Research Article

Factors Affecting Florida Scrub-Jay Nest Survival on Ocala National Forest, Florida

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ABSTRACT One of the main populations of the Florida scrub-jay (*Aphelocoma coerulescens*), a federally threatened species, occurs on Ocala National Forest, Florida. We determined the nest daily survival rate (DSR) of 474 nests of Florida scrub-jays in stands subject to sand pine reforestation management after timber harvesting or wildfire on Ocala National Forest. We used the information-theoretic approach with logistic-exposure modeling to determine the most likely models to account for DSR for the incubation and nestling stages separately. The models consisted of 4 components (temporal, management, habitat, and helpers) with each consisting of one to several specific variables. In the incubation stage all the best models included the temporal component alone or in concert with the habitat, helpers, or habitat and helpers components. Model averaging in the incubation stage indicated support for the year and day × year in the temporal component and stand age in the habitat component. In the nestling stage, top models all included the temporal component alone or with helpers or habitat, helpers, and the interaction of habitat and helpers. Model averaging in the nestling stage showed support for the year, nest age, and to a lesser extent day in the temporal component and helpers. The management component, which consisted of no site preparation, wildfire burn, post-harvest burn, chop and seed, or seed only, had little influence on nest survival for the incubation or nestling stages. However, we identified several other management factors that may increase Florida scrub-jay populations despite having no effect on DSR. First, the proportion of Florida scrub-jay nests was significantly higher than expected in burned habitat based on habitat availability, indicating a potential preferred nesting habitat conducive to population growth. Second, incubation stage DSR with respect to stand age (habitat component) declined to stand age 10 yr and then began to increase, which may be attributed to the higher bird population in the prime habitat in the middle stand ages. The denser population may result in more competition for resources, and possibly may attract more predators, resulting in a lower DSR. Thus, although DSR may be lower at the mid-stand ages, the overall population may actually be optimal. Therefore, to increase the Florida scrub-jay population on Ocala National Forest, we recommend maintaining a mosaic of stands ≤20 yr of age and emphasizing natural reseeding and site preparation via burning. © 2011 The Wildlife Society.

KEY WORDS *Aphelocoma coerulescens*, Florida, Florida scrub-jay, forest management, nest daily survival models, nest survival, Ocala National Forest, reforestation.

The Florida scrub-jay (*Aphelocoma coerulescens*) is a cooperative, monogamous species, living in groups consisting of a mated pair and often ≥1 helpers. Florida scrub-jays are permanent residents and, thus, the quality of their territories can affect them throughout the year. Florida scrub-jay habitat consists of dense thickets of southern scrub oaks (*Quercus* spp.) <3 m tall with bare sand in between, although birds also will use adjacent non-scrub habitats (Fitzpatrick et al. 1991). Such habitat typically develops after clearing by timber harvesting or wildfire. Florida scrub-jays are found in southern scrub oak, sand pine (*Pinus clausa*)—southern scrub oak, and slash pine (*P. elliottii*)—southern scrub oak habitats.

Both sand pine and slash pine scrub, though structurally similar to oak scrub, also contain a layer of pine. For suitable Florida scrub-jay habitat, pine scrub should contain <50% tree (>3 m tall) canopy cover (U.S. Fish and Wildlife Service [USFWS] 1990).

Ocala National Forest contains some of the most important and extensive sand dunes remaining within the geographic range of the Florida scrub-jay (USFWS 1990). Scrub habitats are considered imperiled both worldwide (global rank is G2) and locally (Florida state rank is S2) signifying a community that is imperiled because of rarity or vulnerable to extinction due to natural or human factors (Florida Natural Areas Inventory 2002).

The Florida scrub-jay was listed as a threatened species in 1987 (52 Federal Register 20715–20719) primarily because of habitat loss arising mainly from widespread urbanization and habitat degradation (Woolfenden and Fitzpatrick 1991, Stith et al. 1996, Breininger et al. 1999). Although the full

extent of their decline is unknown, by 1993 approximately 4,000 Florida scrub-jay breeding pairs remained, a decline of about 25% since 1983 and a reduction to about 10% of historical numbers (Woolfenden and Fitzpatrick 1996).

Most of the remaining Florida scrub-jays are found on public lands, with Ocala National Forest containing one of the most important extant populations. It is one of 3 areas (the others being Archbold Biological Station in Highlands County and Merritt Island National Wildlife Refuge in Brevard County) that must support a stable or increasing population before declassification to non-threatened status can be considered (USFWS 1990). Ocala National Forest's Florida scrub-jay population is the largest of the 3 populations and is the only one with sufficient potential habitat to support a population (≥500 breeding groups) that is likely to be viable over the long-term (USFWS 1990).

Historically, fire maintained the low oak scrub vegetation required by the Florida scrub-jay and without fire or similar habitat disturbance, the vegetation becomes too dense and tall to accommodate nesting and foraging requirements (Woolfenden and Fitzpatrick 1996). Because of the adjacency of private lands and other developed areas, large, stand-replacing wildfires are no longer allowed to burn, and the use of prescribed fire is often restricted. For this reason, mechanical treatments, such as sand pine harvesting, are used to manage Florida scrub-jay habitat on Ocala National Forest. Managers of this forest are seeking a balance between having sufficient good quality Florida scrub-jay habitat in the short term by accomplishing little or no sand pine regeneration versus over the long-term by harvesting and purposely regenerating sand pine.

Florida scrub-jay ecology and life history have been studied primarily at Archbold Biological Station and at Merritt Island National Wildlife Refuge. Ocala National Forest is the only one of these 3 areas where sand pine is intentionally regenerated for Florida scrub-jay habitat; the other areas purposely suppress sand pine. Clearcutting is used to regenerate sand pine and create large cleared areas with much open sand substrate. Clearcuts are ≥10 ha and usually result in a mosaic of stand ages from newly cut to about 50-yr old, at which age sand pine would be harvested. Florida scrub-jays begin to use clearcut areas shortly after harvesting and will continue to use such stands until they reach approximately 20 yr of age. After clearcutting the land often is subjected to site preparation to enhance reforestation. To adequately manage the Florida scrub-jay on Ocala National Forest, information is needed on how this species responds to harvest and regeneration of sand pine. Our objectives were to determine what factors, including the effects of various reforestation treatments (site preparation and seeding), may affect Florida scrub-jay nest survival on Ocala National Forest.

