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REPRODUCTIVE ECOLOGY OF THE ISLAND SCRUB-JAY

LUKE CALDWELL[1,4], VICTORIA J. BAKKER[2], T. SCOTT SILLETT[2], MICHELLE A. DESROSIERS[1], SCOTT A. MORRISON[3], AND LISA M. ANGELONI[1]

[1]*Department of Biology, Colorado State University, Fort Collins, CO 80523*
[2]*Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, MRC 5503, Washington, DC 20013-7012*
[3]*The Nature Conservancy, 201 Mission St, 4th Floor, San Francisco, CA 94105*

Abstract. We investigated the reproductive ecology of the Island Scrub-Jay (*Aphelocoma insularis*), which is endemic to Santa Cruz Island, California, and is a species of conservation concern. We documented daily nest survival, probability of renesting, annual fledging success, and breeding behavior, and determined how these factors varied in relation to the habitat characteristics of the jays' home ranges. Clutch sizes, feeding rates, and nest attendance were not correlated with chaparral cover or with home-range size. In contrast, nest predation, which accounted for 92% of documented nest failures, was less likely at nests that were more concealed, at nests of breeding pairs with home ranges that were smaller and had a greater proportion of taller vegetation, and at nests that were initiated earlier in the breeding season. Researchers' activity near nests increased the likelihood of predation, although the effect diminished with a nest's age. Despite relatively low nest survival, the high frequency of renesting allowed pairs to fledge an average of 1.1 ± 0.1 young per year, or 1.8 ± 0.2 young after the effects of the observer were accounted for. Currently, chaparral habitats on Santa Cruz Island are regenerating following the removal of exotic herbivores. This regeneration could in turn increase and improve breeding habitat for this island endemic.

Key words: Aphelocoma insularis*, California, habitat-specific demography, nest survival, observer effects, reproductive ecology, Santa Cruz Island.*

Ecología Reproductiva de *Aphelocoma insularis*

Resumen. Investigamos la ecología reproductiva de *Aphelocoma insularis*, una especie endémica de la Isla Santa Cruz, California, cuyo estado de conservación es preocupante. Documentamos la supervivencia diaria del nido, la probabilidad de anidación repetida, el éxito anual de emplumamiento y el comportamiento de cría, y determinamos cómo estos factores variaron en relación con las características del hábitat del rango de hogar de *A. insularis*. El tamaño de la nidada, las tasas de alimentación y la asistencia del nido no estuvieron correlacionados con la cobertura del chaparral o con el tamaño del rango de hogar. En contraste, la depredación del nido, la cual representó el 92% de los fracasos documentados del nido, fue menos probable en los nidos que estuvieron más ocultos, en los nidos de parejas reproductivas con rangos de hogar que fueron más pequeños y tuvieron una mayor proporción de vegetación más alta, y en nidos que fueron iniciados más temprano durante la estación reproductiva. La actividad de los investigadores cerca del nido aumentó la probabilidad de depredación, aunque el efecto disminuyó con la edad del nido. A pesar de la baja supervivencia del nido, la alta frecuencia de la anidación repetida le permitió a las parejas emplumar un promedio de 1.1 ± 0.1 pichón por año, o 1.8 ± 0.2 pichón luego de que los efectos del observador fueron tenidos en cuenta. Actualmente, los hábitats de chaparral en la Isla Santa Cruz están regenerándose luego de la remoción de los herbívoros exóticos. Esta regeneración podría a su vez aumentar y mejorar el hábitat reproductivo para este endemismo insular.

INTRODUCTION

Unbiased estimates of habitat-specific demographic rates are essential for predicting population trajectories and for effectively managing natural populations (Bradbury et al. 2001, Benson et al. 2010). Habitat-specific demographic rates are especially important for managing species that face an elevated risk of extinction due to small population sizes, habitat change, human-induced catastrophes (e.g., fire, disease), and pressure from exotic species (Frankham 1998, Blackburn et al. 2004, Whittaker and Fernandez-Palacios 2008). The Island Scrub-Jay (*Aphelocoma insularis*) is such a species of conservation concern (USFWS 2008, BirdLife International 2012). This island endemic is currently restricted to Santa Cruz Island, a 250-km^2 island off the coast of southern California (Curry and Delaney 2002); its total population numbers less than 2500 individuals (Sillett et al. 2012). Existing and emerging threats to long-term persistence, such as West Nile virus

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[4]E-mail: lukecaldwell@hotmail.com

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(Boyce et al. 2011), underscore the importance of robust population monitoring and modeling (Morrison et al. 2011).

Island Scrub-Jays are relatively long-lived, nonmigratory, and maintain territories year round in chaparral dominated by oaks (Atwood 1980a, b, Atwood et al. 1990), particularly island scrub oak (*Quercus pacifica*). Like other species of *Aphelocoma* (Woolfenden and Fitzpatrick 1984, Carmen 2004, McCormack and Brown 2008), *A. insularis* is an oak mutualist, and its density is positively associated with the density of chaparral (Sillett et al. 2012). *Aphelocoma* species use scatter hoarding to store acorns for later consumption, a behavior that plays an important role in oak dispersal (Bossema 1979, Carmen 2004). Chaparral is becoming more extensive on the island following the removal of introduced sheep (*Ovis aries*), pigs (*Sus scrofa*), and cattle (*Bos taurus*) within the last 30 years (Klinger et al. 1994, Peart et al. 1994, Morrison 2011). Expansion of native vegetation, especially chaparral, may have resulted in a 20–30% increase in the Island Scrub-Jay population since the 1980s (Sillett et al. 2012).

