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Comparison of Hatching Failure in a Wildland and Suburban Population of the Florida Scrub-Jay (*Aphelocoma coerulescens*)

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Comparison of Hatching Failure in a Wildland and Suburban Population of the Florida

Scrub-Jay (*Aphelocoma coerulescens*)

by

Sonya Christine LeClair

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Biology
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Table of Contents

List of Tables	ii
List of Figures	iii
Abstract	iv
Chapter One Introduction	1
Study organism	6
Study area and general methods	6
Chapter Two Analysis of Historical Data	10
Methods	11
Results	13
Discussion	19
Chapter Three Influence of Ambient and Nest Temperature and Perceived Predation Risk on PHF	25
Methods	28
Study site	28
Treatments	28
Temperature	29
Incubation behavior	30
Statistical analyses	31
Results	32
Temperature	32
Incubation behavior	36
Discussion	41
References	47

List of Tables

Table 1.	Results of Mann Whitney U tests to examine the effects of site, clutch size, presence of helpers, clutch initiation date (i.e. timing of breeding) and year on rates of partial hatching failure in a wildland and suburban population of Florida Scrub-Jays in Highlands County, Florida.	15
Table 2.	AIC values generated from multiple binary logistic regressions to test the effects of year (A), site (B), clutch initiation date (i.e. timing of breeding) (C), presence of helpers (D), and clutch size (E) in explaining the occurrence of partial hatching failure in a wildland and suburban population of the Florida Scrub-Jay in Highlands County, FL. Only those models with each individual variable or models with Δ AIC values <10 are included in this table.	17
Table 3.	Results of ANOVA for analysis of historical demographic data for the effects of clutch size and site on rates of partial hatching failure.	18
Table 4.	Results of ANOVA examining differences in ambient temperatures between treatments. Log transformation was used on maximum temperature.	33
Table 5.	Results of binary logistic regression examining the effects of incubation behavior and ambient temperatures on the occurrence of hatching failure.	35
Table 6.	Results of ANOVA examining differences in frequency and duration of off-bouts, proportion of time spent away from the nest and feeding rates between control suburban, experimental suburban and wildland treatments. Log transformation was used for maximum off-bouts.	37

List of Figures

- Figure 1. Aerial photo of scrub at Archbold Biological Station (“wildland”) on top and Placid Lake Estates (“suburban”) scrub at bottom. 8
- Figure 2. Rates of partial hatching failure (PHF) in a wildland and suburban population of the Florida Scrub-Jay (*Aphelocoma coerulescens*) from 1993-2001. PHF was defined by having an egg(s) survive the incubation period, but subsequently fail to hatch in a nest that produced at least one nestling. The bars represent standard error, and the numbers above the bars indicate sample sizes. 14
- Figure 3. Minimum, mean and maximum ambient temperatures at control suburban, experimental suburban and wildland treatments in 2003 (black) and 2004 (grey). Bars represent standard error, and numbers above the bars represent sample sizes. 34
- Figure 4. Frequency of off-bouts, mean duration of off-bouts and proportion of time off nest in 24-hours in control suburban, experimental suburban and wildland females in 2003 (black) and 2004 (grey). Bars represent standard error, and numbers above the bar indicate sample size. 38
- Figure 5. Minimum duration off-bouts, maximum duration off-bouts and frequency of male incubation feedings in control suburban, experimental suburban and wildland treatments in 2003 (black) and 2004 (grey). Bars represent standard error, and numbers above bars represent sample sizes. 40

Comparison of Hatching Failure in a Wildland and Suburban Population of the Florida Scrub-Jay (*Aphelocoma coerulescens*)

Sonya Christine LeClair

ABSTRACT

Egg hatchability has been correlated with many factors, including clutch size, presence of helpers, timing of breeding and predation risk. Hatching failure is higher in a suburban population of Florida Scrub-Jays than in a wildland population, but the reasons for this pattern are unclear. An analysis of long-term demographic data on scrub-jays in both habitats revealed the factors that best explained variation in hatching failure, and an experiment tested whether two potential site factors, ambient temperature and predation risk, could increase hatching failure in the suburbs.

Although a global model was best supported by the data for occurrence of partial hatching failure (PHF), clutch size and site were the most significant parameters in this model, which is consistent with the analysis of rates of PHF. I further examined two potential site differences, ambient temperature and predation risk, which might increase PHF in the suburbs.

Human activity may increase the perception of predation risk, thus suburban jays may take fewer, longer off-bouts or make fewer incubation feedings to decrease this perceived risk. These behavioral changes may increase nest temperature, thus increase embryo mortality. I placed thermocouples and video cameras at nests during incubation to gauge both ambient and nest temperature and behavior of scrub-jays at each site. I predicted higher ambient temperatures in the suburbs, because suburban areas often serve

as heat islands. I also predicted fewer, longer off-bouts and fewer feedings in the suburbs and where human activity was increased experimentally. Ambient temperatures were higher in the suburbs as a result of higher daily minimums rather than higher maximums. Furthermore, females exposed to increased human activity took fewer but not longer off-bouts than suburban or wildland controls; therefore, they increased their nest attentiveness. Although temperature and incubation behavior varied among treatments, neither explained the occurrence of PHF during incubation; however, temperature differences during the laying period could affect the viability of first-laid eggs. First-laid eggs in the suburbs may be exposed to relatively warmer ambient conditions for an extra day prior to incubation, which may decrease their viability and increase PHF.

Chapter One

Introduction

Egg hatchability can be defined as the proportion of eggs that successfully hatch. The rate of egg hatching success may be influenced by a variety of ecological, geographical and social factors (Koenig 1982). Among species, diminished hatchability, or hatching failure, tends to be slightly higher for cooperative breeders with shared incubation, but tends to be slightly lower for uniparental incubators, monogamous pairs, birds with all-purpose territories and monogamous pairs with helpers (Koenig 1982; Woolfenden and Fitzpatrick 1984; Innes 1996). A variety of factors may contribute to variation in hatching failure among populations within species, including inbreeding depression (van Noordwijk and Sharloo 1981; Bensch et al. 1994), clutch size (Reid et al. 2000; Wiebe and Martin 2000; Erikstad and Tveraa 1995), timing of breeding (Harmeson 1974; Hipfner et al. 2004), female condition (White 1991; Saino et al. 2002), increased population density (Koenig 1982), ambient and nest temperatures (Taylor 1949; Lundy 1969) and predation risk (Martin and Conway 2000).

Inbreeding tends to promote homozygosity, and it can increase the incidence of recessive lethal alleles (Koenig 1982; van Noordwijk and Sharloo 1981). In a population of the Great Tit (*Parus major*), death resulting from increased homozygosity seemed to occur before or at hatching and, as a result, the number of eggs that failed to hatch and the proportion of clutches that experienced hatching failure increased with the degree of inbreeding (van Noordwijk and Sharloo 1981). Furthermore, lifetime reproductive

success decreased in inbred female Song Sparrows (*Melospiza melodia*), and this largely was the result of increased hatching failure (Keller 1998). Hatching failure also was positively correlated with the degree of genetic similarity among mates in the Great Reed Warbler (*Acrocephalus arundinaceus*) (Bensch et al. 1994).

The presence of helpers in cooperative breeding species may contribute to lower rates of hatching failure by decreasing the amount of time a female must spend defending the territory, thereby allowing her to remain on the nest (Woolfenden and Fitzpatrick 1984). This hypothesis parallels a prediction that increased population density contributes to greater egg neglect through increased territorial disputes (Koenig 1982). Periods of neglect may leave the eggs exposed to temperatures outside the range of ideal temperatures for development (35-40° C), leading to developmental abnormalities and embryo death (Lundy 1969).

A relationship also exists between maternal condition and egg hatchability. Unlike mammals, which continue to nourish their young as they develop, birds lay amniotic eggs. Embryo survival depends upon the necessary amino acids derived from maternal proteins and female nutritional deficiencies can affect egg protein quality (White 1991). Various other resources contributed to the egg by the mother, such as lipids, vitamins or immune factors, also have a direct effect on egg quality, which may influence subsequent embryo survival (White 1991; Saino et al. 2002).