STUDY AREA

We conducted our study on the 155,207 ha Ocala National Forest, between Gainesville and Daytona Beach, Florida in Marion, Lake, and Putnam counties. About 1,619 ha of sand pine scrub were regenerated annually on Ocala National Forest, approximately 810–1,215 ha following timber harvest and an additional 607 ha that were treated with prescribed fire.

Managers selected stands for harvest based on site-specific needs for replacement habitat for the Florida scrub-jay. A technique currently used by Ocala National Forest to manage for Florida scrub-jays is to clearcut 10 ha or larger blocks in sand pine stands adjacent to or nearby 3- to 6-yr-old stands occupied by scrub-jays. By the time the stands are harvested (approx. 2 yr after stand selection) and become suitable Florida scrub-jay habitat (approx. 3 yr after harvest), the occupied 3- to 6-yr-old stands are 8- to 11-yr old and presumed to be approaching an age at which Florida scrub-jays find them less suitable (L. Lowery, U.S. Forest Service, personal communication).

Reforestation (regeneration) treatment method refers to the type of site preparation and seeding (if any) that is done after the sand pine on a stand has been harvested. We also evaluated nest success on stands that experienced wildfire. Reforestation techniques used during sand pine regeneration and wildfire include: 1) no site preparation and no seeding; 2) post-harvest burning and no seeding; 3) wildfire burn and no seeding; 4) seeding only; and 5) chopping and seeding. Chopping is a procedure whereby an implement is pulled behind heavy equipment, such as a bulldozer, and chops debris (e.g., limbs, twigs, and stumps) that remains after logging. After harvest of sand pine, these sites may be artificially reseeded with pine seed or left to reseed naturally. Managers used the Continuous Inventory of Stand Conditions database (a U.S. Forest Service database derived from field evaluations of individual stands that included tree species, age, and size) and ArcGIS to assess the area of each treatment type on Ocala National Forest.

METHODS

Nest Monitoring
We selected nests for monitoring by randomly driving or walking slowly along sandy, one-lane tracks that are common in the study area. When we encountered a group of Florida scrub-jays we then observed the birds to locate the nest. Thus, most nests were close to one-track roads, which provided ready access for monitoring of nests. These sandy roads are long-standing and were established independently from their proximity to any particular stand type. Hence, we assumed the roads passed through a random sample of the stand types on Ocala National Forest. By walking these roads to detect Florida scrub-jays, we believe we obtained a nest sample that was unbiased with respect to stand type. Observers monitored nests during the breeding season (Apr–Jul) in 2002 through 2006, visiting them approximately every 3 days and more frequently near the anticipated time of hatching or fledging. Observers recorded the date, location, number of eggs, number of eggs that hatched, number of nestlings, and number of fledglings. We defined an observation interval as a survival score (yes or no) for a sampled nest during varying length intervals (days) between 2 successive inspections of the nest. We determined the

number of fledglings by frequently visiting the nest near the projected time of fledging. We distinguished successful nests from failed nests by looking for feces on the edge of the nest or under it versus signs that the nest had been damaged or disturbed or presence of loose feathers, an indication of predation on nestlings. In some cases ≥1 eggs may have been removed from the nest by predators before we first observed the nest. Nest parasitism by brown-headed cowbirds (*Molothrus ater*) was not observed, possibly because cowbirds are markedly smaller than Florida scrub-jays (Woolfenden and Fitzpatrick 1996).

Modeling Nest Daily Survival Rates

We separated nest data into the incubation and nestling stages because survival may differ between these 2 stages. We used the information-theoretic approach (Burnham and Anderson 2002) with a logistic-exposure model (Shaffer 2004) to assess the effects of 4 components (temporal, management, habitat, and helpers) on nest daily survival rates (DSR). We defined day of the breeding season for a given year as the number of days after initiation of the breeding season with day 1 being the first day in which we observed any nest with ≥1 egg.

A logistic-exposure model is a generalized linear model (Nelder and Wedderburn 1972) that accounts for possible heterogeneity in DSR that may be present due to repeated observations of nests throughout the breeding season, at various days and nest ages, as well as different exposure period lengths. We assumed the binomial probability distribution and a modified logit link function to model the fate of nests during each nest monitoring interval (Shaffer 2004). We used PROC GENMOD (SAS Institute Inc., Cary, NC) to fit the logistic-exposure model separately to the incubation and nestling stages using iterative maximum likelihood estimation.

We used the information-theoretic approach of Burnham and Anderson (2002) for model development and selection. We developed and ranked candidate models based on Akaike information criteria corrected for small sample size (AIC$_c$), the difference in AIC$_c$ between a model and the lowest model (ΔAIC$_c$), and the corresponding Akaike weights (*w*). Preferred models have the smallest AIC$_c$ and ΔAIC$_c$ values, and the highest Akaike weight values, which represent the relative likelihood of a model with respect to those in the candidate pool. We considered a model parameter important if the 95% confidence interval for the odds ratio did not contain 1.0; however, we also considered whether a model parameter was included in the top models, its magnitude, and its relationship with its DSR. We obtained the odds ratio for a parameter of a continuous variable by exponentiating the parameter. We determined importance between all possible levels of a categorical variable by exponentiating the difference between the 2 parameters, which we obtained by using customized contrasts and then exponentiating. We evaluated the global model, which contained all the variables from all the candidate models, based on the Hosmer–Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000) where a large value

of the chi-squared statistic (small *P*-value) indicates lack of fit of the model. We checked the global model for goodness-of-fit before proceeding with model selection (Burnham and Anderson 2002).

We constructed a separate set of a priori candidate models for the incubation stage and the nestling stage. Each set consisted of 16 models that included the 4 single component models, all 6 2-component models, all 4 3-component models, the complete 4-component model, and the constant survival model. These models represented hypotheses concerning effects on DSR of the 4 components. We considered day of the breeding season to be represented by only its linear effect during the breeding season. Had the breeding season been longer, the linear relationship between survival and day of the breeding season would have likely changed, which would have compelled us to also consider the quadratic effect. We hypothesized that for the temporal component, DSR would decrease linearly as day of the breeding season (day) progressed, vary quadratically as nest age in days (age) increased, and vary among years of study (years: 2002–2006). We predicted that the management component (the 5 stand treatments for sand pine regeneration) would have a differential effect, that the habitat component (stand age in years) would have a quadratic effect with maximum DSR at 6–10 yr, and that presence of helpers would increase DSR. In some years, the oak scrub vegetation acquired its new leaves after nests had been constructed and eggs laid, thus providing little concealment and protection for the earlier incubation stage nests and possibly increasing the likelihood of nest predation. In other years the leaves were acquired before eggs were laid, providing increased protection from predators. Hence, we predicted that DSR during incubation would be affected by the day of the breeding season and year interaction (day × year) and, thus, the temporal component included this interaction for the incubation stage. In addition, we assumed that the benefits of helpers for nestlings might vary with stand age and, thus, included a stand age × helpers interaction term for the nestling stage. By comparing support for these 16 models, we drew conclusions concerning our a priori hypotheses about the importance of these effects on DSR. As each component was present in the same number of models, we could evaluate the importance of each component by summing the Akaike weights across all models in which that component occurred (Burnham and Anderson 2002).