Here, we provide the first estimates of habitat-specific nest success and per capita fecundity for the Island Scrub-Jay and address three objectives: (1) quantify the jay's breeding ecology and parental behavior at the nest; (2) evaluate whether attributes of the nest site and home range influence parental behavior, daily nest survival, probability of renesting, and productivity; and, (3) evaluate and account for age and temporal and observer effects in nest survival and overall fecundity estimates. This information is needed to assess the species' long-term population viability in light of the extensive ecological changes occurring on Santa Cruz Island. Atwood (1980b) indicated that Island Scrub-Jays experienced high rates of nest predation from a suite of native species including the gopher snake (*Pituophis catenifer*), yellow-bellied racer (*Coluber constrictor*), western spotted skunk (*Spilogale gracilis*), island fox (*Urocyon littoralis*), Common Raven (*Corvus corax*), and Island Scrub-Jay. We therefore focused on identifying the factors that affect the probability of survival of the jay's nests, such as vegetative characteristics of the nest site and home range, time of year (Verhulst et al. 1995, Siikamäki 1998, Sperry et al. 2008), and nest age or stage (Burhans et al. 2002, Grant et al. 2005). We also examined effects of the presence of a human observer at nests (Rotella et al. 2000, Ibáñez-Álamo and Soler 2010, Carey 2011). Finally, we assessed whether the success of a prior nest attempt, seasonal timing, habitat factors, and observer effects influenced the probability that a pair renests.

METHODS

STUDY SITES

Santa Cruz Island (34° 0′ N, 119° 45′ W) is located approximately 39 km off the coast of Santa Barbara, California, and is the largest of the eight California Channel Islands. The Nature Conservancy owns 76% of the island; the U.S. National Park Service owns the remainder. The island has two rugged mountain ranges that flank a central valley, which marks a fault. The climate is Mediterranean, characterized by cool, wet winters and hot, dry summers. Mean annual precipitation in the central valley is 50 cm (Fisher et al. 2009). We established three study plots on the island (Fig. 1; see Appendix 1 for

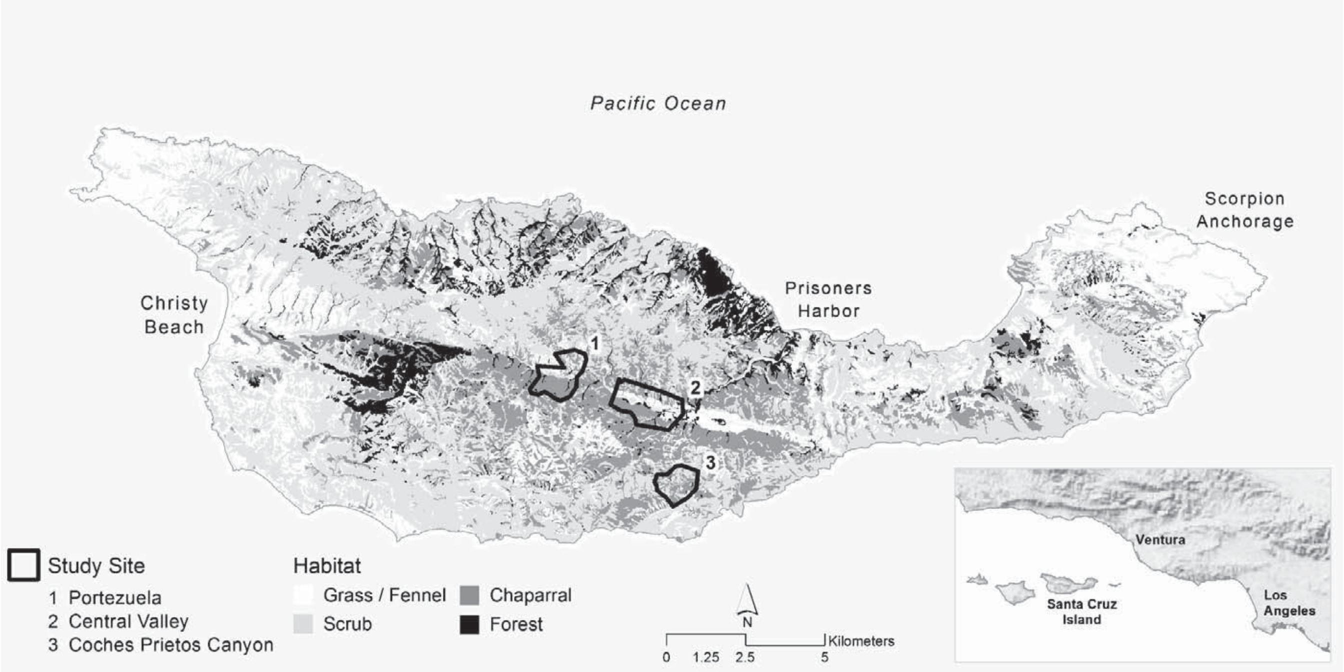

FIGURE 1. Map of Santa Cruz Island, California, showing the three study plots and habitat distribution.

individual home ranges, available at http://dx.doi.org/10.1525/cond.2013.120028): Central Valley (226 ha), which encompasses the study area used by Charles T. Collins and students from the late 1970s through the early 2000s (see references in Curry and Delaney 2002), Coches Prietos Canyon (115 ha), and Portezuela (163 ha). We selected these plots because they encompass a representative gradient of the island's chaparral, which allowed us to assess the effects of habitat characteristics on reproductive success. This gradient ranges from relatively open areas dominated by grassland and coastal sage scrub with isolated patches of chaparral to areas of continuous chaparral cover and little to no grassland and scrub. Within each plot, we studied a minimum of 15 territorial pairs through the breeding season (February–June) in 2008, 2009, and 2010. We captured Island Scrub-Jays opportunistically with box traps and mist nets, each baited with peanuts. We marked each jay with a unique combination of up to four colored plastic leg bands and one numbered aluminum U.S. Geological Survey leg band.

NATURAL HISTORY, NEST OBSERVATIONS, AND PRODUCTIVITY

We attempted to locate and monitor all nesting attempts by each focal pair. During the course of this study, we found 352 nests of 88 pairs. We determined the fate of each nest (whether it failed to fledge young or successfully fledged at least one young) by inspection of the nest, by the adults' behavior, and by visual confirmation of fledglings. To ensure that we found all attempts at second or replacement nests, we monitored breeding pairs after a nest fledged or failed. We periodically flushed incubating females from nests to confirm clutch sizes and the number of nestlings; using a mirror mounted on an extendable pole to check high or otherwise inaccessible nests, and we climbed a small number of nest trees. We checked nests approximately once every three days, except near hatching and fledging, when we monitored a subset of nests daily to determine the lengths of those pairs' incubation and nestling periods. Overall, check intervals were sufficiently variable to allow for the assessment of observer effects. We weighed 33 nestlings from 10 nests between 10 and 13 days after hatching. We averaged the masses of all nestlings in each nest and then averaged across all 10 nests to determine the nestlings' mean mass.