Hatchability also may be related to clutch size. First, a female may be limited in her ability to produce several high-quality eggs (Potti and Merino 1996). In large clutches, last-laid eggs may be smaller, and small eggs may contain insufficient reserves for normal embryonic development, or they may be more vulnerable to fluctuations in

nest temperature (Lundy 1969; Potti and Merino 1996). Therefore, smaller, last-laid eggs may be more likely to experience hatching failure. Second, many species begin incubation on the day the penultimate or ultimate egg is laid. First-laid eggs in large clutches may be vulnerable to hatching failure because they are exposed to ambient conditions for a longer period of time prior to the onset of incubation, and temperature fluctuations can lead to developmental abnormalities or even death (Lundy 1969; Drent 1975). Finally, female passerines may not be able to incubate large clutches efficiently. Large clutches may become warmer or lose more water if females cannot regulate the nest microclimate effectively, and these changes may increase the potential for hatching failure (Reid et al. 2000).

Timing of breeding also is an important factor in reproductive success. First, female condition at the end of the breeding season may be poor relative to early nesters, thus late-nesting females may need to increase the frequency or duration of their off-bouts to meet their foraging needs (Hipfner et al. 2004). Conversely, females nesting early in the season may encounter a food shortage, because food availability often is most scarce at the beginning of the breeding season (Perrins 1970). Therefore, early-nesting females also may increase the duration of their off-bouts to forage (Harmeson 1974). In each case, longer off-bouts increase the time eggs may be exposed to temperatures outside normal incubation temperatures, leading to increased embryo mortality (Lundy 1969; Drent 1975).

Predation risk also influences behavioral patterns during incubation, which may increase the possibility of hatching failure. Increased activity of the adults at nests can lead to an increased risk of nest predation (Skutch 1949). A prediction of this

observation is that birds alter their incubation behavior to decrease activity at the nest in areas of high predation risk. Specifically, males may decrease incubation feedings and females may take fewer, longer off-bouts from the nest (Conway and Martin 2000). Although this strategy decreases the risk of nest predation, it may increase the possibility of partial clutch loss through hatching failure. Eggs are sensitive to prolonged exposure outside the range of 35-40° C, and long off-bouts taken regularly may cause egg temperatures to fall outside this range. This exposure may lead to potential developmental abnormalities and embryo death, thus increased hatching failure (Lundy 1969). As a result, behavioral changes in response to predation risk may increase the potential for hatching failure, but by lowering the risk of nest predation, the behavioral change increases the probability that the nest will successfully fledge at least some young. Therefore, although the changes in incubation behavior with predation risk incur a cost of increased hatching failure, this cost is offset by the benefit of reduced predation.

Although predation risk can be affected by a number of interacting factors, human activity may be perceived by birds in a manner analogous to increased predation risk (Frid and Dill 2002). Many animals change their behavior in response to humans, and this can lead to lower reproductive success if nests or young are neglected for long periods of time (Frid and Dill 2002). If the perception of predation risk increases in urbanized areas as a result of human activity, females may alter their incubation behavior by taking fewer, longer off-bouts to minimize nest activity in suburban areas. This may increase the potential for hatching failure in these areas.

Finally, ambient temperature can affect embryo development and potential hatching failure. Contact with the female's brood patch, as well as her behavior at the

nest relative to both ambient and nest temperatures, helps regulate egg temperature (Drent 1975; Wilson and Verbeek 1995). Consequently, long periods of egg neglect may reduce the regulation of egg temperature relative to ambient temperatures and decrease the hatchability of the eggs. In urban and suburban areas, where temperatures typically are warmer than nearby rural areas (Oke 1987), periods of egg neglect may increase the potential for hatching failure. Embryos are particularly sensitive to overheating (Lundy 1969; Drent 1975); therefore, warm temperatures in urban and suburban areas may increase egg temperatures while the female is off the nest and subsequently increase embryo mortality.

Long-term research on the demography of the Florida Scrub-Jay (*Aphelocoma coerulescens*) in both wildland (Woolfenden and Fitzpatrick 1984, 1996) and suburbs (Bowman et al. 1998; Bowman and Woolfenden 2001) suggest that hatching failure is significantly higher in a suburban population of scrub-jays than a nearby wildland population, but the reason for this pattern is unclear (Bowman and Woolfenden 2001). Few differences in inbreeding and female condition exist between the two populations, thus neither are likely to explain the differences in hatching failure between the two populations. However, other differences exist that could influence hatching failure. The objective of this research was to evaluate the potential effect of these variables (clutch size, helpers, timing of breeding, site and year) on hatching failure. In addition, I conducted an experiment to test the potentially interactive effects of ambient temperature and perceived predation risk on hatching failure in both sites. In Chapter Two, I examine nine years of historical demographic data from both populations to assess the relative strength of the above variables in explaining variation in hatching failure. In

Chapter Three, I conducted an experiment to examine whether ambient temperatures differed between the sites, whether human activity led females to take fewer, longer off-bouts and males to decrease feedings, and whether these factors interacted to increase hatching failure in the suburbs.

Study organism

The Florida Scrub-Jay is a federally Threatened species that occurs only in peninsular Florida (Woolfenden and Fitzpatrick 1984). It is an extremely sedentary habitat specialist, preferring relatively open, low-growing (<2m) oak scrub dominated by sand live oak (*Quercus geminata*), Archbold oak (*Q. inopina*) and myrtle oak (*Q. myrtifolia*) (Woolfenden and Fitzpatrick 1996). Scrub-jays are cooperative breeders that defend territories containing one breeding pair and from zero to several non-breeding helpers. They typically breed from March through May. Scrub-jays build nests predominantly in *Q. geminata*, *Q. inopina* and *Q. myrtifolia* and lay three to five eggs (Woolfenden and Fitzpatrick 1996). Only the female incubates these eggs for approximately 18 days until hatching. Defensive behavior by the male at the nest may be mistaken for incubation (Hailman and Woolfenden 1985). Females begin incubation with the penultimate or ultimate egg is laid. During incubation, the male often perches on sentinel near the nest and feeds the incubating female (Woolfenden and Fitzpatrick 1996).

Study area and general methods

A population of scrub-jays at Archbold Biological Station (hereafter referred to as “wildland”) in Highlands County, FL has been studied since 1969 (Woolfenden and Fitzpatrick 1984, 1996). This habitat is located on a 2000-ha preserve composed

predominantly of xeric oak scrub that is maintained by both natural and prescribed fire (Figure 1). It is connected via contiguous scrub habitat to a suburban study area 8km north.



Figure 1. Aerial photo of scrub at Archbold Biological Station (“wildland”) on top and Placid Lake Estates (“suburban”) scrub at bottom.

A population of scrub-jays in Placid Lake Estates (“suburban”), a 1500-ha residential housing subdivision, has been studied since 1992 (Bowman et al. 1998; Bowman and Woolfenden 2001, 2002). At this site, a gradient exists in the density of human housing, from relatively low density (<10 houses/40ha) to relatively high density (>180 houses/40 ha). Xeric oak scrub patches exist in a matrix of human development and, because of fire suppression and habitat fragmentation, many of these patches are overgrown (Figure 1).

Scrub-jays in each population are uniquely banded, a periodic census is performed and likely every nest in each study area is found and the fate of each of these nests is determined. The majority of nests are found during the building or egg-laying stages, although some nests may be found during incubation. Once a nest is found, it is monitored during brief visits every three to four days to determine building stage or completed clutch size. Once the eggs hatch, the nest is checked every three to four days until day 11 post-hatching, when nestlings are banded with one color band and one aluminum band. After banding, nests are checked only with binoculars until fledging at day 18 post-hatching.

Chapter Two

Analysis of Historical Data

Approximately 30% of extant scrub-jay populations occur in scrub patches surrounded by a suburban matrix (Stith et al. 1996), and their demography differs from that of their wildland counterparts (Bowman et al. 1998; Breininger 1999; Bowman and Woolfenden 2001). Suburban scrub-jays tend to breed earlier and continue breeding later into the season than wildland scrub-jays, and suburban clutches tend to be larger than those of wildland scrub-jays (Bowman et al. 1998). Despite a longer breeding season and larger clutches, suburban scrub-jays experience relatively low reproductive success, including higher rates of hatching failure (Bowman and Woolfenden 2001). The factors that influence this pattern are not yet clear. Hatching failure can be affected by a variety of factors, as discussed in Chapter One; however, some of these hypotheses can be eliminated based upon information about scrub-jay biology and known differences in demographic patterns between suburban and wildland populations.

Close inbreeding rarely occurs in either the suburban or wildland scrub-jay populations (Woolfenden and Fitzpatrick 1984,1996); therefore, inbreeding likely is not responsible for increased hatching failure in the suburbs. Female condition also does not appear to contribute to the observed differences in hatching failure. Females in suburban habitat have *ad libitum* access to human-provided foods. Although qualitative differences in food may exist between the sites, female body condition just prior to

breeding does not differ between the sites, and plasma protein levels of suburban birds are higher than those in the wildlands (Schoech and Bowman 2003).

