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EFFECT OF PREDATION RISK AND FOOD AVAILABILITY ON PARENTAL CARE AND
NEST SURVIVAL IN SUBURBAN AND WILDLAND FLORIDA SCRUB-JAYS

by

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B.S. University of Michigan, 2005

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
at the University of Central Florida
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ABSTRACT

Individual organisms often use cues from their natural environments to determine many behavioral and life-history “decisions.” These “decisions” are usually adaptive, i.e. a response to selection, because the environmental cues on which they are based reliably correlate with increased fitness over time. When the selected behavioral response to a natural cue no longer provides a fitness benefit, then selection for a new response may occur but individuals maintaining the previously selected response may suffer reduced survival and reproduction. Especially in human-modified landscapes individuals making a maladaptive behavioral or life-history choice based on those formerly reliable environmental cues may be faced with an “evolutionary trap”.

In urban, or suburban, environments many factors have been altered in ways that could lead to evolutionary traps. Inappropriate behavioral responses by many individuals could lead to reduced demographic performance of urban populations relative to their wildland counterparts and to the decline of entire urban populations. In birds, maladaptive patterns of nest provisioning or vigilance may occur (a) when human-provided adult foods are easier to feed young because they are more abundant and predictable than foods appropriate for nestlings, or (b) when birds’ perception of predation risk, which can be influenced by human disturbance, is greater than the real risk. By provisioning or attending their nests more or less than what is appropriate given the environmental level of resources and risks, the behavior of suburban parents may be contributing to high levels of nest failure during the nesting stage.

To determine whether maladaptive parental care influences nest survival during the nestling stage, I conducted an experiment using Florida Scrub-Jays (*Aphelocoma coerluscens*).

Suburban scrub-jays have lower nest survival during the nestling stage but higher survival during the incubation stage relative to wildland jays. Both predators and food abundance vary greatly between suburban and wildland scrub. The suburbs have a greater abundance of predators that may prey on both adult scrub-jays and their nests and more foods appropriate for adults but less nestling-appropriate food. This variation in risks and resources should affect the parental care behavior of suburban scrub-jays, which in turn may affect patterns of nest survival. In pre-treatment observations, I found that suburban females spent more time brooding than wildland birds but suburban males did not provision any more than wildland males. Experimentally increasing the perception of adult predation risk reduced parental care in both suburban and wildland females. Increasing the availability of nestling food reduced parental care in suburban females but had no effect in wildland females. Increasing food availability, but not predation risk, decreased call rates but increased call frequency in nestling scrub-jays from both habitats. However, neither parental care nor food availability had much influence on nest survival during the nestling stage. Instead, side nest concealment and the presence of helpers were the most important variables in nest survival analyses prompting other explanations besides maladaptive parental behavior or lack of nestling food resources for the habitat-specific difference in nest survival during the nestling stage.

I dedicate this thesis to my father, John Dexter Niederhauser (1944 - 2011), who passed away suddenly this past winter. He was the best father a son could ever hope for, providing love, support and encouragement every step throughout my life. He helped me through many rough spots I encountered in both school and work, and I always could come to him for advice no matter the subject. He was my most avid supporter in pursuing a graduate degree and always was eager to hear about my adventures in ecological field work. He himself earned a Master's degree in public health but did not do any scientific research like his father, my grandfather, did in the field of chemistry. He really did want to follow in his father's footsteps but never had the ambition or knack to pursue that line of work. He had enormous pride in me that I chose a career in science, and that pride is what continues to motivate me in my academic career even after he has passed. I wish that he was still here so that he could see my finished thesis, but I know that he would be swollen with pride to see this great accomplishment.

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INTRODUCTION

Individual organisms often use cues from their natural environments to determine many behavioral and life-history “decisions.” These decisions may include what to eat, and how much time to invest in foraging, whether to be vigilant, when and where to reproduce, when to hibernate or migrate, and so on. These decisions are adaptive because the environmental cues on which they are based reliably correlate with survival and/or reproductive success over evolutionary time (Williams and Nichols 1984). When the selected behavioral response to a natural cue no longer provides a fitness benefit, then selection for a new response may occur, but individuals maintaining the previously selected response may suffer reduced survival and reproduction.

Behavioral miscues are inappropriate responses to given levels or abundances of natural cues and are often caused by anthropogenic disturbances or changes to an environment. Another term for these miscues is “evolutionary traps,” defined as “in an environment that has been altered suddenly by human activities, an organism makes a maladaptive behavioral or life-history choice based on formerly reliable environmental cues, despite the availability of higher quality options” (Schlaepfer et al. 2002). Evolutionary traps encompass a wide assortment of maladaptive behaviors and have many factors that cause them, but these traps can arise in two general ways.

Evolutionary traps can arise when the environment changes the cues or creates conditions that mimic the cue even when the environmental conditions do not warrant it (Schlaepfer et al. 2002). In highly modified environments, the same cues may exist and they may elicit the same behavioral response; however, in this novel environment that response no longer produces an

adaptive outcome. For example, birds may nest in high densities in man-made forest edges. The structural cues created by these edges are the same as those found in naturally occurring forest edges, but nest success is lower in the man-made edges because of higher predation, brood parasitism and density effects (Gates and Gysel 1978). Another example of this type of trap is the effect of global warming on breeding behavior in Great Tits (*Parus major*). These birds have had reduced nest success and nestling survival because spring temperatures are getting warmer over the past decades and the peak emergence of insect larvae occurs earlier, but the start of egg laying has not changed possibly because they are cueing in on something other than temperature and food availability (Visser et al. 1998, Buse et al. 1999).

Evolutionary traps also can occur when conditions in an altered environment produce novel cues similar to natural cues, but requiring a different behavior response. The formerly adaptive response to the natural cue can be maladaptive in response to the novel cue. For example, sea turtles ingest floating plastic objects because their clear appearance is similar to that of jellyfish, one of their usual prey items, but ingestion of these plastic objects can cause impaction of their intestines and possibly death for those turtles (Fritts 1982, Bjorndal et al. 1994). Though the factors that cause evolutionary traps are numerous, their adaptive consequences may be few and deleterious. In most circumstances the result of these traps could be mortality or reproductive failure.

In urban or suburban environments many factors have been altered in ways that could lead to evolutionary traps. Inappropriate behavioral responses by many individuals could lead to reduced demographic performance of urban populations relative to their wildland counterparts and to the decline of entire urban populations. Roads and other forms of development may create

edge effects leading to evolutionary traps or they may create novel cues that mimic natural cues, such as the cues that lead mayflies to inappropriately lay eggs on asphalt (Kriska et al. 1998). Anthropogenic pollution may cause miscues as well. Light pollution may alter individual perception of photoperiod by individuals resulting in a mismatch between peak resource availability and the timing of breeding (Kempnaers et al. 2010). Noise pollution may alter how and when individuals vocalize, altering the dynamics of mate attraction and mating success (Slabbekoorn and Ripmeester 2007). Bird feeders and garbage containers are abundant within urban and suburban areas and provide an *ad libitum* source of food for a variety of urban organisms (Baker and Harris 2007, Chamberlain et al. 2005). Such a plentiful and predictable food source could cause mismatches between the perceived abundance of food and the abundance of natural foods that are essential during critical periods of life history, such as during nestling development. In addition, these point-source foods could result in altered perceptions of predation because predators may aggregate around these feeders or refuse bins (Prange et al. 2004). Human disturbance in general may cause heightened perceptions of risk (Frid and Dill 2002). A response to a perceived increase in predation risk, such as increasing vigilance at the cost of foraging, when no increase in risk really exists, is a classic example of an evolutionary trap.

The federally Threatened Florida Scrub-Jay is a relatively long-lived species in which nest survival may be vulnerable to behavioral miscues caused by anthropogenic changes in the abundance of food and/or predators in suburban habitats. Overall nest survival does not differ between suburban and wildland scrub-jays, but in the suburbs survival is higher during the egg stage and lower during the nestling stage (Bowman and Woolfenden 2001). In suburban habitats,

adult foods are abundant from human-provided feeders, but lepidopteran larvae, the food appropriate for nestlings, is much scarcer than in wildland habitats (Shawkey et al. 2004). Predator composition differs between suburban areas, with fewer snakes and more felines, canines and native mesopredators (Peifer et al. In Prep). In addition, in our study areas, humans are active in the habitats in which scrub-jays breed, thus the potential for human disturbance is high (pers obs.). In addition, the fire regime is lengthened in suburban habitats, where fire is routinely suppressed. Reduction in fire intervals affects the structure of scrub vegetation (Reinhart and Menges 2004) which has important demographic effects on Florida Scrub-Jays (Breininger et al. 2006). Potentially as a result of changes in habitat structure, the side concealment of nests is lower in the suburbs than the wildlands (Walton 1997) which may have an interactive effect with provisioning rates on nest success. Either the lack of foods appropriate for nestlings, the different communities of real or perceived predators, or the lack of concealment for nests could contribute to the lower nest survival during the nestling stage in suburban habitats. The goal of this study was to determine whether the perception of nestling food abundance and adult predator abundance affected parental care, and whether this, in turn, had a direct effect on variation in nest survival during the nestling stage in Florida Scrub-Jays in wildland and suburban habitats.

CHAPTER ONE: VARIATION IN PARENTAL CARE AND FOOD AVAILABILITY DOES NOT AFFECT DIFFERENCES IN NEST SURVIVAL DURING THE NESTLING STAGE BETWEEN SUBURBAN AND WILDLAND FLORIDA SCRUB-JAYS¹

Abstract

Human modification of habitats can reduce reproductive success by creating “evolutionary traps” that mimic natural cues and cause maladaptive behaviors. Differences in food and predator abundance in urban areas can cause miscues that could potentially lead to a reduction in parental care and reproductive success. By manipulating an adult’s perception of predation risk and the availability of nestling foods in urban and wildland areas, we were able to test whether these factors influenced parental care, nestling begging and nest survival during the nestling stage. Experimentally increasing the perception of adult predation risk reduced parental care in both suburban and wildland females. Increasing the availability of nestling food reduced parental care in suburban females but had no effect in wildland females. Increasing food availability, but not predation risk, decreased call rates but increased call frequency in nestling scrub-jays from both habitats. However, neither parental care nor food availability had much influence on nest survival during the nestling stage. Instead, side nest concealment and the presence of helpers were the most important variables in nest survival analyses prompting other

¹ This chapter will be submitted as a co-authored manuscript. I will be the primary author and I will include Reed Bowman as a co-author.

explanations besides maladaptive parental behavior or lack of nestling food resources for the habitat-specific difference in nestling stage nest survival.

