior subspecies of band-tailed pigeon (Keppie and Braun 2000, Pacific Flyway Study Committee and Central Flyway Webless Migratory Game Bird Technical Committee 2001). Therefore, my initial objectives in this study were to: 1) identify vegetation characteristics and landscape features that influence nest-site selection of band-tailed pigeons, and 2) determine whether these vegetation and landscape characteristics affect nesting success.

Additionally, the band-tailed pigeon is a good species for examining habitat selection at large spatial scales because individuals 1) are apparently willing to travel >100 km between foraging and nesting sites (Keppie and Braun 2000, Kirkpatrick et al. 2005) and 2) do not defend territories like many other montane forest birds. Band-tailed pigeons forage in both oak woodlands and mixed-conifer forest but primarily nest in mixed-conifer forest. Nest predation is a pervasive selective pressure thought to influence avian distribution and breeding habitat selection in birds (Nilsson 1984, Martin 1993a, Sieving and Wilson 1998), and may explain why band-tailed pigeons nest primarily in mixed-conifer forest. I tested two predictions of the hypothesis that band-tailed pigeons are nesting more frequently in areas where they can reduce the risk of nest predation: 1) mixed-conifer forests would have a lower risk of nest predation compared to other plant communities in which they forage, and 2) the relative abundance of avian and mammalian nest predators would be lower in mixed-conifer forests than in oak woodlands. I compared the artificial nest results with results from natural band-tailed

pigeon nests to determine if the difference in nest predation between the 2 plant communities was similar for both artificial nests and natural nests.

Finally, some studies have suggested that variation in predation risk is related to variation in the abundance of main food sources available to nest predators (the alternative prey hypothesis; Lack 1954, Anglestam et al. 1984). I tested a prediction of the alternative prey hypothesis: that cone and acorn abundance would be negatively correlated with the risk of nest predation in mixed-conifer forest and oak woodlands.

PRESENT STUDY

The methods, results, and conclusions are presented in two papers attached to this thesis. The first paper describes nest-site selection in band-tailed pigeons and has been submitted to a peer-reviewed journal. The second paper describes how nest-placement and alternative food sources affect the risk of nest predation in four mountain ranges located in southeastern Arizona. The second paper will also be submitted to a peer-reviewed journal. The following is a summary of the most important findings in these two papers.

Numbers of band-tailed pigeons (*Patagioenas fasciata*) in Arizona have declined 5.1% annually since 1966. Understanding the habitat requirements for the interior subspecies of band-tailed pigeons and identifying potential causes for declines will help management agencies develop plans to recover populations. We located and monitored pigeon nests ($n = 12$) in southeastern Arizona during 2002-2004 and estimated nesting success. We measured and compared habitat features between 1) nest sites and randomly selected sites, and 2) successful and unsuccessful nests. The odds of a band-tailed pigeon nesting in an area increased with more trees >100 cm dbh, and more cover of silverleaf oak (*Quercus hypoleudcoides*) between 2 and 5 m above ground ($P < 0.0001$). Overall nesting success was 32%. Burned areas contained more successful nests than unburned areas ($P = 0.038$) and areas around successful nests contained more snags than areas around unsuccessful nests ($P = 0.011$). Band-tailed pigeon nest sites in southeastern Arizona were in areas with larger trees compared to random sites suggesting that

observed population declines may have been due, in part, to removal of large trees as part of forest management practices over the past century.

Band-tailed pigeons nest more commonly in mixed-conifer forests, but forage in both mixed-conifer forests and oak woodlands. We examined the hypothesis that band-tailed pigeons in Arizona nest more frequently in coniferous forests because the risk of nest predation is lower relative to oak woodlands. We tested two predictions of this hypothesis. We tested the prediction that mixed-conifer forests have a lower risk of nest predation compared to oak woodlands. We used artificial nests baited with quail eggs to compare the relative risk of nest predation between mixed-conifer forest and oak woodlands. We compared the artificial nest results with results from natural band-tailed pigeon nests to determine if the pattern in risk of nest predation observed with artificial nests was similar to the pattern observed with natural nests. We also tested the prediction that the relative abundance of avian and mammalian nest predators was lower in mixed-conifer forests compared to oak woodlands. We used point-count surveys to compare the relative abundance of avian and mammalian nest predators between the 2 plant communities. We also tested the alternative prey hypothesis. We estimated the relative abundance of main food sources (conifer cones, acorns) available to common nest predators to determine if the abundance of these main food sources influences the probability of nest predation within mixed-conifer forest and oak woodlands. In support of the nest predation hypothesis, both the risk of nest predation ($P = 0.0002$) and predator abundance ($P = 0.039$) were lower in coniferous forests than in oak woodlands. Results of the artificial nest experiment were comparable to results from natural nests (interaction

between nest type and plant community, $P = 0.829$). We did not find a relationship between the abundance of main food sources for potential nest predators and the risk of nest predation ($P = 0.156$). Our results suggest that the risk of nest predation likely influences habitat selection in band-tailed pigeons.

We recommend additional studies to further clarify the preferred nest-site characteristics of band-tailed pigeons, identify the factors responsible for population declines, and identify factors responsible for the low nesting success observed during this study. Additionally, forest management practices such as thinning, road building, and prescribed fire can increase the abundance of small mammals (Kyle and Block 2000, Converse et al. 2006a, Converse et al. 2006b) and thereby increase the risk of nest predation. Therefore, research is needed to determine how these practices affect predation risk particularly in mixed-conifer forests and other areas that normally have a lower relative risk of nest predation.

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APPENDIX A

NESTING SUCCESS AND NEST-SITE SELECTION IN BAND-TAILED PIGEONS

Abstract

Numbers of band-tailed pigeons (*Patagioenas fasciata*) in North America have declined nearly 4% per year since 1980. Understanding the habitat requirements for the interior subspecies of band-tailed pigeons and identifying potential causes for declines will help management agencies develop plans to recover populations. We located and monitored band-tailed pigeon nests ($n = 12$) in southeastern Arizona during 2002-2004 and estimated nesting success. We measured and compared habitat features between 1) nest sites and randomly selected sites, and 2) successful and unsuccessful nests. The odds of a band-tailed pigeon nesting in an area increased with more trees >100 cm dbh, and more cover of silverleaf oak (*Quercus hypoleudcoides*) between 2 and 5 m above ground ($P < 0.0001$). Overall nesting success was 32%. Burned areas contained more successful nests than unburned areas ($P = 0.038$) and areas around successful nests contained more snags than areas around unsuccessful nests ($P = 0.011$). Band-tailed pigeon nest sites in southeastern Arizona were in areas with larger trees compared to random sites suggesting that observed population declines may have been due, in part, to removal of large trees as part of forest management practices over the past century. We recommend additional studies to further clarify the preferred nest-site characteristics of band-tailed pigeons, identify the factors responsible for population declines, and identify factors responsible for the low nesting success observed during this study.

Introduction

Nest-site selection has been studied extensively in birds (Cody 1985, Morrison et al. 1998, Hall and Mannan 1999) and recent efforts to document fitness consequences of nest placement (Martin 1998, Clark and Shutler 1999, Jones and Robertson 2001, Martin 2001) have provided important insights for wildlife managers. For example, vegetation and landscape features that correlate with reproductive success provide metrics for assessing habitat quality (Conner et al. 1986, Pidgeon et al. 2003, Sara and Di Vittorio 2003, Borgmann and Rodewald 2004). Identifying the proximate cues that birds use to select nest sites and the ensuing consequences of those choices is critical to managers for conservation planning (Caughley 1994), especially for species of conservation concern.

The band-tailed pigeon (*Patagioenas fasciata*) is a migratory game bird that breeds in two distinct regions within the western U.S. (Braun 1994). The coastal subspecies (*P. f. monilis*) breeds from southern California to British Columbia, whereas the interior subspecies (*P. f. fasciata*) breeds in Colorado, Utah, New Mexico, and Arizona (Keppie and Braun 2000). Information currently available suggests that populations of both subspecies are declining. In the late 1800's, flocks of band-tailed pigeons were compared to those of the passenger pigeon (*Ectopistes migratorius*; Bendire 1892). Flocks greater than 50 birds are now rarely observed away from mineral springs in the Pacific Coast region and numbers have declined nearly 4% annually since 1980 throughout the pigeon's range (Sauer et al. 2005). Breeding populations in Oregon have declined by 70% since 1950 (Keppie and Braun 2000). Reliable trend estimates for the interior subspecies are not available, but recent surveys indicate an 84% decline since the

1970's for the interior subspecies in 1 mountain range in Arizona (Kirkpatrick et al. 2005). Most states still consider band-tailed pigeons game birds, yet annual estimates of both hunter participation and number of pigeons harvested decreased by 87% between 1970 and 1996 (Pacific Flyway Study Committee and Central Flyway Webless Migratory Game Bird Technical Committee 2001). Consequently, the band-tailed pigeon has been identified as a priority species of conservation concern at both the state (Latta et al. 1999) and national (National Audubon Society 2002) level.

Recent research has provided useful information on the natural history of band-tailed pigeon in Oregon (Leonard 1998, Sanders 1999), but knowledge of basic breeding biology and habitat requirements remains poor for the interior subspecies of band-tailed pigeon (Keppie and Braun 2000, Pacific Flyway Study Committee and Central Flyway Webless Migratory Game Bird Technical Committee 2001). This lack of information is largely due to low nesting densities and the difficulty of locating nests which are not easily found using typical nest-searching techniques (Martin and Geupel 1993). More information on the breeding biology, habitat, and potential causes of mortality of band-tailed pigeons is necessary to effectively determine the underlying causes of population declines (Fitzhugh 1970, Braun 1994, Pacific Flyway Study Committee and Central Flyway Webless Migratory Game Bird Technical Committee 2001). Therefore, our objectives in this study were to: 1) identify vegetation characteristics and landscape features that influence nest-site selection of band-tailed pigeons; 2) determine whether these vegetation and landscape characteristics affect nesting success; and 3) examine

whether low reproductive success may be contributing to the observed population declines.

Study Area

We studied band-tailed pigeons within the Coronado National Forest, primarily within the Santa Catalina Mountains, Pima County, Arizona, USA. Our study area was approximately 20 km northeast of Tucson, but we also included 1 band-tailed pigeon nest located in the Chiricahua Mountains, Cochise County, approximately 160 km southeast of Tucson. The Santa Catalina and Chiricahua Mountains are typical of Sky Island mountain ranges; relatively small, high-elevation mountain ranges in the Sonoran desert that are separated from other mountain ranges by desert basins (Marshall 1957, Warshall 1995). The mountains have rugged terrain and elevations range from 900 to 3000 m with desert scrub and encinal oak woodlands at lower elevations, oak-pinyon-juniper (*Quercus* spp.-*Pinus* spp.-*Juniperus* spp.) and pine-oak woodlands at mid-elevations, and ponderosa pine (*Pinus ponderosa*) and mixed-conifer forest at higher elevations. Annual precipitation and temperature vary along an altitudinal gradient ranging from 900 to 3000 m. Low elevations experience temperatures between 4 – 38°C with 30 cm of precipitation annually, whereas higher elevations experience temperatures between -6 – 24°C with 69 cm of precipitation annually (WALTER 2001). Most precipitation falls during the brief but heavy summer monsoon rains and as light rain in the winter.