Egg hatchability also may be influenced by clutch size, presence of helpers or timing of breeding, but the effects of these variables in these populations are not known. Suburban scrub-jays have fewer helpers and tend to breed earlier and continue breeding later than wildland jays (Bowman and Woolfenden 2001). Clutch size also is larger in the suburbs, with a median clutch size of 4 eggs in the suburbs and only 3 eggs in the wildlands (Bowman et al. 1998). Each variable has the potential to contribute to the observed variation in hatching failure between wildland and suburban scrub-jay populations. The objective of this study was to examine basic patterns of hatching failure in a wildland and suburban population of scrub-jays in Highlands County, FL, as well as explore the effects of several variables on observed rates and occurrence of hatching failure.

Methods

Extensive demographic data were available from each population as a result of long-term on-going studies at each site. These data were available in the historical database at Archbold Biological Station maintained by Reed Bowman (suburban) and Glen E. Woolfenden (wildland) and were not extracted from the literature. Although studies began in wildland habitat in 1969, the first year for which complete data were available from the suburban habitat was 1993. Therefore, the years in which concurrent data were available for both sites began in 1993.

Territory-specific data collected between 1993 and 2001 were used to assess the effects of site (suburban vs. wildland), year, incubation initiation date (i.e. timing of

breeding), presence of helpers and clutch size on rates and occurrence of hatching failure. Hatching failure was defined in two ways, partial hatching failure and whole hatching failure. Partial hatching failure (PHF) was defined as an egg(s) surviving the incubation period but subsequently failing to hatch in a clutch where at least one egg hatched successfully. Whole hatching failure (WHF) was defined as all eggs in a clutch surviving the incubation period but subsequently failing to hatch. “Rate” of PHF was defined as the proportion of eggs in a clutch that did not hatch, and “occurrence” of PHF was a binary variable that indicated whether or not a nest experienced PHF.

Data were included for all nests where incubation initiation and hatch dates were known and for nests where incubation initiation dates were unknown, but the hatch date and subsequent hatch success were known. Unknown initiation dates could be determined by counting back 18 days (i.e. the length of the incubation period) from the day the first chick hatched. Data were excluded for nests found after eggs hatched, nests where neither the incubation initiation date nor the hatching date was known, and nests that were depredated or abandoned before hatching.

For an egg to be considered having failed to hatch, it had to have survived incubation and be observed in the nest on or after day two post-hatching. Eggs seen on the hatch date, but missing prior to day two post-hatching may have hatched and then disappeared. Therefore, these were considered partial brood loss rather than hatching failure. I could not be certain whether an egg present on the hatch date but missing by day two had been removed as an egg or as a nestling (dead or alive). This method would tend to underestimate hatching failure and overestimate partial brood loss, but it was a

conservative estimate of hatching failure, and less likely to bias comparisons between sites.

A total of 1726 nests from both sites were examined; 1023 nests from suburban habitat, and 703 nests from wildland habitat. I used individual Mann-Whitney U tests on rates of PHF to examine the relative contributions of the different ecological and social variables listed. Because rates of PHF were not normally distributed and could not be transformed, parametric tests could not be used on rates of PHF. To estimate the relative strength of individual variables used in the rate analysis to explain variation in the occurrence of PHF, I used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) derived from multiple binary logistic regressions. I considered models that included each of the five variables separately, as well as models with all variable combinations, for a total of 29 models. Models with a ΔAIC_i of less than 10 were reported, because those greater than 10 have little support that the fitted model is the best model. Those with ΔAIC_i values between two and seven have some support, and those with ΔAIC_i below two have strong support (Burnham and Anderson 2002).

Results

WHF did not differ significantly between wildland (0.02) and suburban (0.03) habitats, and it was excluded from further analyses. However, rates of PHF were consistently and significantly higher in suburban habitat, even in clutches of the same size (Figure 2). Clutch size and site were the only variables significant in explaining rates of PHF, and I found no effect of year, timing of breeding or presence of helpers on PHF (Table 1).

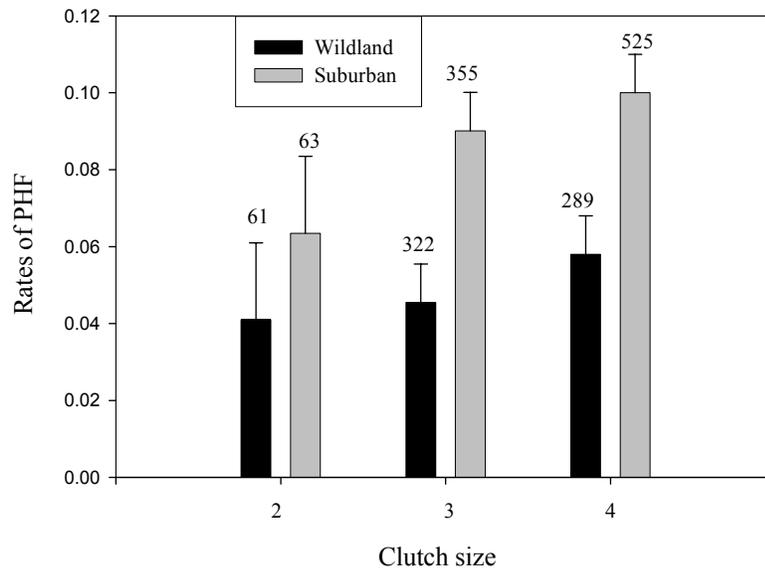


Figure 2. Rates of partial hatching failure (PHF) in a wildland and suburban population of the Florida Scrub-Jay (*Aphelocoma coerulescens*) from 1993-2001. PHF was defined by having an egg(s) survive the incubation period, but subsequently fail to hatch in a nest that produced at least one nestling. The bars represent standard error, and the numbers above the bars indicate sample sizes.

Table 1. Results of Mann Whitney U tests to examine the effects of site, clutch size, presence of helpers, clutch initiation date (i.e. timing of breeding) and year on rates of partial hatching failure in a wildland and suburban population of Florida Scrub-Jays in Highlands County, Florida.

Variable	Z	P
Site	-5.851	0.001
Clutch size	-3.616	0.001
Helpers	-0.122	0.903
Clutch initiation date	-0.745	0.711
Year	-0.376	0.707

Of the 29 models explaining variation in the occurrence of PHF, the model best supported by the data included all five variables (Table 2). The cumulative weight of the individual parameters in the global model suggested that site (0.9978) and clutch size (0.9978) contributed more than year (0.8924), timing of breeding (0.9682) or presence of helpers (0.8843), and this is consistent with the results of rates of PHF. Clutch size and site appear to explain variation in both the rate and occurrence of PHF between suburban and wildland habitats; however, parametric analyses, although invalid because assumptions of normality were violated, showed that no interaction existed between clutch size and site, suggesting that an independent site effect existed other than the known difference in clutch size between the two habitats (Table 3).

Table 2. AIC values generated from multiple binary logistic regressions to test the effects of year (A), site (B), clutch initiation date (i.e. timing of breeding) (C), presence of helpers (D), and clutch size (E) in explaining the occurrence of partial hatching failure in a wildland and suburban population of the Florida Scrub-Jay in Highlands County, FL. Only those models with each individual variable or models with Δ AIC values <10 are included in this table.

Model	-2Log likelihood	AIC _i	Δ (AIC)	w _i
ABCDE	1821.62	1833.62	0.000	0.7870
ABCE	1827.94	1837.94	4.319	0.0908
BCDE	1828.14	1838.14	4.522	0.0821
BDE	1833.54	1841.54	7.917	0.0150
ABE	1833.60	1841.60	7.979	0.0146
BCE	1834.71	1842.71	9.088	0.0083
A	1888.47	1892.48	58.86	1.66×10^{-13}
B	1857.66	1861.66	28.04	8.14×10^{-7}
C	1889.50	1893.50	59.88	9.93×10^{-14}
D	1888.20	1892.20	58.58	1.91×10^{-13}
E	1870.42	1874.42	40.80	1.38×10^{-9}

Table 3. Results of ANOVA for analysis of historical demographic data for the effects of clutch size and site on rates of partial hatching failure.

Source of variance	SS	df	MS	F	p
Model	1.02	9	0.11	4.6	0.001
Site	0.09	1	0.09	3.8	0.053
Clutch size	0.20	4	0.05	2.0	0.092
Site x Clutch size	0.03	4	0.01	0.3	0.884

Discussion

Hatching failure of whole clutches (WHF) did not differ between wildland and suburban habitat. Whole hatching failure was rare in both populations, and although I did not examine WHF specifically, I suspect that its occurrence may be the result of infertility. Inbreeding can lead to infertility (Moseley and Landauer 1949); however, inbreeding is very rare in both populations and isn't likely to differ between the two populations.