Introduction

Parental care is any parental behavior that increases reproductive success (Clutton-Brock 1991). Parental care behaviors range from setting up territories and building nests to provisioning and being vigilant for offspring. These behaviors may vary with the abundance of food and predators perceived among breeding habitats. If food is limited, parents may make more provisioning trips in order to provide sufficient food for their young to survive. Abundant predators may significantly influence parental care by reducing provisioning trips when the risk of predation is high (Martin et al. 2000a, b; Eggers et al. 2008). However, the response to predation may vary depending on relative resource abundance. If food is abundant, parents might be able to reduce provisioning rates, without reducing parental care by increasing the size of the food loads delivered to nestlings (Martin et al. 2000a); however, if food is limiting, the decision to invest in vigilance or parental care might depend on an individual's prospects of future reproduction, either at another site or in a subsequent year. If those prospects are high, birds may be willing to incur reduction in reproductive success to increase the probability of future nest attempts.

In birds, reducing parental care has potential consequences, both direct and indirect. Obviously, reduced parental care means fewer resources for the growing young. However, frequent or long departures from the nest during the nestling stage can increase the risk of failure from starvation or dehydration (Markman et al. 1995). Less food brought to the nest or infrequent provisioning trips may increase the begging calls of the nestlings (Leonard and Horn

1996, 1998, 2001), which may lead to increases in nest predation (Haskell 1994, Briskie et al. 1999, Dearborn 1999). By reducing parental care through fewer visitations or less time spent at the nest, breeding birds may be increasing the risk of nest failure. This is only an adaptive response if the benefits to the adult in reduced predation risk outweigh the costs of reduced fecundity through increased nest failure.

Human modification of natural landscapes has the potential to drastically affect reproductive success by altering parental behaviors. Anthropogenic changes can disrupt behavioral strategies by providing cues similar to ones that normally correlate with survival and reproductive success, but that have different behavior responses. The once appropriate response now does not provide a fitness advantage, and is thus a maladaptive response. These behavioral miscues are termed “evolutionary traps” (Schlaepfer et al. 2002). Human-modified areas are known to vary in food (Blair and Launer 1997, Denys and Schmidt 1998) and predator (Haskell 2001) abundance, and these factors may cause miscues and maladaptively alter investment in parental care.

Differences in predator abundance between urban and wildland habitats may affect parental care by altering the parents’ perception of predation risk. A perception of high predation risk in suburban areas may be caused by real risks, such as domestic cats (Crooks and Soulé 1999, Woods et al. 2003), or perceived risks, such as human activity around nests (Frid and Dill 2002). Predators of both nests and adults vary along an urbanization gradient (Haskell et al. 2001), and in general, mesopredators and domestic animals are more abundant in suburban habitats. Relatively long-lived species that prioritize survival over seasonal fecundity may reduce provisioning trips in order to reduce adult mortality when the perception of predation is high.

When the predation risk to adults is real, such behavioral trade-offs may reduce current reproduction but increase the probability of surviving to a future time when reproduction is more favorable or the predation risk has decreased. If no real threat exists, but the perception of risk is high, then altering provisioning becomes maladaptive because the cost of reduced parental care is incurred without an offsetting increase in survival.

Differences in the abundance and types of food may also cause maladaptive behaviors. Suburban habitats have abundant human-provided food but less natural food (e.g. arthropods; McIntyre 2000) than wildlands. If parents in human-modified habitats perceive higher amounts of adult food, and thus perceive the habitat as high quality, they may defend smaller territories exacerbating the problem of reduced nestling food availability. Human-provided foods are suitable for adults, but may not be appropriate for nestlings because these foods are plant-based and young may have different nutritional needs or digestive capabilities. These foods may not provide the essential nutrients required by nestlings causing them to be in poorer condition and beg more which in turn may increase the provisioning rate of parents and attract more predators. Thus, suburban habitats provide the classic conditions for an evolutionary trap in that scrub-jays may perceive an increased risk of predation, but is not real because of human disturbance, and a food-rich environment, but is not real because not enough nestling-appropriate food exists in the suburbs, so reducing provisioning trips and increasing food payloads will not have the adaptive effect of maintaining or increasing nest success. The ultimate consequence of these maladaptive behaviors may be reduced nest survival due to both starvation and predation in the suburbs.

The Florida Scrub-Jay (*Aphelocoma coerulescens*; hereafter “scrub-jay”) is a relatively long-lived, xeric oak specialist that resides in both wildland and suburban areas that differ in

abundances of food and predators. Scrub-jays do not appear to disperse between suburban and wildland habitats because these birds have short natal dispersal distances (Woolfenden and Fitzpatrick 1984, Fitzpatrick et al. 1999, Coulon et al. 2010), so scrub-jays have existed in suburban habitats as those environments have been modified. Typically, suburban areas are not optimal habitat for scrub-jays because they have fewer dense scrub-oaks to use as nesting sites (Bowman and Woolfenden 2002) and a lower abundance of animal food (e.g. arthropods) than in the wildland areas (Shawkey et al. 2004). However, human-provided supplemental food from feeders and refuse is abundant in the suburbs. This difference in food abundance is important because although human-provided foods are appropriate and even high-quality foods for adults, nestling scrub-jays in the wildlands are fed exclusively animal foods, primarily small arthropods (Stallcup and Woolfenden 1978), most likely because of their rapid digestibility and their high protein and water content (Sauter et al. 2006). Although suburban nestlings are fed mostly arthropods and vertebrates, 15-30 percent of their diet consists of plant-based human provided foods (Sauter 2005). Additionally, scrub-jay territory sizes in the suburbs are smaller than in the wildlands (Bowman 1998) which may further limit the amount of food available to feed nestlings.

Both adult and nest predators are known to vary across urbanization gradients and this is true in suburban and wildland scrub habitats. Bird adult predators such as Cooper's Hawks (*Accipiter cooperii*) (Stout and Rosenfield 2010) and nest predators such as American Crows (*Corvus brachyrhynchos*) (McGowan 2001) as well as mammalian predators such as domestic cats (*Felis domesticus*) and raccoons (*Procyon lotor*) (Prange and Gehrt 2004) are more abundant or in higher densities in suburban than rural areas. Predator abundance has been inferred in a

comparative study between suburban and wildland scrub; the suburbs have greater abundances of domestic cats and canines (Canidae family), but fewer snakes (Peiffer et al., In prep). Fish Crows (*Corvus ossifragus*), Blue Jays (*Cyanocitta cristata*) and Common Grackles (*Quiscalus quiscalus*) are common in the suburban scrub and could be potential nest predators (Bowman and Woolfenden 2001). Cooper's Hawks appear to be common (pers. obs.) and could be a primary adult predator in the suburbs. Differences in food and predator abundance between the habitats make scrub-jays good models to investigate whether predation, food limitation, or nest-site concealment directly affects nest survival during the nestling stage or whether variation in these resources leads to maladaptive parental care resulting in a habitat-specific difference in nest failure during the nestling stage.

Despite the ecological differences that exist between suburban and wildland habitats, the overall success of scrub-jay nests does not differ between the habitats. However, nest failure rates are lower during incubation stage and higher during the nestling stage in the suburbs than the wildlands (Bowman and Woolfenden 2001). To determine the relative importance of maladaptive parental care, food limitation and nest concealment on the difference in nest failure rates during the nestling stage between suburban and wildland populations of Florida Scrub-Jays, we tested three novel hypotheses: the predation risk, food availability and nest site hypotheses.

The predation risk hypothesis states that suburban scrub-jays may invest less time in parental care because the perception of predation risk to adults is higher in the suburbs. Conway and Martin (2000) showed that females that perceived high predation risk reduced the frequency, but increased the length of incubation on and off bouts. In Pied Flycatchers (*Fidecula hypoleuca*), parental care was more strongly influenced by the presence of adult predators than

the presence of a nest predator (Dale et al. 1996). Also, in House Wrens (*Troglodytes aedon*) suburban birds spent less time brooding than rural birds and may bring fewer or smaller food items, possibly because they perceive an elevated risk of predation on adults (Newhouse et al. 2008). The predation risk hypothesis predicts that increasing the perceived predation risk to adults in both habitats should decrease parental care by decreasing the number of trips to a nest (Table 1; Martin et al. 2000a, b, Fontaine and Martin 2006); however in the wildlands, where food appropriate for nestlings is not limiting, birds should respond to the increased risk of predation by increasing the amount of food delivered to the nest per provisioning trip. Because suburban habitat is food limited, we predicted that suburban scrub-jays will spend more time brooding, but bring less food in fewer provisioning trips than wildland scrub-jays. As a result of reduced provisioning, suburban nestlings may be in poorer condition and may beg more (greater power, frequency, and call rate) (Leonard and Horn 2001), relative to wildland nestlings. Increased begging, in turn, may lead to higher rates of predation (Briskie et al. 1999).

The food availability hypothesis states that scrub-jays in suburban habitats have a lower abundance of foods appropriate for feeding nestlings, which could increase nest failure during the nestling stage directly through starvation or indirectly through increased predation because of increased begging. If lepidopteran larvae are supplemented to groups in suburban areas, then provisioning rates should decrease and the amount of food delivered to the nest should increase (Table 1). Because food is limiting in suburban habitat, suburban controls should make more provisioning trips, deliver less food per trip and the nestlings should be in poorer condition than wildland groups. If food-deprived nestlings beg more (Leonard and Horn 2001) and nestlings

that beg more are more likely to be preyed upon (Briskie et al. 1999), then food supplementation should lead to fewer begging calls which should increase nest success (Table 1).

The nest site hypothesis suggests that the shrubs in suburban areas are less suitable for concealing the activity of group members around nests with nestlings and consequently, more nests will fail. Previous work by Walton (1997) found that suburban scrub-jays nests have less side, but equal top concealment than wildland nests. Top cover may decrease exposure to the sun or aerial nest predators and may increase success during the egg stage, but less side cover could allow nest predators to see when group members make provisioning trips. Better side nest concealment may allow parents to make more visits without visually attracting more predators to the nest (Eggers et al. 2008). Concealment has been shown to affect nest success in some species of birds (Martin and Roper 1988, Nalwanga et al. 2004), but few studies examined whether adults vary their parental care based on the concealment of their nest. We predicted that suburban nests should be less concealed on the side than wildland nests, and nests with high provisioning rates that have less side concealment will fail more often than more concealed nests with high provisioning rates. However, parental care may depend on nest site selection, so adults may make fewer provisioning trips to nests that have poor side nest concealment.

