REPRODUCTIVE ECOLOGY OF THE FLORIDA SCRUB-JAY (*Aphelocoma coerulescens*) ON JOHN F. KENNEDY SPACE CENTER/MERRITT ISLAND NATIONAL WILDLIFE REFUGE: A LONG-TERM STUDY

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ABSTRACT

From 1988 to 2002 we studied the breeding ecology of Florida Scrub-Jays (*Aphelocoma coerulescens*) on John F. Kennedy Space Center/Merritt Island National Wildlife Refuge. We examined phenology, clutch size, hatching failure rates, fledgling production, nest success, predation rates, sources egg and nestling mortality, and the effects of helpers on these measures. Nesting phenology was similar among sites. Nests were initiated from late February to mid May with peak initiation during late March. Very few nests remained active beyond mid June. Modal clutch size at T4 was three; modal clutch size at HC and Titan was four. Mean clutch size at Titan was significantly larger than at HC or T4. Clutch size did not influence nest success. Pairs with helpers did not produce larger clutches than pairs without helpers. Fledgling production at T4 was significantly greater than at HC and similar to Titan. However, successful pairs at Titan produced significantly more fledglings than T4 or HC. This is probably a result of the large average clutch size of Titan. Pairs with helpers at HC produced significantly more fledglings than pairs without helpers; helpers did not influence fledgling production at the other sites. Nest success (proportion of nests that produce ≥ 1 fledgling) at HC and Titan was low, 19% and 32 % respectively. Nest success at T4 was 48% and was significantly greater than at HC. Average predation rates at all sites increased with season progression. Weekly means of daily predation rates at HC were higher than T4 during early season and peaked during late April. Titan weekly means were also higher than T4 but did not peak as strongly as HC. Predation rates at all sight rose sharply by early June. The main cause of nest failure at all sites was predation, 93%. Abandonment and hatching failure were small sources of nest failure. Starvation was rare and associated with breeder death or injury.

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INTRODUCTION

A significant population of the threatened Florida Scrub-Jay, *Aphelocoma coerulescens,* occurs along Florida's East coast on John F. Kennedy Space Center/Merritt Island National Wildlife Refuge (KSC/MINWR). This core population has the potential to be one of the three largest metapopulations of the species (Stith 1999, Stith et al. 1996). Although the majority of this metapopulation occurs on protected lands, poor habitat quality poses a serious risk (Stith 1999, Breininger et al. 1999). Optimal Scrub-Jay habitat is dominated by low stature scrub oak species (e.g. *Quercus geminata, Q. myrtifolia,* and *Q. chapmanii*) interspersed with numerous sandy openings and sparse tree cover (Woolfenden and Fitzpatrick 1984, Breininger et al. 1998) and is maintained by frequent fire (Myers 1990, and Hinkle 1992 a). Scrub-Jay habitat on KSC/MINWR differs from habitat as described by Woolfenden and Fitzpatrick (1984) in that it occurs as narrow patches in a matrix of poorly drained pine flatwoods or marshes (Breininger et al. 1991). Also, the Titan site is a distinct coastal scrub community that differs in composition and soils (Schmalzer et al. 1999). Much of the Scrub-Jay habitat (and the surrounding matrix) considered in this study has been degraded due to past fire suppression (Duncan et al. 1999). Scrub patches have become overgrown and lost openings; matrix habitat has experienced increased tree density in pine flatwoods and woody species invasion of marshes. Scrub habitat restoration efforts have been ongoing at KSC/MINWR since 1981.

Historical management differences have made restoration more difficult at HC than T4 (Duncan et al. 1999). As a result, many territories at HC still consist of all tall scrub or contain significant amounts of tall scrub (Breininger and Carter 2003). Titan restoration has also been complicated by invasive exotic species and differing responses of the dominant oak species, *Quercus virginiana*, to management (Schmalzer per. comm.).