We used model-averaging to incorporate the effect of model-selection uncertainty on parameter estimates (Burnham and Anderson 2002). Results from both the incubation and nestling stage models revealed that no one model had the majority of support. Thus, we model-averaged the best candidate models for each stage that had ΔAIC$_c$ <2, yielding parameter estimates, unconditional standard errors, odds ratios, and 95% confidence intervals. We examined the model-averaged parameters for the incubation and nestling stages graphically across years and helpers by plotting DSR versus each variable in the model with the other variables held at their median values for their appropriate stage.

We also conducted a habitat use analysis using a chi-squared test to compare the number of monitored Florida

scrub-jay nests with respect to the amount of scrub habitat ≤20 yr of age that was naturally reseeded versus artificially seeded (Sokal and Rohlf 1995). We made similar comparisons for the number of nests found in stands with different site preparation methods to the number of nests expected based on the proportion of that type of available scrub habitat ≤20 yr of age.

RESULTS

The incubation stage data consisted of 668 observation intervals, 468 without helpers, and 200 with helpers. Over the breeding season there were 488 incubation stage observation intervals through day 45, 173 from days 45 to 90, and 7 beyond day 90. The stand age distribution yielded 122 observation intervals for nests in stands through 5 yr of age, 468 in stands 6–10 yr of age, 62 in stands 11–15 yr of age, and 16 in stands 16–20 yr of age. The average number of incubation stage observation intervals per year was 134. The nestling stage had 1,036 observation intervals, of which 690 were for nests without helpers and 346 with helpers. There were 371 observation intervals through day 45 in the breeding season, 609 from days 45 to 90, and 56 beyond day 90. There were 232 observation intervals for nests in stands through 5 yr of age, 650 in stands 6–10 yr of age, 114 in stands 11–15 yr of age, and 40 for stands 16–20 yr of age. The average number of nestling stage observation intervals per year was 207.

The goodness-of-fit statistic for our global incubation model was 6.1002 with df = 8 and $P = 0.636$, whereas for the global nestling model it was 10.1552 with df = 8 and $P = 0.254$. As we detected no lack of fit, we proceeded with further analysis of possible models.

For the incubation stage 4 models yielded $\Delta AIC_c < 2$ and all contained the temporal component (Table 1). The best fitting model for the incubation stage was a function of the temporal (day of the breeding season, nest age, year, and

day × year) and habitat (stand age) components, which accounted for 31% of the Akaike weight among the 16 candidate models. The second best model contained only the temporal component and had an Akaike weight of 0.24. When we added helpers to the best model, the Akaike weight was 0.23. The fourth best model contained the temporal and helpers components, with an Akaike weight of 0.14.

We used model averaging to combine the 4 best incubation models and incorporate model uncertainty into the parameter estimates and their standard errors. Strong support was shown for $year_{2005}$ and day × $year_{2005}$ as their odds ratios did not contain 1.0 in their confidence intervals (Table 2). The odds ratios for day × $year_{2002}$, day × $year_{2003}$, and day × $year_{2004}$ had confidence intervals that barely covered 1.0, implying support but to a lesser degree. During 2002 DSR was stable over the breeding season, whereas for 2003 and 2004 DSR declined smoothly (Fig. 1). In 2005, DSR changed little with day until approximately mid-season (day 45), at which point DSR dramatically decreased. Conversely, during 2006, DSR was low initially but increased through approximately mid-season and then leveled off. Incubation DSR with respect to day was similar for nests with and without helpers, where survival increased only slightly with helpers (Fig. 1). The odds ratio for the linear component of stand age was 0.6903 (Table 2), resulting in high DSR in the youngest stands (0- to 3-yr old; Fig. 2) for nests with and without helpers. After the initial high rate, DSR declined through about stand age 10 yr at which point the rate began to increase (Fig. 2). Because habitat (stand age) appeared in the top model and had a relatively low odds ratio, there is support for considering stand age as important in the incubation stage in spite of its confidence interval overlapping 1.0. The effect of helpers on incubation survival with respect to stand age was minimal, as survival increased only slightly with helpers (Fig. 2).