We recorded nest height, nest concealment, and nest substrate after a nest failed or after young had fledged. We estimated the proportion of the nest concealed by vegetation at a distance of 1 m in the four cardinal directions (from a standardized height of 1 m), from directly underneath the nest, and from above as the proportion of sky directly over the nest that was concealed by vegetation. The mean of these six measures served as our index of nest concealment.

We used digital video recordings to document adults' behavior and nest predation during the incubation and nestling periods. We placed video cameras a minimum of 3 m away to minimize disturbance to the jays, and we observed birds for 20 min to ensure that they accepted cameras. When adults did not return to a nest within 20 min ($n = 13$), we moved the camera farther away or removed it entirely. We recorded incubation behavior between days 6 and 8 following clutch completion (early stage, $n = 27$) and once between days 14 and 16 (late stage, $n = 33$). After hatching, we recorded nests once between days 6 and 8 (early stage, $n = 32$) and again between days 14 and 16 after hatch (late stage, $n = 24$). All recordings were initiated within 15 min of sunrise and lasted 5 hr. We transcribed videos to quantify nest attendance (the proportion of time a female incubated or brooded) and hourly feeding rates per nestling (the number of feeding trips by both adults per hour divided by the number of nestlings).

HOME RANGE AND HABITAT COMPOSITION

We determined home ranges for each pair on the basis of point-location data recorded weekly over approximately 15 weeks during each breeding season. To minimize disturbance, we mapped locations relative to the GPS location of the observer by using a compass and laser rangefinder to record the angle and distance to the bird. Points were taken once every 5 min for 20 min; we measured a maximum of five locations per day to minimize temporal bias; all locations were taken between 05:30 and 17:00. We used these points to create a 95% and a 100% minimum convex polygon in ArcMap software (ESRI 2009) to delineate the home range of each breeding pair. We used only the 100% polygon estimates of home range in analyses because we found little difference between the two measures, likely because the Island Scrub-Jay's movements during the breeding season are highly localized. Though we followed 88 breeding pairs over our 3-year study, we used 129 home ranges in our analyses of home-range size and habitat composition. This larger number resulted from shifts of home ranges' boundaries from year to year. When the home range of a given pair shifted such that ≥25% of the area was not overlapping the range of the previous year, we designated a new home range for separate inclusion in our analyses. In the few instances ($n = 7$) where <50 data points were recorded, we supplemented data with locations recorded opportunistically in field notes.

We calculated habitat composition within the home range of each breeding pair (see Appendix 2 for habitat types) in ArcMap on the basis of vegetation data recorded in 2005 (Cohen et al. 2009). We calculated mean canopy height (± 7 cm) for each vegetation polygon based on 1-m resolution from LiDAR data recorded and verified in 2010 (Channel Islands National Park, unpubl. data). We estimated the mean canopy height in each home range as the area-weighted average of the mean canopy height for each vegetation polygon within the home range. Similarly, we estimated the proportion of the home range with canopy heights greater than 1 m or 2 m as the proportion of the home range consisting of vegetation polygons with mean heights greater than 1 m or 2 m, respectively.

STATISTICAL ANALYSES

To evaluate whether nest age, observation intensity, or characteristics of the nest site and home range influenced nest survival, we modeled the daily survival rate (DSR) of nests with generalized linear mixed models and a logit link function in Proc NLMIXED software (SAS Institute 2008), using the methods of Rotella et al. (2004, 2007). We tested for seasonal trends in daily nest survival by using days after the earliest initiation of breeding for any of the years of our study (25 February, hereafter "days into season" or *SeasonDay*) as a covariate. We found more support for an effect of nest-attempt number than for days into season, but used days into season in the final analyses because nest-attempt number was not known for all pairs.

Our iterative approach to model building consisted of first evaluating the fit of observer effects, then evaluating the role of home-range and nest-site attributes, and finally building models with all appropriate covariate types. We used a series of binary variables to classify our field methods for collection of survival data at the nest, each coded as 1 or 0 for every day of the nesting cycle: any observation of the nest (*Observed*), whether the female was flushed off the nest (*Flushed*), and whether the nest was examined with an extendable mirror pole, the chicks were handled, the nest tree was climbed, or the nest was videotaped (collectively, *PHCV*). Computationally, observer effects can be estimated when there is variation in the number of days between nest checks (Rotella et al. 2000, 2004, 2007). We modeled observer effects by assessing whether the DSR at *Observed* nests was lower on the day of observation. We also evaluated models in which the more intrusive effects, *Flushed* and/or *PHCV*, were considered additively with *Observed* effects (Appendix 3). We evaluated interactions of observer effects with nest stage (*Stage*) and age of nest (*NestAge*) by considering interactions across the entire interval of nesting, and, if stage-specific interactions were supported, by also considering effects applied only to the egg or nestling stages. Proc NLMIXED allowed inclusion of one random effect, and we considered year and the male's identity (i.e., its unique color-band combination) in separate analyses; the latter helped account for repeated measures of nests attempted by the same male (and usually the same paired female) within and across years, often within approximately the same home range. After identifying the best-fit model of observer effects, we screened potential attributes of the home range, including size (*HRsize*), proportion of chaparral cover (*Chaparral*), mean canopy height (*CanHt*), and proportion with canopy height >2 m (*Prop2*) and >1 m (*Prop1*), with and without interactions with *SeasonDay*, *NestAge*, and *Stage* to identify the best predictor variables and model forms. We assessed nest-site attributes (nest concealment, or *Conceal,* and nest height, or *Height*) similarly. Finally, we built the full model, using the best models of observer, nest-site, and habitat effects, along with days into season in all additive combinations. We also considered an intercept-only model. We followed an information theoretic approach, using Akaike's information criterion (AIC) to guide model selection, and ranked models using second-order AIC adjusted for small sample sizes (AIC_c, Burnham and Anderson 2002). We assessed the goodness of fit of the nest-survival models by the test statistic of Sturdivant et al. (2007).