Scrub-Jays inhabiting suboptimal habitat experience poor demographic performance (Woolfenden and Fitzpatrick 1984, Breininger et al. 1996). During the period of this study T4 has expanded or was stable; HC and Titan have declined (Breininger et al 1996, Breininger pers. comm.). Breininger et al. (1996) investigated the demography of HC and T4 from 1988 to 1993 and speculated that the HC and T4 populations differed from inland populations at Archbold Biological Station (Archbold; Woolfenden and Fitzpatrick 1984) primarily due to differences in predator regimes and predator seasonality at KSC/MINWR. Also, Schaub (1992) found that diurnal snakes and birds were the primary predators of Scrub-Jay eggs and nestlings at Archbold. However, work conducted at KSC/MINWR indicated that predation occurred mainly at night by snakes (LeGare et al. unpbl. data).

Scrub-Jays are cooperative breeders; half of all pairs at Archbold have nonbreeding helpers (Woolfenden and Fitzpatrick 1984) and pairs with helpers at Archbold have increased reproductive success (Woolfenden and Fitzpatrick 1984, Mumme 1992). Pairs with nonbreeders at HC experienced greater reproductive success; nonbreeders did not affect reproductive success at T4 (Breininger et al. 1996).

The populations of Scrub-Jays on KSC/MINWR inhabit a distinctive landscape, potentially encounter unique interspecific interactions (predator species and predation seasonality), and in the case of HC and Titan are experiencing a decline. The purpose of this project was to quantify nesting parameters (i.e. phenology, clutch size, hatching failure, fledgling production, nest success, predation rates, egg and nestling mortality, and the effects of breeder experience and presence of helpers on these measures) of this unique population of Scrub-Jays.

METHODS

Study Sites – This study was conducted in conjunction with long-term demographic monitoring of three populations of Scrub-Jays (HC, T4, Titan) on KSC/MINWR. HC is a 400 ha site consisting of a series of ridges and swales; oak scrub (i.e., *Quercus myrtifolia, Q. geminata,* and *Q. chapmanii*) dominates well drained ridges, saw palmetto (*Serenoa repens*) and ericaceous shrubs (i.e. *Lyonia lucida and Ilex glabra*) dominate transitional areas and marshes dominate troughs (Schmalzer and Hinkle 1992 b). T4 is a 240 ha site similar in topography to HC but with an open canopy of pine, *Pinus elliotii*, (Duncan et al. 1995, 1999). Classic oak scrub dominates high well-drained ridges. Small patches of oaks also occur on lower less well-drained ridges, and marshes occur in swales (Breininger and Oddy 2001). Matrix habitat at T4 is mesic pine flatwoods (Duncan et al. 1999). Titan is a coastal scrub community dominated or co-dominated by Live oak (*Q. virginiana*); other shrubs associated include *S. repens, Myrica cerifera, Bumelia tenax,* and *Forestiera segregata* (Schmalzer et al. 1999).

Field procedures. – Fieldwork was conducted from 1988 to 2002 at HC, 1989 to 2002 at T4, and 1990, 1992 to 2002 at Titan. Most adults were banded with a unique combination of metal and plastic color bands. Most nestlings were banded 11 days after hatching and immigrants were banded within a few months of their arrival. Group composition and status of individuals was determined via observation of behavior (e.g., dominance displays and vocalizations; see Woolfenden and Fitzpatrick 1977).

Nest searches were conducted from late February through mid-June. Nesting status of groups was determined by observation of diagnostic behaviors such as nest building and mate feeding or the absence of the breeder female. Most nests were located before the onset of incubation. Nests were visited weekly until failure or fledging during late morning or afternoon. Additional visits were made to verify clutch size, confirm hatching, band nestlings, and confirm fledging. Partial or complete losses of eggs or nestlings (less than 15 days old) that occurred between visits were estimated to have occurred midway between visits and considered to be acts of predation. Partial losses of nestlings from healthy broods were attributed to predation because starvation (and brood reduction) is rare in Florida Scrub-Jays (Woolfenden 1978, Woolfenden and Fitzpatrick 1984). Eggs were assumed dead if they did not hatch within 48 hours after the first egg hatched. Nests were considered successful if at least one fledgling was produced. The number of fledglings produced was calculated as the number of fledglings observed out of nest or the number of nestlings seen in the nest during the fledging confirmation check (17 days after hatching) in nests that were undisturbed (i.e. no signs of predation) after fledging.