Table 1. Logistic-exposure model-selection results we obtained with PROC GENMOD (SAS Institute 2004) for Florida scrub-jay nest daily survival rates in the incubation stage on Ocala National Forest, Florida (2002–2006). We ranked models based on Akaike's information criterion for small samples (AIC_c), ΔAIC_c, and Akaike weights (w_i); AIC_c is based on $Log_e(L)$, which is the value of the maximized log-likelihood function, and the number of parameters in the model (K). Models with the smallest AIC_c and ΔAIC_c, and highest Akaike weight (w_i) have more support.
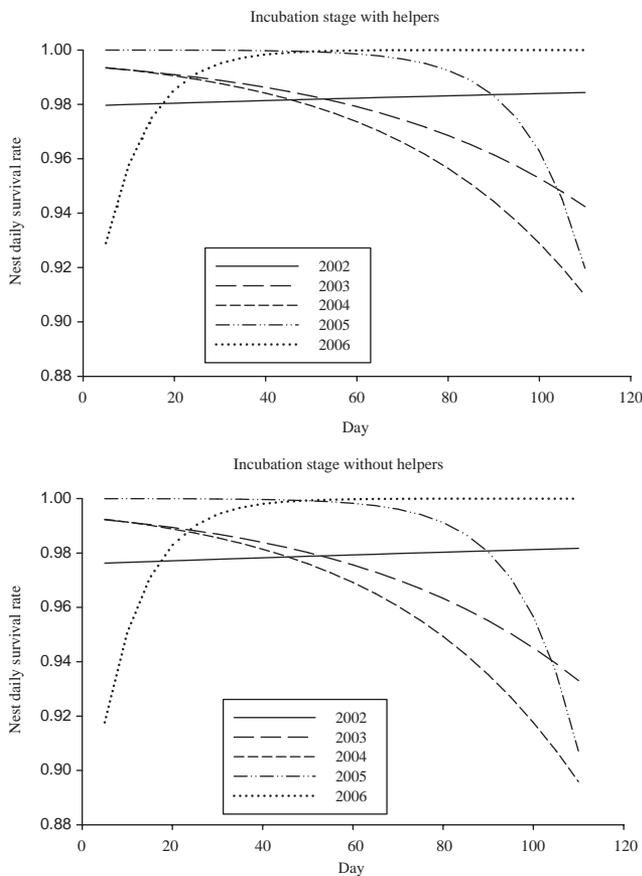
Model[a]	$Log_e(L)$	K	AIC_c	ΔAIC_c	w_i
Temporal habitat	−158.364	14	344.853	0.000	0.3076
Temporal	−160.617	12	345.327	0.474	0.2426
Temporal habitat helpers	−157.632	15	345.407	0.554	0.2332
Temporal helpers	−160.131	13	346.371	1.518	0.1440
Habitat helpers	−171.381	4	350.775	5.922	0.0159
Temporal habitat management	−157.403	18	351.010	6.158	0.0142
Temporal management	−159.569	16	351.301	6.448	0.0122
Habitat	−172.880	3	351.768	6.915	0.0097
Temporal habitat helpers management	−156.819	19	351.865	7.012	0.0092
Temporal helpers management	−158.915	17	352.012	7.159	0.0086
Helpers	−176.164	2	356.332	11.479	0.0010
Constant survival	−177.233	1	356.468	11.615	0.0009
Habitat helpers management	−171.116	8	358.274	13.422	0.0004
Habitat management	−172.692	7	359.418	14.565	0.0002
Helpers management	−173.755	6	359.534	14.681	0.0002
Management	−175.190	5	360.399	15.546	0.0001

[a] Model components: Temporal includes day of the breeding season, nest age and its quadratic term, year, and the interaction of day and year, habitat includes stand age and its quadratic term, helpers (present or absent); and management refers to stand treatment type.
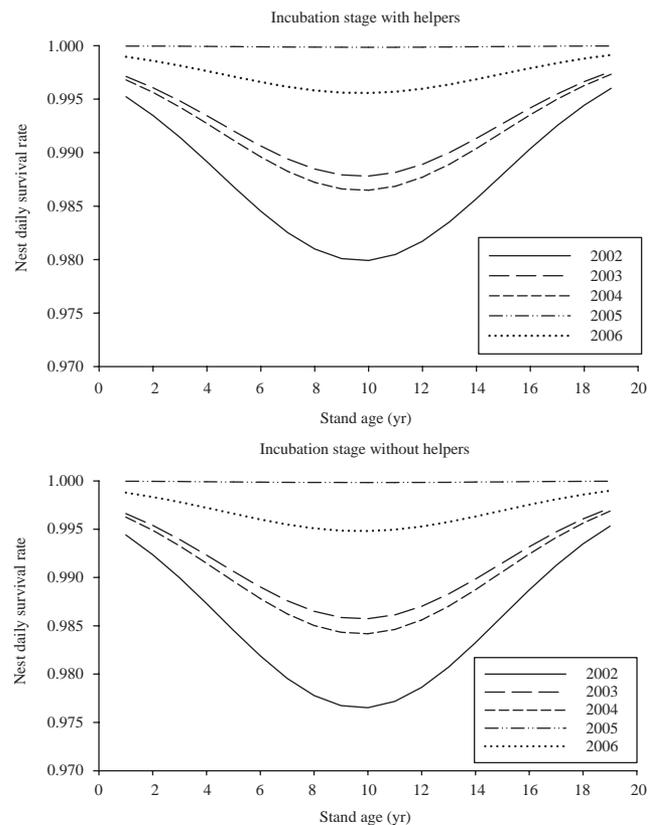
Table 2. Model averaging for Florida scrub-jays nest daily survival rate models in the incubation stage on Ocala National Forest, Florida (2002–2006).

Variable[a]	Estimate	Unconditional SE	Odds ratio	95% CI
Intercept	4.1854	2.5773		
Day	0.1094	0.0692	1.1156	0.9715–1.2811
Age	−0.0526	0.1346	0.9488	0.7249–1.2418
Age^2	0.0007	0.0066	1.0007	0.9876–1.0140
$Year_{2002}$	1.8393	1.6084	6.2922	0.2522–156.9782
$Year_{2003}$	3.0908	1.6846	21.9946	0.7570–639.0148
$Year_{2004}$	3.1379	1.6671	23.0552	0.8218–646.8047
$Year_{2005}$	9.3868	4.0485	11.9293×10^3	3.6320–39.1817×10^6
$Year_{2006}$	0.0000	0.0000	1.0000	1.0000–1.0000
Day × $year_{2002}$	−0.1068	0.0714	0.8987	0.7790–1.0367
Day × $year_{2003}$	−0.1305	0.0705	0.8777	0.7622–1.0107
Day × $year_{2004}$	−0.1353	0.0702	0.8735	0.7590–1.0051
Day × $year_{2005}$	−0.1909	0.0787	0.8262	0.7058–0.9671
Day × $year_{2006}$	0.0000	0.0000	1.0000	1.0000–1.0000
Stand age	−0.3707	0.4045	0.6903	0.3074–1.5502
$Stand\ age^2$	0.0190	0.0216	1.0192	0.9762–1.0641
$Helpers_0$	−0.1596	0.2691	0.8525	0.4977–1.4602
$Helpers_1$	0.0000	0.0000	1.0000	1.0000–1.0000

[a] Variables: Day = day of the breeding season; Age = nest age and its quadratic term age^2; Year = 2002–2006, Stand age (yr) and its quadratic term stand age^2; $Helpers_0$ = helpers absent; $Helpers_1$ = helpers present. Only variables that appeared in models with a change in Akaike's information criterion corrected for small samples (ΔAIC_c) <2.0 are included.

Figure 1. Nest daily survival rate for the incubation stage for nests with and without helpers in relation to day of the breeding season obtained using logistic-exposure and model averaging (Shaffer 2004) for Florida scrub-jays on Ocala National Forest, Florida (2002–2006). The model included the variables day of the breeding season, year, day × year, nest age and its quadratic term, stand age and its quadratic term, and helpers. We evaluated the model at the median value for nest age as 9.0 days and stand age as 8.0 yr.

