

THESIS

REPRODUCTIVE ECOLOGY OF THE ISLAND SCRUB-JAY

(APHELOCOMA INSULARIS)

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ABSTRACT

REPRODUCTIVE ECOLOGY OF THE ISLAND SCRUB-JAY (*APHELOCOMA INSULARIS*)

The small population size and limited range of the Island Scrub-Jay make it a species of conservation concern, yet its reproductive ecology is poorly known. From 2008 – 2010 I investigated factors influencing nest success, quantified annual fecundity per pair, and documented breeding behavior. Nest predation was the major factor influencing nest success, accounting for 92 percent of documented nest failures. Nests that were initiated earlier in the breeding season, nests that were higher and more concealed, and nests of breeding pairs that had smaller home ranges with a greater percentage of oak habitat had higher daily nest survival. Despite a low estimated daily nest survival rate of 0.945 ± 0.004 SE, the high frequency of renesting allowed pairs to maintain a mean fecundity of 1.13 ± 0.15 SE. Island Scrub-Jays may benefit from an increase in breeding habitat and reduced nest predation resulting from the ongoing regeneration of woody vegetation and understory structure following the removal of exotic herbivores on Santa Cruz Island.

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INTRODUCTION

Understanding the factors influencing population dynamics is essential for informing conservation and management efforts (Donovan et al. 1995, Robinson et al. 1995). In particular, the documentation of a species' natural history, behavior, and demographic rates provides a predictive foundation for understanding population dynamics, regulation, and long-term persistence (Holmes et al. 1996). A pressing challenge in predicting long-term demographic trends in response to ecological change is to increase our understanding of habitat-specific demography (Donovan et al. 1995, Holmes et al. 1996, Porneluzi & Faaborg 1999, Benson et al. 2010). Quantifying habitat-specific demographic rates can provide managers and conservation practitioners with more precise information regarding a population's trajectory as well as how to more effectively manipulate these rates by influencing habitat composition, function, and structure (Bradbury et al. 2001).

Species endemic to islands, especially avian species, face an elevated risk of extinction due to natural or human-caused stochastic events (e.g., fire, disease), exotic species, and population fluctuations (Johnson & Stattersfield 1990, Pimm et al. 1993, Frankham 1998, Blackburn et al. 2004, Whittaker & Fernandez-Palacios 2008). Due to the low resiliency found in island ecosystems, the loss of insular species, especially keystone species, can have substantial and lasting impacts on ecosystem functioning and biodiversity (O'Dowd et al. 2003). Because island species are often under greater risk of extinction, data on their vital rates and demography are especially needed to provide effective management.

The Island Scrub-Jay (*Aphelocoma insularis*) is endemic to southern California's Santa Cruz Island, the largest of the eight California Channel Islands. It is North America's sole island-endemic passerine species (Curry & Delaney 2002) and is genetically and

morphologically distinct from its closest relative, the Western Scrub-Jay (*A. californica*; Pitelka 1951, Peterson 1991, Delaney & Wayne 2005). Its restricted range, small population size, and ongoing habitat changes across its range make the Island Scrub-Jay a species of conservation concern. Future conservation and management actions regarding the Island Scrub-Jay will be more effective from having detailed knowledge of fecundity, nest success, and natural history of this species.

In the past three decades, introduced feral ungulates, including sheep (*Ovis aries*), pigs (*Sus scrofa*), and cattle (*Bos taurus*), have been eradicated from Santa Cruz Island, which was managed as a ranch for over 150 years. Their removal has released native vegetation from browsing and grazing pressure and has led to an increase in abundance, density, and recruitment rates of the native flora (Klinger et al. 1994, Peart et al. 1994). Feral pigs, in particular, are known to reduce oak (*Quercus spp.*) recruitment and survivorship through acorn predation and rooting of the soil (Peart et al. 1994, Sweitzer & Van Vuren 2002); indeed, since their removal from Santa Cruz Island in 2006, oak recruitment has increased (L. Laughrin pers. comm.). This may have consequences for the distribution, population size, and reproductive ecology of the Island Scrub Jay, which, like other *Aphelocoma*, is an oak mutualist (Woolfenden & Fitzpatrick 1996, McCormack & Brown 2008, Koenig et al. 2009).

Although they are distributed across a diverse range of temperate and tropical habitats, *Aphelocoma* jays generally maintain a close association with oaks (Woolfenden & Fitzpatrick 1984, Carmen 2004, McCormack & Brown 2008). Oaks are the primary plant species used for nesting sites by several species of *Aphelocoma* (Atwood 1980b, Woolfenden & Fitzpatrick 1996, McCormack & Brown 2008), and oaks provide important food resources for both nestlings and adult jays (Bossema 1979, Woolfenden & Fitzpatrick 1996, Curry et al. 2002, Carmen 2004).

Acorns in particular are a critical food resource, particularly during the non-breeding season (Woolfenden & Fitzpatrick 1984, Carmen 2004, McCormack & Brown 2008, Koenig et al. 2009), and in *A. californica*, interannual variation in masting events can have strong impacts on adult jay density, survival, migration, and reproductive success (Carmen 2004, Koenig et al. 2009).

Differing rates of vegetation recovery across Santa Cruz Island have increased habitat heterogeneity in terms of vegetation density and understory structure (Parkes et al. 2010). The differences in vegetative recovery are likely caused by several factors, including differences in microclimate, soil composition, and the historical intensity of ranching. This allowed me to investigate the influence of the vegetative community on reproductive success and behavior of the Island Scrub-Jay using natural habitat variation among home ranges of breeding pairs. Based on the known association between jays and oak, I predicted that the proportion of oak habitat within home ranges of Island Scrub-Jays would be positively related to their fecundity.