Statistical analysis. – We tested for differences in mean initiation date (Julian) among sites using ANOVA. Differences in the means of clutch size, hatching failure, and fledgling production (fledglings per pair), were analyzed with respect to study area using the Kruskal-Wallis test. Differences in the mean fledgling production were analyzed with respect to presence of helpers using U-tests. Nest success was analyzed with respect to study area, clutch size using contingency table analyses. The apparent level of predation pressure was analyzed with respect to study area, season and presence of helpers using contingency table analyses. We quantified predation pressure at each site as the number of nests that experienced at least one act of predation (i.e., partial predations were included in predation counts). Nests were categorized by season in order to meet cell count assumptions for χ^2 tests (Zar 1996). Season was classified as "early", "middle", and "late" with nests initiated in the first third of the range of initiation dates classified as "early" and so forth. The Tukey test was used for multiple pair-wise comparisons and (Zar 1996). Kolmogorov-Smirnov tests were used to indicate significant departures from normality. Kruskal-Wallis and U-tests were used for samples not meeting the assumptions of ANOVA or t-test (Zar 1996). U-tests were used for multiple comparisons of non-parametric data; experiment wise error was partitioned by number of comparisons. Contingency table analyses were conducted for categorical data (Zar 1996). All results are presented as $\bar{\times}$ ± SE unless otherwise noted. SPSS 10.0 was used for all analyses (SPSS Inc 1999).

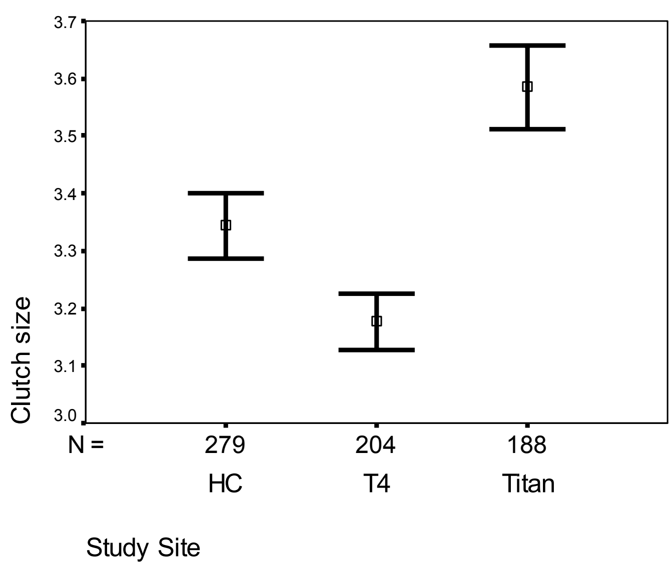
RESULTS

Nesting phenology. – The mean initiation date of first attempts was similar for all sites (F = 0.006, df = 2, P = 0.994). The mean initiation date of first attempts (*n* = 738, all sites pooled) was 31 March (± 0.68 days). Excluding two exceptionally early nests at Titan, 64% of all first attempts (all sites pooled) were initiated in March, 33% in April, and 3% in May. No attempts were initiated after 31 May. Among March nests most groups initiated first attempts during the third week. Second attempts followed 43% of failed first attempts. The earliest recorded second attempt was initiated on 27 March.

Third and fourth attempts were relatively uncommon. Groups at HC had more third (n = 27) attempts than T4 (n = 5) or Titan (n = 6) and the only fourth attempts (n = 4), and initiated nests later into the season. For all site pooled the average number of attempts was 1.46 ± 0.043. Three double broods (i.e., young of a previous attempt alive during a subsequent attempt) were observed at HC and occurred in groups with helpers.