Methods

Trapping and Radio-telemetry

To help locate nests, we placed radio transmitters on adult band-tailed pigeons. We used funnel traps (Braun 1976) baited with millet and sunflower seeds to capture adult male and female pigeons. We trapped pigeons at 5 sites in the Santa Catalina Mountains from 13 June to 22 August of 2002, 2 May to 16 June 2003, and 7 May to 10 August 2004. We placed radio-transmitters on adults with active crop glands indicating reproductive activity. We primarily radio-marked males in 2002 because males incubate eggs for more daylight hours than females (Curtis and Braun 1983) which facilitated finding nests on foot. We primarily radio-marked females in 2003 and 2004 because females incubate eggs during early morning hours (Neff 1947, Keppie and Braun 2000) when telemetry flights were available. We used 7-g and 10-g transmitters in 2002 and switched to 6-g transmitters in 2003 and 2004. We used 3 methods to attach radios to pigeons: backpack, super glue (J. Leonard, Corvallis, Oregon, personal communication), or chest-mount techniques (B. Mueller, American Wildlife Enterprises, personal communication). The University of Arizona's Institutional Animal Care and Use Committee approved all methods (IACUC protocol # 02-010).

We tracked radio-marked pigeons 5 days per week. In addition to tracking radio-marked pigeons from the ground, we located pigeons by flying transects in a fixed-wing airplane (average 1 flight per month) throughout the Santa Catalina Mountains while scanning for radio signals (Leonard 1998). We also made periodic flights outside the Santa Catalina Mountains to search for birds that we were otherwise unable to locate.

We used a Global Positioning System (Garmin emap) receiver to obtain Universal Transverse Mercator (UTM) coordinates for each radio-marked pigeon detected. We searched for nests on foot in areas where we had located radio-marked pigeons.

Breeding Biology and Mortality Factors

We monitored each nest ($n = 12$) every 3 days until the nest failed or offspring fledged. We recorded the presence and behavior of pigeons on each visit to nests to estimate egg-laying dates, incubation and nestling periods, and hatching and fledging success. We also recorded clutch size when we could see eggs through the bottom of nests. We assumed a nest was successful when we observed a squab flying around near the nest, or when we observed pigeon activity throughout the nestling period (25.5 days after hatching) but we observed no activity around the nest after the nestling period ended. We assumed a nest failed when we observed no pigeon activity around the nest or saw no sign of a squab in or around the nest prior to the end of nestling period. When a nest failed, we searched the area under the nest for signs of depredation. We attempted to identify the cause of nest failure (and juvenile and adult mortality) when we found signs of mortality.

Habitat Sampling

Once a nest was no longer active, we measured 13 features to describe characteristics associated directly with the nest (Table A.1). We estimated diameter of the largest supporting stem, nest dimensions, distance to overhead cover, and distance from the nest to the bole when the nest was too high to measure these characteristics directly. We also measured 11 landscape and vegetation features within a 25-m radius of

each nest and at 30 randomly selected points located within the Santa Catalina Mountains (Table A.1). We used ArcView 3.3 to generate random points within the Santa Catalina Mountains with the constraints that points be in undeveloped areas (e.g., not on roads or within housing developments), >1676 m in elevation (lowest recorded elevation of a band-tailed pigeon nest in Arizona; Neff 1947), <45° slopes, ≤1 km from a road (for ease of access), and in areas either not burned or lightly burned during the 2002 Bullock fire or the 2003 Aspen fire. Using point intercept (Elzinga et al. 1998), we estimated percent vegetation cover for 6 height categories (basal, 0-0.5 m, 0.6-2 m, 2.1-5 m, 5.1-10 m, and >10 m) at 5-m intervals along 25-m transects in 4 cardinal directions at each nest and random site. For sampling heights ≥2 m, we estimated the plant species and frequency of hits within our height categories using an imaginary line extending vertically from our eyes. We used U.S. Forest Service GIS data to determine the burn status of nest and random sites.

Analyses

Nesting Success. We used the daily exposure method (Mayfield 1961) to calculate daily nest survival probability and overall nesting success based on a 44.5-day nesting period (19-day incubation period and 25.5-day nestling period; Keppie and Braun 2000).

Habitat Characteristics. We used 2-tailed *t*-tests and Pearson's chi-square tests to compare vegetation and landscape features between nest sites and random sites, and between successful and unsuccessful nests. We also used logistic regression with stepwise variable selection ($P < 0.20$ to enter, $P < 0.10$ to remain) with plot type (nest or

random) as the response variable to identify characteristics that best distinguished nest sites from random sites. We used the same approaches to identify characteristics that best distinguished successful nests from unsuccessful nests, but also included the 13 variables that were nest-site specific for this analysis.

The cover variable “grass 0-0.5 m” was highly correlated with total cover 0-0.50 m ($r = 0.85$), so we excluded grass 0-0.5 m from the analyses. We excluded 5 features associated directly with nests (distance from nest to bole, diameter of largest supporting stem, distance to overhead cover, % overhead cover, and % side cover) from the successful vs. unsuccessful nests logistic regression analysis because we failed to measure these variables at ≥ 1 nest. Because the likelihood of a correlation between burn status and number of snags seemed high, we analyzed the relationship between the number of snags around nest sites and nesting success after accounting for burn status using logistic regression.

We used Watson’s U^2 test for goodness-of-fit to analyze nest aspect relative to the bole, and Watson’s U^2 test for non-parametric 2-sample testing for data containing ties to compare terrain aspect between nest and random sites. Our small sample size of nests prevented meaningful comparison of nest aspect relative to the bole or terrain aspect between successful and unsuccessful nests.

Results

Trapping and Radio-telemetry

We captured 200 band-tailed pigeons (191 after hatch-year birds; 9 hatch-year birds) during 2189 trap hours and radio-marked 50 of those birds (25 males and 2 females in 2002, 1 male and 9 females in 2003, and 6 males and 7 females in 2004). We found 7 of 12 (58%) band-tailed pigeon nests by following radio-marked birds to the nest. We also observed long-distance movements by 3 radio-marked male pigeons during aerial surveys in 2003. These pigeons were captured in the Santa Catalina Mountains and relocated via aerial radio telemetry in the Rincon Mountains (40 km away), Galiuro Mountains (45 km away), and Huachuca Mountains (105 km away).

Breeding Biology and Mortality Factors

Nesting Success. We located 12 band-tailed pigeon nests (6 in 2002, 1 in 2003, 5 in 2004). We estimated that nests were initiated on 15 May, 18 June, 20 June, 28 June, 3 July, 10 July (median), 17 July, 21 July, 23 July, 8 August, and 21 August. Clutch size was 1 for the 3 nests where we could confirm nest contents during incubation, and we assumed clutch size was 1 for 5 nests found during the nestling stage that contained 1 squab each. Apparent nesting success for the 10 nests with known fate was 33%. All 6 nests found in 2002 failed, 1 nest found in 2003 fledged 1 squab, and 2 nests found in 2004 each fledged 1 squab, 2 nests failed, and the fate of 1 nest was unknown. We attributed failures to predation ($n = 4$; 50%), weather ($n = 1$; 12%), and unknown causes ($n = 3$; 38%). Daily nest survival and overall nesting success were 97.5% and 31.9%, respectively.

Mortalities. We confirmed 6 mortalities of pigeons ($n = 1$ juvenile, $n = 5$ radio-marked adults). One pigeon was depredated by a northern goshawk (*Accipiter gentiles*), 1 by an unknown raptor, 1 by a domestic cat, and 2 appeared to have been depredated by foxes (*Urocyon cinereoargenteus*). An unknown predator killed 1 pigeon in a funnel trap.

Habitat Sampling

Nest and Nest-site Features. We measured vegetation and landscape features at 11 of the 12 nests (fire fighters partially destroyed the vegetation around 1 nest in 2002 prior to when sampling could occur). We observed both males and females collecting nesting material. Nests consisted of small diameter (2-5 mm) Douglas fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) twigs. Nest dimensions averaged 24 x 29 cm ($n = 7$, range 15 x 25 cm to 30 x 40 cm) and were located an average of 14.1 m (± 2.3) above the ground in trees 22.9 m (± 3.3) tall (Table A.2).

Nest Sites vs. Random Sites. Nest sites differed from random sites with regards to 13 of 49 features compared (Table A.3). Overall, nest sites were found on steeper slopes, and in areas with higher % canopy closure and larger trees than randomly selected sites. We found no evidence that band-tailed pigeons disproportionately selected nest sites in burned areas ($\chi^2 = 2.1$, $P = 0.148$). The density of trees >13 cm dbh was 30% greater at nest sites (305 ± 67 trees/ha²) compared to random sites (213 ± 21 trees/ha²; $t = -1.7$, $df = 39$, $P = 0.091$). On a community level, fewer nests were placed in stands of encinal oak and ponderosa pine and more nests were placed in stands of mixed-conifer and pine-oak than expected ($\chi^2 = 9.0$, $P = 0.030$). Three variables distinguished nest sites from random

sites. The odds of a band-tailed pigeon nesting in an area increased with more large (54-100 cm dbh) trees, and greater silverleaf oak cover between 2 and 5 m above ground (Table A.4).

Successful vs. Unsuccessful Nests. More successful nests were in burned areas than unburned areas ($\chi^2 = 4.3$, $P = 0.038$) and areas around successful nests contained more snags (151.7 ± 31.3 snags/ha²) than areas around unsuccessful nests (27.9 ± 20.5 snags/ha²; $t = 3.3$, $df = 8$, $P = 0.011$). Snags were more numerous around successful nests even after accounting for burn status ($G^2 = 6.7$, $P = 0.010$).