Island Scrub-Jays are long-lived, non-migratory, and maintain year-round territories in oak-dominated habitat (Atwood 1980a, Atwood 1980b, Atwood et al. 1990). Atwood (1980b) suggested that nest success rates are low because of high rates of nest predation, yet data on reproductive success is limited to nine nests and no data on annual fecundity has been collected. This paucity of knowledge regarding Island Scrub-Jay per-capita fecundity presents challenges for understanding population regulation, and limits the ability to design management plans to mitigate threats to the jay's long-term viability. Here, I provide the first data on habitat-specific nest success, per capita fecundity, and nest site characteristics in *A. insularis*. My study had two objectives: 1) to document per-pair reproductive success and causes of nest failures, 2) to investigate the factors, including habitat composition, influencing nest success. This information

is critical to predicting the species' long-term population stability and viability in light of the extensive ecological changes occurring on Santa Cruz Island.

METHODS

Study Sites - Santa Cruz Island (34° 0'N, 119°45'W) is 24,540 hectares in area and is located approximately 32 km off the coast of southern California. The island experiences a mediterranean-type climate characterized by cool, wet winters and hot, dry summers with a mean precipitation of 50 cm in the central valley (Fisher et al. 2009). I established three study plots on Santa Cruz Island: Coches Prietos Canyon (115 ha), Portezuela (163 ha), and the Central Valley near the University of California, Santa Barbara field station (226 ha). These study plots were selected because they encompass a broad range of the chaparral vegetation gradient on the island thus allowing me to assess the effects of habitat on reproductive success. Within each plot, a minimum of 15 territorial pairs was studied throughout the breeding season (February – June) in 2008, 2009 and 2010. Island Scrub-Jays were captured opportunistically using box traps baited with peanuts. Captured individuals were marked using a unique combination of up to four Darvic color leg bands and one numbered, aluminum U.S. Geological Survey band.

Home range and habitat composition - Home ranges were determined for each pair annually based on locations collected once every 5 minutes for 20 minutes per week for approximately 15 weeks during the breeding season. Individual jays were identified by their unique color band combinations at the time they were located. To minimize disturbance, locations were mapped relative to the GPS location of the observer by using a compass and laser rangefinder to record the angle and distance to the bird. A maximum of 5 locations were collected during any day to minimize temporal bias, and all locations were taken between 0530 and 1600 hours. These points were used to create a 95 percent and a 100 percent minimum

convex polygon in program ArcMap (version 9.2, ESRI) to delineate the home range for each breeding pair. Only the 100 percent polygon estimates of home range were reported and used in analyses because there was little difference between the two measures. This is likely due to the highly territorial behavior of Island Scrub-Jays during the breeding season.

Habitat composition for the home range of each breeding pair was calculated in ArcMap using a vegetation layer created by The Nature Conservancy (2007). The Nature Conservancy delineated the habitat types in the vegetation layer using high-resolution aerial photographs, and the habitat types were ground-truthed in 2006. From these vegetation layers I calculated the percentage of oak-dominated habitat (all oak species were included) within each home range. I focused on oak-dominated habitat because of the high dependency other species of *Aphelocoma* have with oaks (Woolfenden & Fitzpatrick 1984, Carmen 2004, McCormack & Brown 2008).

Nest characteristics, nest survival, and fecundity - All nesting attempts for each pair were located and monitored to determine fecundity and nest success. Nests were found using both behavioral observations and systematic searches. Home ranges were monitored for all re-nesting and double-brooding attempts to quantify annual fecundity per pair. A mirror mounted on an extendable pole was used to check nests to confirm clutch sizes and the number of nestlings. Nests were checked every three days, except near hatching and fledging dates when a subset of nests were monitored daily to confirm the exact lengths of the incubation and nestling periods for those pairs. Thirty-three nestlings were weighed from ten nests between 10 and 13 days post hatching. I averaged the masses of all nestlings in each nest and then averaged across all ten nests to determine the mean nestling mass.

The fate of each nest (whether it failed or successfully fledged at least one young) was determined by visual inspection of the nest, by adult behavior, and by visual confirmation of

fledglings. If, upon visual inspection, the nest was found empty during incubation, it was considered to have been depredated. If a nest was found empty during the nestling period, adult behavior was observed for signs of either nest predation or successful fledging of young. A nest was considered successful if the adults were observed carrying food to a location other than the nest and fledglings were confirmed visually. If adults were observed building a new nest and were not feeding young, then the nest was considered to have been depredated. Nests were considered abandoned if they contained eggs but parental care ended prematurely, excluding two cases of adult mortality. Adult mortality was determined in one case by finding the remains of the adult, and was suspected in another case when an individual took a new mate and left the eggs in the previous nest unattended. In cases where nests were suspected to be abandoned and could be reached, abandonment was confirmed by feeling whether the eggs were cold to the touch. No nests were abandoned during the nestling stage.

Nest height, nest concealment, and the species of the nest substrate were recorded after a nest failed or after young had fledged. Nest concealment was visually estimated as the proportion of the nest concealed by vegetation at a distance of 1 meter in the four cardinal directions (from a standardized height of 1 meter) and from directly underneath the nest. To estimate nest concealment from overhead, the proportion of sky directly over the nest that was concealed by vegetation was visually estimated. I calculated a mean of these six measures (from each cardinal direction, from below and from above) to characterize overall concealment for each nest.

I used five-hour video recording with digital camcorders to document adult behavior at the nest (for a separate study) and to record potential predation events (Coches Prietos Canyon: $n = 31$ nests; Field Station: $n = 25$ nests; Portezuela: $n = 18$ nests). Video cameras were placed a minimum of three meters away to minimize disturbance to the jays, and adult behavior was

observed after the cameras were setup to ensure that the cameras were accepted. Videotaping occurred twice in the incubation period, once between days 6 and 8 (early stage) and once between days 14 and 16 (late stage) for a total of 319.3 hours across all nests and plots.

Videotaping occurred twice during the nestling period, once between days 6 and 8 (early stage) and once between days 14 and 16 (late stage) for a total of 303.4 hours across all nests and plots. All recordings were initiated within 15 minutes of sunrise.