Unlike WHF, partial hatching failure (PHF) was higher in suburban habitat. Several potential causes of variation in rates of hatching failure do not seem applicable to these two populations of scrub-jays (see Introduction); however, my analysis of historical data provides insights into the relative strength of other variables in explaining variation in PHF between the suburban and wildland study sites.

Increased population density may lead to increased intraspecific interactions (Koenig 1982). These interactions may decrease the time a female spends incubating, thus decrease egg hatchability. When eggs are not incubated, they are exposed to ambient temperatures, which may deviate from normal incubation temperatures of 35 to 40° C. Prolonged exposure to temperatures outside this optimum range can increase embryo mortality (Lundy 1969; Drent 1975); therefore, hatching failure may increase if females spend long periods away from the nest. In 1993, the population density of scrub-jays in the suburban site was greater than that of the wildland site. Since then, the number of scrub-jay territories in the suburbs has declined by 65%, and density has decreased accordingly. Despite this decrease in density, year was not significant in explaining

variation in PHF. As a result, differences in population density between the sites likely did not contribute to higher PHF in suburban habitat.

Helpers often assist the breeding pair in territory defense, which may allow the female to spend that time incubating and reduce egg neglect. Female scrub-jays with helpers may be able to increase incubation time, consistent with a previous observation that scrub-jay pairs with helpers experience less hatching failure than those without helpers in previous studies on wildland scrub-jays (Woolfenden and Fitzpatrick 1984). Although fewer scrub-jay pairs in suburban habitat have helpers (Bowman 1998), the presence of helpers did not explain variation in PHF between the sites.

Suburban scrub-jays also begin breeding earlier and continue breeding later in the season than their wildland counterparts (Bowman and Woolfenden 2001). Timing of breeding can influence rates of hatching failure at both times during the breeding season, either because food availability is low early in the season or because body condition worsens as the breeding season progresses. Females that lay early may increase the frequency or duration of off-bouts to spend more time foraging because food often is scarce during this time (Perrins 1970; Harneson 1974). These long periods of foraging increase egg neglect, which may increase hatching failure. Conversely, females breeding late in the season may be in poor condition (Hipfner et al. 2004). Although food may not be limiting at this time, females may be in worse condition if they already have expended energy in previous nest attempts that failed. As a result, these females breeding late in the season also may need to spend more time foraging with similar costs to egg hatchability (Hipfner et al. 2004). Although timing of breeding did not explain variation in PHF between the two sites, human-provided food in the suburbs is predictable in both

space and time, leading to much more efficient foraging by suburban jays (Fleischer et al. 2003). During the pre-breeding season, suburban females decreased the amount of time spent foraging, increased the amount of time spent perching and still maintained the same food intake rate as females in wildland habitats (Fleischer et al. 2003). If suburban females are more efficient foragers than wildland females, they may divert the saved time into incubation. Therefore, by foraging on predictable human-provided foods, they might increase their intake rate without incurring the costs of egg neglect.

Clutch sizes tend to be larger in the suburbs (Bowman et al. 1998), and analyses of both rates and occurrence of PHF suggest that clutch size is a major contributor to PHF in the suburbs. Eggs in experimentally enlarged clutches of the European Starling (*Sturnus vulgaris*) lost more water and that egg temperatures were higher and more variable than those clutches that had not been manipulated, presumably because larger clutches cannot be incubated efficiently (Reid et al. 2000). These enlarged clutches were within the starling's natural range of variation. The combination of higher mean egg temperature and increased water loss likely was responsible for the relatively low hatching success observed in larger clutches (66.7% hatched) than in un-enlarged clutches (90.5% hatched). Scrub-jay eggs in wildland habitat lose approximately 12% of their mass during incubation (Woolfenden and Fitzpatrick 1996), well within the range of normal water loss for passerines (Rahn and Ar 1974). I did not measure the rate of mass loss of suburban eggs or how mass loss varies with clutch size; however, the potential effects of ambient and nest temperatures on PHF are addressed in Chapter Three.

Increased hatching failure with clutch size also may indicate that females are unable to produce an entire clutch of high-quality, viable eggs (Potti and Merino 1996).

In many species, egg size declines in the laying sequence; first-laid eggs are largest and last-laid eggs are smallest. Small, last-laid eggs may not have sufficient reserves to complete development. They also may be more vulnerable to fluctuations in temperature during off-bouts because of their small size (Potti and Merino 1996). Egg size declines with laying order in wildland birds, but not when they are provided with supplemental food (Reynolds et al. 2003). I did not examine patterns of egg-size variation with laying order, but the data of Reynolds et al (2003) suggested that last-laid eggs in the suburbs should be neither smaller nor more vulnerable to hatching failure.

In contrast, first-laid eggs may be increasingly vulnerable to hatching failure in large clutches, especially in species that do not begin incubation until the penultimate or ultimate egg, such as the scrub-jay. The viability of eggs declines with exposure to ambient conditions prior to incubation (Arnold et al. 1987; Arnold 1993), and exposure of first-laid eggs to ambient conditions has been linked to increased hatching failure (Veiga 1992; Stoleson and Beissinger 1999). In larger clutches, first-laid eggs are vulnerable to ambient conditions for even longer periods of time prior to incubation, which may decrease further viability and increase the potential for hatching failure. Clutches in the suburbs tend to be larger than clutches in wildlands (Bowman et al. 1998), and extra exposure to ambient conditions may increase the potential for PHF at this site. Furthermore, ambient temperatures may be warmer in the suburbs, because suburban areas often serve as heat islands (Oke 1987; Dixon and Mote 2003). This temperature difference may have an additive effect to the apparent effect of clutch size, and I explore this possibility in Chapter Three.

In addition to clutch size, site also was a major and independent variable explaining variation in both rates and occurrence of PHF. Several factors may be associated with site differences, including ambient temperature and predation risk. As stated above, the suburban site may serve as a heat island, which occurs when human structures absorb heat and reduce airflow in human-dominated landscapes (Dixon and Mote 2003), causing suburban areas to be warmer on average than nearby rural sites. Nest temperatures are affected by a combination of ambient conditions and patterns of female incubation behavior (Wilson and Verbeek 1995). Because female passerines often take off-bouts to forage, relatively high ambient temperatures in suburban areas may increase nest temperatures while females are off the nest. Because embryos are sensitive to overheating (Lundy 1969; Drent 1975), higher ambient temperatures in suburban areas may result in higher nest temperatures and increased hatching failure.

Additionally, a female's incubation behavior may be affected by her perception of predation risk. As discussed above, females may reduce activity at the nest when the perceived risk of predation is high (Conway and Martin 2000), and they also may perceive human disturbance as increased predation risk (Frid and Dill 2002). In the suburbs, incubating females may be exposed to many types of human disturbance, thus suburban females may perceive a higher risk of predation in response to human activity. If females in the suburbs change their behavior in response to human activity, long off-bouts may leave eggs exposed to ambient conditions for extended periods of time. If females change their behavior and ambient temperatures between the sites are different, these factors may interact to increase hatching failure in the suburbs. Ambient and nest temperatures and incubation behavior at either site previously were unknown, thus I

designed an experiment to assess their effects on hatching failure. The potential effects of these variables will be addressed in Chapter Three.

In conclusion, rates and occurrence of PHF were higher in suburban scrub-jays than in wildland scrub-jays. Clutch size and habitat have significant, but independent effects on differences in the rates and occurrence of PHF between suburban and wildland habitat. Clutches tend to be larger in the suburbs, and PHF may increase in large clutches if they are not incubated efficiently or if first-laid eggs are exposed to ambient conditions for longer periods of time prior to incubation. The next aspect of this research was to evaluate whether ambient temperature and predation risk, two potential site differences, influence variation in PHF.

Chapter Three

Influence of Ambient and Nest Temperature and Perceived Predation Risk on PHF

Variation in PHF between suburban and wildland sites was explained, in part, by differences in clutch size and an independent site effect. Clutch size tends to be larger in suburban than in wildland habitats (Bowman et al. 1998), but PHF is higher in suburban habitat even when controlling for clutch size. Several ecological differences exist between the suburban and wildland sites that could lead to variation in hatching failure, including differences in the number of helpers or timing of breeding; however, my historical analyses suggested that these differences were not associated with variation in PHF. Only differences in clutch size and site were associated with both rates and occurrence of PHF. Ambient temperature and the structure and composition of the predator community differ between suburban and wildland sites and both have the potential to affect PHF. These variables could not be addressed in the analysis of historical data. Therefore, this portion of my research explored potential differences in ambient and nest temperatures. It also tested the prediction, based on the work of Conway and Martin (2000) and Frid and Dill (2002) that incubation behavior changes as a result of real or perceived predation risk.

