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DETERMINANTS OF NEST SURVIVAL IN A MANAGED FLORIDA SCRUB-JAY POPULATION

GEOFFREY M. CARTER[1], DAVID R. BREININGER, ERIC D. STOLEN, AND DONNA M. ODDY

Ecological Program, Mail code: IHA-300, Kennedy Space Center, FL 32899

Abstract. Bird populations occupying managed transitional habitats often have low nest success because optimal habitat conditions are not maintained. In such cases, quantifying determinants of nest survival provides information for habitat maintenance or restoration. Our goal was to determine the current factors affecting nest survival in a managed but declining population of the Florida Scrub-Jay (*Aphelocoma coerulescens*) in Merritt Island National Wildlife Refuge. We used an information-theoretic approach and nest-survival models in program MARK to test a priori hypotheses for survival of Florida Scrub-Jay nests. Failure of Florida Scrub-Jay nests was common; only 35% of 614 were successful in producing at least one fledgling. Ninety-four percent of 399 nest failures were due to predation. Nest survival was highest in oak-dominated territories, varied by population center, and decreased with proximity to forest edges, as the season progressed, and with increasing accumulated rainfall prior to the nesting season. Shrub height, a primary focus of current efforts at habitat-quality assessment and management, was not well supported as a determinant of survival of Florida Scrub-Jay nests at Merritt Island. We suggest hypotheses to explain the lack of support for an effect of shrub height, and we conclude that mitigation of low nest survival at Merritt Island may require additional actions.

Key words: anthropogenic edge, Aphelocoma coerulescens*, Florida Scrub-Jay, program MARK, nest survival, nocturnal predation, snakes.*

Determinantes de la Supervivencia del Nido en una Población Manejada de *Aphelocoma coerulescens*

Resumen. Las poblaciones de aves que ocupan hábitats transicionales manejados tienen a menudo un éxito de anidación bajo debido a que no se mantienen las condiciones óptimas de hábitat. En tales casos, cuantificar los determinantes de la supervivencia de los nidos provee información para el mantenimiento o restauración del hábitat. Nuestra meta fue determinar los factores actuales que afectan la supervivencia de los nidos en una población manejada pero en declive de *Aphelocoma coerulescens* en el Refugio de Vida Silvestre Nacional Isla Merrit. Utilizamos un enfoque de la teoría de la información y modelos de supervivencia de nidos del programa MARK para probar hipótesis a priori sobre la supervivencia de nidos de *A. coerulescens*. El fracaso de nidos de *A. coerulescens* fue común; sólo el 35% de 614 tuvo éxito en producir al menos un volantón. Noventa y cuatro por ciento de 399 fracasos de nidos fue debido a la depredación. La supervivencia de nidos más alta se presentó en territorios dominados por encinos, con variaciones ocasionadas por centros poblacionales, y disminuyó con la proximidad a los bordes del bosque, a medida que la temporada avanzó y con el incremento de precipitaciones acumuladas previo a la temporada de anidación. La altura de los arbustos, un foco primario de los esfuerzos actuales de evaluación y manejo de la calidad de hábitat, no fue apoyada como un determinante de la supervivencia de nidos de *A. coerulescens* en Isla Merrit. Proponemos varias hipótesis para explicar la falta de apoyo a un efecto de la altura de los arbustos, y concluimos que para mitigar la baja supervivencia de nidos en Isla Merrit pueden requerirse acciones adicionales.

INTRODUCTION

Numerous bird species are adapted to intermediate seral stages of ecosystems, and their abundance is limited outside of these particular habitat conditions (Newton 1998). Frequent fire is essential for maintenance of many of these habitats within such ecosystems (Beckage et al. 2005), but anthropogenic influences have interfered with the natural fire regime of many fire-maintained ecosystems (Duncan and Schmalzer 2004, Slocum et al. 2007), causing changes in habitat structure. Human-influenced changes to habitat structure can increase nest-predation rates via changes in the predator community, predator density, the ability of the prey to avoid or deter predators, or changes in predators' searching behavior and ultimately may cause population declines (Newton 1998, Evans 2004).

The Florida Scrub-Jay (*Aphelocoma coerulescens*) exemplifies such circumstances because breeding adults typically defend a single all-purpose territory for life and the

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[1]E-mail: geoffrey.m.carter@nasa.gov

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species prefers an intermediate seral stage of a fire-maintained habitat. Patchy fire at the proper frequency creates an optimal state for Florida Scrub-Jay fitness that is characterized by a mosaic of shrubs of short and medium (2 m) height (Breininger and Carter 2003, Breininger and Oddy 2004) and plentiful sandy openings (Breininger et al. 1998). This habitat structure facilitates predator detection and avoidance by adult Florida Scrub-Jays, which use a sentinel behavior (McGowan and Woolfenden 1989). Adult survival and nest success are greatest in this habitat state (Woolfenden and Fitzpatrick 1984, Schaub et al. 1992, Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. 2009). Insufficiently frequent fire allows shrubs to grow taller and openings to disappear, while an excessive frequency does not allow shrub regeneration sufficient to provide adequate cover. Adult survival and recruitment are lowest (often mortality exceeds recruitment) in these suboptimal states that are now common throughout the species' range and threaten the Florida Scrub-Jay with extinction (Breininger and Carter 2003, Breininger and Oddy 2004, Breininger et al. 2009).