The three hypotheses are not mutually exclusive and a combination of any or all three hypotheses could contribute to the habitat-specific differences in nestling stage nest survival. However, nestling begging may respond differently among the treatments allowing us to differentiate between the hypotheses (Table 1). To study the habitat-specific causes of nest failure in the nestling stage, we conducted an experiment in both suburban and wildland populations of scrub-jays. To determine the relative importance of maladaptive parental care in

predation risk, food abundance and nest sites on nest failure, we manipulated food availability and the perception of predation risk in both suburban and wildland groups and analyzed nest survival during this stage using behavioral and habitat variables.

Methods

Study Organism and Study Sites

Scrub-jays are relatively long-lived, cooperatively breeding birds that form family groups consisting of a monogamous breeding pair and up to six non-breeding helpers (Woolfenden and Fitzpatrick 1996). Scrub-jays defend permanent, year-round territories and are dependent on fire-maintained xeric-oak scrub habitat. Florida Scrub-Jays are federally listed as Threatened due to huge declines in their numbers over the past few decades (Stith et al. 1996), mostly due to the widespread conversion and fire-suppression of xeric-oak scrub habitat (Peroni and Abrahamson 1985).

We compared parental care behaviors and nestling stage nest survival rates of scrub-jay populations in two suburban sites and one wildland site near Lake Placid, Highlands County, Florida. The two suburban sites, Placid Lake Estates (27°15'N, 81°25'W) and Leisure Lakes (27°21'N, 81°27'W), are 1500 ha residential housing subdivisions containing fragmented patches of overgrown, fire suppressed oak scrub habitat with limited to no management of these areas. The wildland site, Archbold Biological Station, is a 2000 ha natural preserve that is maintained with controlled burns to keep the scrub optimal for scrub-jays and other species endemic to Florida scrub habitats. Placid Lakes and Leisure Lakes are separated by only 5 km and the distance between Placid Lakes and Archbold is 8 km. Two suburban sites were necessary

because scrub-jay populations have declined at both sites, reducing the number of breeding pairs necessary for adequate sample sizes. Among the measured variables (proportion of time brooding, number of on/off-bouts, provisioning rate, total food delivered food per provisioning trip, nestling begging call power, call frequency and call rate), nestling begging call rate was the only variable that was significantly different between Placid Lake Estates and Leisure Lakes ($F = 11.643$, $df = 1$, $p = 0.003$), thus I pooled them into one suburban category.

Nest Monitoring

As part of an existing long-term study, nest success was monitored in all three sites for all groups where nests are found (95 percent are found prior to laying) with nest checks done every 3-4 days. A nest was considered to have been successful if at least one nestling survives to the day of fledging, 18 days post-hatch, and was found alive outside of the nest after that day. The nest was considered to have failed if all nestlings are missing (depredated) or all the nestlings are dead but still in the nest (starved). Partial brood loss (brood reduction) also was noted when monitoring nests. Nest monitoring was used in all parts of our study including the habitat comparisons, the predation risk and food availability experiment, and the analysis of nest survival during the nestling stage.

Experimental Design

We conducted the predation risk and food availability experiment in the 2009 breeding season, and repeated the experiment in the 2010 breeding season, with the goal to determine if the perception of adult predation risk, the availability of nestling-appropriate foods, or both affected the parental care of breeding scrub-jays. Our experimental design (Tables 1 and 2)

included food supplementation and predation risk treatments set up in a factorial design to increase the perception of predation risk, increase the availability of nestling foods, or both. Both manipulations were carried out on the fourth and fifth day post-hatch during the nestling stage on the days between nest watches (see below). Predation risk treatments (P) consisted of one of two randomly rotated predator models (owl or robotic domestic cat) covered by a camouflaged cloth presented to a group of scrub-jays at a maximum of 10m from the nest. Any one nest was exposed to both models (owl and cat) on sequential days if the nest was assigned to the predator treatment. We presented the model to the groups by removing the cloth and exposed the group to the predator model until the scrub-jays reacted to the model before removing it from the area. The predation risk controls (PRC) were presented with the camouflaged cloth only. The cloth was necessary to remove the possibility that our presence would affect the group's reaction to the model.

The food supplementation treatment groups (S) were provided with 30g of waxworms placed on a feeder. Supplementation controls (SC) were given one peanut broken up into pieces on a feeder to control for the effect of feeding (Sauter 2005). Feeders were placed no closer than 20 m from a nest, and they were put out on the same day as the first nest watch (see below) and retrieved after the second nest watch was completed. To ensure that the feeder was being used, we placed a few peanuts on it and waited until at least one member of the breeding pair landed on the feeder to retrieve a peanut. In most cases when we put either the waxworms or peanuts out on treatments days at least one if not both of the breeders were waiting by the feeder. We had only a single pair that was reluctant to visit the feeder that we resolved by giving the broken up peanut (unsupplemented control) on the ground. We used a randomized list generator to select

the order in which treatments (supplementation or the predation risk treatment) were assigned to territories. We paired those treatments into four groups: 1) predation risk control, supplementation control (PC/SC); 2) predation risk, supplementation control (P/SC); 3) predation risk control, supplementation (PC/S); and 4) predation risk, supplementation (P/S). Groups from each habitat were randomly assigned into one of those treatment groups. All groups were independent of one another, and only two groups were used in both 2009 and 2010. Neither of those groups had post-treatment observations in 2009, so they were included only once in the analysis of the predation risk and food availability experiment.

Parental Behavior Observations

To collect data on parental behavior, we conducted 1-hr nest observations. The observations were carried out during peak morning feeding times between 30 minutes to 3 hours after sunrise (Stallcup and Woolfenden 1978) twice during the nestling stage. The first observation, 3-5 days post-hatch, was a true, unmanipulated control that was used for habitat comparisons and to ensure that treatment groups did not differ before treatments were applied. The second observation was after the supplementation and/or predation risk treatments had been applied, 6-8 days post-hatch, and was used to determine if the treatments had any effect on the behavioral variables collected. Data from these observations were the main source of data in the factorial analyses. Before we collected observational data, we noted the group size and brood size to account for the presence of helpers and the number of nestlings, which may affect the total number of provisioning trips to nest (Hatchwell 1999). During nest observations, we used a 10x50 pair of binoculars to observe the nest from at least 10m and noted the instantaneous behavior of the breeding females and males at the beginning of each minute of the hour

observation similar to the method used by Rensel et al. (2010). We noted when the female got on or off the nest in order to calculate the proportion of time spent brooding and the frequency of on and off-bouts, and we noted when the breeding male made a provisioning trip and how much food was delivered. We determined the amount of food delivered by ranking bolus sizes (1= unidentifiable foods or small insects, 2= intermediate food items, and 3= large prey like anoles or orthopterans; Stallcup and Woolfenden 1978). We did not use female provisioning trips in our data analysis because females provision very little during the first few days after young have hatched and instead brood heavily because nestlings are naked and cannot thermoregulate. We totaled the proportion of time spent at the nest brooding and how many on and off-bouts were made by the breeding female, and we tallied the number of provisioning trips and the amount of food delivered by the breeding male for the hour watches each divided by the number of nestlings to account for varying brood sizes. Parental behavior observations were used in all parts of our study including the habitat comparisons, the predation risk and food availability experiment, and the analysis of nest survival during the nestling stage.

Nestling Begging and Nestling Condition

During nest watches we recorded nestling begging calls. We attached lapel microphones to the nest shrub approximately 15 cm away from the nestlings similar to the method used in Briskie et al. (1999) and used a Marantz PMD-660 to digitally record the calls. Before recording, we allowed the birds to adjust to the presence of the microphone, and we did not start recording until nestling calls were heard through the microphone or provisioning trips recommenced. After recording the calls, we used RAVEN interactive sound analysis software (Cornell Lab of Ornithology) to determine the power, frequency and rate of the begging calls. Call power was

calculated as the power of calls minus the average power of the ambient noise because ambient noise can affect begging loudness (Leonard and Horn 2005). Call rate was calculated as the number of calls in the hour recording divided by the number of nestlings because brood size may affect the rate of nestling begging (Leonard et al. 2000). Call power, frequency and rate were only calculated when at least one provisioning trip was made. After the begging calls had been recorded, call powers, frequencies, and rates were averaged for each nest watch. Nestling begging call characteristics were used in all parts of our study including the habitat comparisons, the predation risk and food availability experiment, and the analysis of nest survival during the nestling stage.

Nestling condition was determined by weighing the young on the eleventh day post-hatch (Day 11 mass). We used the average mass and mass range for each nest. Nestling condition data were used in only the habitat comparisons.

Nest Concealment

After a nest successfully fledged young or failed, we measured the nest shrub to determine how nest concealment interacts with parental activity to affect nest fate. We measured the nest concealment using the same methods from Walton (1997). The percentage of side concealment was estimated using a density board bearing a grid of 25 10cm-by-10cm squares arranged in 5 rows and 5 columns. The board was centered over the nest from 0.5m from the edge of the nest shrub and viewed from 3 m away in each of the four cardinal directions. We estimated the proportion (0%, 25%, 50%, 75%, and 100%) of each square that was blocked by the vegetation. We totaled the percentage values from each block and averaged the percentages of the four directions for minimum, maximum and average side concealment. Nest concealment

data were used in the habitat comparisons and in the analysis of nest survival during the nestling stage.

Statistical Analysis

We adjusted the provisioning rates for varying brood sizes by calculating the rate as provisioning trips per hour per nestling. The amount of food delivered was calculated as both the total food delivered per nestling and the food delivered per provisioning trip per nestling. Proportional data, like the proportion of time at the nest by females, were arc sin transformed, and variables that were non-normally distributed were log-transformed. The frequency of on- and off-bouts, proportion of time spent at the nest, provisioning rate, food delivered, and nestling begging calls (power, frequency and rate) were compared between habitats in the first observations (unmanipulated control). Both the female parental care variables (proportion of time at the nest and frequency of on- and off-bouts) and male parental care variables (provisioning rate, total food delivered and food per provisioning trip) were highly correlated, so two principle components were developed that represented female (PC1) and male parental care (PC2) and explained 60 and 65 percent, respectively, of the variation within each set of those variables. Female parental care (PC1), male parental care (PC2), and the nestling begging calls (power, frequency and rate) were compared between habitats in the second observations (treatments). Some nests failed before the second watch was completed; those nests were used only in the habitat comparisons.