We used an analogous approach to assess predictors of renesting with Proc GLIMMIX software (SAS Institute 2008). This modeling focused on habitat characteristics within the home range as well as observation intensity and nest fate for the current attempt (expressed by the binary variable *Fledged*). We did not consider nest-site factors in this analysis. Models for subsequent nests were also ranked with AIC_c.

We calculated several additional metrics to summarize the reproductive effort, clutch size, and fecundity of breeding pairs. For pairs for which all reproductive attempts were known, we estimated the mean number of nests attempted per pair per breeding season and the mean number of eggs laid per female per breeding season as measures of reproductive effort. We estimated mean clutch size from nests for which we had complete clutch data. We estimated observed mean annual fecundity per pair by averaging the number of young fledged over the breeding season by the number of pairs whose annual 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. We can know definitively whether a pair fledged offspring because the juvenile plumage is distinct, young stay in their parents' home range for several weeks to months after fledging, and they continue to be fed by their parents (Atwood 1980a, Curry and Delaney 2002).

We estimated corrected fecundity after accounting for observer effects. To do so, we used the mean duration of each stage for successful nests, the estimated mean lag between failure of a nest and the first egg in the next nest attempted, a breeding season of 130 days, and the mean number of fledged young per successful nest. Then, following Grzybowski and Pease (2005), we numerically simulated nesting and renesting throughout the nesting season with or without human observation and flushing of adults from nests, holding habitat factors at their observed means. We allowed demographic stochasticity in all rates, and incorporated parameter uncertainty in model coefficients and lag times before renesting. We report the mean nest success and fecundity from these simulations ($n = 100\,000$ runs).

Last, we determined whether attributes of each pair's home range affected clutch size and whether attributes of both the home range and the nest site affected parental behavior. We tested for the effect of the total area of chaparral habitat in each home range on the size of the first clutch of each pair by assuming a Poisson distribution for clutch size, and we modeled clutch size by using a generalized linear model with a log-link function in JMP software (SAS Institute 2010).

This analysis tested the hypothesis that variation in clutch size was related to total area of chaparral habitat in a home range, which we considered to be a proxy for food availability because Island Scrub-Jays forage predominantly in chaparral and jay density is positively correlated with amount of chaparral cover (Sillett et al. 2012). To understand the factors affecting nest attendance during the incubation period, we used a model based on multiple linear regression to test for effects of home-range size, total area of chaparral in the home range, mean canopy height within the home range, and nest concealment. We also used a multiple linear regression model to determine whether these four independent variables affected the rates at which nestlings were fed. We used separate regression models for early and late nestling periods. We report mean values ± 1 SE.

RESULTS

NATURAL HISTORY

Male and female Island Scrub-Jays built nests jointly, and no cooperative breeding was observed. Twigs of woody plants formed the nest's outer cup, 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 animal hair was sometimes incorporated in the nest lining. Adults occasionally made incomplete nests, as seen in other species of *Aphelocoma* (Woolfenden and Fitzpatrick 1996), and on one occasion we observed the reuse of a completed nest from a prior year. Only females incubated and brooded young, and both adults fed nestlings. Jays built nests in a variety of plant species, with oak being used most commonly (61%), followed by toyon (*Heteromeles arbutifolia*) (10%), lemonade berry (*Rhus integrifolia*) (5%), California lilac (*Ceanothus arboreus*) (4%), mountain mahogany (*Cercocarpus betuloides*) (3%), and 13 other woody species. Mean nest height was 3.1 ± 0.1 m ($n = 323$, range 0.8–16 m).

Breeding pairs occupied home ranges ($n = 129$) that varied widely in size, canopy height, and coverage of chaparral. The mean size of a home range was 3.5 ± 0.2 ha (range 0.4–8.9 ha), and the average area of chaparral in home ranges was 2.1 ± 0.1 ha (range 0.2–6.2 ha), or 63% ± 2% (range 9–100%). The mean height of the canopy within home ranges was 1.2 ± 0.1 m (range 0.2–4.9 m), while the mean percentage of habitat with canopy height >2 m was 18% ± 2% (range 0–100%).

Five species were recorded on video or observed depredating Island Scrub-Jay nests: the island fox ($n = 1$), Cooper's Hawk (*Accipiter cooperii*, $n = 1$), Common Raven ($n = 1$), gopher snake ($n = 1$), and Island Scrub-Jay ($n = 4$). These few cases where the predator could be identified represent a small fraction of all nests that were depredated; in cases where the predator was not seen, identifying the predator from the condition of the nest (Thompson and Burhans 2003) was not possible, preventing us from assigning an overall proportion of cases of predation to any particular class of predator. In two of the instances of conspecific nest predation, the predator was confirmed as the male of the territorial pair, suggesting that the adults had abandoned the nest and simply consumed their own eggs. Because we observed this cannibalism immediately after checking the nest, it may have been the result of disturbance at the nest during the early laying or incubation stage when parental investment is minimal. Circumstantial evidence that Bewick's Wrens (*Thryomanes bewickii*) destroyed nests consisted of four jay nests found with punctured eggs, and wrens are known to cause failures of other birds' nests by puncturing the eggs (Picman 1992).

We quantified the length of nesting stages and adults' behavior at the nest. Mean duration of the incubation period was 18.3 ± 0.2 days ($n = 22$ nests, range 17–21 days), and mean duration of the nestling period was 22.5 ± 0.5 days ($n = 21$ nests, range 19–27 days). Mean nest attendance (proportion of time females brooded) during incubation was 0.79 ± 0.03 ($n = 49$). Mean nest attendance during the early and late nestling periods was 0.45 ± 0.05 ($n = 32$) and 0.07 ± 0.03 ($n = 24$), respectively. The adults' average visitation rate per hour was 1.1 ± 0.2 ($n = 49$) during incubation, 2.7 ± 0.3 ($n = 32$) during the early nestling period, and 3.3 ± 0.3 ($n = 24$) duirng the late nestling period. Mean mass of nestlings 10– 13 days old was 64.5 ± 3.7 g ($n = 33$ nestlings from 10 nests; range 39.8–95.1 g).