Discussion

Movements

Several radio-marked pigeons traveled long distances (up to 105 km) between montane forests in 4 different mountain ranges. Such travels represent the first documentation of long-distance movements between mountain ranges for band-tailed pigeons during the breeding season in southeastern Arizona. Several authors (Neff 1947, Smith 1968, Gutierrez et al. 1975) have mentioned the nomadic tendency of band-tailed pigeons in response to fluctuations in food availability, but breeding site fidelity has also been documented (MacGregor and Smith 1955, Braun 1972, Leonard 1998, C. Kirkpatrick, personal observation). Band-tailed pigeons in Oregon traveled on average 5 km from nest sites to foraging areas and the longest distance traveled was 51 km (Leonard 1998). Band-tailed pigeons in Colorado traveled as far as 65 km from nest sites to foraging areas (Braun 1972). Distances between Sky Island mountain ranges (and available habitat) are relatively large and may force band-tailed pigeons in southeastern Arizona to commute farther to find food or appropriate nesting habitat compared to Oregon and Colorado. Although we were not able to determine activities of pigeons in these other mountain ranges, band-tailed pigeons may be nesting in one range and foraging in another to take advantage of dependable food sources in residential areas.

Breeding Biology and Mortality Factors

Our results agree with those from other studies of breeding band-tailed pigeons in that breeding activity peaked in June and July in the Santa Catalina Mountains (Fitzhugh 1974, Leonard 1998). Only 33% of band-tailed pigeon nests monitored in southeastern

Arizona fledged young. Estimates of band-tailed pigeon nesting success in the Pacific Coast Range were much higher (55%, MacGregor and Smith 1955; 73%, Glover 1953; 69%, Leonard 1998) with little annual variation (Jarvis and Passmore 1992, Leonard 1998).

Recruitment within the interior region may be subject to greater annual fluctuations than recruitment in the Pacific Coast region because of greater annual fluctuation in food resources. Acorn mast, one of the pigeons' main food sources in Arizona (Neff 1947) varies greatly among years in the southwest. Pigeons in the Pacific Coast region rely on elderberries (*Sambucus* spp.) during the breeding season (Leonard 1998), the abundance of which may not fluctuate greatly from year to year. Nesting success for other Columbids varies greatly, both annually and across the species' breeding distribution (Wiley and Wiley 1979, Nellis et al. 1984, Westmoreland and Best 1985, Howe and Flake 1989, James and Clout 1996, Rivera-Milan 1996). Understanding the underlying causes of the low nesting success observed in this study is crucial because pigeons are still being hunted and their populations are declining.

The effect of radio-transmitters on band-tailed pigeon survival has not been examined (Leonard 1998). Several of our radio-marked pigeons exhibited behavior that likely increased the risk of predation. We suspect that poor harness attachment (e.g., over-tightening of straps) may have influenced pigeons' susceptibility to predators as most documented mortalities occurred during the first year of the study when we were refining transmitter-attachment techniques. Future research should consider the effects of

radio-transmitters on the survival of band-tailed pigeons, nesting success of radio-marked birds, and on the bias such effects may have on their results.

Nest-site Characteristics

Nests and Nest Sites. Characteristics at 12 nests in southeastern Arizona were similar to studies from other areas (MacGregor and Smith 1955, Peeters 1962, Curtis and Braun 1983, Leonard 1998). We found similar results between our study and a study in Oregon (Leonard 1998) for nest-tree height, distance to closest overhead cover, and density of trees >13 cm dbh. Some nest-site specific features differed slightly from those in Oregon; the crown base height of Arizona nest trees averaged >3 m higher, nest heights were 4 m greater, and nests were placed 0.5 m farther from the main bole on average than nests found in Oregon. These differences may simply reflect a greater availability of larger trees at our study site compared to the Oregon study site. Average slope across Arizona nest sites (26°) was similar to Colorado nest sites (Curtis and Braun 1983), whereas slopes for Oregon nest sites averaged 18°.

The majority of band-tailed pigeon nests (>73%) in Arizona were found in large, coniferous trees within mixed-conifer forest, which is similar to nest placement in other regions (Glover 1953, MacGregor and Smith 1955, Peeters 1962, Curtis and Braun 1983, Leonard 1998). Nest trees in Arizona had an average dbh over twice that of nest trees in Oregon. Some nests in Oregon were found in shrubs and the inclusion of shrub dbh measurements may have lowered the average nest-tree dbh in Oregon. Another possible explanation for the difference in nest-tree dbh between the 2 regions is that widespread

timber harvesting has not occurred in the Santa Catalina Mountains for over 80 years (Hensel 2003). Consequently, more large trees may be available for nest sites in Arizona.

Nest Sites vs. Random Sites. Band-tailed pigeons nested in areas with a higher density of large trees and more silverleaf oak cover than random sites. The prevalence of both large trees and silverleaf oak are features one would expect in mixed-conifer forests with a history of fire suppression and no timber harvest. Hence management actions and land uses that promote these forest features may benefit band-tailed pigeons. Our results are based on a relatively small sample of nests; additional data would help validate our conclusions.

Successful Nests vs. Unsuccessful Nests. The number of snags and burn status of the area around nests was associated with the probability of nesting success. We documented greater nesting success in the years following the 2 wildfires that occurred during our study. Wildfires may indirectly affect nesting success by causing a delay in predator recolonization of burned areas. Although we did not document the abundance and distribution of band-tailed pigeon nest predators, populations of some potential nest predators (e.g., squirrels and chipmunks) can remain unchanged or be negatively impacted by fire depending on the fire's intensity (Gashwiler 1970, Kyle and Block 2000, Koprowski et al. 2006), whereas others (i.e., raptors) can increase in number after wildfires (Lawrence 1966, Newsome et al. 1975). Future research should more thoroughly examine the effect of fire on band-tailed pigeon nest-site selection and nesting success using a larger sample of nests.

Management Implications

The number of large trees and the amount of silverleaf oak cover in the midstory are both vegetation features that can be greatly affected by forestry practices including timber harvest and various fire management strategies. Much of the nesting habitat of band-tailed pigeons in Arizona is on land managed by the U.S. Forest Service and managers should consider how different forestry practices may affect nesting habitat of band-tailed pigeons. Band-tailed pigeon nest sites in southeastern Arizona were in areas with larger trees compared to random sites. Hence, the observed population declines may be due, in part, to removal of large trees as part of forest management practices over the past century. Although logging in the Santa Catalinas was patchy and never occurred on a large scale, this possibility deserves further investigation. Additional research is necessary to further clarify the preferred nesting and foraging habitat for band-tailed pigeons in Arizona, examine how current forest management practices affect band-tailed pigeons, examine factors contributing to the low nesting success observed in this study, and identify factors limiting population growth of the interior subspecies of band-tailed pigeons. Low nesting success and annual variation in nesting success across the band-tailed pigeon's breeding range suggests a need for appropriate management actions such as periodic hunting moratoriums of some sub-populations (Braun 1994), if population declines continue in Arizona.

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Table A.1. Vegetation and landscape features measured at 11 band-tailed pigeon nests and within a 25-m radius centered on nests in southeastern Arizona, 2002-2004 (the features measured within a 25-m radius of nests were also measured at 30 randomly selected points).

At the nest tree	25-m radius surrounding nest or random point
Nest tree species	Elevation
Nest tree dbh	Aspect of terrain
Height to crown	Slope
Height of nest tree	Dominant plant species
Nest height	Average top canopy height
Diameter of nest	Plant community
Species of twigs used to construct nest	# layers in canopy
Nest aspect (aspect of nest relative to the bole)	Average canopy closure (densiometer measurements in 4 directions)
Distance from nest to bole	Species and dbh of all trees in 4 categories:
Diameter of largest woody stem supporting nest	>13-23 cm, 24-53 cm, 54-100 cm, and
Distance from nest to overhead cover	>100 cm dbh
% overhead cover (estimated from 1 m above nest)	# snags >13cm dbh
% side cover (estimated from 1 m in 4 cardinal directions around nest)	% cover in 6 height categories (from point intercept)

Table A.2. Nest-site characteristics at band-tailed pigeon nests ($n = 11$) in southeastern Arizona, 2002-2004.

Characteristic	mean \pm SE
Nest tree dbh (cm)	64.5 \pm 11.4
Height to crown (m)	8.9 \pm 2.3
Nest tree height (m)	22.9 \pm 3.3
Nest height (m)	14.1 \pm 2.3
Distance from nest to bole (m)	1.6 \pm 0.4
Diameter of largest woody stem supporting nest (cm)	4.8 \pm 0.4
Distance from nest to overhead cover (m)	0.5 \pm 0.1
Overhead cover (%)	49.3 \pm 12.2
Average side cover (%)	54.6 \pm 9.4

Table A.3. Landscape and vegetation features of band-tailed pigeon nest sites and randomly selected points within a 25-m radius of nests or randomly selected points.