Clutch size.– Mean clutch size varied significantly among sites (Kruskal-Wallis test, χ^2 = 46.581, df = 2, P = .000), **Figure 1**. Clutch annual means ranged from 3.29 to 3.94 at Titan, 3.00 to 3.63 at HC, and 2.80 to 3.54 at T4. Modal clutch size at HC and Titan was four; T4 modal clutch size was three. Titan clutch sizes ranged from one to eight; three nests at Titan produced exceptionally large clutches of six (n=2) and eight (n=1) eggs. HC clutch sizes ranged from one to six; one nest had a clutch size of six. T4 clutch sizes ranged from one to five.

Figure 1. Clutch size ($\bar{x}$ ± 95% CI) of Florida Scrub-Jays on KSC was largest in the Titan population followed by HC and T4 respectively.



Egg and nestling mortality. – Among nests in which all losses were of known stage, n = 543 (including partial losses) 61.4% of egg losses and 98.5% of nestling losses were due to predation (**Table 1**). There was no association between study site and the stage at which predations occurred (χ^2 = 3.964, df = 4, P = 0.411). Hatching failure was the second most common cause of egg loss and was similar at all sites (Kruskal-Wallis test, χ^2 = 2.334, P = 0.311). Among all sites 1,590 (86%) eggs hatched out of a possible 1,848 that survived the incubation period (an 11.7% loss of all eggs laid). The mean annual hatching failure rate was 0.13 (±0.01) and ranged from 0.01 to 0.26.

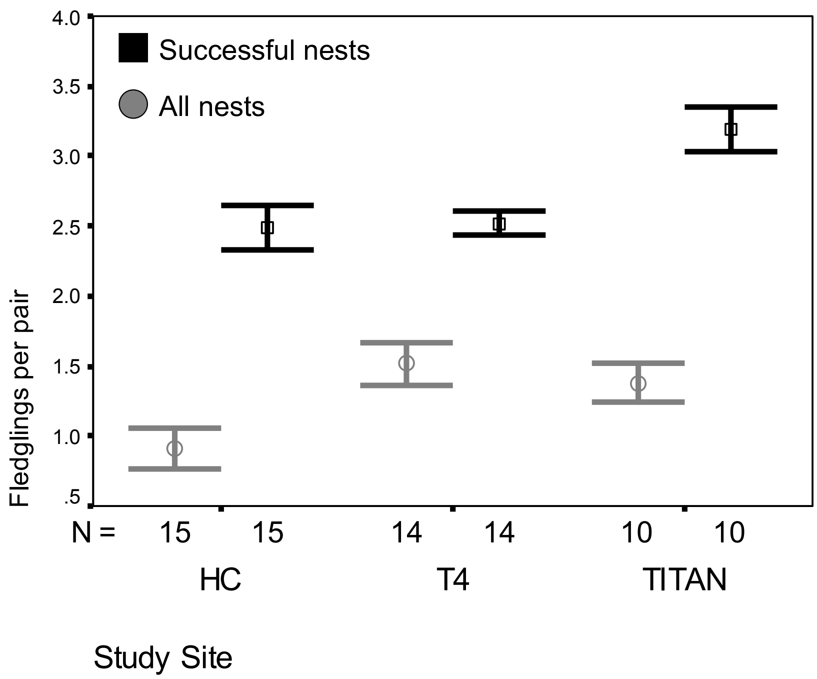
Abandonment was the third most common cause of egg loss. Two cases of abandonment were apparently a result of female breeder death during incubation stage. All other cases of abandonment occurred during the incubation stage for unknown reason. Among nestling losses there were three occurrences of starvation due to breeder death or injury. Other causes of failure included structural failure (n=1) of the nest.

Fledgling production. – T4 mean annual fledgling production was significantly greater than HC, and similar to Titan (F = 5.139, df = 2, P = 0.01), **Figure 2**. However, among successful nests, Titan produced significantly more fledglings than HC or T4 (F = 7.14, df = 2, P = 0.002; Fig. 2). Fledgling production ranged from 0.59 to 2.5 at T4, 0.17 to 1.97 at HC, and 0.54 to 1.91 at Titan. Fledgling production was not related to clutch size at any site (HC, Kruskal-Wallis test, χ^2 = 2.35, df = 4, P = 0.672; Titan, Kruskal-Wallis test, χ^2 = 4.96, df = 4, P = 0.291; T4 χ^2 = 8.47, df = 4, P = 0.076).