Decreased natural land cover, increased pavement and an abundance of structures that create and absorb heat can lead to an increase in ambient temperatures in suburban and urban areas (Oke 1987; Dixon and Mote 2003). Nest temperatures are influenced by ambient temperature (Wilson and Verbeek 1995), and nest temperatures have an effect on

developing embryos. Prolonged exposure to temperatures above the upper critical temperature ($> 40^{\circ}\text{C}$, UCT) can lead to embryo death (Lundy 1969). If suburban habitat is warmer and nests are warmer, the potential for embryo death, or hatching failure, may be higher in suburban areas. This potential might increase if nests are exposed to ambient temperatures for longer periods in the suburbs. This might occur if birds alter their incubation behavior because they perceive the risk of predation to be higher in suburban habitats.

Predation causes fewer nest failures during incubation in the suburban site than in the wildland site (Bowman and Woolfenden 2001). Therefore, according to Martin's hypotheses (see Chapter One), wildland jays should decrease the frequency and increase the duration of their off-bouts, thereby decreasing their risk of predation but increasing their rates of hatching failure; however, hatching failure rates are higher in suburban habitat. Although the real risk of predation may not be higher in suburban habitat, it is possible that human activity in the suburbs alters the jays' perception of predation risk.

Human activity affects the behavior of birds both directly and indirectly (Frid and Dill 2002). European Oystercatchers (*Haematopus ostralegus*) spent less time incubating eggs when disturbed by humans (Verhulst et al. 2001), and many Charadriiformes (Class Aves) left their nests when disturbed by humans, exposing eggs to extremely warm ambient conditions and potential embryo death (Grant 1982). Human activity also may alter a bird's perception of predation risk. Predation risk is the probability that a predation event will be successful, and organisms use a variety of cues to assess how this probability changes over time or space (Frid and Dill 2002). Organisms should tend to overestimate predation risk, rather than underestimate it, because the consequences of

underestimating predation risk are far greater than overestimating it. Human activity is a poor indicator of real predation risk in scrub-jays, because humans rarely depredate nests or kill adult scrub-jays intentionally; however, activity may be misconstrued by the scrub-jays as an indication of increased predation risk if it resembles a cue that they formerly used to assess this risk. If scrub-jays perceive a greater risk of predation in the suburbs, they may alter their incubation behavior to minimize nest activity; however, in the absence of a real threat of predation, this behavior only may increase the potential for hatching failure without the benefit of decreased predation. In this sense, altering incubation behavior as a response to human disturbance may be maladaptive in suburban habitats.

Differences in both perceived predation risk and ambient temperatures between the suburban and wildland population might lead to the observed differences in hatching failure. If ambient temperatures in the suburbs are at or above the upper critical temperature more often than wildlands, and suburban females are off the nests for longer periods of time to decrease nest activity, embryo death may increase as a result. These losses may be an additive effect to the apparent effect of clutch size found in Chapter Two.

In Chapter Three, I examined variation in nest microclimate and parental behavior during incubation relative to habitat and human disturbance to determine whether differences in these variables are consistent with increased hatching failure in suburban habitat. I predicted that ambient temperatures would be higher in suburban habitat, and as a result, nest microclimate would be more variable (i.e. higher mean and greater range of temperatures) both in suburban habitat and where human activity is increased. I also

predicted that females would take fewer, longer off-bouts and males would have lower rates of incubation feedings in suburban habitat and when human activity is increased.

Methods

Study site. Fieldwork was conducted in both suburban and wildland sites (see Chapter Two). Nests in both habitats were located and monitored between February and June 2003 and 2004, and experiments were conducted during that time frame. The fate of all nests found was known as a result of on-going long-term demographic studies in both sites.

Treatments. Within the suburban habitat, nests were assigned to one of two treatments, normal visitation (“control suburban”) or increased visitation (“experimental suburban”) to determine if human activity during this stage could alter incubation behavior. Within the wildland population, nests were assigned only to normal visitation (“wildland”). Normal visitation consisted of one visit during laying, one at clutch completion and one visit at mid-incubation (day nine). Nests in the increased visitation treatment were visited on the same schedule; however, visits were added twice daily (1000-1200 and again 1300-1600) three consecutive days before evaluation of nest microclimate or incubation behavior beginning on day seven post-clutch completion. Because early incubation is considered a critical period of development for some avian eggs (Deeming 1991), alterations in female behavior during this time may be more likely to affect hatching failure. Consequently, increased visitation occurred during early incubation (days four, five and six). Earlier days were not chosen because the final clutch completion visit was made on the day a fifth egg, if one existed, would be laid. Because incubation begins with the ultimate or penultimate egg and depending on the

actual clutch size, this clutch completion visit could occur on the first, second or third day of incubation.

Temperature. Thermocouples were placed in 13 control suburban, 15 experimental suburban and 14 wildland nests in 2003; and 10 control suburban, 15 experimental suburban and 19 wildland nests in 2004 for a total of 23 control suburban, 30 experimental suburban and 33 wildland nests.

On day seven post-clutch completion, a thermocouple (HOBO H8 Pro Series) with two probes capable of measuring ambient and nest temperature simultaneously was placed in nests in both wildland and suburban habitats. This provided measurements of temperature every 12 seconds for 24 hours. The thermocouple unit and wires were colored with paint to resemble vegetation prior to placement to minimize detection and disturbance to the jays. One probe was placed in the lining of the nest by weaving it through the twigs at the bottom of the nest and positioning it horizontally through the lining as close to the eggs as possible without being visible or palpable to the female jay (usually <5mm). The second probe, which measured ambient temperature, was placed in the nest tree below the nest in an area that was shaded and camouflaged with vegetation when possible. All wires were clamped with twist or zip ties to branches to minimize the chance of the probe falling out of or being removed from the nest. This also helped disguise the wires. Placement and removal of the thermocouple occurred between 1000 and 1400, and the probe was left in the nest for 24 hours. Cameras were placed at some nests with thermocouples, but equipment was limited, thus not all nests that had thermocouples also had cameras.

Incubation behavior. Cameras were placed at a total of four control suburban, five experimental suburban and five wildland nests in 2003; and six control suburban, seven experimental suburban and eight wildland nests in 2004, for a total sample size of 10 control suburban, 12 experimental suburban and 13 wildland nests.

On day seven post-clutch completion, as with the thermocouples, a time-lapse remote video camera (Fuhrman Diversified Fieldcam or Sandpiper Technologies Basic Sentinel System) was placed near the nest to measure parental activity at the nest. These activities included the timing and duration of on and off bouts by the female and incubation feedings by the male. The small camera was attached to a retractable arm in a camouflaged sleeve and mounted in a shrub within 0.5 to 2 m of the nest. The video recording device was placed in a waterproof and dustproof Pelican case and concealed 10 to 15 m from the nest (on the ground) to prevent theft, vandalism or damage by wildlife. All other equipment, including the battery and wire case, also was camouflaged with vegetation. The camera recorded in monochrome images during both day and night; it was able to record some female activity at night via infrared lighting when the camera could be placed within 0.5 to 1 m of the nest. The camera was placed at the nest between 1000 and 1400 and was left in place for a 24-hour period. Each camera was placed at a nest with a thermocouple.

From the videotapes, I began recording behavior approximately 15 minutes after the tape began to ensure that the female had resumed her normal activities following the disturbance from placing the camera. All off-bouts were recorded in minutes, and feedings were recorded as the number of feedings per daylight hours. In addition, I noted any unusual or unexpected activity. A female was considered “on” the nest when she

was settled on the eggs or shading them. She was considered “off” the nest when she was on the rim of the nest and clearly not attempting to incubate or shade the eggs or off the nest and out of sight. The duration of “off time” began when her feet touched the rim of the nest. She was considered back “on” the nest when she settled back onto the eggs or was clearly attempting to shade them (i.e. holding out wings, panting). I considered an incubation feeding any time the male arrived at the nest with food and offered it to the female. If I could not see the exchange, I considered it a feeding if I observed the female swallowing after the male departed. If the male simply arrived at the nest and departed without feeding the female, I did not consider it a feeding.