Figure 2. Nest daily survival rate for the incubation stage for nests with and without helpers in relation to stand age (yr) obtained using logistic-exposure and model averaging (Shaffer 2004) for Florida scrub-jays on Ocala National Forest, Florida (2002–2006). The model included the variables day of the breeding season, year, day × year, nest age and its quadratic term, stand age and its quadratic term, and helpers. We evaluated the model at the median value for nest age as 9.0 days and day of the breeding season as 31.5.

Table 3. Logistic-exposure model-selection results we obtained with PROC GENMOD (SAS Institute 2004) for Florida scrub-jay nest daily survival rates in the nestling stage on Ocala National Forest (2002–2006). We ranked models based on Akaike's information criterion for small samples (AIC$_c$), ΔAIC$_c$, and Akaike weights (w_i); ΔAIC$_c$ is based on Log$_e$(L), which is the value of the maximized log-likelihood function, and the number of parameters in the model (K). Models with the smallest AIC$_c$ and ΔAIC$_c$, and highest Akaike weight (w_i) have more support.

Model[a]	Log$_e$(L)	K	AIC$_c$	ΔAIC$_c$	w_i
Temporal helpers	−303.989	9	626.024	0.000	0.3246
Temporal	−305.389	8	626.814	0.790	0.2187
Temporal habitat helpers habitat × helpers	−301.744	12	627.567	1.543	0.1501
Temporal habitat	−304.321	10	628.697	2.673	0.0853
Helpers	−312.757	2	629.516	3.492	0.0566
Temporal habitat helpers management habitat × helpers	−299.347	16	630.832	4.808	0.0293
Habitat helpers habitat × helpers	−310.500	5	631.015	4.991	0.0268
Temporal helpers management	−302.496	13	631.085	5.060	0.0258
Temporal management	−303.753	12	631.585	5.561	0.0201
Constant survival	−314.832	1	631.665	5.641	0.0193
Temporal habitat management	−301.890	14	631.887	5.863	0.0173
Habitat helpers management habitat × helpers	−307.731	9	633.508	7.484	0.0077
Habitat	−313.804	3	633.614	7.590	0.0073
Helpers management	−310.916	6	633.853	7.829	0.0065
Management	−312.856	5	635.728	9.703	0.0025
Habitat management	−311.082	7	636.192	10.168	0.0020

[a] Model components: Temporal includes day of the breeding season, nest age and its quadratic term, and year; habitat includes stand age and its quadratic term; helpers (present or absent); and management refers to treatment type.

The modeling for the nestling stage revealed that 3 models had ΔAIC$_c$ < 2 among the suite of potential models (Table 3). The top model included the temporal and helpers components, with an Akaike weight of 0.32. The other 2 models consisted of the temporal component alone ($w_i = 0.22$) and the temporal, habitat, and helpers components along with the interaction of habitat and helpers ($w_i = 0.15$).
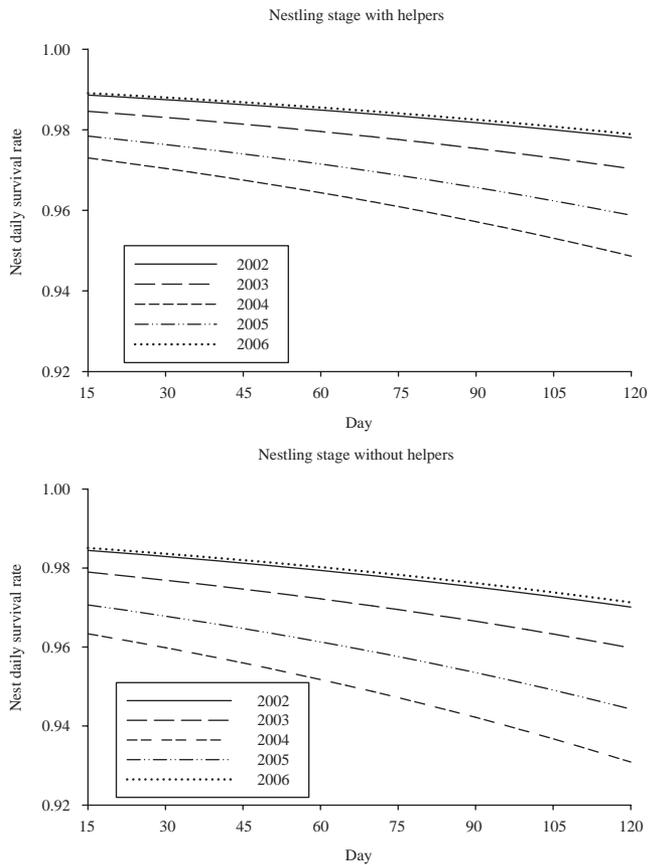
In the nestling stage, model averaging showed support for year because year$_{2004}$ was different from year$_{2002}$ and year$_{2006}$ (contrasts not shown) with odds ratios of 0.4148 and 0.3979, respectively (Table 4). Although the odds ratio for day of the breeding season was 0.9936, its narrow confidence interval of 0.9818–1.0056 (Table 4) and the graphic relationship of DSR with day (Fig. 3), gave some support for day of the breeding season in the nestling stage. As day of the breeding

season progressed, DSR for nestlings slightly declined each year with and without helpers (Fig. 3). The odds ratio for nest age was 0.6500 with a confidence interval slightly exceeding 1.0, indicating support for nest age being important in determining nest survival (Table 4). The model shows that when nestlings were first hatched, they had high survivability, but DSR declined until about nest age 27, at which point DSR rapidly increased until the nestling stage was completed (Fig. 4). We observed this pattern for nests with and without helpers, but DSR was lower for nests lacking helpers throughout the nestling period (Fig. 4). Odds ratios for stand age and its quadratic term were close to 1.0, with confidence intervals that included 1.0, indicating little support (Table 4). The odds ratio for helpers was 0.6105 with a confidence interval 0.2104–1.7717 (Table 4). From the magnitude of this odds ratio for helpers and the relationship of

Table 4. Model averaging for Florida scrub-jay nest daily survival rate models in the nestling stage on Ocala National Forest, Florida (2002–2006).