TABLE 1. Sources of egg and nestling loss from Florida Scrub-Jay nests on KSC in which all losses were of known stage (i.e., egg or nestling; all sites pooled).

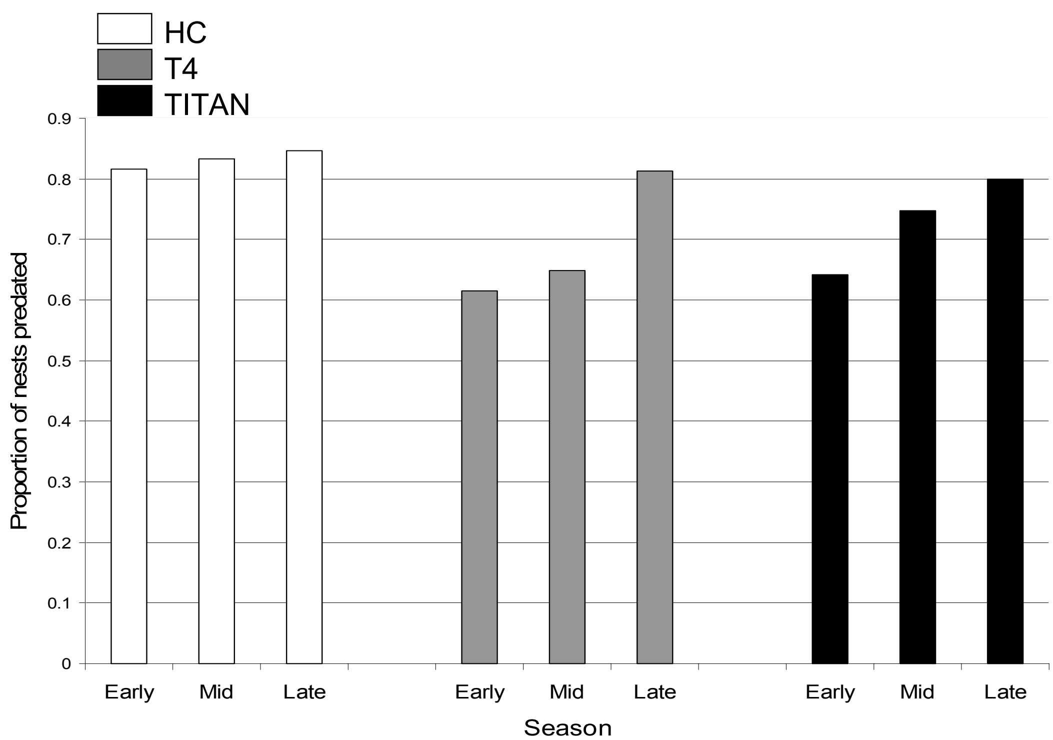
	No. individuals	% of individuals	% of losses
Eggs laid	1815	100	-
Predated	358	19.7	61.4
Abandonment	37	2	6.3
Hatching failure	188	10.4	32.2
Total egg losses	583	32.1	100
Nestlings produced	1232	100	
Predated	718	58.3	98.5
Starvation	8	0.6	1.1
Structural failure	3	0.2	0.4
Total nestling losses	729	59.2	100
Fledglings produced	503		

Figure 2. Among all Florida Scrub-Jay nests on KSC the T4 population produced significantly more fledglings per pair ($\bar{x}$ ± 95% CI) than the HC population and was similar to the Titan population. However, among successful nests the Titan population produced significantly more fledglings than T4 or HC.