Statistical Analyses - I used nest survival models in Program MARK (White & Burnham 1999, Rotella et al. 2000) to estimate daily nest survival and to evaluate whether nest site and home range covariates influenced nest survival. I also tested for a seasonal trend in daily nest survival using the Julian day of clutch completion as a covariate. An information theoretic approach (Burnham & Anderson 2002) was used to evaluate support for 32 *a priori* models. This set of models included all additive combinations of the explanatory variables: nest height, nest concealment, home range size, Julian day of clutch completion, percentage of oak-dominated habitat within the home range, and a null model. I restricted the nest survival analysis to 254 nests for which all variables were measured. I fit all models with a logit link function, and ranked them using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). Models were considered to be competitive with the top model (i.e. the model with a ΔAIC_c value of zero) if a ΔAIC_c value was ≤ 2 . I used model averaging to estimate the daily nest survival rate; this incorporates model uncertainty by weighting the estimated daily nest survival rate from each model by the Akaike weight (w_i) associated with each model. I also calculated the relative variable importance weights by summing the Akaike weights of models that included a particular variable. Variable importance weights can provide insight into which variables are the strongest predictors of the dependant variable (Burnham & Anderson 2002).

I calculated several additional breeding metrics to summarize the reproductive effort, clutch size and fecundity of breeding pairs. Using the subsample of pairs for which all reproductive attempts were known, I estimated the mean number of nest attempts per pair per breeding season and the mean number of eggs laid per female per breeding season as measures of reproductive effort. Mean clutch size was estimated using a subsample of nests that were documented to contain at least one egg. Mean annual fecundity per pair was estimated by averaging the number of young fledged over the breeding season for pairs whose fecundity was known. Our regular monitoring of pairs every three days made it possible to count fledged young even in cases where the nest was not found. This is because young of the year have distinct plumage characteristics, stay in their parent's home range for several weeks post-fledging, and continue to be fed by their parents. These statistics were calculated in program JMP (SAS Institute, 2009). For all variables, I report mean values $\pm$ 1 standard error.

RESULTS

Natural history - Male and female Island Scrub-Jays built nests jointly, and no cooperative breeding attempts were documented (see Atwood 1980b, Curry & Delaney 2002). Twigs of woody plants formed the outer nest cup material, and these twigs were always collected from standing vegetation rather than from the ground; oak twigs were most commonly used. Nests were lined with rootlets and/or grass collected from the ground, and, in at least two nests, animal hair was incorporated in the lining. Adults occasionally made incomplete nests, and on one occasion I observed the reuse of a completed nest from a prior year. Only females incubated and brooded young, and both adults fed nestlings. Nests were placed in variety of plant species with *Quercus* spp. being used most commonly (62%), followed by toyon (*Heteromeles arbutifolia*) (9%), *Rhus* spp. (5%), *Ceanothus* spp. (4%), mountain mahogany (*Cercocarpus betuloides*)

(4%), and 12 other woody species. Mean nest height was 3.07 ± 0.11 m ($n = 254$, range = 0.8 – 16 m).

I calculated the mean duration of the incubation stage and nestling stages from nests that were checked daily at transitions between stages. The incubation period lasted 18.33 ± 0.22 days ($n = 22$ nests, range: 17 – 21 days), and the nestling period lasted 22.52 ± 0.50 days ($n = 21$ nests, range: 19 – 27 days). The mean nestling mass was 64.51 ± 3.71 g ($n = 10$ nests, range = 39.8 – 95.1 g).

This study included breeding pairs that occupied home ranges that varied widely in size, total amount of oak habitat, and percentage of oak. The mean home range of breeding Island Scrub-Jays was 3.44 ± 0.15 hectares ($n = 137$, range = 0.61 – 8.85 hectares). The mean area of oak habitat within home ranges was 1.85 ± 0.09 hectares ($n = 137$, range = 0.16 – 5.4 hectares). The mean percent of oak within home ranges was $56\% \pm 2\%$ ($n = 137$, range = 9% - 100%).

Five species were recorded on video depredating Island Scrub-Jay nests: Island Fox (*Urocyon littoralis*, $n = 1$), Cooper's Hawk (*Accipiter cooperii*, $n = 1$), Common Raven (*Corvus corax*, $n = 1$), Gopher Snake (*Pituophis catenifer*, $n = 1$), and Island Scrub-Jay ($n = 4$). In two of the nest predation events by conspecifics, the predator was a confirmed member of the territorial pair, suggesting that the adults had abandoned the nest and simply consumed their own eggs. There is also circumstantial evidence that Bewick's Wrens (*Thryomanes bewickii*) were nest predators: four jay nests were found with punctured eggs, and wrens are known to cause nest failures in other avian species through egg puncture (Picman 1992). Based on visual examinations of depredated nests that were videotaped, none of the documented nest predators left punctured eggs behind.

Nest survival - I found 352 nests, of which 55 successfully fledged at least one young. The major cause of failure for the 235 nests that failed during the egg or nestling stages was predation (92%), followed by abandonment (6%), adult mortality (0.9%), and substrate failure (0.4%). Forty-six nests were completed but were never seen to contain eggs, and 16 nests were never completed. I did not include these 62 nests in statistical analyses of nest survival because the causes of these nest failures were not known.

My results indicated some model selection uncertainty and strong support for three candidate models (with ΔAICc values ≤ 2 ; Table 1). The top model included nest height, nest concealment, home range size, and the Julian day of clutch completion. The percentage of oak-dominated habitat was also included in one of the three competitive models. Nest height (Figure 1), nest concealment (Figure 2), and the percentage of oak-dominated habitat within home ranges of breeding pairs (Figure 3) were positively associated with daily nest survival, while home range size (Figure 4) and the Julian day of clutch completion (Figure 5) were negatively associated with daily nest survival (see Table 2 for beta values and 95% confidence intervals). Based on the relative variable importance weights, home range size ($w_i = 0.999$) and nest concealment ($w_i = 0.995$) were the most important explanatory variables, followed by, in order of importance, Julian day of clutch completion ($w_i = 0.89$), and nest height ($w_i = 0.62$); there was weak support for an effect of the percent of oak-dominated habitat within home ranges ($w_i = 0.30$) on daily nest survival. The model-averaged estimate of daily nest survival was 0.945 ± 0.004 ($n = 254$).