The persistence of this species depends on restoring and maintaining sufficient habitat in an optimal state (Breininger and Carter 2003). Effective population management requires identifying the most limiting factor and removing or reducing it (Newton 1998). For successional ecosystems, such management requires an understanding of the ecology and dynamics of resident populations (James et al. 1997) and the habitat features that limit declining species (Martin 1992, Marzluff et al. 2000). The guild of predators on Florida Scrub-Jay nests varies from population to population (see Schaub et al. 1992, Breininger et al. 1996, Carter et al. 2007) and thus requires investigation and action at the population scale (Thompson and Burhans 2003, Evans 2004).

We used 20 years of demographic, habitat, and environmental data to infer the current ecological determinants of nest survival of a large Florida Scrub-Jay population in an area of east-central Florida altered by fire suppression. Much of the oak scrub structurally succeeded to xeric hammock, density of pines increased in flatwoods, and many swale marshes were invaded by woody species (*Acer rubrum*, *Salix caroliniana*; Duncan et al. 1999). Subsequently, mechanical cutting and prescribed burns have been used to restore scrub (Schmalzer and Boyle 1998), but pine density remains high in some areas, and many marshes are not yet restored. Despite scrub-restoration efforts, in some population centers Florida Scrub-Jay recruitment is still low (Breininger and Carter 2003), mainly because of low nest survival (Carter et al. 2005).

We specified a set of a priori models of how daily nest survival was affected by a set of habitat factors, annual and seasonal variation, and sociobiological factors. Our goal was to enhance our understanding of nest survival in the population and to determine the relative importance of factors. In particular we wanted to test hypotheses regarding which habitat factors (and related anthropogenic changes) influence nest survival to provide a foundation for a mechanistic understanding of these factors. The merit here is twofold. First, we emphasize the need to understand nest survival on a local scale because the guild of predators on Florida Scrub-Jay nests varies spatially. Second, we use a robust, long-term data set, advanced nest-survival models (Dinsmore et al. 2002), and current model-selection methods (Anderson 2008) to estimate parameters accurately and make solid inferences.

Our chief hypothesis was that habitat factors such as the percentage of oak cover, the distance to habitat edges, and shrub height in particular are important determinants of the survival of Florida Scrub-Jay nests. We focused on shrub height and oak cover because both are heterogeneous at the territory scale, figure prominently in assessment of the quality of Florida Scrub-Jay habitat, and both are bases for recommendations for management and conservation (Breininger and Carter 2003, Breininger and Oddy 2004). We predicted that nest survival should follow a pattern similar to that of adult survival and should be greatest when shrub height is optimal (Breininger et al. 2009). We predicted that nest survival should be highest in territories dominated by oaks because recruitment of yearlings is typically greater in such areas (Breininger and Oddy 2004). We included edges as habitat factors because these features may affect nest survival via changes in rates of predator interactions (Weatherhead and Blouin-Demers 2004). We predicted a positive relationship between survival of Florida Scrub-Jay nests and the distance to three types of edge (forest, marsh, and ruderal) because these landscape features may provide alternate prey for, or facilitate foraging of, nest predators, thus increasing the abundance of nest predators or the probability of interactions between the jays and predators on their nests.

Annual variation in the success of Florida Scrub-Jays is primarily a function of predation rates (Woolfenden and Fitzpatrick 1984). We used rainfall to model annual variation because nest success is correlated with rainfall preceding the nesting season, perhaps by affecting predator populations, populations of alternate prey, the jays' vigilance behavior, or vegetation cover at nest sites (Woolfenden and Fitzpatrick 1984). We hypothesized that rainfall might affect Florida Scrub-Jay nest survival by shifting the focus of snakes to amphibians breeding in adjacent ephemeral marshes. We were unsure of the temporal aspect of this relationship. Therefore, we modeled the cumulative rainfall 10, 6, and 3 months prior to the beginning of the nesting season to represent different lag times. Viewing this factor as exploratory, we did not predict a direction of the effect. Seasonally, we were aware that nest-predation rates increased through the season and, on the basis of a previous study, used a linear trend to model this increase (Carter et al. 2005).

Sociobiological factors included the experience of a breeder and the presence of helpers. We included these factors to improve our overall understanding of nest success. From previous studies that demonstrated these relationships, we predicted a positive influence of the presence of helpers and greater experience, (Woolfenden and Fitzpatrick 1984, Mumme 1992).