NEST SURVIVAL AND PROBABILITY OF RENESTING

Fifty-five of 352 nests found successfully fledged at least one young; 16 nests were never completed; 46 were completed but were never observed with eggs; and the remaining 235 nests failed during the egg or nestling stage. The major cause of failure during the egg or nestling stages was predation (92%), followed by abandonment (6%), death of the adults (0.9%), and failure of the substrate (0.4%). We used 254 nests for analyses of daily nest survival and probability of renesting and excluded those that failed for unknown reasons, i.e., the 16 nests that were incomplete and the 46 nests that never had eggs, and those for which we did not measure all nest-site and home-range variables. We made 1467 total observations of these 254 nests ($\bar{x} = 5.7$ per nest), checked at a mean frequency of 2.9 days (range 1–21 days).

Our observation of nests lowered their DSR (Table 1). The best-supported observer-effects model contained negative consequences of nest observation (of any type) and of flushing during the egg stage. However, the negative effects of observation and flushing of females diminished as the nest aged, over time making the DSR of observed nests more similar to that of unobserved nests (Fig. 2). A model that applied an effect of flushing across the entire nesting period had similar support but predicted greater survival for nests at which the female was flushed than for those where she was not; we rejected this model as biologically implausible on the basis of our

TABLE 1. Results of selection of models predicting daily survival of Island Scrub-Jay nests on the basis of observer effects and nest age. Shown are the 12 highest-ranked models and the intercept-only model. Column headings give model notation, number of estimable parameters (*K*), differences in second-order Akaike's information criterion (ΔAIC_c), and AIC_c weights (w_i). Variables considered were *Observed* (indicating nest observation by any method), *Flushed* (indicating female was flushed off nest), *PHVC* (indicating disturbance of the nest by mirror pole, handling of eggs or nestlings, videotaping of nest, or climbing of nest tree), *NestAge* (starting at day 1 on day first egg laid), *Stage,* a binary variable indicating the egg or nestling stage; "/" indicates effect applied only to the egg or nestling stage. All models also include *Male ID* as a random effect. Number of nest observations = 1467, and effective sample size = 3742.

Model	K	ΔAIC_c	w_i
Observed, NestAge, Stage, Egg/Flushed, Observed × NestAge, Egg/(Flushed × NestAge)[a]	8	0.0	0.50
Observed, NestAge, Stage, Egg/Flushed, Observed × NestAge	7	1.6	0.23
Observed, NestAge, Egg/Flushed, Observed × NestAge, Egg/(Flushed × NestAge)	7	1.7	0.21
Observed, NestAge, Stage, Flushed, Observed × NestAge	7	6.5	0.02
Observed, NestAge, Stage, Flushed, PHVC, Observed × NestAge	8	7.6	0.01
Observed, NestAge, Stage, Flushed, Observed × NestAge, Observed × Stage	8	8.1	0.01
Observed, NestAge, Stage, Flushed, PHVC, Observed × NestAge, Observed × Stage	9	9.2	0.01
Observed, NestAge, Flushed, Observed × NestAge	6	10.2	0.00
Observed, NestAge, Stage, Observed × NestAge	6	11.4	0.00
Observed, NestAge, Flushed, PHVC, Observed × NestAge	7	11.4	0.00
Observed, NestAge, Stage, Observed × NestAge, Observed × Stage	7	12.7	0.00
Observed, NestAge, Stage, PHVC, Observed × NestAge	7	13.1	0.00
Intercept	2	32.9	0.00

[a] AIC_c of top model = 1128.3.

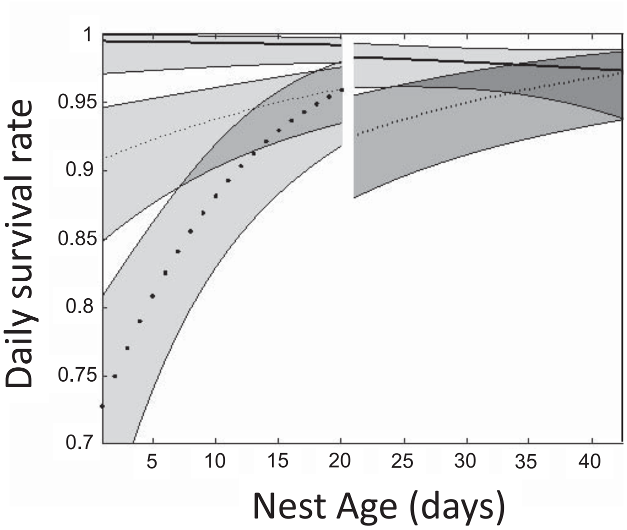

FIGURE 2. Predicted effects of human observation (dashed curve), flushing of incubating females (dotted curve), and no human presence (solid curve) on daily survival rate (DSR) of Island Scrub-Jay nests. For this graph, we specified 21 days after the first egg was laid as the hatch date, although the actual data were more variable than this. Days 1–20 represent the incubation period and days ≥21 represent the nestling period. Modeling indicated flushing affected DSR only during the egg stage. Therefore, effects of flushing are depicted only prior to day 21. Estimates of DSR (and 90% CI) are for nests initiated at the start of the breeding season and are based on parameters in Table 3, assuming the mean values for all variables. Break in plot at day 21 results from the effect of *Stage* on DSR.

observations of predators' behaviors. Fitting of the effect of flushing at the nestling stage was based on very few data points (instances of flushing during the nestling stage were few), and an effect of flushing was not supported if nestling-stage data were analyzed separately.