Characteristic	Nest (<i>n</i> = 11)		Random (<i>n</i> = 30)		<i>t</i>	<i>P</i>
	Mean	± SE	Mean	± SE		
Elevation (m)	2441.8	± 114.3	2228.6	± 73.3	-1.5	0.135
Top canopy height (m)	25.8	± 3.3	25.2	± 2.0	-0.3	0.757
Average canopy closure (%)	83.3	± 3.4	63.5	± 5.8	-2.9	0.005
Slope (°)	25.9	± 1.8	16.7	± 1.1	-3.7	0.003
Trees >13 cm dbh	61.0	± 13.3	42.6	± 4.3	-1.3	0.213
Trees and snags >13 cm dbh	75.5	± 16.2	46.8	± 4.7	-2.3	0.026
Snags >13 cm dbh	14.5	± 4.7	4.2	± 0.8	-2.1	0.057
Trees 13-23 cm dbh	29.3	± 10.3	20.8	± 2.7	-1.1	0.269
Trees 24-53 cm dbh	21.6	± 4.1	19.5	± 2.2	-0.5	0.630
Trees 54-100 cm dbh	8.7	± 2.6	2.2	± 0.5	-2.4	0.034
Trees >100 cm dbh	1.4	± 0.5	0.1	± 0.1	-2.6	0.028
Average dbh for plot (cm)	39.8	± 3.2	26.3	± 1.9	-2.4	0.037
Number of layers in canopy	2.1	± 0.2	2.5	± 0.1	1.6	0.129
Percent cover [†] :						
Basal bare ground	10.5	± 4.4	5.8	± 1.3	-1.4	0.176
Basal litter	70.0	± 3.6	78.3	± 2.4	1.8	0.074
Basal rock	12.3	± 4.5	8.0	± 1.7	-1.1	0.279
Basal log	1.4	± 1.0	1.2	± 0.4	0.0	0.823
Basal small woody debris	20.0	± 4.3	28.8	± 4.4	1.1	0.265
Brush 0-0.5 m	1.4	± 1.0	1.2	± 0.6	-0.2	0.869
Fern 0-0.5 m	2.7	± 1.6	5.5	± 1.3	1.2	0.246
Forb 0-0.5 m	25.5	± 6.2	14.3	± 2.4	-1.7	0.116
PSEMEN 0-0.5 m	1.8	± 1.0	0.0	± 0.0	-1.8	0.104
SYPSP 0-0.5 m	2.7	± 1.6	0.7	± 0.3	-1.3	0.223
Total 0-0.5 m	68.2	± 7.1	47.8	± 5.6	-2.0	0.053
ABICON 0.5-2 m	2.7	± 1.0	5.8	± 1.6	1.6	0.113
Grass 0.5-2 m	1.4	± 0.7	0.3	± 0.3	-1.5	0.146
QUEEMO 0.5-2 m	0.0	± 0.0	0.7	± 0.5	0.8	0.447
QUEGAM 0.5-2 m	0.0	± 0.0	0.7	± 0.7	0.6	0.552
SYMSP 0.5-2 m	4.1	± 2.8	0.2	± 0.2	-1.4	0.187
Total 0.5-2 m	22.3	± 5.7	19.3	± 2.2	-0.5	0.641
ABICON 2-5 m	6.8	± 2.4	10.3	± 2.8	0.7	0.472
PINPON 2-5 m	4.1	± 3.6	5.0	± 1.8	0.2	0.807
PINSTR 2-5 m	3.6	± 1.5	3.8	± 0.9	0.1	0.912
PSEMEN 2-5 m	4.5	± 1.7	11.0	± 2.5	2.1	0.039
QUEHYP 2-5 m	2.3	± 1.0	0.2	± 0.2	-2.0	0.071
Snags 2-5 m	5.0	± 3.4	2.3	± 0.7	-0.8	0.454
Total 2-5 m	36.4	± 6.6	44.3	± 3.7	1.1	0.278
ABICON 5-10 m	8.2	± 3.0	10.7	± 2.8	0.5	0.626
PINSTR 5-10 m	2.3	± 1.2	7.8	± 1.8	1.8	0.073
PINPON 5-10 m	3.6	± 2.7	12.5	± 2.7	1.8	0.073
PSEMEN 5-10 m	9.5	± 3.3	14.0	± 2.9	0.8	0.401
Snags 5-10 m	4.1	± 2.8	2.5	± 0.6	-0.6	0.586
Total 5-10 m	39.5	± 4.9	47.3	± 4.6	0.9	0.348
ABICON >10 m	10.0	± 4.2	7.2	± 2.1	-0.7	0.515
PINPON >10 m	5.5	± 3.1	12.5	± 2.8	1.4	0.171
PINSTR >10 m	3.6	± 3.2	4.3	± 1.4	0.2	0.816
PSEMEN >10 m	21.8	± 8.3	10.8	± 2.3	-1.3	0.230
Snags >10 m	1.8	± 1.2	1.7	± 0.5	-0.1	0.891
Total >10 m	51.4	± 6.1	35.5	± 4.3	-2.0	0.056

[†]Species codes: PSEMEN = Douglas fir (*Pseudotsuga menziesii*), ABICON = white fir (*Abies concolor*); PINSTR = southwestern white pine (*Pinus strobiformis*); PINPON = ponderosa pine (*Pinus ponderosa*); QUEEMO = Emory oak (*Quercus emoryi*); QUEGAM = Gambel oak (*Quercus gambelii*); QUEHYP = silverleaf oak (*Quercus hypoleucoides*); Symspp = snowberry (*Symphoricarpos spp.*); Total = all species pooled.

Table A.4. Logistic regression models for band-tailed pigeon nest sites vs. random sites in southeastern Arizona, 2002-2004. The model estimates are for the likelihood of nest sites vs. random sites. The full model for nest sites vs. random sites was significant (log-likelihood = 2.1, $G^2 = 43.6$, $P < 0.0001$).

Explanatory variable	$\beta \pm SE$	G^2	P
Intercept	3.8 \pm 1.1		
# trees 54-100 cm dbh	-0.4 \pm 0.2	17.2	< 0.0001
Silverleaf oak cover 2-5 m	-0.9 \pm 0.3	14.5	0.0001

APPENDIX B

DOES RISK OF NEST PREDATION INFLUENCE NEST-SITE SELECTION IN
BAND-TAILED PIGEONS?**Abstract**

Band-tailed pigeons have declined throughout their breeding range. Understanding the factors that influence nest-site selection is important for effective management efforts. We examined the hypothesis that band-tailed pigeons in Arizona nest more frequently in coniferous forests because the risk of nest predation is lower relative to oak woodlands. We tested two predictions of this hypothesis. We tested the prediction that mixed-conifer forests have a lower risk of nest predation compared to oak woodlands. We used artificial nests baited with quail eggs to compare the relative risk of nest predation between mixed-conifer forest and oak woodlands. We compared the artificial nest results with results from natural band-tailed pigeon nests to determine if the pattern in risk of nest predation observed with artificial nests was similar to the pattern observed with natural nests. We also tested the prediction that the relative abundance of avian and mammalian nest predators was lower in mixed-conifer forests compared to oak woodlands. We used point-count surveys to compare the relative abundance of avian and mammalian nest predators between the 2 plant communities. We also tested the alternative prey hypothesis. We estimated the relative abundance of main food sources (conifer cones, acorns) available to common nest predators to determine if the abundance of these main food sources influences the probability of nest predation within mixed-conifer forest and oak woodlands. In support of the nest predation hypothesis, both the

risk of nest predation ($P = 0.0002$) and predator abundance ($P = 0.039$) were lower in coniferous forests than in oak woodlands. Results of the artificial nest experiment were comparable to results from natural nests (interaction between nest type and plant community, $P = 0.829$). We did not find a relationship between the abundance of main food sources for potential nest predators and the risk of nest predation ($P = 0.156$). Our results suggest that the risk of nest predation likely influences habitat selection in band-tailed pigeons.

Introduction

Habitat preferences are presumably adaptive (Jones and Robertson 2001) because selecting an appropriate breeding site can provide an individual with the resources necessary for successful reproduction (Martin 1998). Habitat selection has likely evolved, in part, as a result of differential reproductive success in different environments (Clark and Shutler 1999). When choosing where to breed, birds seem to make a series of choices at several spatial scales (Hilden 1965, Hutto 1985, Orians and Wittenberger 1991). Although birds likely use proximate cues to make these choices, ecological processes such as competition for nest sites and food (Nilsson 1984), predation (Martin 1993a), and climate (Martin 2001) can ultimately explain these selective choices. Some birds, such as crossbills (*Loxia* spp.), choose where to breed based on variation in food abundance at regional scales (Benkman 1987). For other birds, such as band-tailed pigeons (*Patagioenas fasciata*), the ecological processes responsible for habitat preferences (and the spatial scales on which they operate) remain unknown.

The band-tailed pigeon is a good species for examining habitat selection at large spatial scales because individuals: 1) are apparently willing to travel >100 km between foraging and nesting sites (Keppie and Braun 2000, Kirkpatrick et al. 2005), and 2) do not defend territories like many other montane forest birds. Moreover, the band-tailed pigeon has been identified as a species of conservation concern at both the state (Altman 1999, Latta et al. 1999, Colorado Partners in Flight 2000, New Mexico Partners in Flight 2001) and national level (Rich et al. 2004, U.S.F.W.S. 2005, National Audubon Society 2002). Band-tailed pigeons are migratory game birds whose populations have declined

1.8% annually throughout North America and 5.1% annually in the southwestern U.S. since 1966 (Sauer et al. 2005). A >84% decline is reported for 1 mountain range in Arizona (Kirkpatrick et al. 2005). Throughout their range, band-tailed pigeons usually place their nests in firs or pines (MacGregor and Smith 1955, Peeters 1962, Leonard 1998, Hughes et al., in review) within forested areas dominated by conifers (Leonard 1998, Hughes et al., in review). They also nest and forage in oak woodlands in Arizona (Neff 1947), but less frequently. One hypothesis that might explain why band-tailed pigeons prefer to nest in coniferous forests compared to other plant communities is to avoid areas with high risk of nest predation.

Nest predation is a pervasive selective pressure thought to influence avian distribution and breeding habitat selection in birds (Nilsson 1984, Martin 1993a, Sieving and Wilson 1998). For example, nest predation accounts for up to 80% of nest failures across a wide range of bird species within all major plant communities (Ricklefs 1969, Martin 1993a, Sieving and Wilson 1998). Probability of nest predation can be affected by nest height and nesting substrate (Ricklefs 1969, Nilsson 1984, Martin 1993a, Borgmann and Rodewald 2004), plant composition and cover (Martin 1993b), forest patch size (Andren and Angelstam 1988, Hoover et al. 1995, Keyser et al. 1998), and aspect of the surrounding landscape (Rauter et al. 2002). Despite recognition of nest predation as an important selective pressure, relatively few empirical studies have examined how nest predation varies among different plant communities within a region (but see Martin 1993a, Sietz and Zegers 1993, Bayne et al. 1997, Sieving and Willson 1998, Pidgeon et al. 2003) and the mechanisms responsible for such variation.

One step in evaluating whether the risk of nest predation potentially influences a bird's decision regarding where to breed is documenting the influence of nest placement on the probability of nest predation. To test the hypothesis that band-tailed pigeons are nesting more frequently in areas where they can reduce the risk of nest predation, we predicted that mixed-conifer forests (where band-tailed pigeons usually nest) would have a lower risk of nest predation compared to other plant communities in which they forage (e.g. oak woodlands). We used artificial nests baited with quail eggs to compare the relative risk of nest predation between mixed-conifer forest and oak woodlands in southeastern Arizona. We compared the artificial nest results with results from natural band-tailed pigeon nests to determine if the pattern in risk of nest predation observed with artificial nests was similar to the pattern observed with natural nests. We also tested a second prediction of the predation-risk hypothesis. We predicted that the relative abundance of avian and mammalian nest predators would be lower in coniferous forests compared to oak woodlands. We conducted point-count surveys to compare the relative abundance of avian and mammalian nest predators between plant communities.

We were also interested in why the risk of nest predation might differ between plant communities. Some studies have suggested that variation in predation risk is related to variation in the abundance of main food sources available to nest predators (the alternative prey hypothesis; Lack 1954, Anglestam et al. 1984). In particular, variation in the abundance of acorns and conifer seeds have been implicated in affecting the probability of nest predation because these are the main food sources for common nest predators in forested systems but their availability varies annually (Martin and Joron

2003, Nour et al. 1993, Ostfeld et al. 1996). However, the relationship between food abundance for potential nest predators (in the form of conifer seeds and acorns) and nest predation has rarely been tested (McShea 2000). We tested a prediction of the alternative prey hypothesis: that cone and acorn abundance would be negatively related to the risk of nest predation in mixed-conifer forest and oak woodlands.