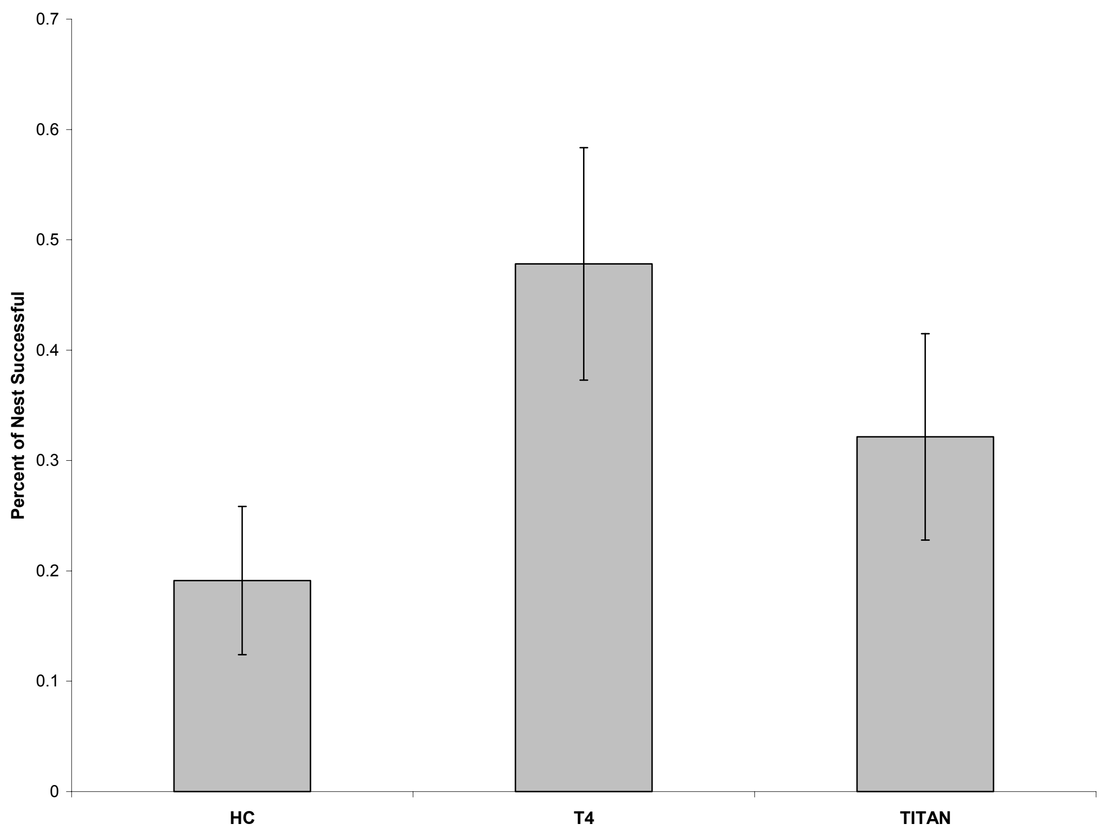
Predation and nest success. – There was a significant association between study area and nest predation during the early (χ^2 = 8.275, df = 2, P = 0.016) and middle (χ^2 = 7.096, df = 2, P = 0.029) seasons (**Figure 3**). Examination of residuals indicated that significantly more nests were predated than expected at HC during the early and middle seasons and significantly fewer nests were predated than expected at T4 during the middle season. There was no association between study area and nest predation during the late season (χ^2 = 0.258, df = 2, P = 0.879). There was also no association between season and nest predation at any site (HC, $\chi^2 = 0.212$, df = 2, P = 0.9; T4, $\chi^2 = 2.250$, df = 2, P = 0.325; Titan $\chi^2 = 2.79$, df = 2, P = 0.248). Among all sites pooled, predation accounted for 93% of nest failure.

Figure 3. Among Florida Scrub-Jay nests on KSC predation pressure (proportion of nests predated including partial predations) was greater than expected during the early and middle season at HC and less than expected at T4 during the middle season.