In the initial screening of candidate variables, the best-supported habitat effect was the proportion of home range with canopy heights >2 m (*Prop2*) and *Prop2* × *SeasonDay* (Appendix 4). We used the model with this structure in building the full model (see below). An effect of home-range size on DSR was supported without interactions with any habitat variables. The support for proportion of home range covered by chaparral (*Chaparral*) was weakly improved by an interaction with age of nest, and we considered models with and without this interaction in building the final model. Nest concealment was statistically supported as a nest-site effect, but we found no support for nest height, which we did not consider in the full model (Appendix 5).

Overall, the best-supported model of DSR included nest-initiation date, i.e., days into season (*SeasonDay*), home-range size (*HRsize*), nest concealment (*Conceal*), proportion of canopy height >2 m (*Prop2*) and *Prop2* × *SeasonDay* (Tables 2 and 3). Greater nest concealment increased DSR (Fig. 3a) while a larger home range decreased DSR (Fig. 3b). Similarly, *Prop2* increased DSR (Figs. 4a, b), while advancing *SeasonDay* decreased DSR (Figs. 4c, d), but the two variables interacted with each other: the importance of canopy height was greater later in the breeding season. Although the method of Sturdivant et al. (2007) to assess goodness of fit cannot incorporate observer effects, the

TABLE 2. Results of selection of models predicting probability of daily survival of Island Scrub-Jay nests on the basis of nest-site and habitat factors. See Table 1 for descriptions of column headings. All models considered included ObsEffect, the best model from Table 1 (*Observed, NestAge, Stage, Egg/Flush, Observed × NestAge, Egg/Flush × NestAge*), except for the intercept only-model, and all include *Male ID* as a random effect. Variables considered were *Conceal* (mean nest concealment), *HRsize* (home range size), *Prop2* (proportion of the home range with canopy height >2 m), *SeasonDay* (number of days into season starting 25 February), and *Chaparral* (proportion of the home range covered by chaparral). Number of nest observations = 1467; effective sample size = 3742. Shown are the 12 highest-ranked models, out of 60, and the ObsEffect and intercept-only models.

Model	K	ΔAIC_c	w_i
SeasonDay, HRsize, Prop2, Prop2 × SeasonDay, Conceal[a]	13	0.0	0.40
SeasonDay, HRsize, Prop2, Chaparral, Prop2 × SeasonDay, Conceal	14	1.0	0.24
SeasonDay, HRsize, Prop2, Chaparral, Prop2 × SeasonDay, Chaparral × NestAge Conceal	15	1.6	0.18
SeasonDay, HRsize, Prop2, Conceal	12	3.5	0.07
SeasonDay, HRsize, Prop2, Chaparral, Conceal	13	4.5	0.04
SeasonDay, Prop2, Chaparral, Prop2 × SeasonDay, Conceal	13	6.7	0.01
SeasonDay, Prop2, Prop2 × SeasonDay, Conceal	12	6.8	0.01
SeasonDay, HRsize, Prop2, Prop2 × SeasonDay	12	8.1	0.01
SeasonDay, HRsize, Prop2, Chaparral, Prop2 × SeasonDay	13	8.3	0.01
HRsize, Prop2, Chaparral, Chaparral × NestAge, Conceal	13	8.8	0.00
HRsize, Prop2, Conceal	11	8.9	0.00
HRsize, Prop2, Chaparral, Conceal	12	9.5	0.00
ObsEffect	8	32.3	0.00
Intercept	2	65.5	0.00

[a] AIC_c of top model = 1096.0.

fit of the best model, excluding observer effects, was acceptable (cubic kernel $Z\hat{s} = -0.40$, $P = 0.688$). On the basis of the relative weights of the variables' importance, *Prop2* ($w_i = 0.99$), *Prop2 × SeasonDay* ($w_i = 0.86$), *HRsize* ($w_i = 0.96$), *Conceal* ($w_i = 0.98$), and *SeasonDay* ($w_i = 0.98$) were all highly important predictors of daily nest survival, and we found some support for *Chaparral* ($w_i = 0.50$) and the interaction *Chaparral × NestAge* ($w_i = 0.19$). After negative observer effects were statistically removed, the estimate of DSR was 0.98 ± 0.01 for nests with mean nest-site and habitat conditions and initiated at the beginning of the breeding season, averaged over the mean nesting period of 44 days (we considered the nesting period to start the day the first egg was laid). The estimated overall probability of nest survival, after observer effects were removed, for a nest with mean nest site and habitat conditions and initiated at the start of the breeding season was 0.42 ± 0.13.

The best-supported model for probability of renesting (Appendices 6 and 7) included a strong negative effect of

TABLE 3. Parameter estimates (β) for the best-supported model (Table 2) predicting the daily survival rate of Island Scrub-Jay nests. See Tables 1 and 2 for descriptions of variables; df = 78.

Parameter	Estimate	Standard error	t	$P > \lvert t \rvert$	Lower 95% CI	Upper 95% CI
Intercept	5.298	1.103	4.80	<0.0001	3.102	7.493
Observed	–3.015	1.263	–2.39	0.0194	–5.529	–0.501
NestAge	–0.024	0.033	–0.73	0.4665	–0.090	0.041
Stage	–0.654	0.357	–1.83	0.0709	–1.365	0.057
Egg/Flushed	–1.383	0.369	–3.74	0.0003	–2.118	–0.647
Observed × NestAge	0.070	0.038	1.82	0.0722	–0.006	0.147
Egg/(Flushed × NestAge)	0.070	0.032	2.15	0.0348	0.005	0.134
SeasonDay	–0.015	0.004	–3.61	0.0005	–0.023	–0.007
Conceal	1.109	0.349	3.18	0.0021	0.414	1.804
HRsize	–0.151	0.049	–3.05	0.0031	–0.250	–0.053
Prop2	–0.792	0.871	–0.91	0.3657	–2.526	0.941
Prop2 × SeasonDay	0.040	0.016	2.47	0.0156	0.008	0.072
MaleID (random effect)	0.151	0.131	1.16	0.2513	–0.109	0.412

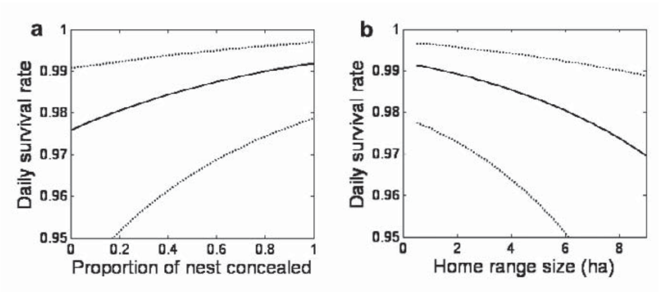

FIGURE 3. Relationship between environmental variables and daily survival rate (DSR) for Island Scrub-Jay nests during the incubation stage. Plots depict the influence of (a) nest concealment (Conceal), and (b) home-range size (HRsize) on DSR for a 20-day-old nest, 60 days into the breeding season. Estimates of DSR (and 90% CI) are based on parameters in Table 3, assuming no nest observation or flushing, and all other variables at their mean values.