This study has important implications for the effective management of band-tailed pigeons within coniferous forests of the western U.S. Identifying the proximate and ultimate factors that influence nest placement in band-tailed pigeons will help develop management plans to maximize reproductive success and reverse population declines. This information can also help identify natural and anthropogenic events that have caused habitat degradation (Caughly 1994, Paine et al. 1996, Koko and Sutherland 2001) for band-tailed pigeons. Additionally, comparing the probability of nest predation among plant communities may help explain patterns of nest-site selection in other canopy-nesting species within montane woodlands of the southwestern U.S.

Methods and Materials

We conducted this study within the Santa Catalina (Pima County), Pinaleno (Graham County), Huachuca, and Chiricahua (both in Cochise County) Mountain Ranges in the Coronado National Forest, Arizona in 2003 and 2004. These are typical Sky Island mountain ranges; high-elevation mountain ranges that are separated from one another by low-elevation desert basins (Warshall 1995). The 4 mountain ranges have rugged terrain and elevations range from 900 to 3000 m with desert scrub and encinal oak woodlands at lower elevations, oak-pinyon-juniper (*Quercus* spp.-*Pinus* spp.-*Juniperus* spp.) and pine-oak woodlands at mid-elevations, and ponderosa pine (*Pinus ponderosa*) and mixed-conifer forest at higher elevations (Marshall 1957, Warshall 1995). Temperatures vary between 4 – 38°C with 30 cm of precipitation annually at lower elevations, and between -6 – 24°C with 69 cm of precipitation annually at higher elevations (WALTER 2001). Most precipitation falls during 2 distinct time periods: brief but heavy summer monsoon rains and light winter rains.

Potential mammalian nest predators include red squirrels (*Tamiasciurus hudsonicus grahamensis*), Abert's squirrels (*Sciurus aberti*), Arizona gray squirrels (*Sciurus arizonicus*), Chiricahuan fox squirrels (*Sciurus nayaritensis chiricahuae*), coatis (*Nasua nasua*), and ringtails (*Bassariscus astutus*). Potential avian nest predators include Steller's jays (*Cyanocitta stelleri*), Mexican jays (*Aphelocoma ultramarine*), house wrens (*Troglodytes aedon*), Bewick's wrens (*Thryomanes bewickii*), and common ravens (*Corvus corax*).

Artificial Nest Experiment

We placed artificial nests in each of two plant communities (mixed-conifer forest and oak woodland) within 4 mountain ranges over a two-year period. Artificial nests have been used in many studies to examine relative predation risk (Martin 1987, Yahner and Cypher 1987, Sieving and Willson 1998, Berry 2002, Borgmann and Rodewald 2004) and researchers using both natural and artificial nests have shown that the risk of nest predation often differs between plant communities (Janzen 1978, Picman 1988, Sieving and Willson 1998) and among nesting substrates (ground, shrub, canopy; Martin 1993a). However, studies using artificial nests are criticized for not accurately measuring the true risk of predation because they lack important parental behaviors such as nest defense and egg concealment by brooding parents. Additionally, predators of artificial nests have differed from those of natural nests in some studies (Willebrand and Marcstrom 1988, Thompson and Burhans 2003) which may lead to erroneous patterns of predation risk that do not reflect patterns of predation risk on natural nests. Nevertheless, the daily predation risk of artificial nests was similar to that of natural nests in some studies (Thompson and Burhans 2003), and spatial patterns of predation risk was similar for natural and artificial nests in other studies (Moore and Robinson 2004). The experimental value provided by artificial nests may outweigh the drawbacks as long as their validity as surrogates for natural nests is evaluated (Major and Kendal 1996).

We used cluster sampling to compare nesting success between mixed-conifer and oak woodlands. We used ArcView 3.3 to generate random points within these 2 plant communities with the constraints that points were: 1) 100 – 1000 m from a passable road

(i.e., no jeep trails), 2) on slopes $<45^\circ$, 3) ≥ 400 m apart, and 4) within one of the following Arizona GAPVEG forest types: Englemann spruce (*Picea engelmannii*)-mixed conifer, ponderosa pine-mixed conifer, Douglas fir (*Pseudotsuga menziesii*)-mixed conifer (madrean), Douglas fir-mixed conifer (Rocky Mountain), encinal oak (madrean evergreen forest). An a priori power analysis for a comparison of proportions revealed that a sample size of 408 nests per plant community was sufficient to detect a 10% difference between plant communities ($\alpha = 0.05$, $\beta = 0.20$). We placed 3-6 ($\bar{x} = 5.8$) artificial nests near each random point (hereafter referred to as nest cluster) and used a different random point for each nest cluster (Table B.1). We placed and checked artificial nests during 3 discrete time periods occurring within the band-tailed pigeon breeding season placing nest clusters. We only placed artificial nests during the mid-season nesting period in 2003 (8 July - 16 August) and placed artificial nests during all 3 nesting periods in 2004 (23 May - 26 June 2004, 30 June - 4 August 2004, 9 August - 11 September 2004).

We constructed artificial nests that simulated band-tailed pigeon nests by gluing together Douglas fir and white fir (*Abies concolor*) twigs (10 to 150 twigs per nest; Keppie and Braun 2000) and fastened the nests to branches with fishing line. We dusted the nests with fine soil to eliminate glue shine. Because band-tailed pigeon nests in Arizona have been found 100 m apart (Kirkpatrick et al. 2005), we spaced nests within a cluster 100 m apart in locations with the most cover (Figure B.1). Band-tailed pigeons place their nests 2 – 36 m above the ground (Leonard 1998). Therefore, we used a ladder to position artificial nests between 2 – 11 m above the ground. Band-tailed pigeons have

a clutch size of 1, so we used 1 fresh bobwhite quail (*Colinus virginianus*) egg per artificial nest. Band-tailed pigeon eggs are 40 mm in length and bobwhite quail eggs are 25% smaller (30 mm in length; Ehrlich et al. 1988). We marked nests with flagging an average of 6.0 m (95% C.I. = 5.6 - 6.4 m) from each nest.

We measured characteristics surrounding each artificial nest including elevation, nest height, nest tree dbh, and percent nest concealment. Nest concealment was calculated as the average of 6 visual estimates: percent cover at 1 m in 4 cardinal directions, and percent cover from 1 m above and below the nest (Martin et al. 1997). Although we attempted to make average-sized band-tailed pigeon nests (24 x 29 cm; K. Hughes, unpublished data), nest sizes varied slightly, so we also recorded relative sizes (small = 1, medium = 2, large = 3) for each artificial nest.

We checked nest status 19 days (range = 17 – 22) after placement (the average incubation period of band-tailed pigeons is 19 days; Braun 1994). We considered nests depredated when: 1) no egg was found in the nest or on the ground within 10 m of the nest, 2) eggs found on the ground showed signs of predation (e.g., puncture marks), or 3) eggs found in the nest showed signs of predation.

Nest Predator Abundance and Distribution

We estimated the relative abundance of avian and mammalian nest predators by conducting 10-minute point-count surveys at 2 locations spaced 200 m apart within each nest cluster both at the beginning and the end of the artificial nest experiment (Figure B.1). On each survey, we recorded the number of four potential mammalian nest predators seen or heard: red squirrels, Abert's squirrels, Arizona gray squirrels, and

Chiricahuan fox squirrels. In addition to recording all mammals heard or seen during point-count surveys, we systematically recorded all visual observations and sign of squirrels and coatis while placing and checking artificial nests. We also recorded the number of four potential avian nest predators seen or heard: Steller's jays, Mexican jays, house wrens, and Bewick's wrens.

Cone and Acorn Abundance

In 2004, we used methods similar to Brotons and Herrando (2003) to estimate the relative abundance of conifer cones and acorns, the main food sources of potential nest predators in this system (Hoffmeister 1986, Erlich et al. 1988). Within each nest cluster, we walked 2 100-m long, 10-m wide belt transects separated by 100 m (Figure B.1). We used a 2-tiered approach to estimate relative abundance of cones or acorns and recorded 1) the proportion of branches on each tree that had cones or acorns present within 5 classes, and 2) the density of cones or acorns on these branches (light, medium, or heavy) because the density of cones or acorns varied from branch to branch within a tree and among trees. For each tree (oak ≥ 15 cm dbh; conifer ≥ 20 cm dbh), we recorded the dbh and estimated the proportion of branches that had cones or acorns according to the following classification scale: 0 = no cones or acorns present; 1 = $< 5\%$ of branches contain at least 1 cone or acorn; 2 = 6-25% of branches contain cones or acorns; 3 = 26-50% of branches contain cones or acorns; 4 = 51-75% of branches contain cones or acorns; 5 = $> 75\%$ of branches contain cones or acorns (tier 1). We rated and recorded the density (heaviness) of the acorn or cone crop on each tree on a load scale: 1 = light, 2 = medium, or 3 = heavy (tier 2). Finally, we multiplied the class scale (tier 1) by the load

scale (tier 2) for each tree within the plot to obtain cone or acorn abundance for each tree. We averaged the relative abundance of cones and acorns for all trees within each nest cluster (for the 2 transects combined) for each of the 2 visits. We used the estimate of relative abundance for cones and acorns within each nest cluster that was highest for the 2 visits as the index of cone and acorn abundance for that nest cluster. Both cones and acorns were used in both plant communities because mixed-conifer forests contain oaks in the understory, and encinal oak woodlands often contain pinyon pines.

Analyses

We used logistic regression and all artificial nests with known fate ($n = 767$ nests) to evaluate whether 2 criticized features of artificial nests affected the risk of nest predation: distance from flagging to each nest and nest size. We also investigated the relationship between random placement of nest clusters and the probability of nest predation because 13 of the 136 nest clusters were placed non-randomly for logistical reasons.

We used double-observer trials in 2004 (Nichols et al. 2000, Conway and Simon 2003) to estimate detection probability for potential avian nest predators. Personnel conducting point-count surveys in 2003 were more experienced and than those in 2004. Therefore, we used results from the double-observer trials to adjust the 2004 observer estimates for avian nest predator detection probability. We did not adjust the number of mammals detected because we had too few mammal detections to calculate detection probability and most mammals were detected visually while placing and checking nests. We used the maximum number of avian (adjusted for detection probability) and

mammalian (unadjusted) nest predators detected within 150 m for the two visits combined (4 point-count surveys) for an estimate of nest predator abundance. We used *t*-tests with nest cluster as the sample unit to compare predator abundance for each group of nest predators between the two plant communities.

We used *t*-tests, chi-square tests, and simple linear regression analyses to examine the relationship between the response variable (depredated or intact) and each of 9 explanatory variables. We used all nests with known fate for *t*-tests and chi-square tests ($n = 767$ nests). For linear regressions, we used the proportion of nests depredated per nest cluster as the response variable ($n = 136$ nest clusters). We used logistic regression for binomial counts with stepwise variable selection ($P = 0.20$ to enter, $P = 0.10$ to remain) to select a model that best explained the probability of nest predation for all nests with known fate. We modeled the response variable as the proportion of nests depredated/the proportion of nests with known fate per nest cluster and accounted for 8 additional variables: year, nesting period, mountain range, plant community, and 5 characteristics measured at each artificial nest (the average elevation, nest tree dbh, nest height, nest concealment, and nest size per nest cluster) along with all 2-way interactions.