We used three-way factorial ANCOVAs based on post-treatment data to assess the effects of habitat, food supplementation, predation risk, presence of helpers (covariate) and interactions between those factors on female brooding behavior, male provisioning, and nestling

begging. Because the treatment groups did not differ in their pre-treatment behaviors within both habitats, it was not necessary to use the difference (delta) between pre- and post-observations, so only post-treatment observations were used in all analyses. We used a linear regression to examine the relationships between begging calls and brooding behavior, provisioning rates and the amount of food delivered.

Also, we compared provisioning and begging to nestling condition to understand how condition related to those factors. We used linear regressions to relate provisioning rates, food delivered and the begging call variables to the mean and range of masses at each nest on day 11.

We modeled nest survival during the nestling stage as a function of parental care (proportion of time at the nest (Pan), number of on-/off-bouts (NB), provisioning rate (PR) and food delivered (FPT)), nestling begging (call power (CP), frequency (CF) and rate (LCR)) and nest concealment (average side concealment (Conc)) using both a multiple binary logistic regression and Program MARK (White and Burnham 1999; www.phidot.org/software/mark). All of the assumptions from Dinsmore et al. (2002) and Dinsmore and Dinsmore (2007) were met to run the nest survival analyses in MARK. Our 19 models were developed based on the main, additive and interactive effects of our variables based on the three hypotheses tested. Suburbs and wildlands were formatted as two groups and the variable representing the difference (Sg) was included in all of the models. Also, the effect of year (Yr) and the presence of helpers (Hlp) were included in models as potential covariates. We used the maximum log-likelihood estimate from these models to determine which provided a better explanation of variation in the nest survival data using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). Models with $\Delta AICc$ values less than two have the most support, models with values between two

and seven have partial support, and values greater than 10 have no support and were excluded. Site was included in most models except the null model and models with individual variables because the point of this study was to understand differences within the suburban and wildland habitats. All analyses were done in either R, version 2.7.2 (www.r-project.org), or in MARK.

Results

Habitat Comparisons (Pre-Treatment)

Parental care behaviors of male and females were observed during the control observations that occurred prior to treatment at 47 nests over the 2009 and 2010 breeding seasons; 24 nests in the suburbs and 23 nests in the wildlands. Suburban females spent more time brooding ($F = 5.069$, $df = 1$, $p = 0.029$; Fig. 1A), but with marginally fewer bouts ($F = 3.874$, $df = 1$, $p = 0.055$; Fig. 1B) than wildland females. Suburban males provisioned at the same rate as wildland males but brought fewer food items per trip. We found a marginally significant interaction between year and site for male provisioning rates ($F = 3.213$, $df = 1$, $p = 0.080$); despite provisioning rates that were not significantly different between suburban and wildland sites in 2009 or 2010. For both years, food delivered per provisioning trip was lower ($F = 4.693$, $df = 1$, $p = 0.036$; Fig. 2), and nestling masses were marginally lighter in the suburbs than the wildlands ($F = 3.035$, $df = 1$, $p = 0.091$). Overall, female parental care (PC1) tended to be higher in the suburbs than the wildlands ($F = 3.355$, $df = 1$, $p = 0.074$), but male parental care (PC2) did not differ between habitats.

Out of the 47 nests observed during our pre-treatment control observations, we recorded nestling begging calls in 45 nests, 23 suburban and 22 wildland, where at least one provisioning

trip took place. None of the nestling call characteristics (power, frequency and rate) differed between the habitats, but call rates differed between the suburban sites. Suburban nestlings from Leisure Lakes begged significantly more than Placid Lake Estates ($F = 11.643$, $df = 1$, $p = 0.003$) and wildland nestlings, but Placid Lakes did not differ from the wildlands. Under both the predation risk and food availability hypotheses, nestlings should make fewer, softer calls with greater provisioning rates and more food brought to the nest, but provisioning rates by the breeding male did not correlate with call power, frequency or rate in either habitat. The relationship between call power and food delivered per provisioning trip marginally differed by site. In the wildlands call power tended to be positively related to food delivered per trip ($R^2 = 0.151$, $p = 0.083$, $n = 21$), but in the suburbs no relationship existed. The only other relationship between parental care behavior and a nestling call characteristic was the correlation between proportion of time brooding and call power. Although call power for all nests was negatively related with time spent brooding ($R^2 = 0.088$, $p = 0.051$, $n = 44$), the relationship was significant only in the suburbs ($R^2 = 0.185$, $p = 0.041$, $n = 23$) and not in the wildlands ($R^2 = 0.031$, $p = 0.443$, $n = 21$).

Of the 47 nests monitored in 2009 and 2010, nestling condition (Day 11 mass) was collected for 36 nests. Mean Day 11 masses for suburban nests were marginally lighter and mass ranges were marginally greater than wildland nests (Mean: $F = 3.035$, $df = 1$, $p = 0.091$; Range: $F = 3.051$, $df = 1$, $p = 0.090$). Although call power did not differ by site, it tended to vary positively with mass range ($R^2 = 0.097$, $p = 0.082$, $n = 32$).

Nest concealment was measured in all 47 nests monitored from 2009 to 2010. All side nest concealment variables (minimum, maximum and average) were strongly correlated with one

another, so average side concealment was the only variable used in analyses. Average side nest concealment did not differ between suburban and wildland nests. Parental care behaviors were marginally related to nest concealment but in the opposite direction than what we predicted. Both the frequency of bouts by females and male provisioning rates tended to decrease with increasing side concealment (Bout frequency: $R^2 = 0.063$, $p = 0.088$, $n = 47$); Prov. rate: $R^2 = 0.080$, $p = 0.054$, $n = 47$), but no interaction existed between habitat and concealment on the frequency of bouts or provisioning rates.

Predation Risk and Food Availability Experiment (Post-Treatment)

A total of 42 nests were used in the experimental manipulations of adult predation risk perception and nestling food availability over the 2009 and 2010 breeding seasons (Table 2). We attempted to collect six replicates (two in 2009 and four in 2010) of the experiment in each treatment group for both habitats, but due to a poor season in 2009, we did not get all of the sample sizes to get at least two replicates in 2009 and four replicates in 2010. 2010 was a better year than 2009, so we were able to collect nearly all four replicates in each of the treatment groups for both the suburbs and the wildlands. The sole exception for that year was in the wildland Supplementation group that had only three replicates instead of four.

Both suburban and wildland females decreased their parental care ($F = 8.274$, $df = 1$, $p = 0.007$; Table 3, Fig. 3) when the perception of predation risk was increased but only when supplemental food was not provided. Suburban females tended to decrease parental care with increasing food availability ($F = 2.941$, $df = 1$, $p = 0.096$; Table 3, Fig. 3) but only when predation risk perception was not increased; increasing food availability had no effect on

wildland females. Neither suburban nor wildland males changed their parental care when only predation risk or food availability was increased.

Increasing food availability influenced nestling begging by increasing the frequency (pitch) ($F = 5.384$, $df = 1$, $p = 0.027$; Table 5, Fig. 4) and reducing the rate of calls ($F = 5.300$, $df = 1$, $p = 0.028$; Table 6, Fig. 5) for both suburban and wildland nestlings with no differences in nestling behavior between the habitats. Marginal interactions between predation risk and supplementation occurred for both call frequency (Site x Predation Risk x Supplementation: $F = 3.665$, $df = 1$, $p = 0.065$) and rate (Predation Risk x Supplementation: $F = 3.496$, $df = 1$, $p = 0.070$). Call power (loudness) was significantly reduced in presence of helpers ($F = 5.707$, $df = 1$, $p = 0.023$) but was not affected by the predation risk or food availability treatments in either habitat.

Nest Survival during the Nestling Stage

Of the 47 nests with nestlings monitored in 2009 and 2010, significantly fewer nests survived ($F = 4.010$, $df = 1$, $p = 0.051$) and daily survival rates were lower in the suburbs (0.025 daily survival rate) than wildlands (0.216 daily survival rate). From the MARK analysis, four models best explained the difference in nest survival during the nestling stage between the suburbs and contained site, the presence of helpers, average side concealment, and interactions between those variables (Table 7). From the cumulative weights, site was the most important factor ($\sum w_i = 1.00$), but it was included in all of the models. Of the remaining factors side concealment ($\sum w_i = 0.778$) seemed to be explain the most residual variation for nest survival during the nestling stage, followed by the presence of helpers ($\sum w_i = 0.459$) and breeding male provisioning rate ($\sum w_i = 0.152$).

Discussion

Habitat Comparisons (Pre-Treatment)

Suburban females spent more time brooding and made fewer on- and off-bouts than wildland females. This pattern is consistent with a previous study (Aldredge 2008) in which suburban females reduced the amount of incubation on and off-bouts, but were able to increase the overall amount of time incubating and reduce the amount of time off the nest. Aldredge (2008) suggested this pattern was a response to an increased perception of predation risk, but that predictable sources of supplemental food allowed females to reduce both the frequency and duration of off-bouts enabling them to simultaneously reduce their exposure to predation while continuing to maintain incubation. As in previous studies, our data suggest that suburban scrub-jays are food-limited. Suburban males provided less food per provisioning trip and nestlings are lighter in the suburbs than wildlands.

Parental care varied with nest concealment but in the opposite direction of our predictions: parents tended to provision at higher rates at less concealed nests. Variation in habitat quality, both within and between sites may influence the quality of food and thus provisioning rates, as well as nest concealment. Klein (unpubl. data) found fewer arthropods in overgrown scrub than in shorter, more open scrub and found that males provision at higher rates in those overgrown sites. Males might be attempting to compensate for poor quality foods in those habitats, but nests are logically better concealed in those overgrown habitats.

The behavior of breeding males and females seemed to have little influence on nestling begging. Neither male provisioning rates, the total amount of food delivered by the male, or the number of on- and off-bouts by the female affected the power (loudness), frequency (pitch) or

rate of nestling begging calls in either suburban or wildland scrub-jays. In the suburbs, call power was negatively related to the proportion of time spent brooding by the female; the more a female brooded, the softer the nestlings begged. This suggests that as suburban females brood more, they may be muffling the begging of their young. In the wildlands only, call power increased with the amount of food delivered per provisioning trip; larger boluses of food were associated with louder begging calls. This may suggest that more competition existed with larger amounts of food in wildland nestlings. However, neither of these patterns may have much biological meaning. Both run opposite the predictions based on habitat-specific nest survival patterns and the range of call powers was very small (3 – 5 dB).