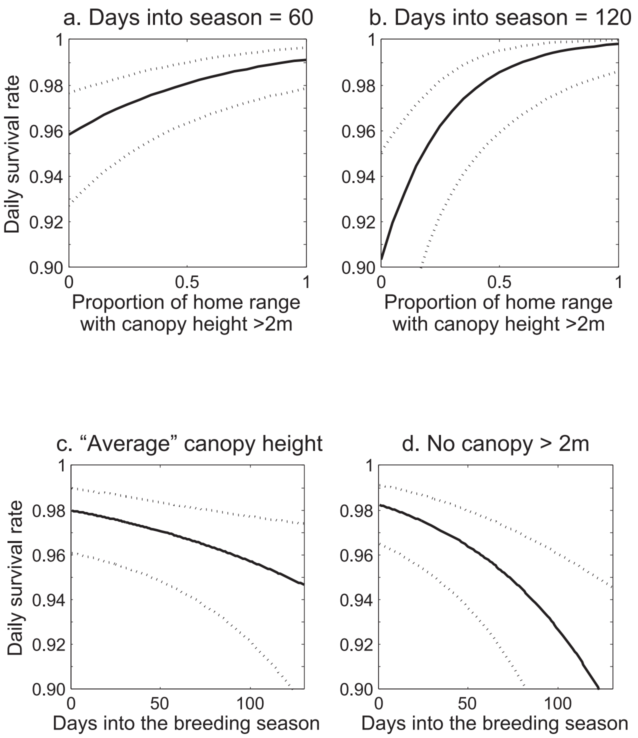

FIGURE 4. Relationship between environmental variables and daily survival rate (DSR) for Island Scrub-Jay nests during the nestling stage. Upper plots depict the influence of the proportion of the home range with canopy height >2 m (Prop2) on DSR for nests at (a) 60 days and (b) 120 days from the start of the breeding season. Similarly, lower plots depict the influence of days into the breeding season (SeasonDay) on DSR for nests in home ranges with differing values of Prop2: (c) the mean (0.18), and (d) none. Estimates of DSR (and 90% CI) are based on the parameters in Table 3 and assume 30-day-old nests, no nest observation or flushing, and all other variables at their mean values.

success of the previous nest (*Fledged*, $w_i = 0.98$), *SeasonDay* ($w_i = 0.98$), and the age of the nest at the end of the current attempt (*NestAge*, $w_i = 0.96$). As with DSR, we found a positive effect of the proportion of the home range with canopy height >2 m (*Prop2*) ($w_i = 0.21$), which interacted with *SeasonDay* (*Prop2* × *SeasonDay* interaction $w_i = 0.16$), such that the beneficial effect of *Prop2* on probability of renesting increased as the breeding season progressed. We found little support for an effect of the intensity or number of flushes on probability of renesting ($w_i = 0.07$).

REPRODUCTIVE EFFORT AND ANNUAL FECUNDITY

The mean number of eggs laid per pair was high relative to the mean number of young fledged. The mean clutch size was 3.6 ± 0.1 ($n = 223$ nests, range 2–5 eggs), and the mean number of eggs laid per female per breeding season was 7.2 ± 0.4 ($n = 82$, range 2–18). The mean number of young fledged per successful nest was 3.2 ± 0.3 ($n = 16$ nests), and the observed mean fecundity was 1.1 ± 0.1 young fledged per pair per year ($n = 132$, range 0–5). We commonly observed attempts at renesting within days after the failure of an earlier nest (estimated mean lag from failure to first new egg = 8.3 ± 0.3 days), resulting in 2.7 ± 0.1 nests attempted per pair per year ($n = 82$ pairs, range 1–6). Renesting accounted for 41% of nests that successfully fledged young ($n = 54$ successful nests). We documented attempts at double brooding (nesting again after a previous brood fledged) in two pairs, both in 2008. Using daily nest survival and probability of renesting to extrapolate seasonal reproductive performance yielded an estimated mean probability of nest success of 0.29 ± 0.001 and a fecundity of 0.9 ± 0.1 young fledged per pair for nests observed every 3 days throughout the nesting interval and observed via flushing every 6 days during the egg stage. For an unobserved pair, the mean estimated probability of nest success was 0.56 ± 0.001 and fecundity was 1.8 ± 0.2 young fledged.

EFFECTS OF HOME-RANGE SIZE AND NEST-SITE CHARACTERISTICS ON PARENTAL BEHAVIOR AND CLUTCH SIZE

None of the home-range or nest-site variables we measured explained a statistically significant amount of variation in either clutch size or parental behavior. Nest attendance during incubation was not associated with home range-size, area of chaparral within home ranges, mean canopy height of home range, and nest concealment (whole model: $F_{4,36} = 1.95$, $P = 0.12$; nest concealment $P = 0.10$, all other $P > 0.49$). None of these covariates were significantly associated with nestling-feeding rates in the early nestling period (whole model: $F_{4,21} = 1.52$, $P = 0.23$; area of chaparral $P = 0.07$, home-range size $P = 0.07$, all other $P > 0.16$). Neither were these covariates significantly associated with the duration of the late nestling period (whole model: $F_{4,15} = 1.19$, $P = 0.36$; nest concealment $P = 0.07$, all other $P > 0.58$). We found no effect of these covariates on clutch size ($\chi^2_4 = 0.40$, $P = 0.98$; for all covariates $P > 0.50$).