We examined natural band-tailed pigeon nests in the Catalina Mountains ($n = 10$, data collected from 2002-2004, Kirkpatrick et al. 2005) to determine if the probability of predation differed between artificial nests (data from 2004 in Catalina Mountains) and natural nests. We examined both nest fate through hatching (nest building and incubation stages) and nest fate through fledging (building, incubation, and nestling stages). We then examined whether differences in nest predation between plant communities within

the Catalina Mountains were consistent for both artificial and natural nests. We used logistic regression with stepwise variable selection ($P = 0.20$ to enter, $P = 0.10$ to remain) and nest fate through hatching as the response variable and plant community, nest type (natural or artificial), nest tree dbh, nest height, and all 2-way interactions as possible explanatory variables.

To determine if alternative food abundance influenced the probability of nest predation within mixed-conifer and oak woodlands, we used data collected from the 4 mountain ranges in 2004 only ($n = 109$ nest clusters) because we only collected data for cone and acorn abundance during 2004. We used logistic regression for binomial counts with stepwise variable selection ($P < 0.20$ to enter, $P < 0.10$ to remain) to obtain a second nest predation risk model for 2004 only. We modeled the response variable as the proportion of nest depredated/the proportion of nests with known fate per nest cluster, and included the following explanatory variables: nesting period, mountain range, plant community, the 5 characteristics measured at each artificial nest, the of index cone and acorn abundance, and all 2-way interactions. For statistical tests, we transformed variables where appropriate to better meet assumptions of parametric tests. We used JMP IN statistical analysis software for all analyses (SAS Institute, Inc. 2003). We report untransformed means and odds with 95% confidence intervals in parentheses.

Results

We placed a total of 784 artificial nests ($n = 157$ in 2003, $n = 627$ in 2004; Table B.1) in 136 nest clusters. We placed nests an average of 2.8 m (95% C.I. = 2.7 - 2.9 m) off the ground in 18 different tree species with an average dbh of 22 cm (95% C.I. = 21 - 23 cm). Average nest concealment around nests was 31% (95% C.I. = 30 - 32%). We were able to determine fate for 767 nests: 80% of all nests were depredated, 17% remained intact, and 3% had unknown fate (nest or egg likely destroyed by weather).

The distance at which we placed flags from nests did not differ between depredated and intact nests (Table B.2; $t_{741} = -1.3$, $P = 0.196$). Larger nests had a lower risk of nest predation than smaller nests (Table B.2; $t_{729} = 1.9$, $P = 0.057$) so we included nest size as a possible explanatory variable in the models for nest predation risk. The probability of predation did not differ between randomly placed nest clusters and non-randomly placed nest clusters (Table B.2; $G^2 = 1.2$, $P = 0.279$), therefore we used all nests with known fate in the analyses.

Nest Predation in Mixed-Conifer Forest and Oak Woodlands

The probability of nest predation differed among mountain ranges, plant communities, elevation, nest tree dbh, and nest size, and was positively related to jay abundance and total predator abundance (Table B.2). Logistic regression resulted in a model for the risk of artificial nest predation containing the main effect plant community and the following interactions: year and nest concealment, mountain range and dbh, and mountain range and nest concealment (Table B.3; $G^2 = 84.2$, $P < 0.0001$).

The odds of a nest being depredated for artificial nests placed in mixed-conifer

forest were 1.6 times (95% C.I. = 1.2, 2.0) lower than in oak woodlands ($G^2 = 13.6$, $P = 0.0002$). The risk of nest predation was negatively related to nest concealment in 2003 and positively related to nest concealment in 2004 (Figure B.2). The relationship between the risk of nest predation and nest concealment also differed among mountain ranges (Figure B.3, $G^2 = 9.6$, $P = 0.002$). A high risk of nest predation in the Chiricahuas ($\bar{x} = 0.91$, 95% C.I. = 0.87 - 0.93) was associated with lower than average nest concealment ($\bar{x} = 29\%$, 95% C.I. = 27% - 31%), whereas in the Huachucas, a relatively low risk of nest predation ($\bar{x} = 0.85$, 95% C.I. = 0.79 - 0.91) was associated with higher than average nest concealment ($\bar{x} = 34\%$, 95% C.I. = 30% - 38%).

The relationship between the risk of nest predation and nest tree dbh differed among mountain ranges (Figure B.4; $G^2 = 3.4$, $P = 0.064$). However, average nest tree dbh did not differ among mountain ranges (ANOVA, $F = 2.1$, $P = 0.100$) and the odds of artificial nest predation were 1.02 times (95% C.I. = 0.99 - 1.05) higher in the Chiricahua and Huachuca Mountains compared to the Catalina and Pinaleno Mountains.

Artificial vs. Natural Band-Tailed Pigeon Nests

The risk of nest predation did not differ between natural and artificial nests when we used the entire nesting cycle (nest building through nestling stages; $G^2 = 0.2$, $P = 0.660$). Sixty seven percent of natural nests vs. 74% of artificial nests were depredated during the entire nesting cycle. However, predation risk differed between natural and artificial nests when we only used the nest building and incubation stages for comparisons ($G^2 = 11.5$, $P = 0.0007$). Twenty percent of natural nests vs. 74% of artificial nests were depredated during the incubation stage. The odds that natural nests

were depredated were 0.21 times lower (95% C.I. = 0.07, 0.61) during the building and incubation stages. However, the pattern in risk of nest predation in mixed-conifer forests and oak woodlands did not differ between natural and artificial nests; the interaction between nest type and plant community was not significant (Wald $\chi^2 = 0.4$, $P = 0.829$).

Abundance of Avian and Mammalian Nest Predators

Average detection probability for observers in 2004 was 0.34 (range 0.30 – 0.48). We detected more predators overall ($\bar{x} = 5.4$, 95% C.I. = 4.7 - 6.2; $t_{134} = -2.1$, $P = 0.039$) and more jays ($\bar{x} = 4.3$, 95% C.I. = 3.8 - 4.8; $t_{134} = -3.9$, $P < 0.0001$) in oak woodlands than in mixed-conifer forests (all predators $\bar{x} = 4.5$, 95% C.I. = 3.9 - 5.1; jays $\bar{x} = 2.9$, 95% C.I. = 2.4 - 3.4). However, we detected more wrens in mixed-conifer forest ($\bar{x} = 1.3$, 95% C.I. = 1.0 - 1.5) than in oak woodlands ($\bar{x} = 1.1$, 95% C.I. = 0.8 - 1.4), although this difference was not significant ($t_{134} = 0.9$, $P = 0.361$). Although we detected very few mammals ($n = 23$) during point-count surveys and incidentally while checking artificial nests, I detected more mammals in mixed-conifer forest ($\bar{x} = 0.3$, 95% C.I. = 0.2 - 0.5) than in oak woodlands ($\bar{x} = 0.0$, 95% C.I. = -0.1 - 0.1; $t_{134} = 3.9$, $P = 0.0002$).

Cone and Acorn Abundance and the Probability of Nest Predation

The abundance of cones and acorns did not vary between plant communities ($t_{107} = 1.2$, $P = 0.242$) nor among mountain ranges ($F_{3, 105} = 0.3$, $P = 0.807$). Nest predation risk for 2004 was very similar to that for both years combined. Plant community, and the interactions between mountain range and nest concealment, nesting period and dbh, and dbh and nest size influenced the risk of nest predation in 2004 (Table B.3; $G^2 = 65.6$, $P < 0.0001$). The abundance of cones and acorns was not related to the risk of nest predation,

after accounting for these other variables (Figure 5; $G^2 = 2.0$, $P = 0.156$).

Discussion

Few studies address ultimate causation underlying observed patterns in habitat selection at the landscape level because habitat quality measurements (e.g., nesting success) combined with population abundance data are typically lacking at this scale (Pidgeon et al. 2003). Birds may first make decisions regarding where to breed at large spatial scales (e.g., at the scale of the plant community) prior to making decisions regarding nest placement at finer spatial scales (Kotliar and Wiens 1990). However, nest placement at fine spatial scales is the focus of most habitat selection studies in birds. Therefore, predation may influence nest-site selection on a landscape scale in addition to influencing decisions at the scale of the nest (nest height, concealment, nest substrate; Marini 1997, Martin and Joron 2003).

The risk of nest predation was lower in mixed-conifer forest than in oak woodlands in southeastern Arizona. This pattern is the opposite of patterns observed in coniferous forests and deciduous woodlands in more northern latitudes (Bayne et al. 1997, Seiving and Willson 1998). The difference may be in part due to the difference in predator assemblages between southeastern Arizona and other regions. Nevertheless, my results support the hypothesis that the risk of nest predation influences habitat selection in band-tailed pigeons. The risk of nest predation was lower in plant communities where band-tailed pigeons occur most frequently and are known to commonly nest (mixed-conifer forest) than in plant communities where they have been known to forage (Neff 1947) but are detected and nest less frequently (Kirkpatrick et al. 2005).

The relationship between nest concealment and the risk of nest predation differed

between 2003 (negative relationship) and 2004 (positive relationship). The relationship between nest concealment and the risk of nest predation also varied among mountain ranges. Nest concealment has been shown to affect the risk of nest predation in some studies (Nice 1937, Nolan 1978, Best and Stauffer 1980, Martin and Roper 1988) but not others (Clark and Nudds 1991, Filliater et al. 1994, Willson and Gende 2000, Remes 2005a). Poorly concealed nests have a higher probability of being depredated by birds than other nest predators (Clark and Nudds 1991, Remes 2005a). The realization that nest concealment may stymie visually stimulated predators (i.e., birds; Yahner and Wright 1985) but not systematic searchers and olfactory stimulated predators (e.g., mammals) has lead some authors to suggest that placing nests in highly concealed locations is not always the best nest-placement strategy (Filliater et al. 1994).

Although we placed nests in locations with the most cover relative to other places in close proximity, our nest placement choices were constrained by a lack of available cover below 6 m within both mixed-conifer forest and oak woodlands due to their physiognomy. Additionally, mixed-conifer forests in southeastern Arizona are mature stands containing many large trees with high canopy cover and a sparse understory (Brown 1994). Most oaks in Arizona's woodlands are evergreen but can be drought deciduous in the late spring; leaves are replaced with the onset of the monsoon in mid to late summer (McClaren and McPherson 1999, K. Hughes, pers. observation). The interval between leaf drop and replacement is extremely variable annually and sometimes replacement begins before leaf drop is complete. The amount and onset of summer monsoon rains (and hence leaf drop and replacement) can vary greatly among the

mountain ranges in the region. This variation could explain why nest concealment and risk of nest predation differed between years and among mountain ranges. Additionally, years of high mammal or corvid abundance may increase the risk of nest predation in this system whether or not nests are well concealed if nests are placed in trees containing cones or acorns for which these taxa are foraging. The relationship between the risk of nest predation and nest tree dbh differed among mountain ranges but the differences were small. Therefore, these relationships may not be biologically meaningful.