Predation Risk and Food Availability Experiment (Post-Treatment)

Scrub-jay behavior seemed to be influenced by the perception of adult predation risk but only in females and their behavior did not differ by habitat. Under experimentally increased perception of predation risk to adults, both suburban and wildland females decreased the amount of parental care provided, but only in the P/SC group and not in the P/S compared to controls (PC/SC). These results run essentially the opposite of the pattern observed during incubation, but under the normal predation risk of the suburban environment. The reduction in parental care may be explained by the predator models (cat, owl) used in the predation risk treatments. Domestic cats are ground predators and prey on both adults (Woods et al. 2003) and nests (Stracey 2011), whereas owls are primarily crepuscular, aerial predators that prey only on adults. Adult birds may avoid ground predators by reducing the amount of time spent in easily locatable and reachable places, and aerial predators may be avoided by being vigilant against an ambush attack. Females may reduce brooding to limit the time they spend in a predictable location but

this may come at the cost of increasing the frequency of trips to and from the nest. This may reduce the chance that if a cat finds the nest it will kill the brooding female, but females may be able to reduce brooding only marginally because a minimum threshold for thermoregulating nestlings exists. Brooding less than that threshold may reduce nestling development or cause death due to hyperthermia. Females may have a different response to the presence of owls. They may be readjusting their positions more often to locations that have better visibility to be vigilant against owls, so increasing their frequency of on/off-bouts should not reduce nest survival but will increase survival for the female. The lack of change in the P/S group compared to controls in both suburban and wildland females is harder to explain. Though patterns of female behavior with increasing predation risk and food availability run the same direction, when these two treatments are brought together they have an interactive effect that results in an intermediate effect on the behavior. The possibility exists that the two treatments creates a conflict within the female, so that she can get off the nest more frequently and longer to be vigilant for predators or to eat a high quality food source.

When the amount of nestling-appropriate food was increased, neither suburban nor wildland males did not alter their parental care in response to food supplementation. That trend is surprising in the suburbs because we know that suburban habitats have fewer arthropod larvae available to feed their young (Shawkey et al. 2004). We were not surprised that wildland males did not respond to food supplementation because nestling-appropriate foods should be abundant in these habitats. This lack of response in wildlife that reside in fair to good condition habitat has been seen in numerous studies (Reviewed by Boutin 1990). Male provisioning rates may be constant no matter the quantity or the quality of food available. Interestingly, suburban females

reduced brooding time when supplemental food was provided, possibly to take advantage of a high-quality food source to improve their own condition and survival.

Increasing food availability, but not predation risk, influenced nestling behavior but this effect did not differ by habitat. In both suburban and wildland habitats, supplemented nestlings (PC/S) begged less and at higher pitches than did controls. Increasing the amount of higher quality food should decrease begging call rates, but that does not explain why call rates were not lower in the P/S group as well. This may be a result of males not feeding the supplemental food to nestlings in this treatment group. If these males perceived a high risk of predation, they may not have fed the high quality food to their young over the two treatment days and thus, without changing provisioning rates, begging rates would not be any lower in this group compared to the PC/SC group. The increase in pitch of begging calls is opposite to what was found in food-deprived nestling Tree Swallows (Leonard and Horn 2001), and we do not have a good explanation for this trend. This small frequency difference (~0.3 Khz) between supplemented (PC/S and P/S) and unsupplemented groups (PC/SC and P/SC) trend may not have any biological meaning, but minimally, it along with the change in call rates suggest that supplementation does affect nestling behavior.

For the most part, both adult and nestling scrub-jays do not react differently in suburban and wildland habitats to increased perceptions of predation risk and nestling food availability. This trend suggests that either the behavioral reactions of scrub-jays are evolutionarily conserved no matter the habitat, or that these populations are not distant enough from one another or the habitat they reside in is not different enough to cause changes in parental care or begging behavior in scrub-jays.

Nest Survival during the Nestling Stage

In addition to site, nest concealment was the most important variable associated with nest survival; however, no interaction existed between concealment and site, thus this parameter was not likely to explain habitat-specific differences in nest survival during the nestling stage.

Although we did not find a difference in nest concealment between suburban and wildland nests, this conflicts with previous findings (Walton 1997). We measured nest concealment in July, sometimes months after a nest fledged or failed. The nesting season of scrub-jays overlaps the period of leaf fall and new leaf development in scrub oaks, the species in which most scrub-jays nest (Bowman and Fleischer unpubl. data). In both sites, most scrub-oaks drop all or some of their leaves by the end of March and the beginning of April. Because breeding is considerably earlier in the suburbs than in the wildlands (Bowman 1998, Reynolds et al. 2003, Schoech 1996, Schoech and Bowman 2001, 2003, Schoech et al. 2004), nestlings are present in suburban nests when many oaks are losing their leaves (Fig. 6A). In contrast, in the wildlands, nestlings often are not present until late March or April, when the scrub oaks have new, relatively dense leaves (Fig. 6B). Thus the habitat-specific variation in nest survival as it relates to nest concealment may be more a function of the differences in nesting phenology between the two sites rather than a difference in the structural characteristics of the oak shrubs.

The presence of helpers was the second most important variable and the proportion of groups with helpers was lower in the suburbs than the wildlands. In the suburbs, fewer young are produced and those have lower survival rates to yearlings. In addition, breeder mortality rates are higher, so a greater proportion of those young surviving recruit into breeding positions, thus reducing the number of helpers in the suburbs (Bowman 1998). Helpers provision nestlings and

contribute to nest vigilance that may aid detecting and deterring nest predators (Stallcup and Woolfenden 1978). Shawkey et al. (2004) also found that the presence of helpers reduced rates of brood reduction in both wildlands and suburbs. In the predation risk and food availability experiment of this study, we found that the presence of helpers reduced begging call power (loudness). Having fewer helpers in the suburbs may increase the risk of starvation, resulting in increased begging, which together with the reduction in vigilance, might lead to increased rates of nest predation.

The difference in scrub-jay nest survival that exists between wildland and suburban habitats during the nestling period does not appear to have been influenced by variation in parental care or food availability or any maladaptive response by the parents to the suburban environment. None of the parental care behaviors had any major support within the MARK analysis suggesting that no matter how often parents visited the nest, they did not affect the risk of nest failure. Although the availability of nestling foods influenced the behavior of suburban females, it does not seem to subsequently influence nestling-stage nest survival. Suburban nestlings appear to be food deprived, but the amount of food per trip also appeared to have little influence on nest survival. We reanalyzed food supplementation data from Sauter (2005); food supplementation reduced rates of brood reduction but did not improve nest success, suggesting that the two variables respond to different environmental pressures. Brood reduction likely occurs because suburban nestlings are food deprived, but poor rates of nest success seem to be independent of food levels and may be driven more by patterns that increase the vulnerability of suburban nests to predation. This is strongly supported by our results that nest concealment and

the presence of helpers were the most important factors in our nest survival analyses, whereas variables related to food, provisioning rates, food loads, or nestling begging had far less support.

Bowman and Woolfenden (2001) suggested differences in nest predators between sites could explain the habitat specific difference in nestling stage nest failure. Predators may differ both spatially and temporally between the habitats. Fewer snakes and more mammalian predators are found in suburban than wildland scrub (Peiffer et al., In prep). In wildland scrub, the seasonal activity of snakes increases as the breeding season progresses, but mammal activity is fairly high early in March, peaks in early to mid-April and then declines later in the season (Schaub 1992). Although few studies exist on the seasonal activity of nest predators in suburban environments, some suggest that activity of mammalian nest predators may be equal or greater in suburbs than in wildlands early in the season. For example, the movement of adult male foxes across road dominated landscapes is greater in drier than wetter months (Baker et al. 2007), and bobcats in Florida seem to move through human-modified areas to get to scrub habitats during the dry season and not during the wet season (Thornton et al. 2004). These studies lead to a possibility that the activity of mammalian nest predators in suburban areas may be greater in the suburbs from early March to mid April, coinciding with the period in which more nestlings occur in nests in the suburbs than in the wildlands. This may increase the probability of a predator encountering a nest. The timing of predator activity, combined with poorly concealed nests that may be easily detected because of the frequent begging of nestlings, as well as the reduced vigilance because of the paucity of helpers, all likely contribute to the reduced nest survival of suburban nests during the nestling stage.

Our study provided little evidence that suburban scrub is an evolutionary trap for Florida Scrub-Jays, at least as far as supplemental food and predation risk influence parental care and nest survival during the nestling period. The major causes of nest failure during the nestling stage had little to do with parental care, but with demographic (fewer helpers) and habitat (different vegetative structure resulting in less nest concealment) differences. However, because our data do not support suburban habitats as evolutionary traps for one aspect of their life cycle does not mean they still might not function as traps. Suburban scrubs are probably not ecological traps because scrub-jays rarely choose to reside in those habitats. Jays were present before development began and their sedentary habitats and life-long defense of territories, ensures that some jays will be present, at least until the population declines and is eventually extirpated. Data exist that show Florida Scrub-Jays do not emigrate from native habitats and settle in suburban habitats (Thaxton and Hingten 1996). However, suburban habitats may be evolutionary traps because anthropogenic food sources are far more predictable, both spatially and temporally, and are of excellent quality for adults, but not for raising nestlings. This may result in a perception that these are food-rich environments, leading to changes in life histories that may not be adaptive to the suburban environment. Even though these habitats have less food for raising nestlings, suburban birds have smaller territories (Bowman 1998), lay earlier and larger clutches (Bowman 1998; Schoech and Bowman 2003), lay larger eggs (Reynolds et al. 2003) that result in larger hatchlings (Sauter 2005) and increase their rate of double brooding (Bowman 1998), all decisions consistent with food-rich environments, but the opposite strategy in an environment in which food for successful reproduction is limiting. This perception may also influence disperse strategies; instead of dispersing from the suburbs, scrub-jays might stay in these habitats because

they perceive this high quality, high protein food source from feeders. Anthropogenic food may also lead to better body condition for breeders(Reynolds et al. 2003, Schoech and Bowman 2003). Because of the rapid rate and extensive nature of ecological changes that accompany urbanization, the risk of evolutionary traps seems particularly high, even if we could not support that perspective in this study. Our study adds to the big picture by reaffirming that humans can have profound impacts on species by affecting their reproductive phenologies. Mismatches between breeding phenologies and resource abundances are becoming more common in the literature, but much of that work is focused on the large-scale human effects such as global climate change (reviewed in Walther et al. 2002). Our study shows that even a relatively small effect like feeder food can have drastic effects on reproductive success within local populations.