METHODS

We studied two centers of the Florida Scrub-Jay population on the wild lands of the John F. Kennedy Space Center that are managed by the United States Fish and Wildlife Service as the Merritt Island National Wildlife Refuge. These populations occupied two habitats: oak scrub (hereafter scrub) and scrubby flatwoods (hereafter flatwoods), which are distinguished by an open canopy of slash pine (*Pinus elliotii*; Schmalzer et al. 1999, Abrahamson and Hartnett 1990). These communities are distributed along well-drained ridges in a matrix of mesic habitats or marshes in adjacent swales (Schmalzer et al. 1999). The shrub composition of scrub and flatwoods is similar, consisting primarily of scrub oaks (*Quercus myrtifolia, Q, geminata, Q. chapmanii*) and saw palmetto (*Serenoa repens*), but the abundance of scrub oaks is correlated with soil moisture that is determined by the size and elevation of the ridge. Scrub oaks dominate larger, drier ridges; saw palmetto abundance increases with soil moisture (Schmalzer et al. 1999). The demography of these population centers has been studied since 1988 with the goal of linking habitat conditions to the population's vital rates (Breininger and Carter 2003, Breininger and Oddy 2004; Breininger et al. 2009). The metapopulation of the Florida Scrub-Jay in the Merritt Island refuge is one of the three largest remaining and thus is important to the conservation of the species (Stith et al. 1996).

NEST DATA

We located Florida Scrub-Jay nests at Merritt Island from 1988 to 2008 and marked most adults with a unique combination of metal and celluloid leg bands. We determined the status (breeder or helper) of all individuals and the sex of each breeder through field observations. We considered breeders experienced after their first nesting season. We determined nesting status by observing diagnostic behaviors and by the cryptic behavior of the female breeder during visits to territories. We located nests during building or by observing the incubating female return to the nest. We aged nests by finding them during egg laying, observing hatching, or aging nestlings. For nests found after laying, we calculated initiation dates by assuming a 17-day incubation period, synchronous hatching, and a 17-day brooding period (Carter et al. 2005). We monitored nests weekly until fledging or failure. We also made visits to verify clutch size, confirm hatching, and confirm fledging. We assumed loss of eggs or nestlings (<15 days old) between visits to be due to predation. We considered a nest successful if nestlings were seen in the nest during the fledging-confirmation check (17 days after hatching) or if fledglings were observed out of the nest.

HABITAT DATA

We recorded the location of each nest by interpreting the location of the nest site on digital orthophotos (resolution 1 m) or by a GPS receiver. We digitized nest locations with ArcGIS 9.2. We assigned nests to categories of shrub height and percent oak cover by attributes of territories (see Woolfenden and Fitzpatrick 1984) that were mapped each year. We defined height classes as short (all shrubs in territory recently burned and <120 cm), optimal (territory a mosaic of shrubs of short and medium height, 120–170 cm), and tall (territory contains shrubs >170 cm), as described by Breininger and Carter (2003). We defined oak-cover classes as oak (50% or more of territory covered by oak shrubs) and oak–palmetto (territory <50% oak), as described by Duncan et al. (1995). We classified territory attributes and defined edges operationally by photo interpretation of digital orthophotos overlaid with territory maps. We measured distances to forest edge, marsh edge, and ruderal edge by mapping these features, overlaying nest data, and using the NEAR tool in ArcGIS 9.2. Through the study, marsh edges and ruderal edges changed little relative to the precision of nest locations, so only one map for each was necessary. Forest edges did occasionally change with management, so we updated maps as necessary to reflect this.

STATISTICAL ANALYSES

We used the nest-survival analysis implemented in program MARK (White and Burnham 1999; Dinsmore et al. 2002) to calculate estimates of daily survival rate, model-selection statistics, and to estimate model parameters with associated confidence intervals. MARK uses adjusted Akaike's information criterion (AIC_c) statistics to rank models (Burnham and Anderson 2004), relative to other models in the set, and the model with the minimum AIC_c value ranks best. We based our inferences on model weight and evidence ratios. Model weight is the probability that a given model is the best model (conditional on the data and the model set) and is a function of the difference between the AIC_c of a given model and the lowest AIC_c; evidence ratios are simply a ratio of model weights and can be thought of as a weight of evidence for a model relative to any other model in the set (Anderson 2008).

The range of conditions of occupied habitat that we attempted to model represented two population centers in different habitats, one in scrub and the other in flatwoods. We were aware of variation in nest-predation rates between these two sites (Breininger et al. 1996, Carter et al. 2005), and we wanted to account for this variation in our models, so we treated study site as a fixed factor, grouped our data by site, and included it in all models. We also grouped our data by shrub height and oak cover because we wanted to obtain direct estimates of daily survival rate for these important habitat classifications (Breininger and Carter 2003, Breininger and Oddy 2004). The set of models consists of additive models of shrub height and oak cover (separately and together) with the fixed site factor, a linear trend, and the same hypothesized combinations of distance to edges, cumulative rainfall, breeder experience, and presence of helpers.