Annual nest success at HC was low (0.19 ± 0.03) and ranged from 0.03 to 0.4. Titan nest success was 0.32 ± 0.04 and ranged from 0.17 to 0.64. T4 nest success was 0.48 ± 0.05, ranged from 0.14 to 0.64, and was significantly greater (U = 23; P < 0.001) than HC nest success (Kruskal-Wallis test, $\chi^2 = 2$, P = 0.001), **Figure 4**. Clutch size did not influence nest success at any site (HC, $\chi^2 = 3.318$, df=4 P = 0.506; T4, $\chi^2 = 5.569$, df = 3, P = 0.135; Titan, $\chi^2 = 2.127$, df=6, P = 0.712).

Figure 4. Florida Scrub-jay nest success ($\bar{x}$ ± 95% CI) of the T4 population on KSC was significantly greater than the HC population and similar to the Titan population.



Helper effects. – There was no association between presence of helpers and nest predation ($\chi^2 = 0.089$, df = 1, P = 0.766). Pairs with helpers produced significantly more fledglings at HC than pairs without helpers, (1.25 ± 0.67 and 0.69 ± 0.57, respectively, U = 60, P = 0.029). Helpers did not influence fledgling production at T4 (U = 89.5, P = 0.701) or Titan (U = 40.5, P = 0.481).

DISCUSSION

Most aspects of Florida Scrub-Jay breeding biology such as phenology and hatching failure were relatively invariable among the sites studied; the exceptions being clutch size, fledgling production, and the influence of helpers. Collectively, Florida Scrub-Jay populations on KSC experienced strong nest predation pressure (89% of all egg and nestling losses are due to predation) but predator composition and density vary among the sites considered here (see Breininger et al. 1996). We speculate that the observed differences in reproductive traits are primarily due to different levels of nest predation pressure, timing of predation, predator composition, and possibly reduced effectiveness of Florida Scrub-Jay antipredator behavior (e.g., helper effectiveness), or a combination thereof.

Phenology, clutch size, and mortality. – The phenology of the Florida Scrub-Jay nesting season was very similar among study sites. Mean initiation date of first attempts was 31 March and peak nest initiation occurs during the third week of March. Although initiation of Florida Scrub-Jay nesting is at least partly influenced by climate (Woolfenden and Fitzpatrick 1996), locally variable factors such as foraging success or food supply are probably more significant in controlling nest initiation (Fleischer et al. 2003; Reynolds et al. 2003; Schoech and Bowman 2003) and in natural settings breeding most likely occurs during maximal food availability.

Nesting at all sites on KSC ended by late May. Woolfenden and Fitzpatrick (1984) suggested that the relatively brief breeding season may function to allow completion of feather molt prior to acorn ripening and the fall peak in territoriality. The brief nesting season may also alleviate the peak in adult mortality, during June and July at

ABS, thought to be associated with care of dependant young and feather molt (Woolfenden and Fitzpatrick 1984). However, peak breeder mortality at KSC coincides with spring and fall hawk migration (Breininger et al. 1996) supporting the former explanation.

Although food abundance does appear to influence the timing of nesting it is apparently not the only factor determining clutch size of Florida Scrub-Jays. Woolfenden and Fitzpatrick (1984) found contradictory evidence for an optimal clutch size among the Archbold population. Modal clutch size at ABS is smaller than the most productive clutch size (Woolfenden and Fitzpatrick 1984, 1996) and starvation of nestlings is rare (Woolfenden and Fitzpatrick 1984, 1996) suggesting that other factors are important in determining optimal clutch size (De Steven 1980). The case for an optimal clutch size in the KSC populations is also ambiguous. At all sites on KSC nest success was the same for all clutch sizes and all clutches were equally productive (except at T4 where four egg clutches produced more fledglings than two egg clutches).

Nest predation influences the clutch size of some bird species (e.g., Smith and Andersen 1982, Slagsvold 1984) and may also influence Florida Scrub-Jay clutch size. The universal prediction of the nest predation hypothesis states that clutch size varies inversely with predation pressure (Slagsvold 1982). Based on experiments Slagsvold (1984) concluded that all other factors being equal, populations exposed to high predation rates should lay smaller clutches. Florida Scrub-Jays typically experience high nest predation rates (Woolfenden and Fitzpartick 1984) and it is reasonable to assume that Florida Scrub-Jay pairs that lay smaller clutches might benefit because of the relatively short breeding season and the steady increase of predation rates with season progression

(Woolfenden and Fitzpatrick 1984). However, our data does not agree with the prediction of the nest predation hypothesis, because higher mean clutch sizes occurred in populations (i.e., HC and Titan) where predation was greatest. Furthermore, there was no association between nest success and clutch size.