Reproductive effort and annual fecundity - I estimated mean clutch size, the mean number of renesting attempts per pair per breeding season, the mean number of eggs laid per female per breeding season, and mean annual fecundity per breeding season. Mean clutch size was $3.62 \pm$

0.07 ($n = 223$, range = 2 – 5 eggs). I commonly observed renesting attempts following nest failures, but rarely documented double-brooding attempts (nesting again after a previous nest fledged). Renesting attempts often occurred within days after the failure of an earlier nesting attempt, resulting in 2.73 ± 0.14 nesting attempts per pair per year ($n = 82$ pairs, range = 1 – 6 attempts). In 2008, I documented, for the first time, double-brooding attempts for two separate pairs. No double-brooding was observed in 2009 or 2010. The mean number of eggs laid per female was 7.18 ± 0.38 eggs per breeding season ($n = 82$ females, range = 2 – 18). The mean number of young fledged per pair was 1.33 ± 0.15 young per year ($n = 132$ pairs, range = 1–5), which was low relative to the mean number of eggs laid.

DISCUSSION

My results indicate that Island Scrub-Jay fecundity was limited by nest predation, and that nest survival varied seasonally and was affected by attributes of both the home range and the nest site. By contrast, I documented no instances of nestling starvation, indicating that a lack of food was not a source of nest failure. As I discuss in more detail below, the covariates affecting nest success, such as nest concealment and home range size, are likely to be related to the complexity of vegetation structure and to understory and canopy density. My results therefore suggest that the ongoing regeneration of woody vegetation on Santa Cruz Island is likely to increase the long-term viability of the Island Scrub-Jay population by increasing nest survival rates and fecundity, and perhaps, by increasing the carrying capacity of the island.

As in many passerine species (Ricklefs 1969, Martin 1995), I found that nest predation was the leading cause of nest failure for the Island Scrub-Jay. I identified attributes of both nest sites and home ranges that influenced nest survival. At the scale of the nest site, both nest concealment and nest height had a positive influence on daily nest survival. These results are

consistent with other studies of passerines that have shown that higher and more concealed nests experience reduced predation (Hatchwell et al. 1999, Colombelli-Négrel & Kleindorfer 2009 although see Howlett & Stutchberry 1996). However, it is likely that the influence of nest height and nest concealment on daily nest survival is species-specific as there are various factors that limit nest success for different species. Home range size was negatively related to daily nest survival, indicating that smaller territories were more likely to fledge young. Previous studies have found home range size to be inversely related to food abundance and habitat quality (Simon 1975, Smith & Shugart 1987, Marshall & Cooper 2004 but see Van Horn 1983). Smaller home ranges can also incur lower energetic costs (Johnson & Gaines 1990) and potentially fewer encounters with predators (Yoder et al. 2004) than larger home ranges. However, it may be necessary to maintain larger home ranges in low quality habitats in order to obtain sufficient food (Anich et al. 2010). In my study plots, pairs generally had smaller home ranges in areas that had more continuous woody vegetation, a higher density of oak trees, and a more complex vertical structure, with shrub and canopy layers. The importance of the effect of home range size on daily nest survival may therefore suggest that the complexity of vegetation within a home range affects nest predation risk. Although the percentage of oak in home ranges had a positive influence on nest survival, its lower importance suggests that species composition may play a reduced role compared with overall vegetation structure. If the Island Scrub-Jay's major nest predators are visually-oriented, it seems likely that the overall density of vegetation within home ranges, along with nest concealment, would affect nest survival by making it more difficult for predators to see nests.

Another possible explanation for higher nest survival in smaller home ranges with more dense vegetation is the potential prey-site hypothesis, which predicts a negative relationship

between nest predation rates and the availability of potential nest sites (Martin & Roper 1988, Martin 1993, Chalfoun & Martin 2009). This negative relationship is expected if the probability that a predator will successfully find a nest decreases with the number of potential nest sites that must be searched. However, this pattern appears to be dependent upon the habitat type, the predator community, and the search strategies employed (i.e. visual or olfactory) by the potential nest predators (Mezquida & Marone 2002, Martin & Joron 2003). On Santa Cruz Island, areas with more dense vegetation would provide more potential locations to place a nest, which may reduce the ability of predators to locate nests. This hypothesis would predict that as vegetation continues to regenerate, the number of suitable nest sites should increase, thereby reducing the ability of predators to find nests.

I also found strong support for a seasonal decline in nest success. This pattern has been well documented in many other avian species (Hochachka 1990, Verhulst et al. 1995). Seasonal declines in avian reproduction may be caused by a variety of factors including changes in food availability (Siikamäki 1998), changes in predator behavior or activity (Sperry et al. 2008), and climatic factors (Monadjem & Bamford 2009).

My results suggest that Island Scrub-Jay reproductive success is most strongly limited by nest predation, rather than by other factors. Given the mediterranean climate of Santa Cruz Island, food abundance for the Island Scrub-Jays may be correlated with rainfall, and the effects of resource abundance on reproductive success would predict that Island Scrub-Jay fecundity would be positively correlated with rainfall. However, contrary to this expectation, Island Scrub-Jay reproductive success was not appreciably higher in 2010 (1.45 ± 0.26 SE), which had a wetter winter than 2008 (1.21 ± 0.26 SE) and 2009 (1.80 ± 0.37 SE). However, I lack reproductive data from an extremely wet or dry year, and little is known about how the jay's

predator and prey communities respond to extreme weather conditions. Indeed, the high inter-annual variability in rainfall on Santa Cruz Island, coupled with a lack of information on the jay's community ecology, emphasizes the need to continue monitoring the reproductive success and survival of *A. insularis*.