RESULTS

MODEL SELECTION

During the 20 years of monitoring, we located 614 Florida Scrub-Jay nests for a total of 12 623 exposure days during the period 1 March–7 July. The mean number of nests located annually was 31 ± 15 (SD) and ranged from 9 to 54. Among our habitat factors, information-theoretic model selection indicated that rates of daily survival of Florida Scrub-Jay nests at Merritt Island were most influenced by oak cover and distance to the nearest forest edge (Table 1). There was less support for an effect of shrub height; the evidence ratio indicated that the best oak-cover model was 18.67 times more likely to be the most parsimonious model than the model with shrub height instead of oak cover (Table 1). Collectively, oak-cover models had 19.26 times more support than height models and 3.75 times more support than models that contained both shrub height and oak cover. There was also strong support for a forest-edge effect. Models with distance to forest had over 6.16 and 11.57 times more support than models with distance to marsh and distance to ruderal edge, respectively (Table 1).

Annual variation was best represented by cumulative rainfall in the 3 months prior to the nesting season. Models with cumulative rainfall 3 months prior to the nesting season had 11.06 and 11.40 times the support of models with cumulative rainfall 6 or 10 months prior to the nesting season (Table 1). There was strong support for a seasonal trend (Table 1); models without a seasonal trend had virtually no support. Among sociobiological factors, the female's experience was the most important, but in general models with these factors had very little support (Table 1). The β_i, standard error, and 95% CI for the best model are given in Table 2. The directions of all β_i were consistent with our predictions, and none of the 95% CI overlapped zero (Table 2). The small β_i estimate of distance to forest edge (Table 2) is an artifact of the units (m) used to measure distance.

TABLE 1. Model-selection results for models of rate of daily survival of Florida Scrub-Jay nests at Merritt Island National Wildlife Refuge. Models include grouping variables and individual covariates[a].

Model	ΔAIC_c[b]	ΔAIC_c weight	K[c]	Deviance
Oak + site + T[d] + distf + rain3	0.00	0.36	6	1879.65
Height + oak + Site + T + distf + rain3	2.75	0.09	8	1878.39
Oak + site + T + rain3	2.98	0.08	5	1884.63
Oak + site + T + distm + rain3	3.62	0.06	6	1883.27
Oak + site + T + distf	3.71	0.06	5	1885.36
Oak + site + T + distf + rain6	4.68	0.03	6	1884.32
Oak + site + T + distf + rain10	4.78	0.03	6	1884.43
Oak + site + T + distr + rain3	4.98	0.03	6	1884.63
Height + oak + site + T + rain3	5.28	0.03	7	1882.92
Height + site + T + distf + rain3	5.85	0.02	7	1883.50
Height + oak + site + T + distm + rain3	5.92	0.02	8	1881.56
Oak + site + T + fexp	6.27	0.02	5	1887.92
Height + oak + site + T + distf	6.71	0.01	7	1884.35
Oak + site + T	6.73	0.01	4	1890.38
Oak + site + T + fexp + help + fexp × help	7.25	0.01	6	1886.90
Height + oak + site + T+ distr + rain3	7.28	0.01	8	1882.92
Oak + site + T + distm	7.60	0.01	5	1889.25
Height + oak + site + T + distf + rain6	7.63	0.01	8	1883.27
Height + oak + site + T + distf + rain10	7.69	0.01	8	1883.34
Oak + site + T + help	7.71	0.01	5	1889.36
Oak + site + T + rain10	7.88	0.01	5	1889.54
Oak + site + T + rain6	7.90	0.01	5	1889.55
Oak + site + T + fexp + mexp + fexp × mexp	8.24	0.01	6	1887.89
Oak + site + T + mexp	8.57	<0.01	5	1890.22
Oak + site + T + distm + rain6	8.67	<0.01	6	1888.32

[a]Oak, coverage of territory by oak (<50% or >50%); height, height of shrubs in territory by three categories (all <120 cm, some 120–170 cm but none >170 cm, or some >170 m); distf, distance to nearest forest edge; distm, distance to nearest marsh edge; distr, distance to nearest ruderal edge; fexp, female experience; mexp, male experience; help, helpers, rain3, rain6, and rain10 = accumulated rainfall 3, 6, 10 months prior to nesting season, respectively.
[b]AIC_c of best model was 1891.66.
[c]Number of parameters.
[d]Linear seasonal trend.