Statistical analyses. The thermocouples recorded temperature continuously over a 24 h period. From those data I was able to calculate the maximum, minimum and mean ambient and nest temperatures. When temperature data were not normally distributed (minimum and maximum temperatures), they were log-transformed. To test for differences in temperatures between sites and treatment, I used ANOVA. Because many temperature variables were correlated, I ran a Principal Components Analysis (PCA) to extract the significant factors. I used binary logistic regression to examine the effects of temperature and behavior on observed occurrences of PHF during the field seasons. I also used ANOVA to test for differences in behavior between treatments, but I did not test for behavioral differences between sites. I had only one treatment in wildland habitat because of limited sample sizes. Therefore, including site in the ANOVA was inappropriate because the sites were not treated identically. Maximum duration of off-bouts were not normally distributed; therefore, they were log-transformed. I repeated measurement for 11 breeding females between the two years; however, analyses

excluding these females did not differ qualitatively from analyses in which they were included. Therefore, I did not exclude these females from the analyses.

Results

Temperature. Ambient temperatures differed significantly with treatment and year. Mean ambient temperatures were higher in both control and experimental suburban treatments than in the wildland treatment, largely because minimum temperatures were approximately 5° C higher in the suburbs (Table 4), (Figure 3). Maximum temperatures did not differ between treatments or years. The range in ambient temperatures was greater in the wildland treatment (24.31°C) than either the control (18.67°C) or experimental suburban (18.85°C) treatments because minimum temperatures were lower in wildlands (Table 4). Nest and ambient temperatures were highly correlated (Pearson, $p=0.001$); therefore, nest temperatures followed similar trends, but no temperature variables explained variation in PHF during the study period (Table 5).

Temperature variables were highly correlated, and thus a PCA was run to extract significant factors. Factor one was associated with minimum and mean ambient and nest temperatures and explained 67.3% of the variance in temperature data. Factor two was associated with maximum ambient and nest temperatures and explained 21.8% of the variance. Together, they explained 89.1% of the variance; however, neither Factor 1 ($p=0.199$) nor Factor 2 ($p=0.825$) was significant in explaining the occurrence of PHF during 2003 and 2004.

Table 4. Results of ANOVA examining differences in ambient temperatures between treatments. Log transformation was used on maximum temperature.

Variable	df	F	p
Minimum ambient	5	8.8	0.001
Treatment	2	9.3	0.001
Year	1	19.4	0.001
Treatment x Year	2	0.5	0.58
Maximum ambient	5	1.2	0.30
Treatment	2	0.1	0.96
Year	1	0.2	0.64
Treatment x Year	2	2.8	0.07
Mean ambient	5	6.3	0.001
Treatment	2	8.9	0.001
Year	1	10.3	0.002
Treatment x Year	2	1.2	0.32
Range ambient	5	10.3	0.001
Treatment	2	8.1	0.001
Year	1	20.7	0.001
Treatment x Year	2	3.3	0.04

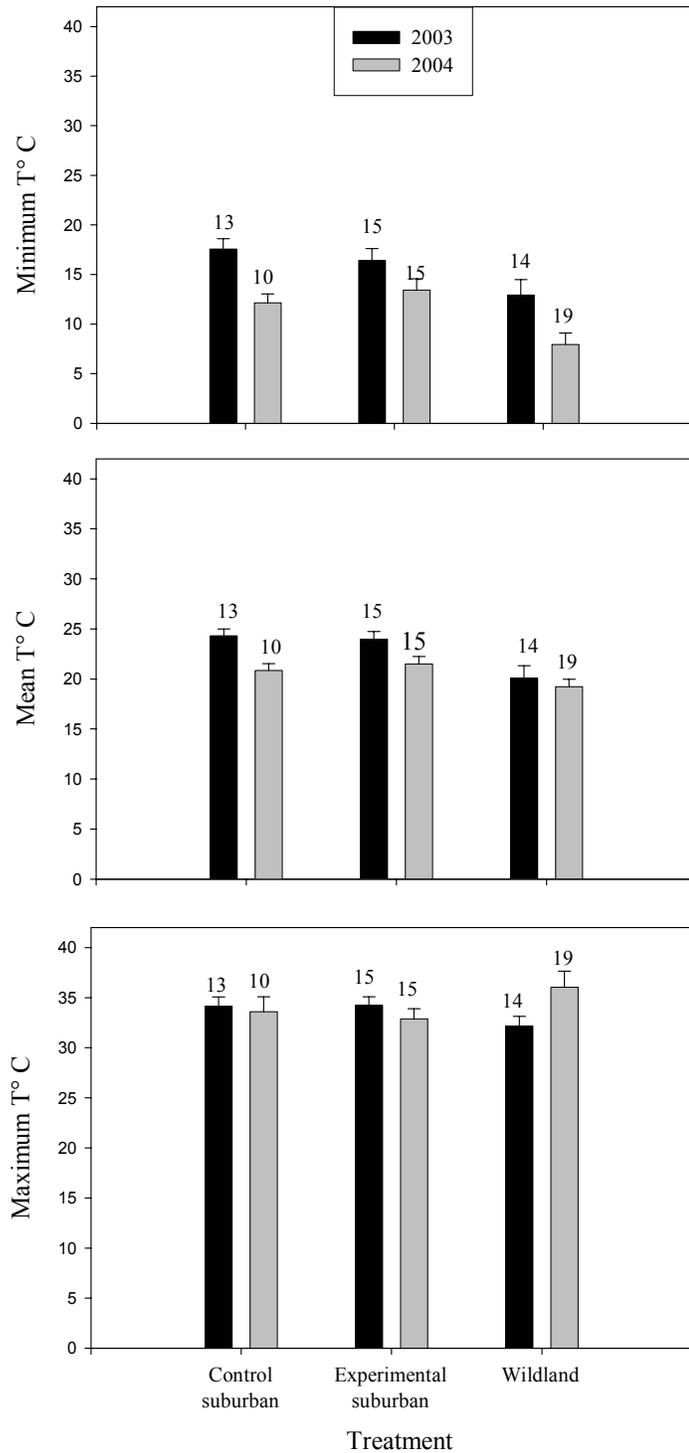


Figure 3. Minimum, mean and maximum ambient temperatures at control suburban, experimental suburban and wildland treatments in 2003 (black) and 2004 (grey). Bars represent standard error, and numbers above the bars represent sample sizes.

Table 5. Results of binary logistic regression examining the effects of incubation behavior and ambient temperatures on the occurrence of hatching failure.

Variable	df	R ²	p
Frequency off-bouts	1	0.16	0.06
Minimum duration off-bouts	1	0.16	0.79
Maximum duration off-bouts	1	0.16	0.66
Mean duration off-bouts	1	0.16	0.94
Proportion 24-hrs off nest	1	0.16	0.83
Frequency incubation feedings	1	0.16	0.11
Minimum ambient	1	0.02	0.21
Maximum ambient	1	0.001	0.74
Mean ambient	1	0.03	0.15

Incubation behavior. Three incidents of nest predation were recorded during the study period. In 2003, in the suburbs, a gray fox (*Urocyon cinereoargenteus*) successfully depredated a nest of three eggs. The female left the nest seconds before the fox became visible and made no attempts at nest defense. In the wildlands, also in 2003, a Swallow-tailed Kite (*Elanoides forficatus*) attempted to depredate a nest but was driven off by the defending male jay; the female never appeared to leave the nest. In 2004, I observed a scrub-jay depredate a nest in the wildland habitat. The female left the nest, and moments later an unidentified scrub-jay appeared at the nest and attempted to remove an egg. The female returned to the nest and defended it against the intruder, but she was not successful. The intruder removed and ate two eggs within meters of the nest and within sight of the camera. I was not able to determine the identity of the intruding scrub-jay, because the band combinations were not clear on the videotape.

Incubating females always remained on the nest during the night, except when disturbed by a potential predator as noted above. Increased human activity significantly decreased the frequency of off-bouts, but an interaction existed between treatment and year (Table 6), (Figure 4). The interaction existed because of year differences in control suburban and wildland females. In 2003, control suburban females took more off-bouts than wildland females, but in 2004, wildland females took more off-bouts than control suburban females. In both years, experimental suburban females took significantly fewer off-bouts than either control suburban or wildland females (Duncan's post-hoc test). Mean duration of off-bouts did not differ by treatment, but year was significant (Table 6), because in both the experimental suburban and wildland treatments,

Table 6. Results of ANOVA examining differences in frequency and duration of off-bouts, proportion of time spent away from the nest and feeding rates between control suburban, experimental suburban and wildland treatments. Log transformation was used for maximum off-bouts.