Variable[a]	Estimate	Unconditional SE	Odds ratio	95% CI
Intercept	10.6546	3.4875		
Day	−0.0064	0.0066	0.9936	0.9818–1.0056
Age	−0.4307	0.2544	0.6500	0.3908–1.0812
Age^2	0.0080	0.0046	1.0081	0.9987–1.0175
Year$_{2002}$	−0.0417	0.4688	0.9592	0.3756–2.4494
Year$_{2003}$	−0.3499	0.4318	0.7048	0.2971–1.6716
Year$_{2004}$	−0.9216	0.4130	0.3979	0.1742–0.9088
Year$_{2005}$	−0.6916	0.4231	0.5008	0.2149–1.1672
Year$_{2006}$	0.0000	0.0000	1.0000	1.0000–1.0000
Stand age	−0.0563	0.0991	0.9452	0.7752–1.1525
Stand age^2	0.0022	0.0041	1.0022	0.9941–1.0104
Helpers$_0$	−0.4935	0.5327	0.6105	0.2104–1.7717
Helpers$_1$	0.0000	0.0000	1.0000	1.0000–1.0000
Stand age × helpers$_0$	0.0254	0.0473	1.0257	0.9332–1.1274
Stand age × helpers$_1$	0.0000	0.0000	1.0000	1.0000–1.0000

[a] Variables: Day = day of the breeding season; Age = nest age and its quadratic term age^2; Year = 2002–2006, Stand age (yr); Helpers$_0$ = helpers absent; Helpers$_1$ = helpers present. Only variables that appeared in models with change in Akaike's information criterion for small samples (ΔAIC$_c$) <2.0 are included.

Figure 3. Relationship of nest daily survival rate with day of the breeding season for nests with helpers and those without helpers in the nestling stage using logistic-exposure and model averaging for Florida scrub-jays on Ocala National Forest, Florida (2002–2006). The model included the variables day of the breeding season, year, nest age and its quadratic term, stand age and its quadratic term, helpers, and stand age × helpers. We evaluated the model at the median value for nest age as 27.5 days and stand age as 7.0 yr.

Figure 4. Relationship of nest daily survival rate with nest age for nests with and without helpers in the nestling stage using logistic-exposure and model averaging for Florida scrub-jays on Ocala National Forest, Florida (2002–2006). The model included the variables day of the breeding season, year, nest age and its quadratic term, stand age and its quadratic term, helpers, and stand age × helpers. We evaluated the model at the median value for day of the breeding season day as 52.0 days and stand age as 7.0 yr.
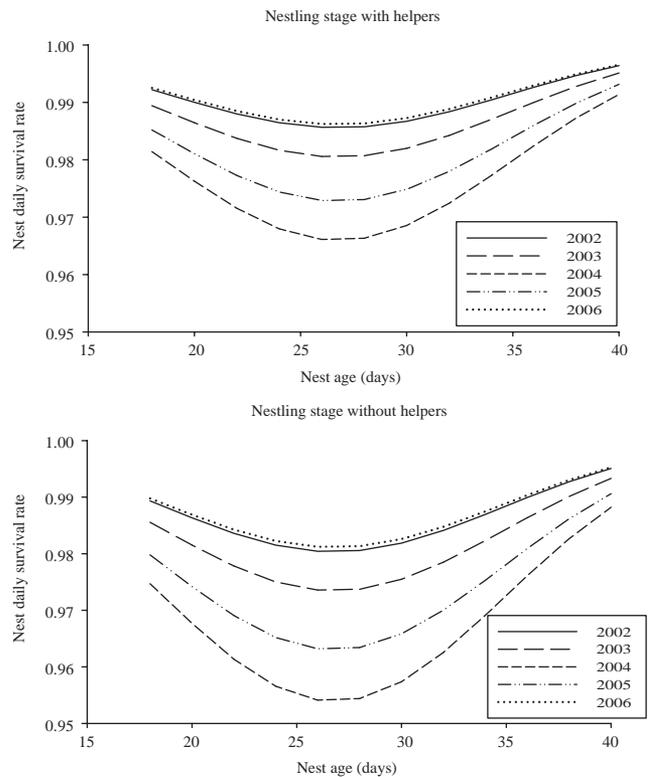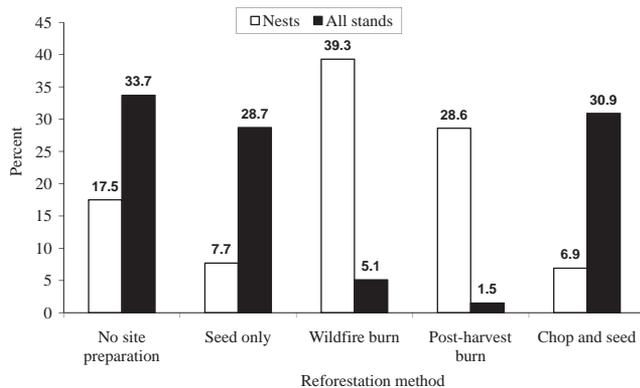
nest age and helper status that was evident in each of the years (Fig. 4), there is support for concluding that helper presence has a positive effect on DSR.

The relative importance of model components differed between incubation and nestling stages (Table 5). In both stages, the temporal component had the highest importance value and management (treatments) had lowest importance. Conversely, the habitat component (stand age) was more

Table 5. Relative importance of the 4 model components for predicting nest daily survival rates of Florida scrub-jays on Ocala National Forest, Florida (2002–2006).

Component[a]	Incubation stage	Nestling stage
Temporal	0.9716	0.8712
Management	0.0451	0.1112
Habitat	0.5904	0.3258
Helpers	0.4125	0.6274

[a] Model components: Temporal includes day of the breeding season, nest age and its quadratic term, year, and the interaction of day and year for the incubation stage; habitat includes stand age and its quadratic term; helpers (present or absent); and management refers to stand treatment type.

important in the incubation stage than in the nestling stage, whereas the helper component (presence of helpers) was more important in the nestling stage than in the incubation stage.

Approximately 39.5% of available oak scrub habitat ≤20 yr of age on Ocala National Forest was allowed to reseed naturally (J. Hinchee, U.S. Forest Service, personal communication) and contained 84.0% of monitored nests. The remaining 16.0% of nests were located in 60.5% of the area that was artificially reseeded. There was a disproportionately high number of nests in the naturally reseeded areas in relation to availability ($\chi_1^2 = 393.2$, $P < 0.001$).