Nevertheless, predation does influence Florida Scrub-Jay reproduction because it was the primary cause of egg and nestling loss. Collectively, predation accounts for 82% of egg and nestling losses at KSC demonstrating the significant predation pressure experienced by some of the sites at KSC. The high predation rate of eggs and nestlings at KSC reduced average fledgling production and all sites on KSC produced less young per pair than the stable population at ABS. Other sources of loss such as hatching failure and starvation are similar.

Predation pressure and nest success. – Although there was no significant association between season and nest predation it is clear from examination of Fig. 3 that predation pressure at T4 and Titan was relatively low during the early and middle seasons and steadily increased. Florida Scrub-Jays at HC did not have this window of relatively low predation pressure in which to fledge young. The additional predation pressure on nests at HC during the early and middle season certainly contributed to the significantly lower nest success at HC. The higher predation during the early and middle seasons at HC was may have been due to higher densities of predators and possibly differing predator composition. Snakes are considered the primary nest predators at KSC (Breininger et al. 1996) and recent data using remote-operated video cameras confirm that yellow rat snakes (*Elaphe obsoleta*) are the primary predator of Florida Scrub-Jay eggs and nestlings at Happy Creek (M. Legare, unpubl. data). During a two-year study, 75% of eggs and nestling lost to predation were consumed by yellow rat snakes (M. Legare unpubl. data).

Helper effects. – Similar to Breininger et al. (1996) we found that the presence of helpers was not consistently associated with fledgling production on KSC; only at HC did helpers influence fledgling production. Groups with helpers produce more fledglings presumably because helpers reduce nest predation by acting as sentinels and assisting in mobbing of predators (Francis et al. 1989, McGowan and Woolfenden 1989, Schaub et al. (1992). However, predation studies at HC indicated that predation often occurred at night (Legare unpubl. data). Florida Scrub-Jays are probably not able to defend nests against nocturnal predation (Woolfenden and Fitzpatrick 1984) perhaps explaining why there was no association between helper presence and nest predation and no consistent association between helper presence and fledgling production.

In summary, the observed variation in clutch size at KSC may be related to variation in predation pressure but apparently not as predicted by the predation hypothesis. Variation in helper effects was possibly due to variation in predator composition, predator density, or timing of predation (i.e. nocturnal). Further research should be directed at identifying important Florida Scrub-Jay nest predators on KSC, measuring densities of those predator populations, and understanding how habitat quality effects predator populations or Florida Scrub-Jay vulnerability to nest predation.

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14. ABSTRACT

From 1988 to 2002 we studied the breeding ecology of Florida Scrub-Jays (Aphelocoma coerulescens). on John F. Kennedy Space Center/Merritt Island National Wildlife Refuge. We examined phenology, clutch size, hatching failure rates, fledgling production, nest success, predation rates, sources egg and nestling mortality, and the effects of helpers on these measures. Nesting phenology was similar among sites. Mean clutch size at Titan was significantly larger than at HC or T4. Pairs with helpers did not produce larger clutches than pairs without helpers. Fledgling production at T4 was significantly greater than at HC and similar to Titan. Pairs with helpers at HC produced significantly more fledglings than pairs without helpers; helpers did not influence fledgling production at the other sites. Nest success at HC and Titan was low, 19% and 32 % respectively. Nest success at T4 was 48% and was significantly greater than at HC. Average predation rates at all sites increased with season progression. Predation rates at all sight rose sharply by early June. The main cause of nest failure at all sites was predation, 93%.

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Florida Scrub-Jay, Aphelocoma coerulescens, nesting ecology, predation, clutch size, nest success, nest predators

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