The risk of nest predation was influenced by whether or not a nest was natural or artificial. Artificial nest studies have been criticized because they often do not provide accurate estimates of predation risk in natural nests (Willebrand and Marcstrom 1988, Reitsma et al. 1990, Burke et al. 2003, Whelan and Burhans 2003, Moore and Robinson 2004). Adult behavior may both provide cues to predators (Inglis 1977, Vickery et al. 1992, Conway and Martin 2000, Martin et al. 2000, Tewksbury et al. 2002) and deter predation (Samelius and Alisauskas 2001, Remes 2005b, Andersson and Waldeck 2006). Lower predation risk has been reported in nests with increased nest attendance (Inglis 1977, Samelius and Alisauskas 2001, Remes 2005b, Andersson and Waldeck 2006). Band-tailed pigeons have nearly constant nest attendance with only 2 obvious periods of parental activity (incubation switch between male and female in morning and afternoon) during the incubation stage. The lack of nest attendance at artificial nests may facilitate predation by some nest predators (i.e., wrens) that would otherwise not have access to eggs if adults were defending the nest (Davison and Bollinger 2000). Additionally, incubating birds may provide additional camouflage while on the nest (Burke et al.

2003), but few studies have adequately tested this hypothesis. Because band-tailed pigeons sit extremely still while on nests and activity at the nest is limited, the lack of concealment from a brooding adult at artificial nests and a high rate of nest attendance at natural nests likely contributed to the difference in predation risk between natural and artificial nests. Despite the difference in risk of nest predation between natural and artificial nests in this study, the differences in predation risk between plant communities was consistent for both natural and artificial nests.

Overall predator abundance was greater in oak woodlands than in mixed-conifer forest. Both wrens and mammals tended to be relatively more abundant in mixed-conifer forest than in oak woodlands. Although we lack evidence indicating that birds were the main predators of artificial nests in this study, low overall nest concealment and high relative abundance of jays in both oak woodlands and mixed-conifer forests is consistent with this assumption (jays are visual predators; Yahner and Wright 1985). Even so, we observed a squirrel attacking a natural band-tailed pigeon nest while an adult was incubating (Kirkpatrick et al. 2005).

We found no relationship between cone and acorn abundance and nest predation risk. The lack of relationship could be because: 1) our measures of cone and acorn abundance were inaccurate, 2) cone and acorn abundance does not affect the risk of nest predation in this system, 3) predation risk is affected by cone and acorn abundance the previous year rather than the same year, or 4) cone and acorn abundance affect nest predation via a numerical response. A study in the eastern United States found that acorn crop in one year accurately predicted the risk of nest predation among artificial nests the

following year (McShea 2000). Higher numbers of granivorous mammals (including squirrels) as a result of increased food abundance from the previous fall led to increased predation risk the following summer.

Conclusion

The risk of artificial nest predation varied between oak woodlands and mixed-conifer forest across four mountain ranges in southeastern Arizona. This pattern was consistent for both artificial nests and natural band-tailed pigeon nests in the Santa Catalina Mountains. These results suggest that nest predation may be an important factor involved in habitat selection of band-tailed pigeons at a landscape level. Band-tailed pigeons across their range are declining, and most band-tailed pigeon nests in Arizona fail due to predation (Hughes et al., in review). Forest management practices such as thinning, road building, and prescribed fire can increase the abundance of small mammals (Kyle and Block 2000, Converse et al. 2006a, Converse et al. 2006b) and thereby increase the risk of nest predation. Therefore, research is needed to determine how these practices affect predation risk particularly in mixed-conifer forests and other areas that normally have a lower relative risk of nest predation.

More research on the effects of variability in predation risk across the landscape is needed to determine how nest placement and nest predation influence habitat selection at the landscape scale. Artificial nests provide an easy way to test patterns of relative predation risk across large spatial scales. Future research examining why the risk of nest predation varies across the landscape in southeastern Arizona may expand our understanding of distributional patterns of nesting birds.

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Table B.1. Number of artificial nests placed within each of 4 mountain ranges and 2 plant communities in southeastern Arizona during 2003 and 2004.

Mountain Range	Oak Woodlands	Mixed-Conifer Forest	Total per Mountain Range
Catalinas	23	139	162
Chiricahuas	123	118	241
Huachucas	145	57	202
Pinalenos	78	101	179
Total	369	415	784

Table B.2. The risk of nest predation for artificial nests in southeastern Arizona varied among mountain ranges and plant communities, and was influenced by elevation, nest tree features, nest size, and abundance of potential nest predators. Results are based on 2-tailed *t*-tests, likelihood ratio chi-square tests, and simple linear regressions.

Explanatory variable	intact	depredated	<i>n</i>	<i>F</i>	<i>t</i>	<i>G</i> ²	<i>P</i>
	(<i>x</i> ± SE)	(<i>x</i> ± SE)					
Year			767 *			<0.01	1.000
Mountain Range			767 *			26.3	< 0.0001
Plant Community			767 *			46.5	< 0.0001
Nesting Period			767 *			2.0	0.370
Random Placement of Nest Clusters			767 *			1.2	0.279
Flagging Distance	5.6 ± 0.4	6.1 ± 0.2	741 *		-1.3		0.196
Elevation	2227 ± 41	1978 ± 19	765 *		5.7		< 0.0001
Nest Tree dbh	20.6 ± 0.8	22.4 ± 0.3	765 *		-2.2		0.030
Nest Height	2.9 ± 0.1	2.8 ± 0.0	763 *		0.8		0.397
Nest Concealment	30.4 ± 0.8	30.9 ± 0.4	761 *		-0.8		0.430
Nest Size	1.9 ± 0.0	1.8 ± 0.0	729 *		1.9		0.057
Jay Abundance			136 **	4.7			0.032
Wren Abundance			136 **	2.3			0.135
Mammal Abundance			136 **	0.4			0.514
Combined Predator Abundance			136 **	5.2			0.025
Cone and Acorn Index			109 **	0.2			0.686

*Nest is sample unit. Sample sizes vary due to missing data.

**Nest cluster is sample unit. Cone and acorn index includes nest clusters from 2004 only.

Table B.3. Results of two logistic regressions for binomial counts using stepwise variable selection ($P = 0.20$ to enter, $P = 0.10$ to remain). In each model, the risk of artificial nest depredation within forests in southeastern Arizona was the response variable. The two models were based on 1) nest clusters ($n = 136$) from 2003 and 2004 pooled, and 2) nest clusters ($n = 109$) from 2004 only.

Error! Not a valid link.

Figure B.1. Layout of an artificial nest cluster showing location of artificial nests, point-count survey stations, and food abundance transects. I sampled 136 of these nest clusters in 2003 and 2004 in southeastern Arizona.

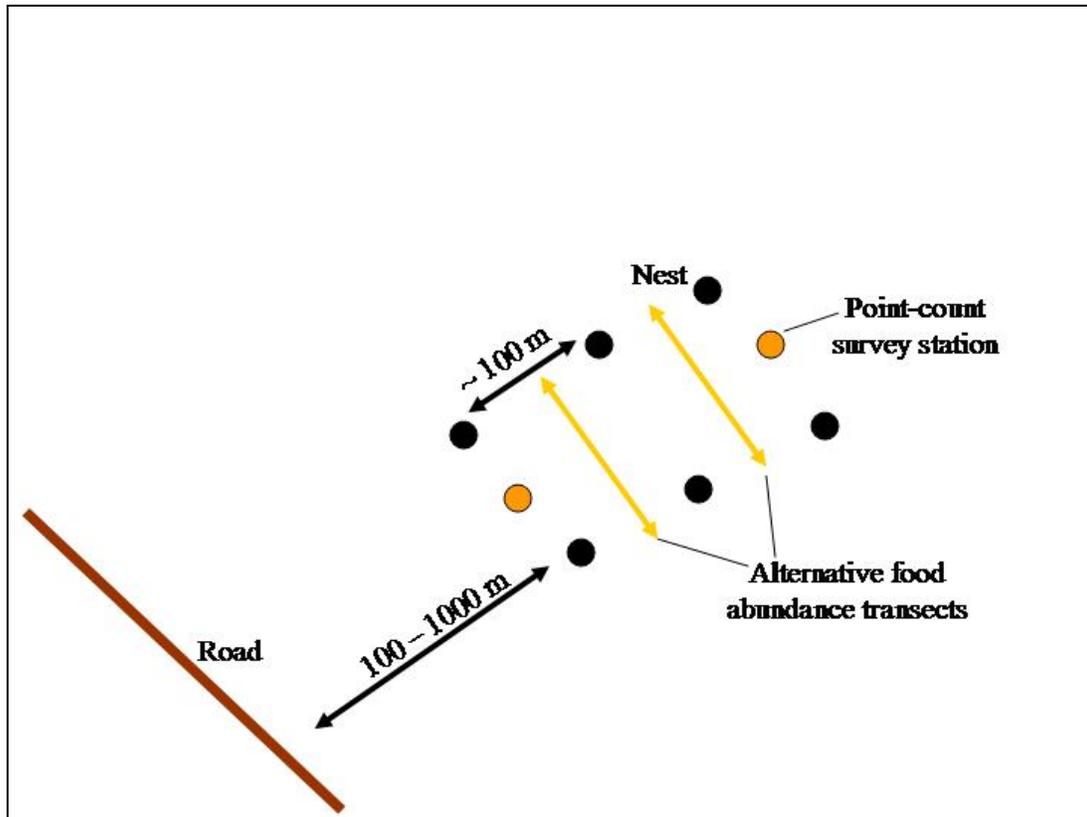


Figure B.2. The probability of artificial nest predation was positively related to nest concealment in 2004, but negatively related to nest concealment in 2003, southeastern Arizona.