DAILY SURVIVAL RATES

Failure of Florida Scrub-Jay nests was common; only 35% of nests ($n = 215$) were successful in producing at least one fledgling. Of 399 nest failures, 94% were due to predation. Model predictions of Florida Scrub-Jay nest survival were higher in oak territories and in flatwoods (Fig.1). There was a positive relationship between survival of Florida Scrub-Jay nests and distance to forest edge (Fig. 2). On an annual basis the accumulated rainfall in the 3 months prior to the nesting season had a negative influence on daily survival rate (Fig. 3). Seasonally, the trend in nest survival was negative (Fig. 4).

DISCUSSION

As predicted, survival of Florida Scrub-Jay nests at Merritt Island was related to oak cover, distance to forest edge, and subject to annual and seasonal variation. However, contrary to our predictions and previous findings, we found that the importance of shrub height and sociobiological factors was not supported. These results demonstrate the need for examining nest survival at the population level and could have implications for management of Florida Scrub-Jay habitat. The unexplained variation related to site may provide clues to the direction of further inquiry.

The evidence for an effect due to oak cover (model support and direction of effect) agrees with Breininger and Oddy

TABLE 2. Beta estimates of best-supported model of daily survival rates of Florida Scrub-Jay nests at Merritt Island National Wildlife Refuge.

Variable[a]	β_i	Estimate	SE	LCI	UCI
Intercept	β_0	1.336	0.064	1.210	1.462
Oak	β_1	0.078	0.032	0.014	0.141
Site	β_2	0.123	0.032	0.060	0.186
T	β_3	–0.004	0.001	–0.005	–0.002
distf	β_4	0.00023	0.00010	0.00003	0.00043
rain3	β_5	–0.008	0.003	–0.014	–0.001

[a]See Table 1 for definitions.

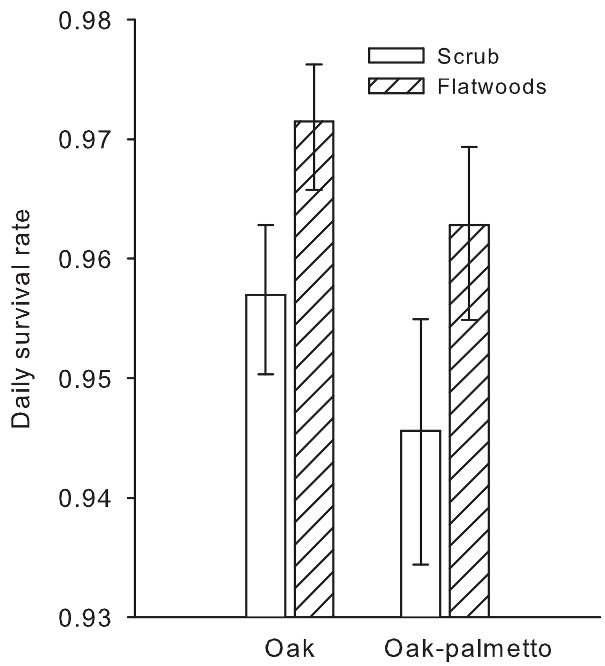

FIGURE 1. Prediction of rates of daily survival of Florida Scrub-Jay nests by community type at Merritt Island National Wildlife Refuge, according to the best-supported additive model that included percentage of oak cover, site, a linear seasonal trend, and two individual covariates (distance to nearest forest edge and accumulated rainfall in the 3 months prior to the initiation of the nesting season). These rates were highest in territories where scrub oaks dominated and in the flatwoods community type. Predictions are calculated with the median date and mean values for covariates. Error bars are 95% CI.

(2004), who found that territories on large ridges with well-drained soils (represented by our oak class) performed better (yearlings produced minus breeders' deaths) than territories on smaller, poorly drained ridges with less oak cover (represented by our oak–palmetto class). Our results indicate that at least part of the difference in demographic performance

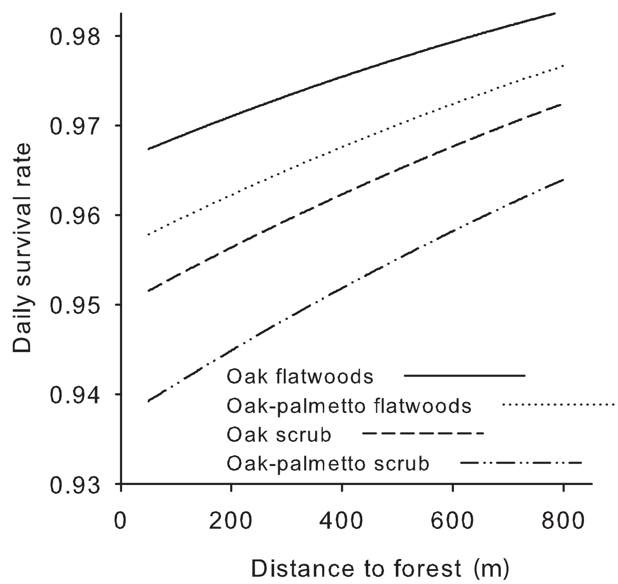

FIGURE 2. The rate of daily survival of Florida Scrub-Jay nests increased with increasing distance to the nearest forest edge at Merritt Island National Wildlife Refuge, as predicted by the best-supported model (described in Fig. 1). Reported rates are for nests on the median date on the basis of the mean accumulated rainfall in the 3 months prior to the initiation of the nesting season (25 cm).