In all three years of the study, the mean number of young fledged per breeding pair was low relative to the mean number of eggs laid which appears to be caused by high nest predation. Despite low nest survival, the ability of females to renest multiple times and lay up to 18 eggs throughout the breeding season allows the Island Scrub-Jay to have comparable fecundity to what is observed in other *Aphelocoma* species. Averaged across all pairs and years, the Island Scrub-Jay's mean annual fecundity (1.13 ± 0.15) was comparable to that of the Western Scrub-Jay (1.16 ± 1.5 SD, Carmen 2004) and lower than that of the cooperative breeding Florida Scrub-Jay (*A. coerulecens*, 1.90 (range 0.9–2.8), Woolfenden and Fitzpatrick 1996).

My results provide mixed support for prior findings on the Island Scrub-Jay's mating system and natural history. This study confirms that Island Scrub-Jays are non-cooperative breeders that rely on oak-dominated habitat and that predation is the leading cause of nest failure (Atwood 1978, 1980a, 1980b). Additionally, mean clutch size and nest height were similar to that reported by Atwood (1980b). However, I documented home range sizes substantially larger than previously described (Kelsey and Collins 2000). Kelsey and Collins (2000) used their estimate of home range size based on 23 pairs to infer global population size of the Island Scrub-Jay. If their measured home range sizes were underestimates, then the population size of jays on Santa Cruz Island may have been overestimated.

Further research on the Island Scrub-Jay and the ecological communities of Santa Cruz Island would benefit future management and conservation efforts. Currently, there are large gaps

in our knowledge of the Island Scrub-Jay's natural population fluctuations, and little is known about how adult survivorship may respond to changes in vegetative community or to variation in climatic variables. Future studies of habitat-specific demography should include more detailed data on both vegetation structure and composition, to explicitly test the hypothesis that these variables affect both home range sizes and nest survival rates. Additionally, population projection modeling is needed to determine if the per-pair fecundity that I have documented for *A. insularis* is sufficient maintain a stable or growing population.

The increases in oak recruitment and area of woody vegetation that are now occurring on Santa Cruz Island is likely to be beneficial to the Island Scrub-Jay. Our research suggests that Island Scrub-Jay reproductive success may increase as vegetation regenerates. This regeneration is likely to provide additional high quality breeding habitat, may decrease nest predation rates, and may increase food resources. Further, since home range sizes were smaller in areas with denser oak habitat, it is possible that an increase in oak habitat will allow the island to support greater numbers of breeding pairs. However, it will be important to investigate the effects of vegetation regeneration on the demography, density, habitat use, and foraging behavior of potential nest predators to more clearly understand the impacts of habitat change on the Island Scrub-Jay. Additional data on the habitat-specific demography of the Island Scrub-jay will allow researchers to more precisely predict how jays may respond to changes in habitat composition and structure, and thereby develop more informed and effective management strategies for this island endemic species.

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TABLES

Table 1. AIC model selection results to predict daily survival of Island Scrub-Jay nests. AICc values, Δ AICc values, model weights (w_i), and number of parameters (K) are presented for the top 9 models (out of 32); models $> 10 \Delta$ AICc are not listed.

Model ¹	AICc	Δ AICc	K	w_i
Height, Concealment, Size, Date	1137.0	0	5	0.39
Concealment, Size, Date	1138.1	1.05	4	0.23
Height, Concealment, Size, Date, % Oak	1138.7	1.70	6	0.17
Concealment, Size, Date, % Oak	1139.8	2.72	5	0.10
Height, Concealment, Size	1141.5	4.43	4	0.04
Concealment, Size	1142.0	4.94	3	0.03
Height, Concealment, Size, % Oak	1142.8	5.79	5	0.02
Concealment, Size, % Oak	1143.4	6.35	4	0.02
Height, Date, Size	1146.9	9.87	4	0.003

¹Height = nest height; Concealment = nest concealment; Size = area of home range; Date = Julian day of clutch completion; % Oak = percent of home range covered by oak-dominated habitat.

Table 2. Beta values and 95% confidence intervals of all covariates from the top model investigating factors influencing daily nest survival in Island Scrub-Jays using program MARK. The direction column refers to whether the variable is positively or negatively related to daily nest survival.

Covariates in top model	β Values	Lower 95% C.I.	Upper 95% C. I.	Direction
Nest Height	0.08	- 0.01	0.17	+
Nest Concealment	1.13	0.48	1.78	+
Home Range Size	- 0.19	- 0.27 ⁻⁴	- 0.10 ⁻⁶	-
Julian Day of Clutch Completion	- 0.01	- 0.014	- 0.002	-