About 67.9% of the 474 monitored nests were located in areas that had undergone a wildfire (39.3%) or post-harvest burn (28.6%), although such areas comprised only 6.6% of the available 39,211 ha of habitat (Fig. 5). Stands that were artificially seeded (28.7% of area) or chopped and then artificially seeded (30.9% of area) contained 14.6% of monitored nests (Fig. 5). Distribution of nests was different from that expected based on availability of treatment types ($\chi_5^2 = 3686.2$, $P < 0.001$). Sites subjected to burning (wildfire or prescribed) appeared to be selected for nesting by Florida scrub-jays, whereas sites that were only artificially seeded or lacked site preparation were used less than expected based on availability.

Figure 5. Percent of Florida scrub-jay nests ($n = 474$) versus percent of available scrub habitat (39,211 ha) by reforestation method (site preparation and seeding) for stands ≤20 yr of age on Ocala National Forest, Florida (2002–2006).

DISCUSSION

We found that the reforestation methods used on the Ocala National Forest, including site preparation and seeding, had little effect on Florida scrub-jay nest DSR. The most important variables in determining nest DSR in the incubation stage were temporal, especially year and day × year, and also habitat (stand age). The influence of day × year may be partly related to how early in the breeding season the oak scrub obtained its leaves, as leaves provided some protection for the nest against inclement weather and concealment from predators. During the nestling stage, the variables with the most support for influencing nest DSR were the temporal component (year, nest age and its quadratic term, and to a lesser extent day) and helpers.

In a 10-year study conducted at the Archbold Biological Station, Woolfenden and Fitzpatrick (1984) found extensive annual variation in nest survival ranging from a low 0.267 in 1972 to a high of 0.778 in 1970. Bowman and Woolfenden (2001) found that nest failure for Florida scrub-jays in wildland habitat varied annually and that nest failure in the incubation stage was similar to that in the nestling stage. Our estimate for nest survival cannot be directly compared to the average life span of nests as calculated by Woolfenden and Fitzpatrick (1984) because methodologies differed. However, our data also show substantial annual variation in DSRs, as year (via the day × year interaction only in the incubation stage) was included as a variable in the models for the incubation and nestling stages. Florida scrub-jay hatching is not highly synchronized, as incubation may begin prior to the laying of the fourth egg in a clutch, which can result in young hatching about 1–2 days after its nest mates and thus putting it at a competitive disadvantage for survival if food delivered by the parents is insufficient. However, starvation, though the second most common cause of nestling loss, only accounted for approximately 13% of nestling mortality (Woolfenden and Fitzpatrick 1984); thus, there may be other factors that account for observed annual differences between DSRs in the incubation and nestling stages.

In Florida scrub-jays, nest failure has been found to be primarily related to the level of predation (Schaub et al. 1992, Woolfenden and Fitzpatrick 1996, Carter et al. 2007, Franzreb 2007). Further, Schaub et al. (1992) found that nest predation on Florida scrub-jay nests increased as the season progressed. Annual variation in DSRs can be affected by predation, which may be influenced by variability in yearly rainfall. Woolfenden and Fitzpatrick (1984) found that the proportion of nests that yielded ≥1 fledgling was positively correlated with rainfall levels in the 10 months immediately preceding the nesting cycle. Woolfenden and Fitzpatrick (1984) proposed that the amount of rainfall may influence the level of nest predation by affecting the density and activity of nest predators, availability of alternative foods for predators, time budgets of nest vigilance by Florida scrub-jays, or amount of vegetative protective cover for the nests.

Woolfenden and Fitzpatrick (1984) noted that presence of helpers had a positive effect on nest survival in both the incubation and nestling stages but that this effect was only evident during a pair's first nesting attempt of the season. Mumme (1992) conducted experimental removals of Florida scrub-jay helpers and found no significant effect on breeder survival, egg survival, or hatching success. However, Mumme (1992) did observe higher rates of predation on nestlings in 1 of the 2 years of the study and lower fledgling survival in both years for nests in which helpers had been removed versus the control where helpers were not removed. The results of our study concur more with those of Mumme (1992) than those of Woolfenden and Fitzpatrick (1984), as we found that helpers provide a benefit to nest survival only in the nestling stage, not unexpected, as helpers play no role in the incubation process. Further, Woolfenden and Fitzpatrick (1984) found that pairs with helpers had a significantly greater chance of producing ≥1 fledgling than did nests without helpers ($\bar{x} = 2.44$ fledglings with helpers vs. 1.56 without helpers). On Ocala National Forest, groups with helpers on average produced 0.7 fledglings more per pair than nests lacking helpers (Franzreb 2007).

Nest age was not an important variable in our incubation stage model but was in the nestling stage model. During incubation there are fewer trips by the incubating female to the nest and no begging young that might attract the attention of potential predators. Increased visits to the nest during the nestling stage by adults to feed young and presence of noisy young may increase the likelihood that the nest will be detected and lost to predation. In other species, increased begging has been correlated with an increase in the likelihood of predation during the nestling stage (Halupka 1998, Dearborn 1999). When eggs first hatched in our study, the nest had a high likelihood of daily survival but then the rate rapidly declined until approximately day 27, at which point it increased throughout the remainder of the nestling period. Helpers fed the young and protected nestlings from predation, which may explain why the DSR was higher with helpers versus without helpers. However, as we observed this pattern in nests with and without helpers, it is not likely to be solely the result of the presence and activity of helpers; it may be the result of the behavior of nestlings themselves in that, as they age, they

tend to become more cautious and less likely to beg until they actually see their parents at the nest with food. This more restrained behavior may reduce the loss of nestlings to predators that rely on sound or movement to detect prey.

For many bird species, eggs and nestlings resulting from first nesting attempts within a breeding season are more likely to survive than those produced from later attempts (Lack 1954, 1966). Survival rates do not remain constant throughout the nest cycle and tend to decline with time in the nest (Ricklefs 1969, Caccamise 1976). In some species, nests in the incubation stage experienced higher mortality (Zimmerman 1984, Winter 1999), whereas in others higher mortality occurred in the nestling stage (O'Grady et al. 1996, Lloyd 2003). Many studies, however, detected no difference in survival between nest stages (Wray et al. 1982, Pietz and Granfors 2000). In the case of the Florida scrub-jay, Woolfenden and Fitzpatrick (1984) calculated that daily nest survival decreased with the number of days into the breeding season. In comparing wildland to suburban habitats, Bowman and Woolfenden (2001) found that in both habitats nest success of Florida scrub-jays declined throughout the breeding season. Schaub et al. (1992) noted that predation on Florida scrub-jay nests increased as the breeding season progressed. Based on our models, for 3 of the years for the incubation stage and each year in the nestling stage, nest success declined as day of the breeding season increased. In the incubation stage, we observed the influence of day on DSR via its interaction with year. In the nestling stage, DSR declined slightly as the day of the breeding season progressed.