DISCUSSION

The Island Scrub-Jay's fecundity was strongly limited by nest predation, the rate of which from 2008 to 2010 was higher than that documented for some mainland species of *Aphelocoma* (Carmen 2004, Woolfenden and Fitzpatrick 1996, McCormack and Brown 2008). Nevertheless, the annual, mean fecundity of the Island Scrub-Jay was comparable to that of other species of *Aphelocoma* because of the high frequency of renesting in *A. insularis*. We documented females renesting up to 6 times and laying up to 18 eggs in a single breeding season. Averaged across all pairs and years, our estimate of the Island Scrub-Jay's mean annual fecundity for breeding adults (1.1 ± 0.1, or 1.8 ± 0.2 after accounting for observer effects) was similar to that of the Western Scrub-Jay (*A. californica*; 1.2 ± 1.5, Carmen 2004) as well as that of the cooperatively breeding Florida Scrub-Jay (*A. coerulescens*; 1.9, range 0.9–2.8, Woolfenden and Fitzpatrick 1996). Although a rigorous analysis of survival of adult Island Scrub-Jays is needed, our data suggest that the species' abundance is not strongly limited by annual fecundity.

The nest-site and habitat predictors of nest success revealed in our study were probably related to the nest's detectability by predators. Nest concealment had a positive influence on the DSR of nests at the scale of the nest site, consistent with several studies of other passerines (e.g., Hatchwell et al. 1999, Colombelli-Négrel and Kleindorfer 2009). Canopy height was also positively associated with DSR at the scale of the home range. Other studies have shown that dense vegetation and nest concealment affect nest survival positively by making it more difficult for predators to detect nests or requiring that predators expend more energy searching more potential nest sites (Martin and Roper 1988, Martin 1993, Chalfoun and Martin 2009).

The continuing recovery of chaparral on Santa Cruz Island will likely increase the amount of habitat suitable for breeding jays. Predicting the effects of these changes on the demography and viability of the Island Scrub-Jay, however, will require a better understanding of how revegetation of the island will affect the jay's predator and prey species. For example, denser vegetation may increase nest concealment and have a positive effect on nest survival, but succession may also affect the distribution, abundance, and foraging strategies of nest predators, such as the island fox.

Our results suggest that habitat quality and food availability have less of an effect on the reproductive success of *A. insularis* than does nest predation. We did not detect habitat-specific effects on clutch size, nest attendance, or feeding rates, and we documented no instances of nestlings starving. Furthermore, the mean number of young fledged per pair was not statistically higher in 2010 (1.5 ± 0.3), which followed a wetter winter and when the availability of food was probably greater (e.g., Morrison and Bolger 2002, Langin et al. 2009), than in either 2008 (1.2 ± 0.3) or 2009 (1.8 ± 0.4). However, habitat quality and food availability may have affected reproductive success indirectly by affecting home-range size and predation risk. We found that jays with smaller home ranges were more likely to fledge young than ones that occupied larger home ranges. Previous studies have found territory size to be inversely related to food abundance and habitat quality (Simon 1975, Smith and Shugart 1987, Marshall and Cooper 2004), suggesting that in low-quality habitats larger territories are necessary for the birds to obtain sufficient food (Anich et al. 2010). In *A. insularis*, larger home ranges, in general, had more grassland and coastal sage scrub and a less dense understory, possibly making it easier for predators to find nests; alternatively, the density of predators may be higher in more open habitats, although we have no data on habitat-specific density for the predator community.

Testing for and documenting observer effects have two important implications for management. First, it allows managers and scientists to design research that minimize its detrimental effects on nest success. Second, it allows for a proper accounting of observer effects and can yield unbiased estimates of annual fecundity for use in population modeling. We did not anticipate the negative effect of flushing incubating or brooding females on nest survival that we documented. Indeed, several studies of passerines' nesting ecology have not found a statistically significant observer effect (Mayer-Gross et al. 1997, Lloyd et al. 2000, Weidinger 2008), and Schaub et al. (1992) found no observer effects on nest predation in the Florida Scrub-Jay. Moreover, in a recent meta-analysis of observer effects on nest success, Ibáñez-Álamo et al. (2012) found no negative effect and even a positive effect in coastal areas and for ground-nesting species. Our findings therefore suggest that observer effects might need to be assessed for individual species in different environments where the communities or behaviors of predators vary.

Flushing of females off nests was strongly supported as a predictor of nest survival, but all forms of nest observation were associated with an increased risk of nest failure (Table 1). We suspect that predators, especially the unusually tame island fox, followed our scent trails to jay nests and were perhaps cued to the sound of the flushing jays. Nest observations were also associated with nest abandonment, and two of eight observed nest failures were due to filial cannibalism (when adults consume their own offspring). Adult jays may have been more likely to end a nest attempt when researchers observed their nests prior to substantial investment (e.g., Garrettson et al. 2011). Filial cannibalism has rarely been observed in birds (Gilbert et al. 2005), and we do not know the full extent of egg removal or filial cannibalism by the Island Scrub-Jay.

In summary, our study contributes data and analyses important for the conservation management of the Island Scrub-Jay, building upon earlier work on the species' mating system and natural history. We confirmed that the Island Scrub-Jays is a noncooperative breeder that relies on oak-dominated habitat and that predation is the leading cause of nest failure (Atwood 1978, 1980a). We found mean clutch size and nest height to be similar to that reported by Atwood (1980b), but we found mean home-range size to be substantially larger than what Kelsey and Collins (2000) reported (range 0.59–2.24 ha, mean = 1.35 ± 0.52 ha, $n = 23$) from the late 1990s. Although the continuing regeneration of chaparral on Santa Cruz Island is likely to benefit the Island Scrub-Jay, threats to its viability from disease and climate change, as well as the species' extremely limited range, raise conservation concern (Morrison et al. 2011). Given the dynamic ecological change already underway on the island, our results emphasize the importance of long-term monitoring for understanding this species' reproductive ecology.

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