FIGURES

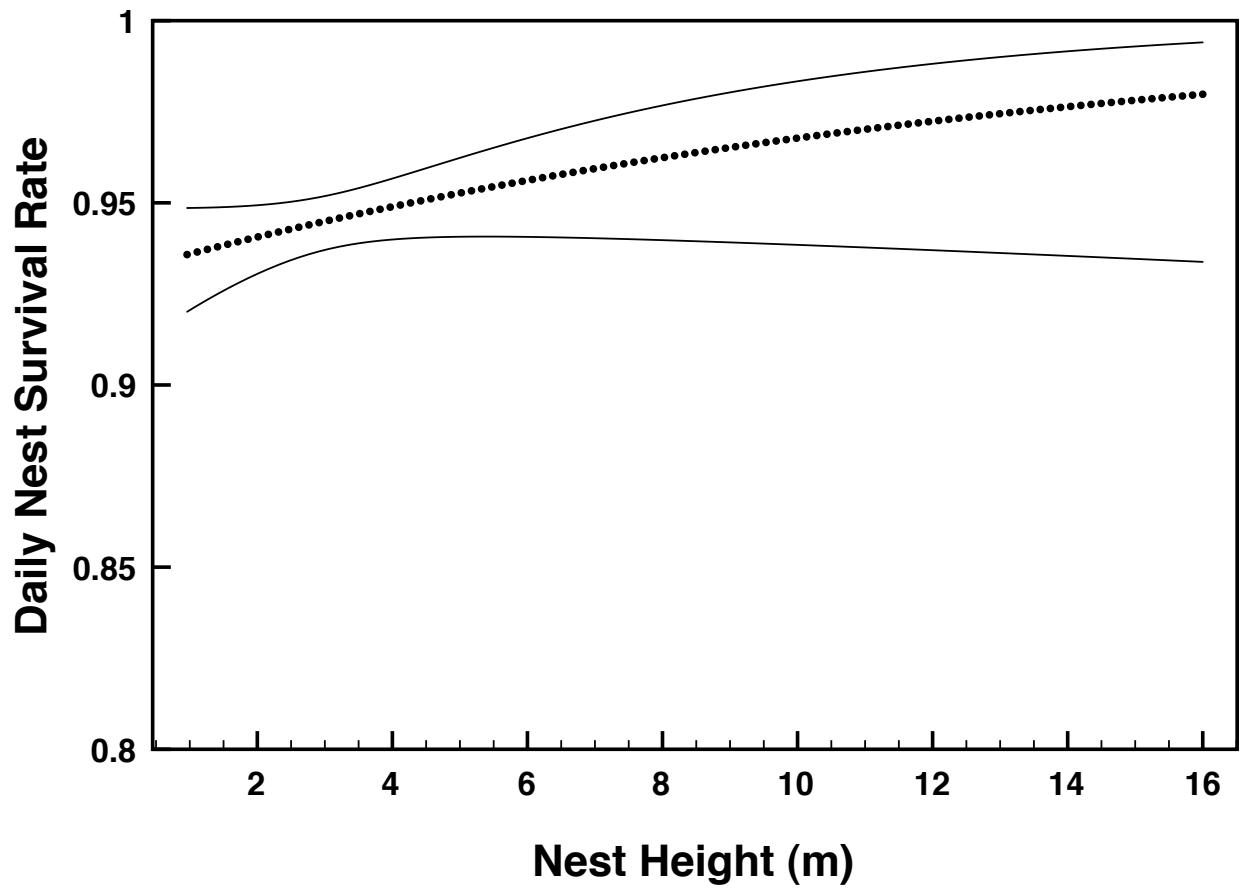


Figure 1. The effect of nest height on Island Scrub-Jay daily nest survival rate. The dashed line represents the estimated daily nest survival rate. Solid lines represent the upper and lower 95% confidence intervals.

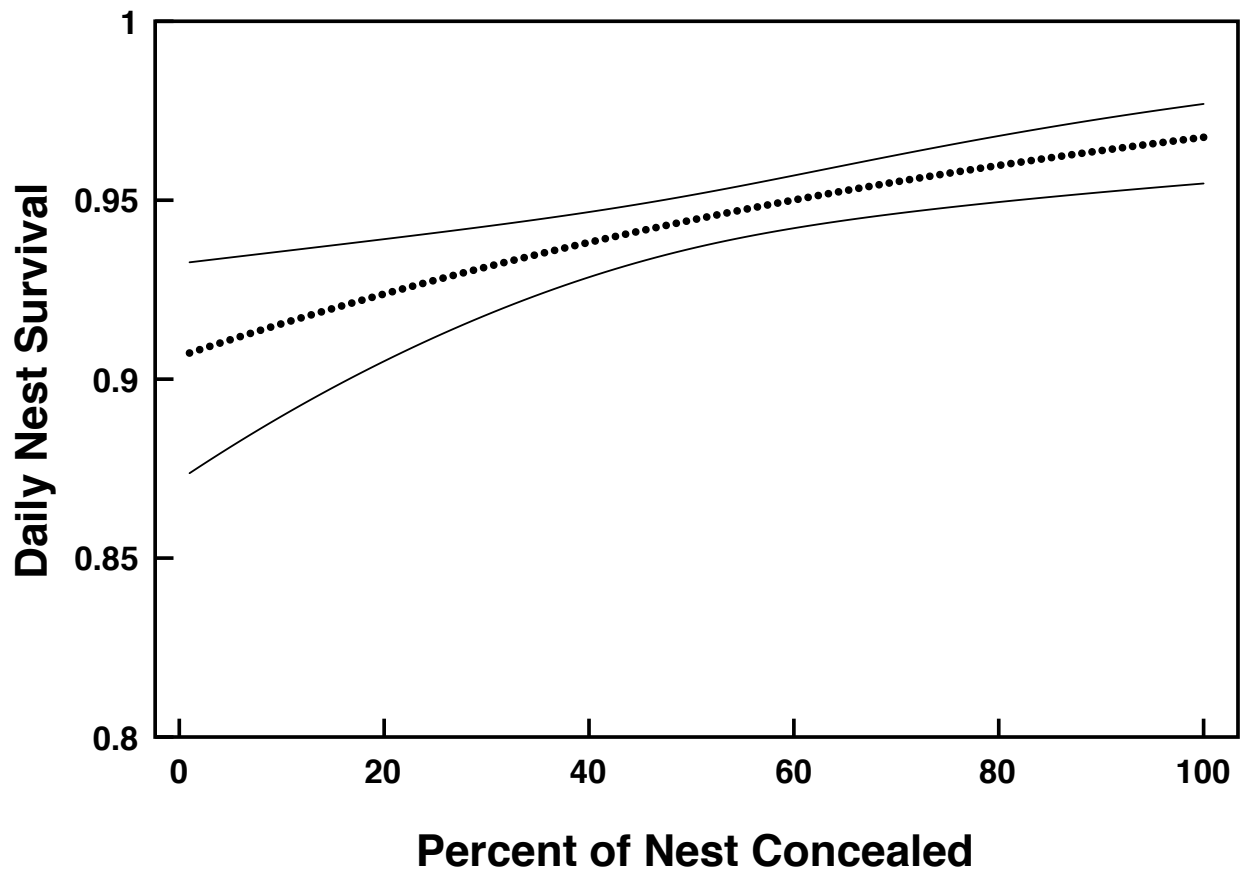


Figure 2. The effect of nest concealment on daily nest survival rate for Island Scrub-Jays. The dashed line represents the estimated daily nest survival rate. Solid lines represent the upper and lower 95% confidence intervals.