between oak and oak–palmetto territories is realized during the nest stage. However, it is important to note that despite this difference, oak–palmetto habitat is still important for Florida Scrub-Jay conservation, because oak–palmetto territories can sometimes function as sources (where production of yearlings is greater than mortality of breeders), and occupied oak–palmetto territories increase the meta-population's size and act as demographic buffers (Sutherland 1996), thereby decreasing risk of extinction (Breininger and Oddy 2004).

In relation to edges, we found that survival of Florida Scrub-Jay nests was influenced primarily by distance to forests. Snakes use forest edges (Blouin-Demers and Weatherhead 2001, Weatherhead and Blouin-Demers 2004), and snakes are currently the main predators of Florida Scrub-Jay nests at Merritt Island (Carter et al. 2007). The increase of forest edges in the refuge due to fire suppression may have increased the density of snakes. Forests reduce the suitability of habitat for the Florida Scrub-Jay (Duncan et al. 1995, Breininger et al. 1998); our results indicate that some of the effect of forests on the jay's fitness is on nest survival.

We included site in all of our a priori models by design, but a post hoc fit of the best model without the site effect had virtually no support. This indicates the site effect is important and needs further examination. We presume the site effect is ultimately tied to some difference in predator–prey interactions, because 94% of failures of Florida Scrub-Jay nests at Merritt Island were due to nest predators. The direction of the site effect is consistent with an earlier study (Breininger et al. 1996) that

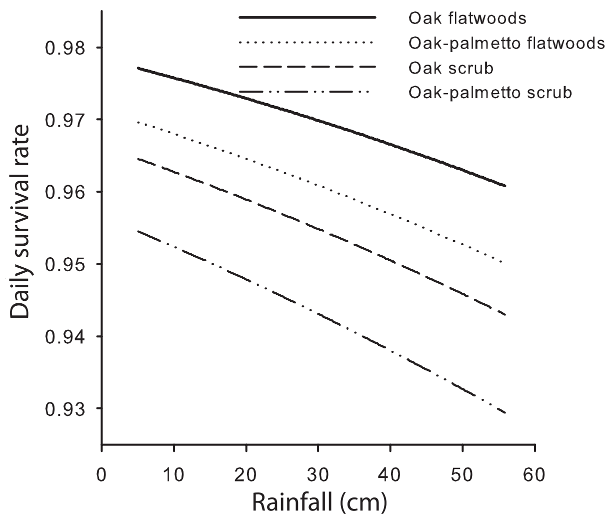

FIGURE 3. The rate of daily survival of Florida Scrub-Jay nests decreased with increasing amount of rainfall in the 3 months prior to the nesting season at Merritt Island National Wildlife Refuge. Reported rates are for nests on the median date on the basis of the mean distance to nearest forest edge (218 m), as predicted by the best-supported model (described in Fig. 1).

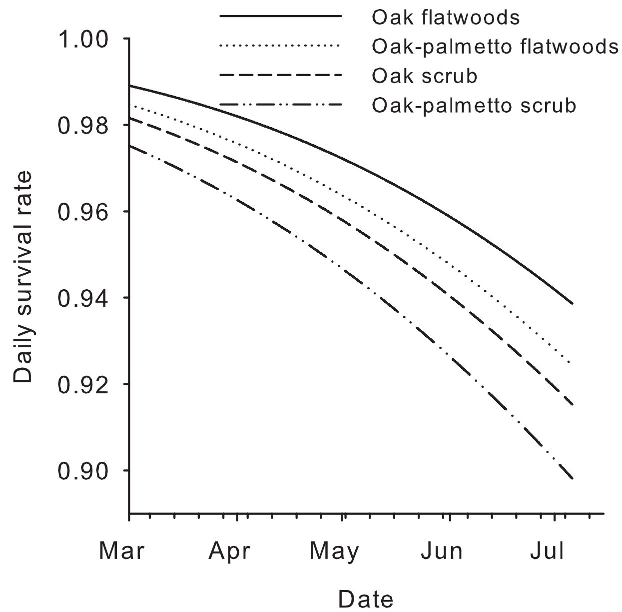

FIGURE 4. The rate of daily survival of Florida Scrub-Jay nests declined through the season at Merritt Island National Wildlife Refuge. Reported rates are based on the mean distance to nearest forest edge and mean accumulated rainfall in the 3 months prior to the initiation of the nesting season, as predicted by the best-supported model (described in Fig. 1).

attributed higher rates of nest predation in the oak-scrub site to abundant tall shrubs and few openings. Habitat restoration has reduced the extent of tall shrubs in the oak-scrub site, but openings are still scarce because they disappear relatively quickly following fire. Openings are more abundant in the flatwoods site because of more frequent fire (Duncan et al. 1999) and possibly because the cast limbs and needles of pines also help create openings by producing hotspots during fires (Myers 1990).