CONCLUSION

This study showed that although the parental care behavior of breeding male and female suburban Florida Scrub-Jay was affected by adult predation risk perception and especially by nestling food availability, nest survival during the nestling stage was not influenced by variations in parental care and food availability. Suburban females brooded more with fewer bouts than wildland females supporting the predation risk hypothesis, that parents maladaptively reduce parental care because of a false adult predation risk. Suburban and wildland females brooded less and increased the frequency of on/off-bouts as adult predation risk perception was increased, but only suburban females decreased brooding when nestling food availability was increased. Nestling begging call rates were lowest in the groups that were only supplemented with nestling foods suggesting that the food availability hypothesis (i.e., the lack of nestling-appropriate foods is driving the lower survival of nests with nestlings) should have more support over the predation risk hypothesis in explaining the lower nestling stage nest survival in suburban habitats as compared to wildlands. However, most of the behavioral responses to the treatments were similar and none of the parental care variables held much support in a MARK AIC analysis, nor did supplementation have any effect on nest survival during that stage of development (Sauter unpubl. data).

The most important factors in explaining nest survival during the nestling stage were average side nest concealment, though concealment did not differ between the suburbs and wildlands, and the presence of helpers. Nest concealment should be an important factor

regardless of the stage. If the lack of difference in concealment was due to inappropriate timing of concealment data collection because of season leave drop (Fig. 7), then the nest site hypothesis (i.e., the interaction of poor side concealment and high male provisioning rates contributes to the lower nestling stage nest survival in the suburbs) would have the most support among the three hypotheses we developed. The presence of helpers was significantly different between the habitats, so fewer helpers in the suburbs may reduce overall provisioning and vigilance leading to higher predation rates during this stage in the suburbs. The most likely explanation for the difference in nest survival during the nestling stage is a combination of all these factors. High male provisioning rates from a reduced availability of high quality, nestling-appropriate foods may cause high rates of nestling begging calls. These high rates in conjunction with poor side nest concealment during that time of the season may increase the probability that a nest predator locates a nest. The lack of helpers in this habitat, in addition to reducing provisioning, reduces the chance of detecting and deterring predators from eating those nestlings. But, this supposition cannot necessarily be supported or rejected given our data, and other explanations (e.g., differences in nest predators between habitats), could explain the difference in nest survival during the nestling stage between suburban and wildland habitats.

What we can say unequivocally is that neither parental care behavior nor nestling food availability had any effect on the nestling stage nest survival. Food does have a significant impact on the survival of individual scrub-jay nestlings (Shawkey et al. 2004), but appears to not have any effect on the survival of the nest as a whole. The conservation implication of this result suggests that making sure there is enough nestling food for scrub-jays to feed their young is not enough to improve nest survival in this species. Instead, returning habitats to a more natural state

with more natural predator communities or conserving habitat may be more important than manipulating nestling-appropriate food abundance. Alone, supplementation of nestling foods or surveys of nestling food abundance are not adequate measures to ensure the conservation of the Florida Scrub-Jay. Though having enough food resources for your young is important, it is only one factor in many that determines whether an organism's reproductive bout is successful or not.

APPENDIX: TABLES AND FIGURES

Table 1: Experimental design and predictions for the predation risk and supplementation treatments. Up arrows indicate higher means, down arrows indicate lower means, and equal signs indicate the same means as the control groups for each treatment.

Supplementation Treatment	Predation Risk Treatment	
	Predation Risk Control	Predation Risk
Supplementation Control	= Provisioning Trips/ Brooding Frequency = Brooding Time = Food per Trip = Begging	↓ Provisioning Trips/ Brooding Frequency ↑ Brooding Time ↑ Food per Trip ↑ Begging
Supplementation	↓ Provisioning Trips/ Brooding Frequency ↑ Brooding Time ↑ Food per Trip ↓ Begging	↓↓ Provisioning Trips/ Brooding Frequency ↑↑ Brooding Time ↑↑ Food per Trip = Begging

Table 2: Experimental design and sample sizes for the predation risk and supplementation treatments. Treatments were applied in a 3-way factorial design, where all possible combinations of habitat (wildland or suburban), supplementation (control or supplemented) and predation risk (control or predator model) occurred. Numbers show the actual sample sizes collected for the 2009 and 2010 scrub-jay breeding season in each habitat category. PLE = Placid Lake Estates and LL = Leisure Lakes.

Supplementation Treatment	Predation Risk Treatment	
	Predation Risk Control	Predation Risk
Supplementation Control	6 Wildland groups 6 Suburban groups • 3 PLE • 3 LL	7 Wildland groups 5 Suburban groups • 3 PLE • 2 LL
Supplementation	4 Wildland groups 6 Suburban groups • 3 PLE • 3 LL	3 Wildland groups 5 Suburban groups • 3 PLE • 2 LL

Table 3: 3-way factorial ANCOVA table for the overall parental care (PC1) provided by breeding female scrub-jays after the predation risk and supplementation treatments. Source = Factor, covariate or interaction between factors, df = degrees of Freedom, SS = sum of squares, MS = mean squared, F = F distribution and p = p value. Factors include site (wildland or suburban), presence of helpers (helpers, no helpers) as a covariate, supplementation (control or supplemented) and predation risk (control or predator model).

Source	df	SS	MS	F	p
Site	1	14.790	14.790	8.828	0.006
Presence of Helpers	1	0.036	0.036	0.218	0.644
Pred. Risk	1	13.862	13.862	8.274	0.007
Supplementation	1	0.054	0.054	0.032	0.859
Site x Pred. Risk	1	0.436	0.436	0.261	0.613
Site x Supplementation	1	4.928	4.928	2.941	0.096
Pred. Risk x Suppl.	1	4.301	4.301	2.567	0.119
Site x Pred. Risk x Suppl.	1	0.021	0.021	0.013	0.911
Residuals	33	55.291	1.675		
Total	41	93.719	2.286		

Table 4: 3-way factorial ANCOVA table for the begging call powers (loudness) of nestling scrub-jays after the predation risk and supplementation treatments. Source = Factor, covariate or interaction between factors, df = degrees of Freedom, SS = sum of squares, MS = mean squared, F = F distribution and p = p value. Factors include site (wildland or suburban), presence of helpers (helpers, no helpers) as a covariate, supplementation (control or supplemented) and predation risk (control or predator model).

Source	df	SS	MS	F	p
Site	1	1.080	1.080	0.100	0.754
Presence of Helpers	1	61.65	61.65	5.707	0.023
Pred. Risk	1	3.870	3.870	0.359	0.553
Supplementation	1	26.21	26.21	2.427	0.129
Site x Pred. Risk	1	0.940	0.940	0.087	0.770
Site x Supplementation	1	5.220	5.220	0.484	0.492
Pred. Risk x Suppl.	1	3.740	3.740	0.347	0.560
Site x Pred. Risk x Suppl.	1	44.67	44.67	4.136	0.050
Residuals	32	345.7	10.80		
Total	40	493.1	12.33		

Table 5: 3-way factorial ANCOVA table for the begging call frequency (pitch) of nestling scrub-jays after the predation risk and supplementation treatments. Source = Factor, covariate or interaction between factors, df = degrees of Freedom, SS = sum of squares, MS = mean squared, F = F distribution and p = p value. Factors include site (wildland or suburban), presence of helpers (helpers, no helpers) as a covariate, supplementation (control or supplemented) and predation risk (control or predator model).

Source	df	SS	MS	F	p
Site	1	0.010	0.010	0.051	0.823
Presence of Helpers	1	0.724	0.724	3.814	0.060
Pred. Risk	1	0.024	0.024	0.128	0.723
Supplementation	1	1.022	1.022	5.384	0.027
Site x Pred. Risk	1	0.462	0.462	2.432	0.129
Site x Supplementation	1	0.018	0.018	0.095	0.760
Pred. Risk x Suppl.	1	0.021	0.021	0.108	0.745
Site x Pred. Risk x Suppl.	1	0.696	0.696	3.665	0.065
Residuals	32	6.075	0.190		
Total	40	9.052	0.226		

Table 6: 3-way factorial ANCOVA table for the begging call rate of nestling scrub-jays after the predation risk and supplementation treatments. Source = Factor, covariate or interaction between factors, df = degrees of Freedom, SS = sum of squares, MS = mean squared, F = F distribution and p = p value. Factors include site (wildland or suburban), presence of helpers (helpers, no helpers) as a covariate, supplementation (control or supplemented) and predation risk (control or predator model).

Source	df	SS	MS	F	p
Site	1	0.027	0.027	0.016	0.901
Presence of Helpers	1	0.011	0.011	0.006	0.937
Pred. Risk	1	2.004	2.004	1.162	0.289
Supplementation	1	9.137	9.137	5.300	0.028
Site x Pred. Risk	1	0.559	0.559	0.324	0.573
Site x Supplementation	1	0.068	0.068	0.039	0.844
Pred. Risk x Suppl.	1	6.029	6.029	3.496	0.070
Site x Pred. Risk x Suppl.	1	0.480	0.480	0.279	0.601
Residuals	33	56.91	1.725		
Total	41	75.23	1.835		

Table 7: Nest survival models for suburban and wildland Florida Scrub-Jay nests during the nestling stage, created in Program MARK, using Akaike's Information Criterion corrected for small sample sizes (AIC_c). k is the number of parameters in each model, ΔAIC_c is the difference between each model and the best-fitting model, and ω_i is the weight of the model. Covariates: Sg = site (Suburbs, Wildlands), Yr = year, Hlp = presence of helpers, Conc = average side nest concealment, PR = breeding male provisioning rate, FPT = amount of food delivered per provisioning trip, Pan = proportion of time spent brooding by breeding female, NB = number of brooding bouts made by breeding female, CP = nestling begging call power (loudness), CF = nestling begging call frequency (pitch), LCR = log-transformed nestling begging call rate.