Variable	df	F	p
Frequency off-bouts	5	3.7	0.01
Treatment	2	3.9	0.03
Year	1	0.1	0.74
Treatment x Year	2	5.4	0.01
Min duration off-bouts	5	2.6	0.04
Treatment	2	0.1	0.88
Year	1	1.6	0.22
Treatment x Year	2	4.8	0.02
Max duration off-bouts	5	2.0	0.11
Treatment	2	2.2	0.13
Year	1	2.7	0.11
Treatment x Year	2	1.7	0.20
Mean duration off-bouts	5	3.1	0.02
Treatment	2	0.8	0.47
Year	1	7.8	0.01
Treatment x Year	2	2.8	0.08
Proportion time off nest in 24-hrs	5	2.9	0.03
Treatment	2	3.6	0.04
Year	1	4.9	0.04
Treatment x Year	2	1.6	0.21
Frequency incubation feedings	5	1.0	0.43
Treatment	2	1.6	0.22
Year	1	0.3	0.57
Treatment x Year	2	0.7	0.50

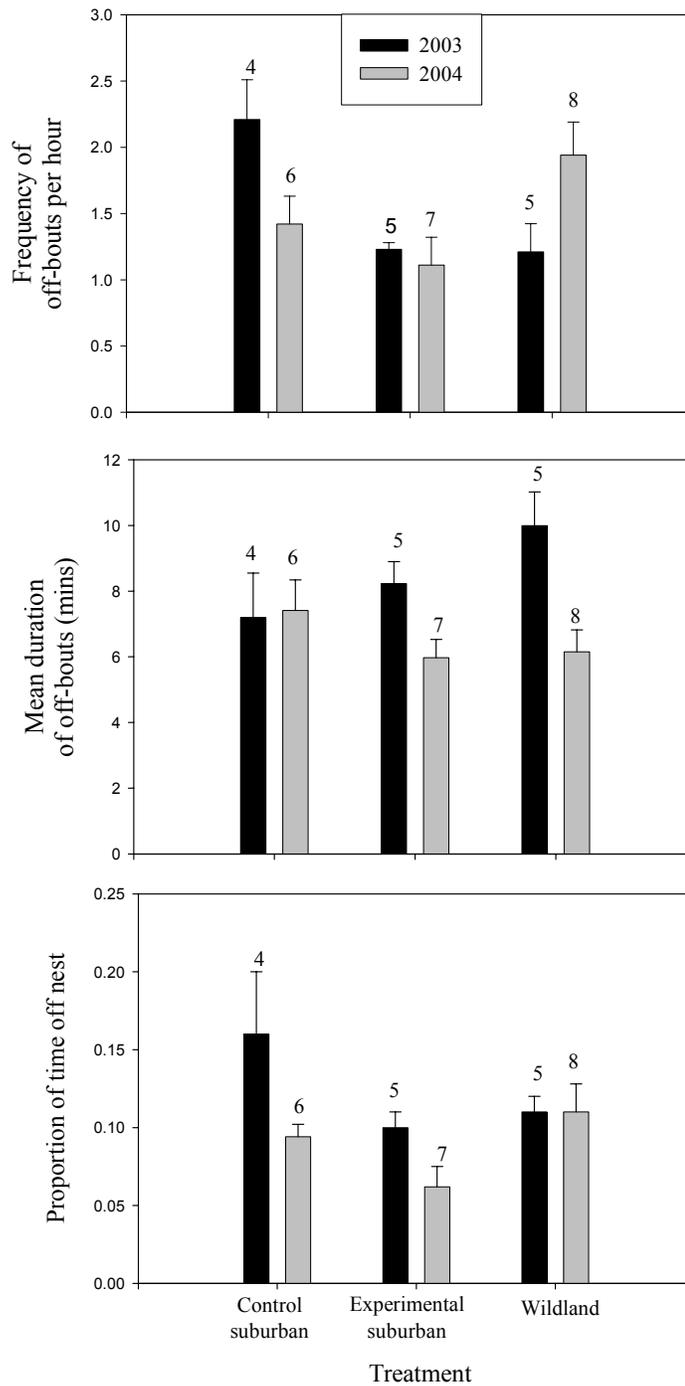


Figure 4. Frequency of off-bouts, mean duration of off-bouts and proportion of time off nest in 24-hours in control suburban, experimental suburban and wildland females in 2003 (black) and 2004 (grey). Bars represent standard error, and numbers above the bar indicate sample size.

the duration of off-bouts tended to be longer in 2004 than in 2003. Because the frequency of off-bouts differed with treatment, but the duration of those off-bouts did not differ, the proportion of time that females spent off the nest in a 24-hour period also differed significantly with treatment and year (Table 6). Experimental suburban females spent a smaller proportion of their time off their nests than females in any other treatment, but this difference was significant only between experimental and control suburban females (Duncan's post hoc test).

The minimum duration of off-bouts was not significantly different between treatments or year, but an interaction existed between treatment and year (Table 6), (Figure 5). Again, this interaction existed as a result of year differences in control suburban and wildland females. In 2003, the minimum duration of off-bouts was much greater in wildland females than those of control suburban females, but in 2004, minimum duration of off-bouts was greater in control suburban than wildland females. Maximum duration of off-bouts did not differ between control suburban, experimental suburban or wildland females or between years (Figure 5).

Although at experimental nests females took fewer off-bouts and were off their nests for a shorter proportion of the day, they did not experience less hatching failure than females in other treatments. Rates of hatching failure were highest in control (0.1270) and experimental suburban (0.0996) treatments and lowest in the wildland treatment (0.0537). Only the frequency of off-bouts was marginally significant in explaining the occurrence of PHF during 2003 to 2004 study period (Table 5).

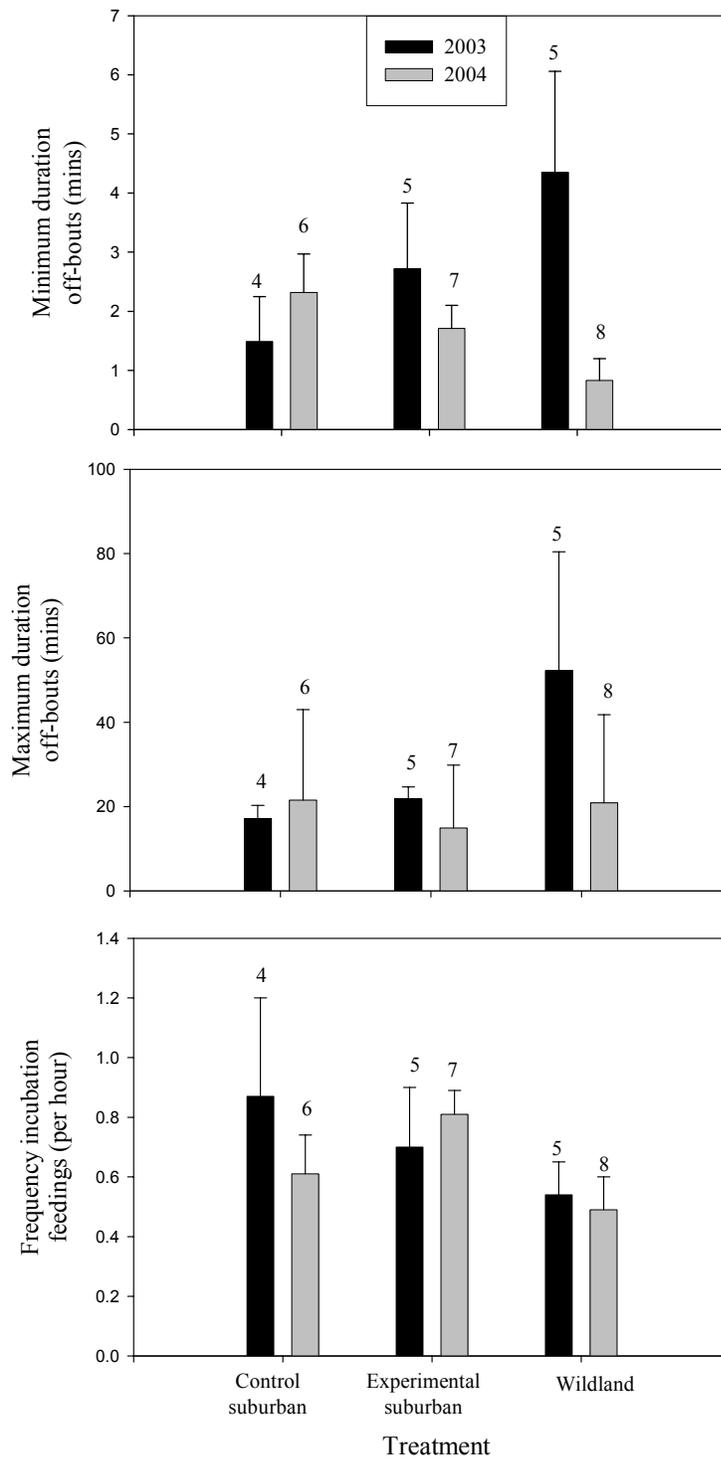


Figure 5. Minimum duration off-bouts, maximum duration off-bouts and frequency of male incubation feedings in control suburban, experimental suburban and wildland treatments in 2003 (black) and 2004 (grey). Bars represent standard error, and numbers above bars represent sample sizes.