The direction of estimates of the shrub-height parameter agreed with past studies (Breininger and Carter 2003, Breininger et al. 2009), but the precision of the estimates was poor and the 95% confidence intervals overlapped zero, suggesting a weak relationship. Our data span 20 years, so we believe that this result is not due to a small sample. One possible explanation is predation taking place at night, when the jays are unable to detect predators and defend their nests regardless of shrub height (Carter et al. 2007). It is also possible that the positive influence on nest survival expected at optimal height (Schaub et al. 1992, Breininger et al. 1996, Carter et al. 2005) may be negated by premature loss of openings. Many of the openings in restored oak scrub last for <2 years after a fire, after which the canopy becomes continuous (Schmalzer and Hinkle 1992). Openings often disappear before scrub reaches heights considered optimal for the Florida Scrub-Jay; this may have confounded our results.

The negative seasonal trend was consistent with previous studies and our expectations and may be best explained by predator activity increasing through the season (Woolfenden and Fitzpatrick 1984, Schaub et al. 1992). The negative annual effect of accumulated rainfall in the 3 months prior to the initiation of the nesting season differs from the result of Woolfenden and Fitzpatrick (1984) of a positive correlation of rainfall accumulated in the 10 months prior to the nesting season with nest success. Our models with an equivalent measure of rainfall in the 10 months prior to the nesting season had little support. It is not clear how annual rainfall affects survival of Florida Scrub-Jay nests negatively but a direct effect on the young (e.g., food availability) seems implausible because nest failure due to starvation is rare (Carter et al. 2005). Rather, it seems more likely that rainfall affects nest survival via some effect on predator populations (e.g., increased predator density or activity). It is clear that the mechanism by which rainfall affects nest survival in the population we studied differs from that in the one studied by Woolfenden and Fitzpatrick (1984).

We were surprised to find, in contrast to previous findings (Woolfenden and Fitzpatrick 1984, Mumme 1992, Schaub et al. 1992, Breininger et al. 1996), little support for any of the sociobiological factors that we incorporated into our model set. Presumably the presence of helpers and greater experience improves breeders' vigilance, mobbing, avoidance, and defense of nest predators (Francis et al. 1989, McGowan and Woolfenden 1989, Mumme 1992). However, the Florida Scrub-Jay's main forms of vigilance (detecting predators visually) and nest defense (mobbing) are probably not effective in a closed habitat or at night, thus reducing any advantage that experience or helpers might provide.

To conclude, our results suggest that forest edges reduce the survival of Florida Scrub-Jay nests, but shrub height, a habitat feature commonly used to assess habitat quality and guide management, is alone a poor determinant of the jay's nest survival at Merritt Island. It is possible that the influence of shrub height has been uncoupled from nest survival either by the presence of snakes hunting nocturnally or by openings being ephemeral. Ephemeral openings do appear to be a symptom of anthropogenic interference with fire regimes, and it is possible that nocturnal nest predation is as well. We also suspect that the site effect we observed was related to a premature loss of openings, which highlights the need for better understanding of the occurrence of openings at Merritt Island and the mechanism that relates openings to the survival of Florida Scrub-Jay nests. Ideally this need would be met by incorporating nest monitoring with efforts to optimize restoration of openings via an adaptive management plan (Marzluff et al. 2000, Kendall 2001). Similarly, restoration of forested marshes to reduce forest-edge effects could also be part of an adaptive management plan that incorporates monitoring of snake abundance. These actions may provide a more mechanistic understanding of the factors affecting nest survival.

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LITERATURE CITED

Abrahamson, W. G., and D. C. Hartnett. 1990. Pine flatwoods and dry prairies, p. 103–149. *In* R. L. Myers and J. J. Ewel [eds.], Ecosystems of Florida. University of Central Florida Press, Orlando, FL.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York.

Beckage, B., W. J. Platt, and B. Panko. 2005. A climate-based approach to the restoration of fire-dependent ecosystems. Restoration Ecology 13:429–431.

Blouin-Demers, G., and P. J. Weatherhead. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. Ecology 82:2882–2896.

Breininger, D. R., V. L. Larson, D. M. Oddy, R. B. Smith, and M. J. Barkaszi. 1996. Florida Scrub-Jay demography in different landscapes. Auk 113:617–625.

Breininger, D. R., V. L. Larson, B. W. Duncan, and R. B. Smith. 1998. Linking habitat suitability to demographic success in Florida Scrub-Jays. Wildlife Society Bulletin 26:118–128.

Breininger, D. R., and G. M. Carter. 2003. Territory quality transitions and source–sink dynamics in a Florida Scrub-Jay population. Ecological Applications 13:516–529.