Model	AIC_c	ΔAIC_c	ω_i	k
Site + Conc	140.5109	0	0.2185	3
Site + Hlp x Conc	140.7113	0.2004	0.19767	5
Site + Hlp + Conc	141.232	0.7211	0.15236	4
Site + PR + Conc	142.3616	1.8507	0.08661	4
Site x Hlp + Conc	142.6969	2.186	0.07324	5
Site + PR x Conc	143.4676	2.9567	0.04982	5
Site	143.9478	3.4369	0.03919	2
Site + Hlp	144.121	3.6101	0.03594	3
Site + Yr	144.4973	3.9864	0.02977	3
Site + FPT	145.6562	5.1453	0.01668	3
Site + CP	145.7848	5.2739	0.01564	3
Site + LCR	145.7859	5.275	0.01563	3
Site + Pan	145.8131	5.3022	0.01542	3
Site + PR	145.8505	5.3396	0.01513	3
Site + NB	145.8777	5.3668	0.01493	3
Site + CF	145.9472	5.4363	0.01442	3
Site + CP + LCR	147.5356	7.0247	0.00652	4
Site + CP x LCR	149.444	8.9331	0.00251	5

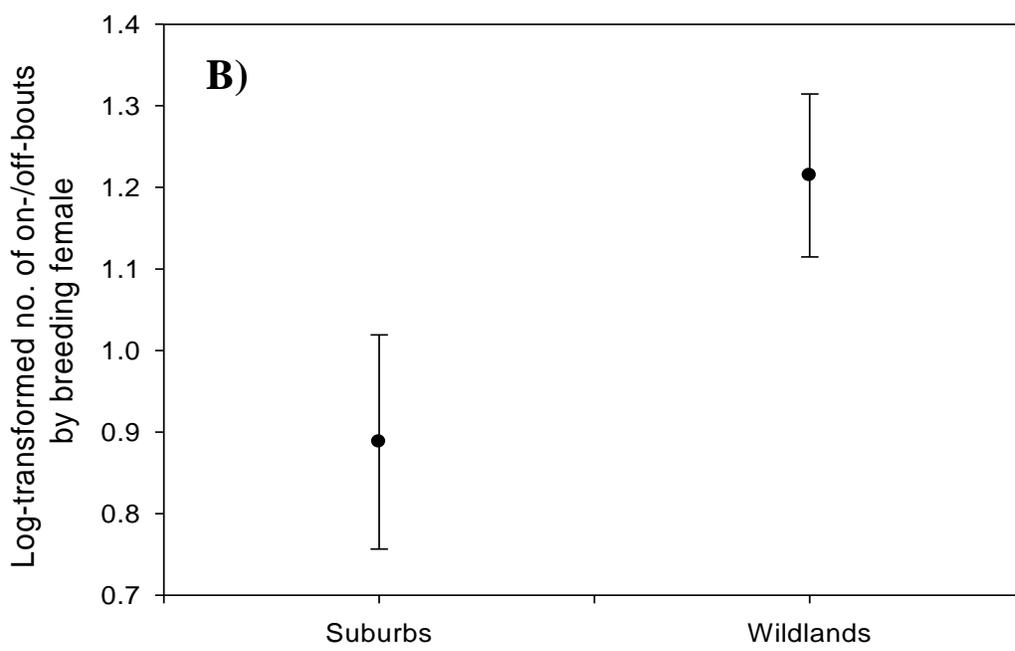
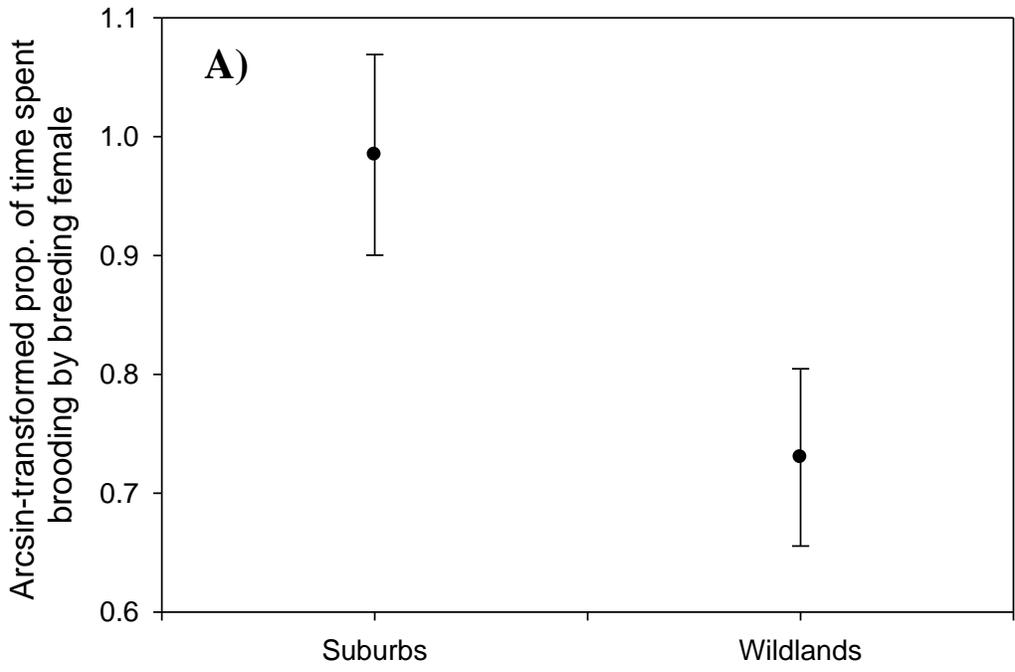


Figure 1: The arcsin-transformed proportion of time spent brooding (A) and log transformed number of on-off-bouts (B) by breeding female scrub-jays in suburban and wildland habitats.

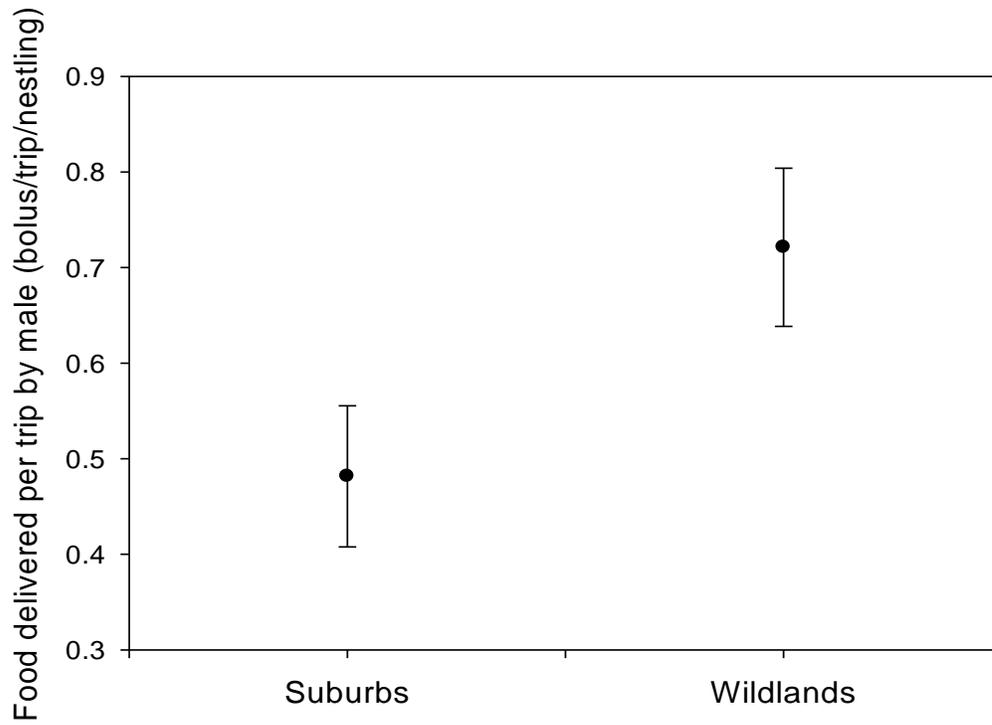


Figure 2: The food delivered per provisioning trip by breeding male scrub-jays in suburban and wildland habitats.

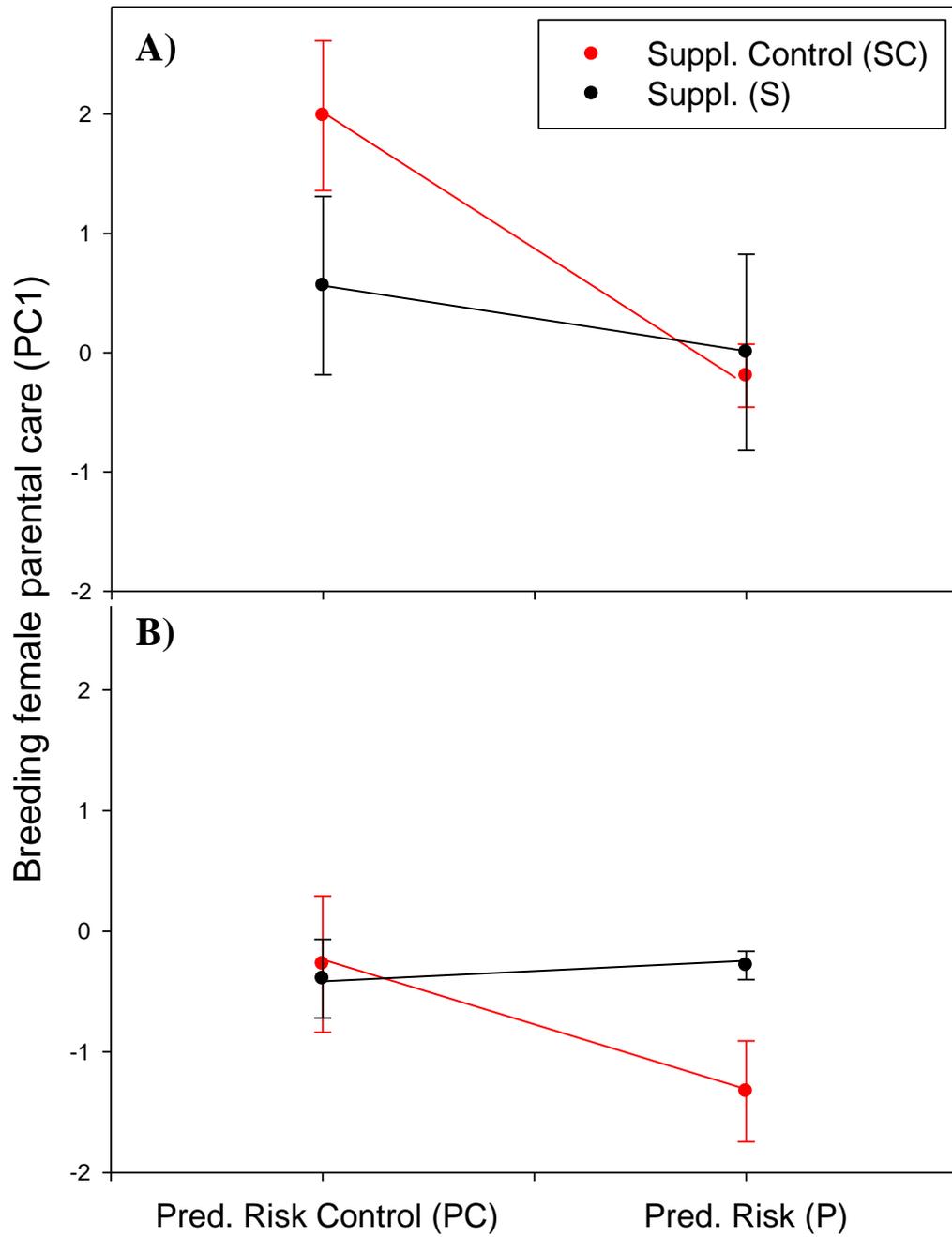


Figure 3: The effect of the treatment groups on the overall parental care (PC1) by breeding female scrub-jays in suburban (A) and wildland (B) habitats.