Experimental suburban males tended to have slightly higher rates of incubation feedings than control suburban or wildland males, but these differences were not significant (Figure 5). Feeding rates were correlated negatively with mean duration of off-bouts (Pearson $p=0.011$), but they were not correlated with any other female behavior. No differences existed among incubation feeding rates between years (Table 6), and feeding rates were not significant in explaining occurrence of PHF during the study period (Table 5).

Discussion

The data supported the hypothesis that a difference in ambient and nest temperatures would exist between the sites; however, the difference was not in the expected direction. Although a difference in mean ambient temperature existed between the sites, the differences resulted from higher minimum temperatures in the suburbs rather than higher maximums. The differences in minimum temperatures between the sites occurred at night when all females had 100% attendance. As a result, minimum temperatures likely had little effect on PHF. Although maximum ambient temperatures did not differ between the sites, they still may influence PHF if females left their eggs exposed to those conditions for long periods of time; however, the length off-bouts did not differ between suburban and wildland sites. Therefore, I was unable to detect any apparent interactions between incubation behavior and ambient temperatures that would increase rates of PHF in the suburbs.

Female scrub-jays exposed to increased human activity near their nests consistently took fewer off-bouts, but they did not increase the length of these bouts as expected. As a result, they increased their overall nest attentiveness when exposed to

extra visitation. This finding is in contrast to those of Conway and Martin (2000), who noted that increased risk of nest predation led female passerines to decrease the frequency and increase the duration of their off-bouts to minimize nest activity, but it did not change overall proportion of nest attendance. In part, this finding might be explained by the scrub-jays' access to predictable human-provided food sources and their perception of humans as potential predators.

The strategy employed by females in the experimental suburban treatment, short, infrequent off-bouts, may seem like an ideal strategy to minimize predation and maximize time on the nest; however, this strategy often places severe constraints on incubation behavior in most habitats (Conway and Martin 2000). Females must balance their needs with those of the developing embryos, and short off-bouts may not leave females enough time to satisfy their own nutritional requirements. Therefore, if females take fewer off-bouts, they often must increase the length of these bouts to devote more time to foraging (Conway and Martin 2000). This strategy minimizes the risk of predation, but incurs the cost of egg neglect; however, in the suburbs, where human-provided food is predictable both in space and time, scrub-jays may be able to forage very efficiently (Fleischer et al. 2003), meeting their own nutritional needs in less time. As a result, females exposed to increased human disturbance may decrease the frequency of their off-bouts without changing their duration and still meet their nutritional needs.

Nest attentiveness also may be influenced by the way in which suburban jays view humans as predators. If a female can deter potential predators without risking her own survival, she benefits from maximizing her time at the nest (Conway and Martin 2000). High nest attentiveness often is associated with lower predation risk (Conway and

Martin 2000), and some species commonly use physical intimidation to deter potential predators (Thompson and Raveling 1987). Scrub-jays give chase to mockingbirds and blue-jays, both of which are potential nest predators but unlikely predators on adults (Woolfenden and Fitzpatrick 1996). Their behavior suggests that scrub-jays will defend their nest if they do not risk their own survival in doing so. This idea is consistent with my videotape of a gray fox depredating a jay nest; the female left and did not physically defend the nest at all. In contrast, when another scrub-jay depredated a nest, the female defended it vigorously. Additionally, suburban females generally tend to remain on the nest to defend the contents during our scheduled nest visits, although most wildland females leave the nest during these visits (pers. observation). In many comparisons, the behavior of control suburban females was more similar to wildland than to the experimental suburban females. This similarity in behavior suggests that suburban scrub-jays may habituate to normal human activity and view humans as a threat only when their activity increases near a nest. Furthermore, if adults remain on the nest or chase only potential nest predators they believe they can deter, but escape from predators that might kill them as well, the behavior of suburban females during visits suggests that they perceive increased activity as a threat to the nest contents, but not to themselves. As a result, experimental females may have increased nest attentiveness to deter potential human predators, but without increasing their own risk of predation.

Female nest attentiveness also can be affected by the behavior of her mate. Incubation feedings by the male may provide an important nutritional benefit to the incubating female (Smith et al. 1989), and a positive correlation often exists between nest attentiveness and rate of incubation feedings (Halupka 1994; Martin and Ghalambour

1999); however, incubation feedings may decrease in areas of high predation risk. Feeding rates were correlated negatively with nest predation in several hole- and open-nesting species in Arizona and Montana (Martin and Ghalambour 1999), and rates also decreased in two species of nuthatches after exposure to a common egg predator (Ghalambour and Martin 2000). By decreasing feeding rates, males may decrease nest activity, and thus decrease predation risk (Conway and Martin 2000). Contrary to expectation, feeding rates were similar for males in all treatments. Therefore, increased human activity did not appear to decrease feeding rates. Males may not have changed their rates of feeding if they did not perceive a higher risk of predation relative to increased human activity. Moreover, feeding rates were not correlated with nest attentiveness in this study, and as a result, male behavior likely has little consequence on egg temperatures and PHF in suburban habitat.

If ambient conditions differ only as a result of minimum temperatures, which occur at a time when all females are incubating, and females exposed to increased human activity do not leave their eggs exposed to ambient conditions for long periods of time, then temperature and behavior during incubation likely do not interact to increase PHF in the suburbs. Although temperature differences did not affect PHF during incubation, they may have an important influence on egg hatchability prior to the onset of incubation. The pre-incubation stage was not addressed in this study, but it may be the next logical step in examining trends in PHF between the populations.

The egg viability hypothesis states that hatching success can be maximized if parents begin incubation prior to clutch completion, because the viability of eggs declines over time (Arnold et al. 1987; Arnold 1993). Embryo development can occur prior to

incubation if ambient temperatures are above physiological zero (PZT), and this can cause unsynchronized tissue growth and eventual embryo death (Lundy 1969). Egg viability declines more slowly at low ambient temperatures, and eggs may tolerate warm daily temperatures as long as temperatures become cool again overnight (Arnold 1993).

Scrub-jays begin incubation with the penultimate or ultimate egg; therefore, their first-laid eggs are exposed to ambient temperatures for longer periods of time prior to incubation than other eggs in the clutch. Eggs exposed to ambient conditions for three or more days prior to incubation in the Green-rumped Parrotlet (*Forpus passerinus*) (Stoleson and Beissinger 1999), and for two days in the House Sparrow (*Passer domesticus*) (Veiga 1992) experienced lower hatching success than eggs exposed for shorter periods of time. Suburban clutches tend to contain four eggs. Therefore, these eggs are exposed to ambient conditions for an average of three days prior to incubation; however, clutches in wildland habitat normally contain only three eggs (Bowman et al. 1998). Therefore, eggs in the wildlands are exposed for only two days prior to incubation. An extra day of exposure to temperatures above PZT in the suburbs may increase PHF at this site, and the combination of larger clutch size and different ambient temperatures between sites could explain the effects of both clutch size and site found in Chapter Two.

In conclusion, differences in ambient temperatures between the sites were related to higher minimum temperatures rather than higher maximums in suburban habitat. Differences in minimum temperature likely do not increase PHF, and because duration of off-bouts did not differ, ambient temperatures had no effect on PHF. Additionally, females exposed to increased human activity took fewer but not longer off-bouts, thus

they spent more time on their nests than females in other treatments. Male behavior did not differ between treatments. If temperature differences occurred only when females were incubating, and females exposed to extra human activity did not increase time away from the nest, then temperature and behavior during incubation likely did not interact to increase PHF in the suburbs; however, the observed temperature differences could affect egg viability during the pre-incubation period, and an extra day of exposure to temperatures above PZT in the suburbs could increase PHF at this site.

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