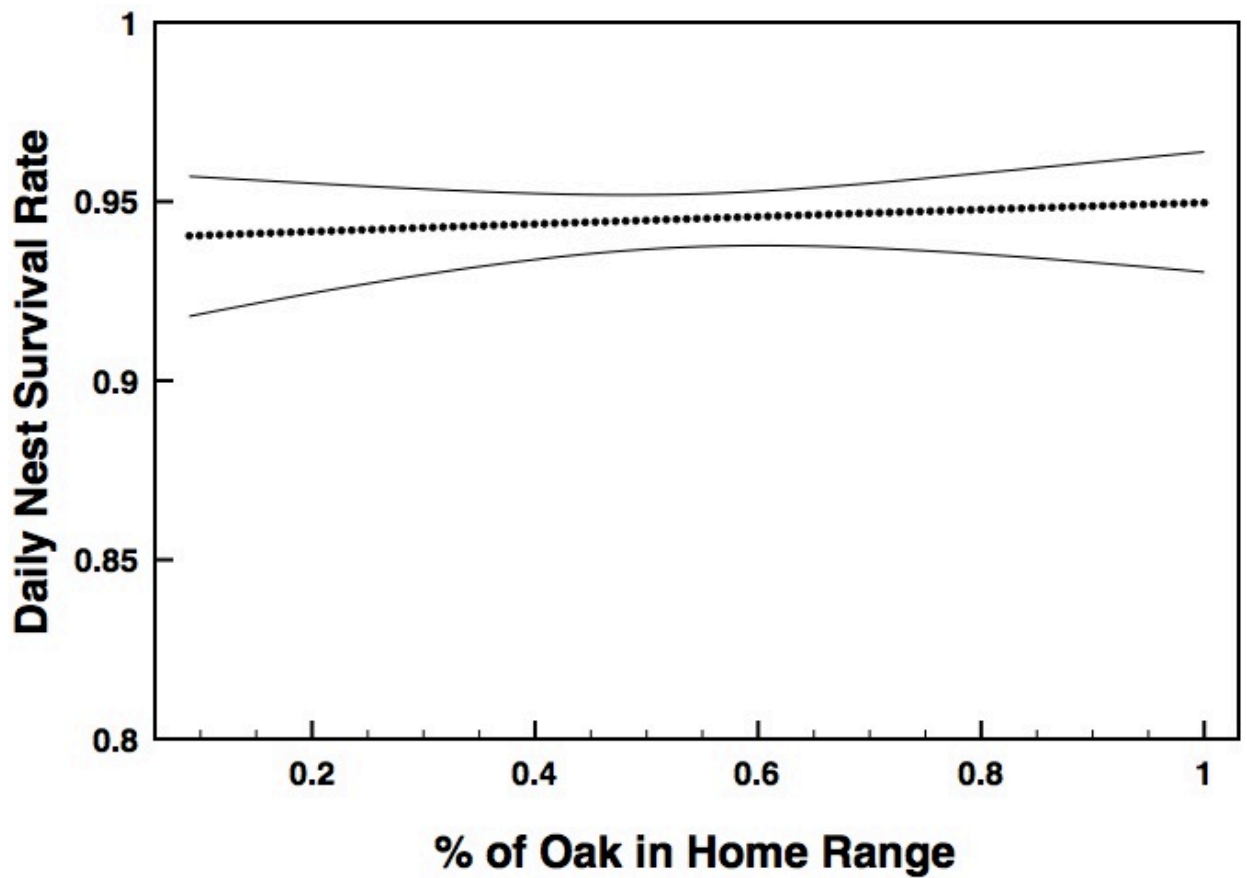


Figure 3. Effect of the percent of oak habitat in home ranges on Island Scrub-Jay daily nest survival rate. The dashed line represents the estimated daily nest survival rate. Solid lines represent the upper and lower 95% confidence intervals.