Breininger, D. R., and D. M. Oddy. 2004. Do habitat potential, population density, and fires influence Scrub-Jay source–sink dynamics? Ecological Applications 14:1079–1089.

Breininger, D. R., J. A. Nichols, G. M. Carter, and D. M. Oddy. 2009. Habitat-specific breeder survival of Florida Scrub-Jays: inferences from multistate models. Ecology 90:3180–3189.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Carter, G. M., D. R. Breininger, V. L. Larson, D. M. Oddy, R. B. Smith, and E. D. Stolen. 2005. Reproductive ecology of the Florida Scrub-Jay (*Aphelocoma coerulescens*) on John F. Kennedy Space Center/Merritt Island National Wildlife Refuge: a long-term study. NASA Technical Memorandum 2005-212562, Kennedy Space Center, FL.

Carter, G. M., M. L. Legare, D. R. Breininger, and D. M. Oddy. 2007. Nocturnal nest predation: a potential obstacle to recovery of a Florida Scrub-Jay population. Journal of Field Ornithology 74:390–394.

Dinsmore, S. J., G. C. White, and F. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Duncan, B. A., S. Boyle, D. R. Breininger, and P. A. Schmalzer. 1999. Coupling past management practice and historical landscape change on John F. Kennedy Space Center. Landscape Ecology 14:291–309.

Duncan, B. W., D. R. Breininger, P. A. Schmalzer, and V. L. Larson. 1995. Validating a Florida Scrub Jay habitat suitability model, using demography data on Kennedy Space Center. Photogrammetric Engineering & Remote Sensing 61:1361–1370.

Duncan, B. W., and P. A. Schmalzer. 2004. Anthropogenic impacts on potential fire spread in a pyrogenic ecosystem of Florida, USA. Landscape Ecology 19:153–164.

Evans, K. L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146:1–13.

Francis, A. M., J. P. Hailman, and G. E. Woolfenden. 1989. Mobbing by Florida Scrub Jays: behaviour, sexual asymmetry, role of helpers, ontogeny. Animal Behaviour 38:795–816.

James, F. C., C. A. Hess, and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on Red-cockaded Woodpeckers. Ecological Applications 7:118–129.

Kendall, W. L. 2001. Using models to facilitate complex decisions, p. 147–169. *In* T. M. Shenk and A. B. Franklin [eds.], Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, DC.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management?, p. 455–473. *In* J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington DC.

Marzluff, J. M., M. G. Raphael, and R. Sallabanks. 2000. Understanding the effects of forest management on avian species. Wildlife Society Bulletin 28:1132–1143.

McGowan, K. J., and G. E. Woolfenden. 1989. A sentinel system in the Florida Scrub Jay. Animal Behaviour 37:1000–1006.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida Scrub Jay. Behavioral Ecology and Sociobiology 31:319–328.

Myers, R. L. 1990. Scrub and high pine, p. 150–193. *In* R. L. Myers and J. J. Ewel [eds.], Ecosystems of Florida. University of Central Florida Press, Orlando, FL.

Newton, I. 1998. Population limitation in birds. Academic Press, London.

Schaub, R., R. L. Mumme, and G. E. Woolfenden. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. Auk 109:585–593.

Schmalzer, P. A., and C. R. Hinkle. 1992. Species composition and structure of oak–saw palmeto scrub vegetation. Castanea 57:220–251.

SCHMALZER, P. A., AND S. R. BOYLE. 1998. Restoring long-unburned oak–mesic flatwoods requires mechanical cutting and prescribed burning. Restoration and Management Notes 16:96–97.

SCHMALZER, P. A., S. R. BOYLE, AND H. M. SWAIN. 1999. Scrub ecosystems of Brevard County, Florida: a regional characterization. Florida Scientist 62:13–47.

SLOCUM, M. G., W. J. PLATT, B. BECKAGE, B. PANKO, AND J. B. LUSHINE. 2007. Decoupling natural and anthropogenic fire regimes: a case study in Everglades National Park, Florida. Natural Areas Journal 27:41–55.

STITH, B. M., J. W. FITZPATRICK, G. E. WOOLFENDEN, AND B. PRANTY. 1996. Classification and conservation of metapopulations: a case study of the Florida Scrub-Jay, p. 187–216. *In* D. R. McCullough [ED.], Metapopulations and wildlife conservation. Island Press, Covelo, CA.

SUTHERLAND, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford, England.

THOMPSON, F. R., AND D. E. BURHANS. 2003. Predation of songbird nests differs by predator and between field and forest habitats. Journal of Wildlife Management 67:408–416.

WEATHERHEAD, P. J., AND G. BLOUIN-DEMERS. 2004. Understanding avian nest predation: why ornithologists should study snakes. Journal of Avian Biology 35:185–190.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton University Press, Princeton, NJ.