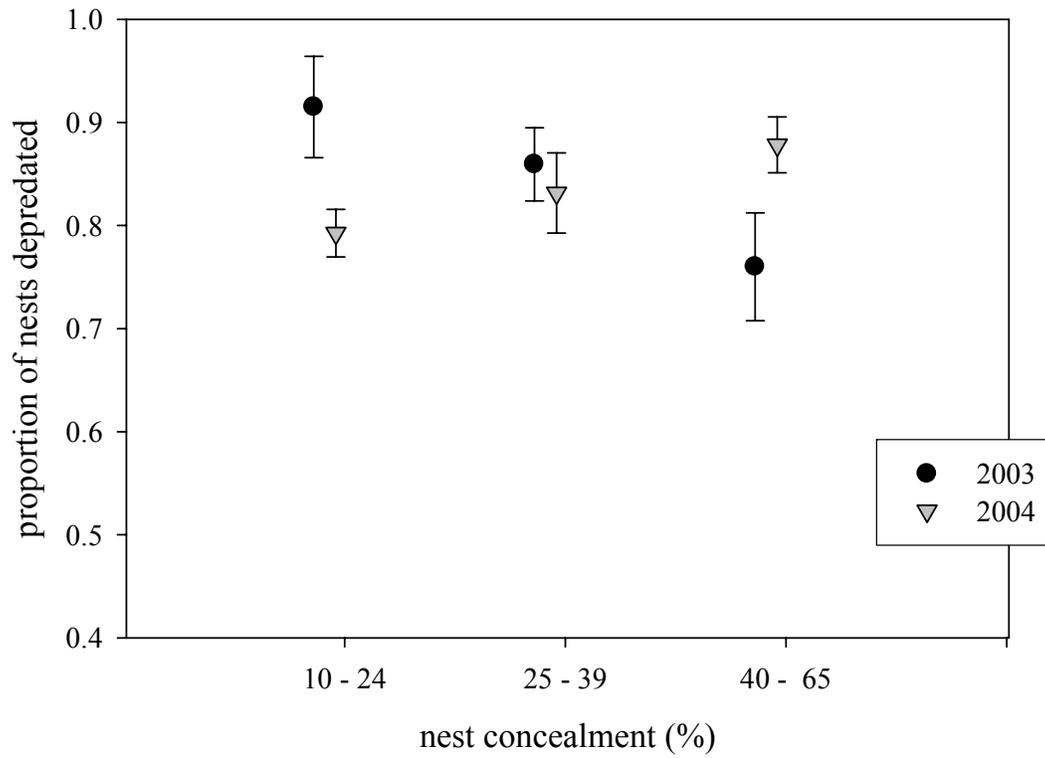


Figure B.3. The relationship between the probability of artificial nest predation and nest concealment differed among mountain ranges in southeastern Arizona.

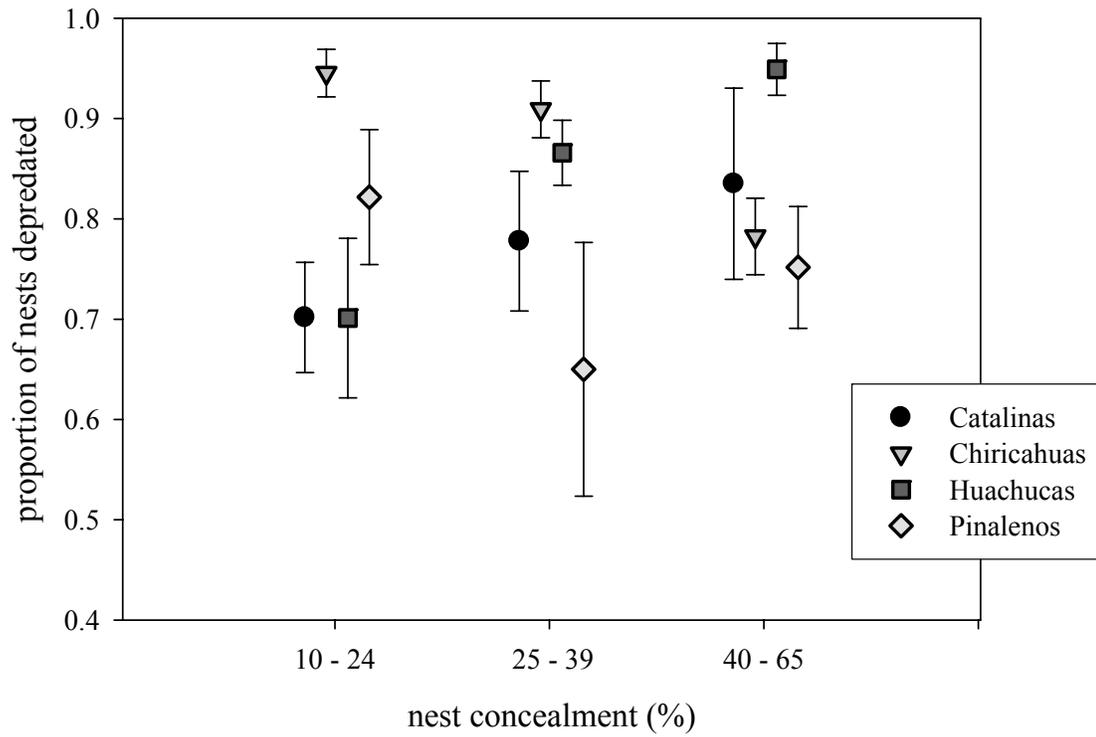


Figure B.4. The relationship between the probability of artificial nest predation and nest tree dbh differed among mountain ranges in southeastern Arizona.

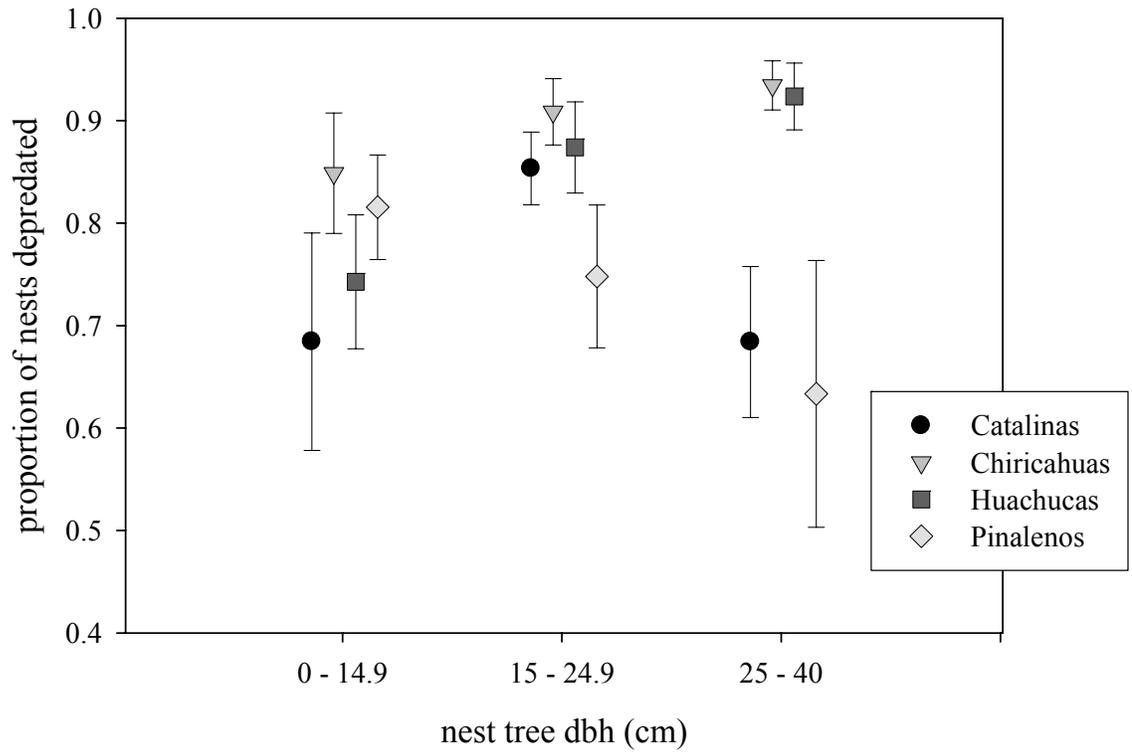
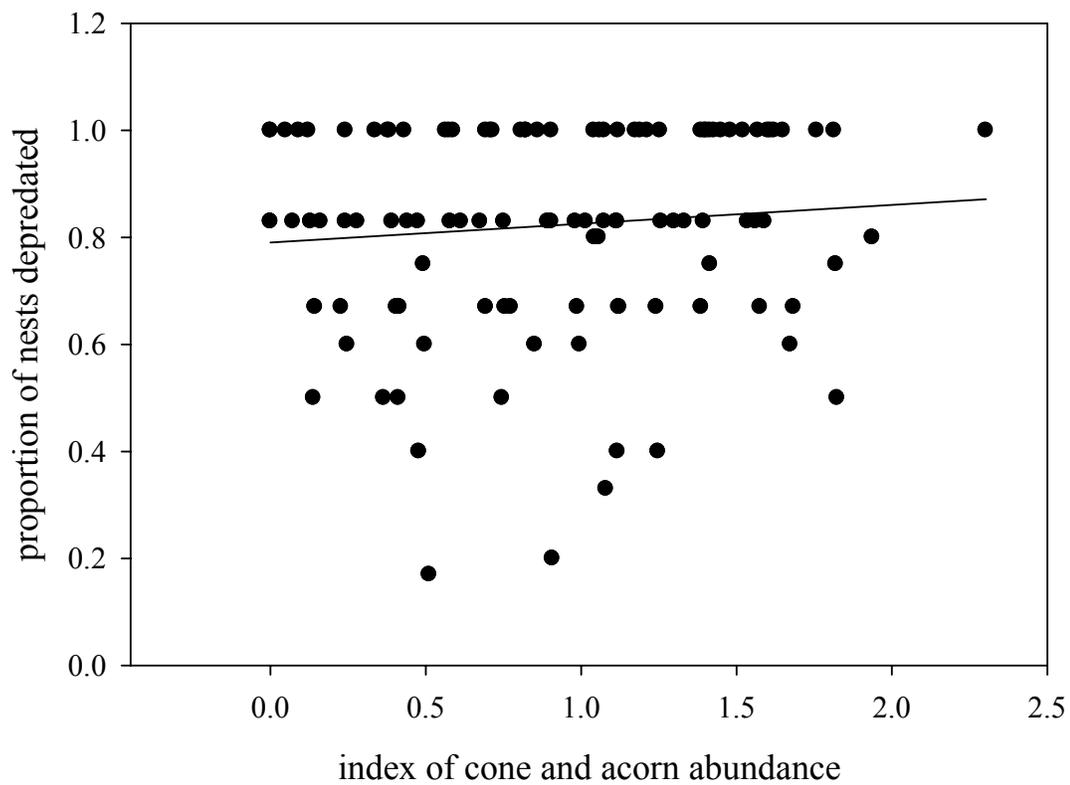


Figure B.5. The probability of artificial nest predation was not related to cone and acorn abundance after accounting for other variables that explain nest predation risk, southeastern Arizona.



APPENDIX C.
THE INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE (IACUC)