The decline in DSRs as the breeding season progressed may have been a response to the availability of food resources. However, because the decline also was apparent during the incubation stage for at least some of the years studied, prevalence of food resources may not be the entire explanation. It may be that as the season progresses, predation pressure may increase or higher daily maximum ambient temperatures may adversely impact the eggs or nestlings. It is possible that both the availability of food and the prevalence of predators play substantial roles in nest success for Florida scrub-jays. It is clear from our study that in most years there are substantial nest survival benefits for a pair to nest early in the season.

Even though Florida scrub-jays appeared to prefer to nest in naturally seeded stands, the models did not indicate that seed treatment had an influence on DSR in either the incubation or nestling stages. It is not clear why this would affect the location but not the survival of nests except that naturally reseeded areas may have had higher plant species diversity and more structural diversity that Florida scrub-jays found attractive for nesting. Also, some artificially reseeded areas were chopped and a small percentage were chopped and burned. Regardless of whether a chopped and seeded stand was burned or left unburned, Florida scrub-jays avoided locating nests in stands that had been subjected to chopping. The areas that had undergone natural reseeding included those that were subjected to a wildfire burn or a post-harvest burn, and these burned areas were strongly preferred for nesting by Florida scrub-jays.

During scrub fires, some patches of vegetation are burned while others are left unburned, forming a mosaic of scrub patches of different ages. Florida scrub-jays spend a substantial amount of time foraging on the ground, where they avoid areas of heavy leaf litter or herbaceous cover (Fitzpatrick et al. 1991). For 3–4 yr after an area is burned, oak scrub produces few acorns, and inadequate nest site cover (Ostertag and Menges 1994, Woolfenden and Fitzpatrick 1996). As stands age, vegetation growth increases the percent of canopy cover, thus resulting in a decline in the amount of bare sandy ground that Florida scrub-jays require for foraging and acorn caching. Scrub habitat recovers to pre-burn conditions very rapidly (Abrahamson 1984), so burned areas can provide good foraging habitat once acorn production has resumed. As scrub reaches approximately 20 yr of age, acorn production and the amount of open ground used by Florida scrub-jays for caching acorns decrease, whereas tree density and nest predation increase (Woolfenden and Fitzpatrick 1996). Scrub with pine cover >15% is rarely used by Florida scrub-jays (Cox 1987, Breininger 1992). As the canopy cover for trees >3 m reaches and then exceeds 50%, the habitat becomes unsuitable for Florida scrub-jays. Breininger et al. (2009) examined whether habitat quality within territories affected survival and detection probabilities of breeding Florida scrub-jays. They found that most available habitat is only marginally suitable across most of the species' range and conclude that average survival rates are such that the population will continue to decline. This is because the less suitable habitat with taller vegetation structure is resistant to change and the optimal habitat is an intermediate transitional stage that is short-lived without some form of habitat disturbance.

On Ocala National Forest, Greenberg et al. (1995) compared bird species densities in mature sand pine forest to stands in 3 disturbance treatments from 3- to 7-yr old. Treatments included: 1) high intensity wildfire, salvage logging, natural regeneration; 2) clearcutting, roller chopping, and broadcast seeding; and 3) clearcutting and bracke-seeding. Greenberg et al. (1995) found Florida scrub-jays only in areas that had been disturbed and found no significant differences in densities of scrub-jays among the 3 treatments. Likewise, in our study, data on DSR for the incubation and nestling stages showed no significant difference between treatment types. Even though Florida scrub-jays appear to prefer burned areas for nesting habitat (higher proportion of nests) over those with no site preparation, seeding, or chopping with seeding, a nest appears to be no more likely to survive in a stand that had undergone any particular type of treatment.

Stands 6–10 yr of age contained approximately 77.6% of the nests in our study, although only 17.4% of available habitat was in this stand age group (K. Franzreb, U.S. Forest Service, unpublished data). The patterns for DSR versus stand age were unexpected because we anticipated that DSR would be highest in middle-aged stands where the acorn crop would be better and cover for nest protection would be higher than in younger stands, and the vegetation would not have grown enough to reduce the open sandy areas needed for acorn caching as in the oldest stands. We noted that Florida scrub-jays frequently nested in the hedge-like

vegetation that was not removed during logging along the edges of clearcut stands, which increased use of very young stands and appeared to be particularly good habitat for nest survival in the incubation stage.

Although good quality habitat in the middle stand age classes had the highest usage for Florida scrub-jay nesting, birds nesting there did not seem to have a reproductive advantage. From a selective perspective, pairs should prefer to nest in stands that offer the highest probability of nest success. In the case of nests in the incubation stage, DSR was highest in stands ≤5 yr of age and in stands 16–20 yr of age. Stands ≤5 yr comprised about 17.8% of available scrub habitat and contained 18.4% of nests. Only 12 nests (0.6%) were located in stands 16- to 20-yr old even though these stands comprised 33.9% of available scrub habitat (K. Franzreb, unpublished data). It is possible that the high DSR in stands 16- to 20-yr old may be an artifact of a low sample size in that stand age range. Perhaps the lower Florida scrub-jay densities in the older stands resulted in less competition for space and food resources. It may be that high Florida scrub-jay density, food availability, or predator densities may be responsible for the lower than expected DSRs in middle stand ages, but the actual cause remains elusive.

MANAGEMENT IMPLICATIONS

Use of young stands appears to be associated with presence of hedge rows, and high DSR in older stands may be an artifact of the low sample size of nests. We therefore recommend that a mosaic of stand ages be provided, with the understanding that even though middle-aged stands have lower DSRs, they produce more Florida scrub-jay nests, and subsequently more fledglings, than older-aged stands. Although the models indicated that stand treatment in terms of site preparation or seeding did not significantly influence DSRs, Florida scrub-jays seem to prefer burned and naturally reseeding habitat for nesting. Hence, to increase the actual number of nests, prescribed burning may be a valuable tool for Florida scrub-jay management.

ACKNOWLEDGMENTS

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