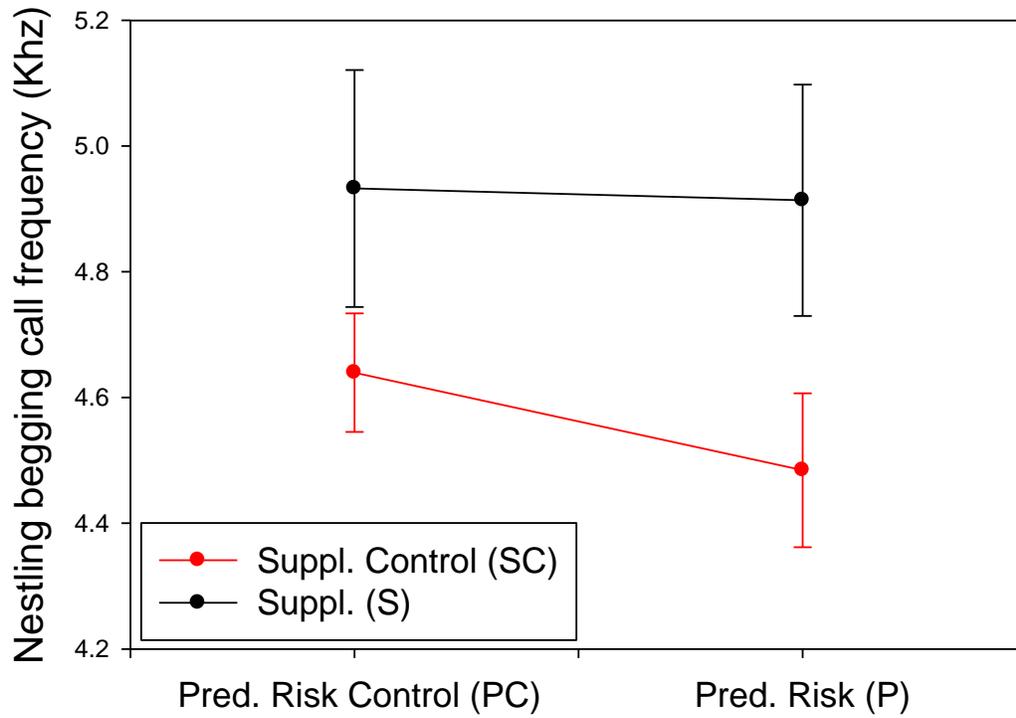


Figure 4: The effect of the treatment groups on the begging call frequencies (pitch) of nestling scrub-jays in both suburban and wildland habitats together.

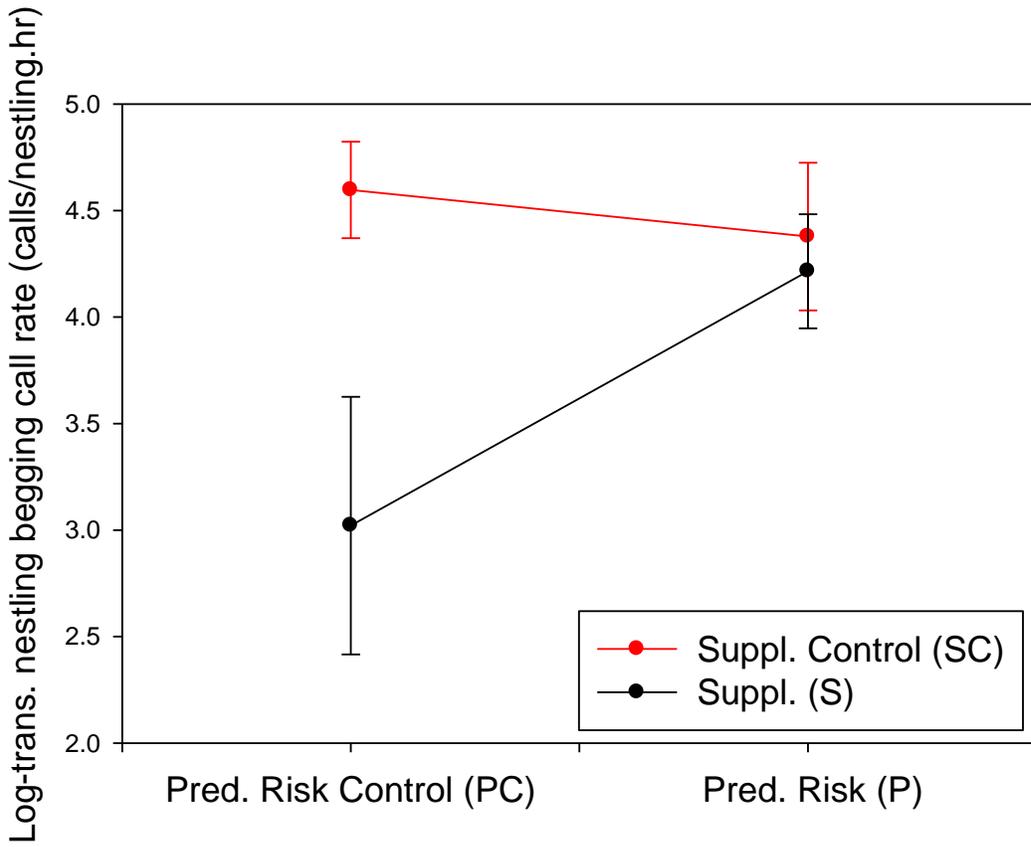


Figure 5: The effect of the treatment groups on the log-transformed begging call rates of nestling scrub-jays in both suburban and wildland habitats together.

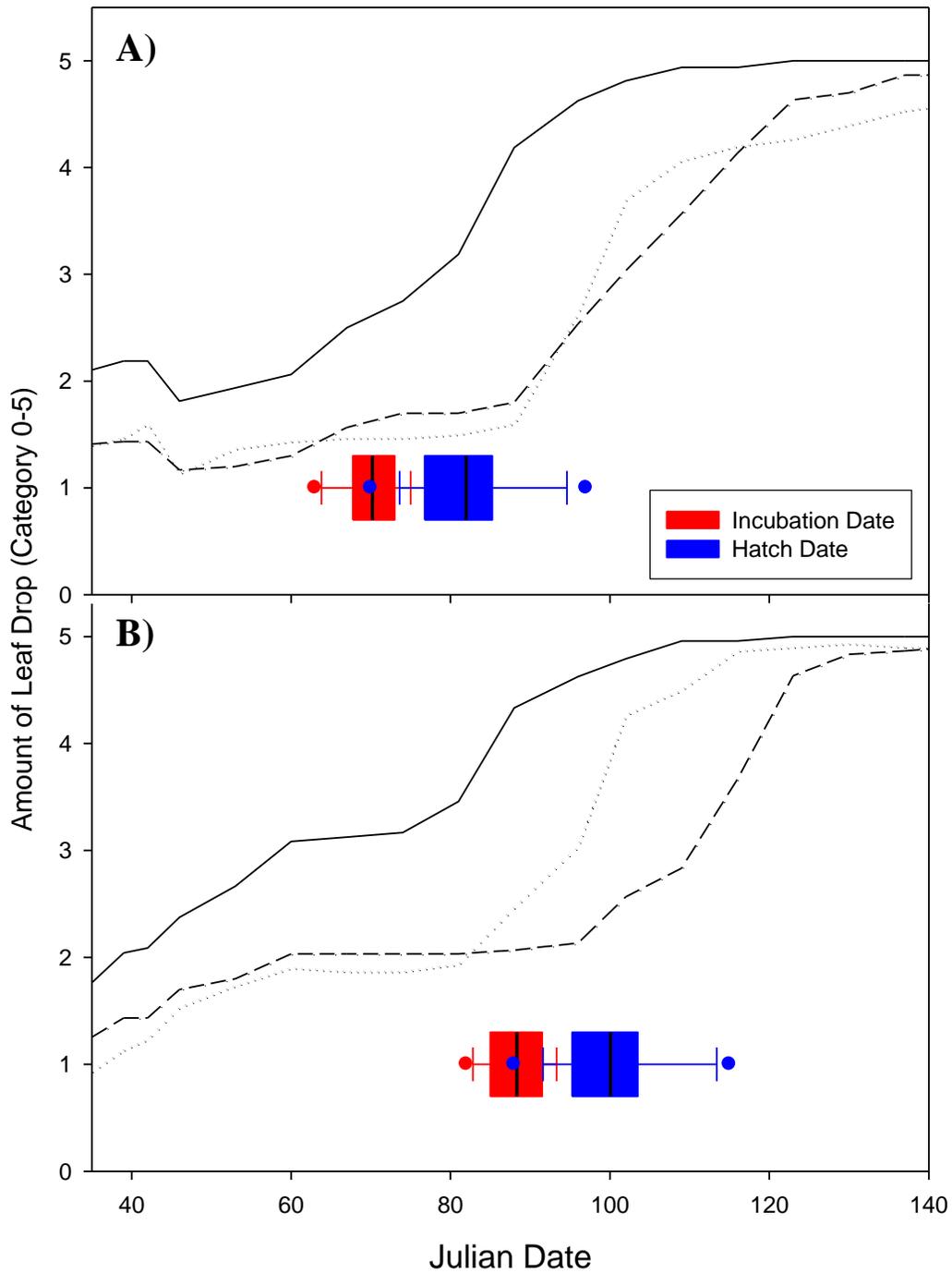


Figure 6: The amount of leaf drop by *Quercus chapmanii* (solid lines), *Quercus geminata* (dotted lines), and *Quercus inopina* (dashed lines) scrub-oak shrubs in comparison to scrub-jay median incubation and hatch dates from 1994 to 2010 in suburban (A) and wildland (B) habitats. Leaf drop categories: 0 = 0%, 1 = 1 – 25%, 2 = 26 – 50%, 3 = 51 – 75%, 4 = 76 – 99%, and 5 = 100%.

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