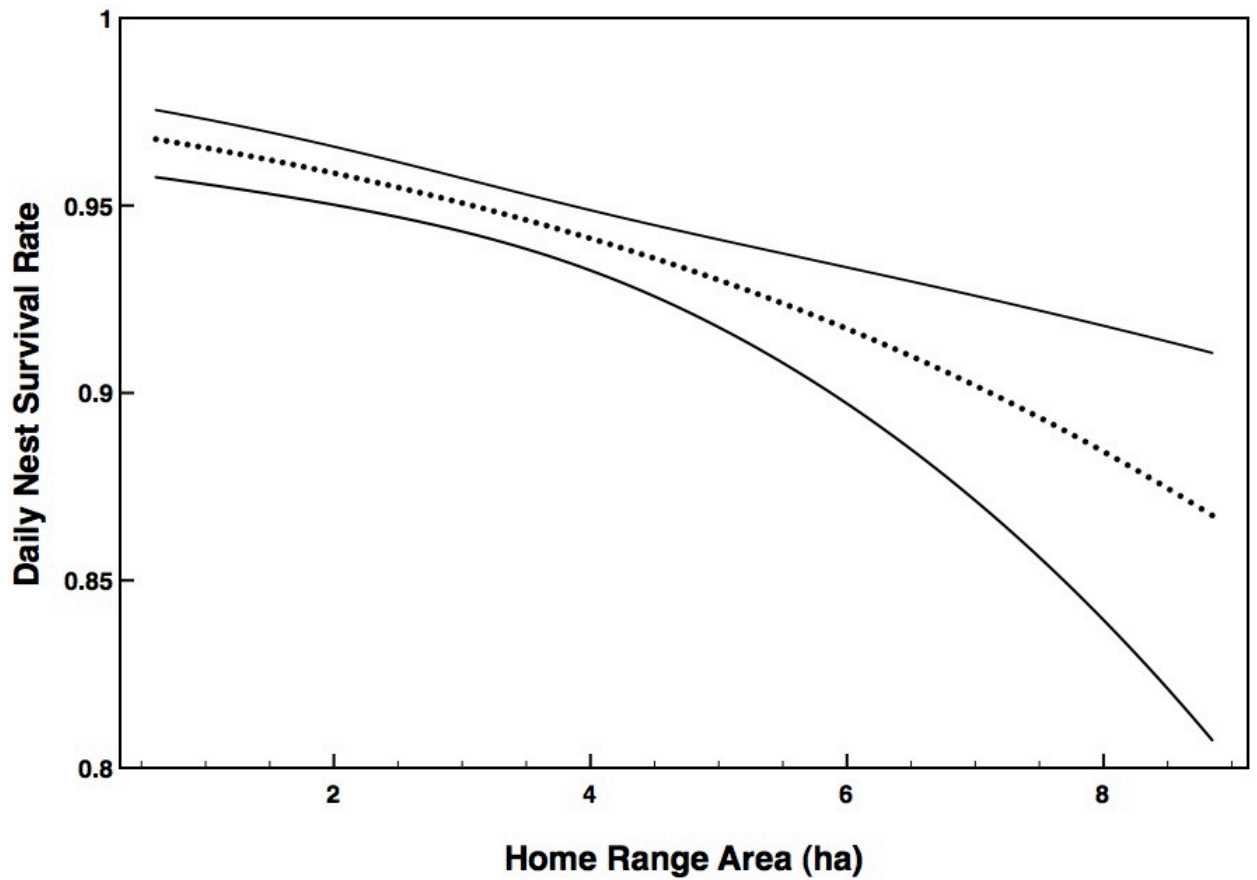


Figure 4. The effect of Island Scrub-Jay home range size on daily nest survival rate. The dashed line represents the estimated daily nest survival rate. Solid lines represent the upper and lower 95% confidence intervals.

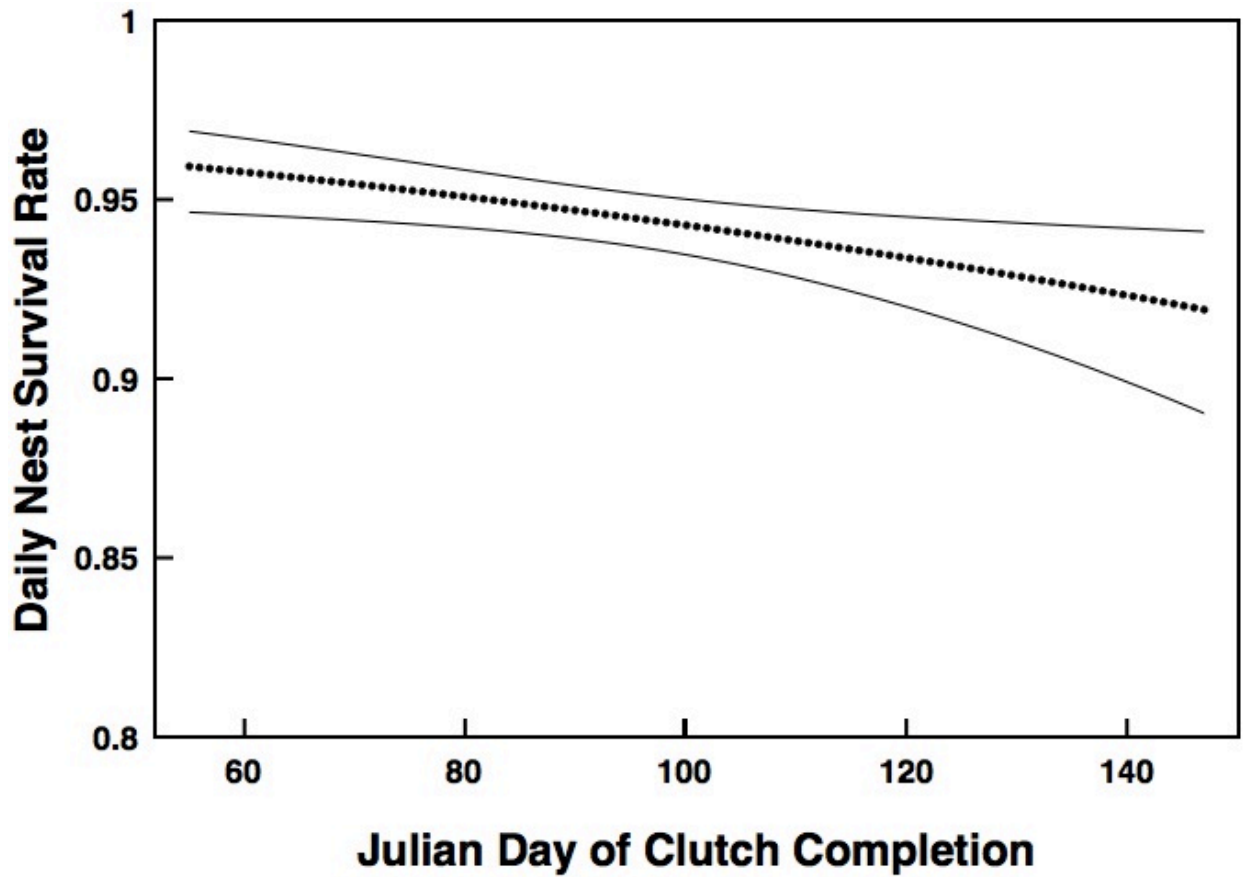


Figure 5. Effect of seasonality on the daily nest survival rate of the Island Scrub-Jay. The dashed line represents the estimated daily nest survival rate. Solid lines represent the upper and lower 95% confidence intervals.