

LIFE IN AN ALTERED LANDSCAPE: REPRODUCTIVE SUCCESS AND
FORAGING EFFICIENCY OF FLORIDA SCRUB-JAYS (*APHELOCOMA*
COERULUESCENS) IN REGENERATING PASTURE

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ABSTRACT

The challenge of protecting habitat for imperiled species amidst continuing, excessive habitat alteration constrains our conventional definition of 'suitable' habitat. Certain endangered species are known to persist on modified habitat, especially where their native habitat is largely destroyed. I examined reproductive success and foraging efficiency of Florida Scrub-Jays (*Aphelocoma coerulescens*) in a human modified habitat – regenerating pasture – along a pasture-native scrub interface. From 1985 to 2003, Florida Scrub-Jays were equally successful at producing young in regenerating pasture and native scrub. Production of eggs, nestlings, fledglings, independent young, and yearlings per nest were not statistically different between pasture and scrub, but consistently trended higher in the former. Nest success in pasture was significantly higher among pairs lacking nonbreeding helpers compared to pairs with helpers. Breeding males preferred pasture for their overall daily activities, and foraged equally frequently in pasture and scrub. Foraging efficiency of breeding males was significantly higher for small prey items, but significantly lower for medium and large prey items when they foraged in pasture compared to when they foraged in scrub. Availability of small prey items was significantly higher in pasture than in scrub; the availability of medium and large prey items were not significantly different between habitat types. These results suggest that regenerating pasture can provide suitable habitat for Florida Scrub-Jays when in close proximity to native scrub. The definition of suitable habitat for this habitat-limited species should be expanded to include areas of pasture containing regenerating oak shrubs.

BIOGRAPHICAL SKETCH

Maria (Marita) Davison was born in Ellicott City, Maryland, but moved to Lima, Peru at the age of 2 months. Daughter to John and Rosario Davison and sister to Albert Davison, she grew up living in various countries throughout South America, but considers La Paz, Bolivia (her mother's hometown) her enduring home. During her eight years in Bolivia, she traveled extensively throughout the country, discovering a curiosity and love for the wonders of nature. It wasn't until she visited her grandmother's village in the Amazonian valley of Yungas in La Paz that she faced the reality of human impacts on the landscape and the steady extermination of some of the most enchanting natural places on Earth. As a result of this realization, Marita developed a profound passion for conservation and a commitment to pursue a path directed at maintaining our ecological integrity. She pursued an interdisciplinary course of study Vanderbilt University and received her B.S. in Environmental Science with a minor in Latin American Studies in May of 2000. During her undergraduate career, she took part in the "Opportunities in Conservation" program (designed to train young conservationists) at the Tennessee Chapter of The Nature Conservancy. She was involved with designing an ecologically sound plan for maintaining populations of the near-extinct Tennessee Coneflower (*Echinacea tennesseensis*). This first exposure to the application of science to address real conservation issues confirmed her passion for conservation and chosen career path. Upon graduating, Marita managed a natural history training program at the Smithsonian Museum of Natural History for a year and a half, and then spent six months working on a biodiversity inventory in northern Costa Rica. She enrolled as a graduate student at Cornell University in August 2002.

Dedicated to my mom, Rosario, who has been a source of unconditional love, support, and friendship.

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I would like to thank the staff at Archbold Biological Station for tremendous support during my fieldwork. Financial support from Archbold allowed me to spend an entire breeding season with Florida Scrub-Jays at a world-class research facility, an opportunity that I did not take for granted. I specifically would like to thank Dr. Glen Woolfenden for access to an amazing study system and for challenging me to experience the world from a Florida Scrub Jay’s perspective. Special thanks also go to Dr. Reed Bowman, Larry Riopelle, and Roberta Pickert for guidance with project development, implementation, and help with GIS considerations, respectively. In addition, this project would likely not have been possible without the contribution of countless interns at Archbold over the years, whose hard work helped to generate the comprehensive dataset used in this study.

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INTRODUCTION

The rate of alteration of natural ecosystems by human activities is increasing worldwide, resulting in unprecedented degradation of natural habitats and loss of species (Wilson 1988; Vitousek et al. 1997; McIntyre & Hobbs 1999; Pitman et al. 2002). Effects of disturbances such as habitat alteration on individual species are scale-dependent and have been the subject of detailed research (Wiens 1989; Hansen et al. 1993; Andren 1994). On a local scale, narrowly distributed endemic species and those that specialize on a limited range of environmental conditions are exceedingly vulnerable to habitat alterations and notably prone to extinction (Pimm & Askins 1995; Pitman et al. 2002; Thomas et al. 2004). Proper conservation management of such species requires knowledge of how they respond to various kinds of landscape alterations at the local level (Morrison et al. 1998; McIntyre & Hobbs 1999).

Given the rapid pace of landscape alterations, it has often become unrealistic to focus conservation efforts on securing large tracts of pristine habitat (Morrison & Humphrey 2001); therefore, research and conservation efforts have more recently expanded to include modified habitats (Marzluff & Ewing 2001; Rosenzweig 2003). The majority of these research efforts have examined the ecology of birds and other species in urban landscapes (Koenig et al. 2001; Melles et al. 2003; Zerbe et al. 2003) and agricultural landscapes (Martinez et al. 1998; Petit et al. 1999; Garcia et al. 2006), which globally are the most dominant human land-use types. Numerous studies have shown that urban and agricultural landscapes can support high species richness and abundance (Petit et al. 1999; Marzluff & Ewing 2001; Melles et al. 2003; Zerbe et al. 2003). Management of agroecosystems in particular has been suggested as a viable conservation approach when large tracts of pristine habitat are no longer available (Wuerthner 1994; Jules & Dietsch 1997; Vandermeer & Perfecto 1997; Warren 1998). Some studies have shown that certain species may favor agricultural habitats over

native habitats (Morrison & Humphrey 2001; Garcia et al. 2006), commonly citing reduced predation rates, enhanced breeding sites, and greater food availability due to high prey abundance, facilitated prey capture, or both.

Food availability, in particular, is considered one of the major determinants of successful reproduction in birds. Although various studies have addressed the relationship between food availability and reproduction in the context of human-modified landscapes in general, and agricultural habitats in particular, research in these altered landscapes has mostly focused on habitat generalists (Holloway & Schnell 1997; Cosson et al. 1999; Drapeau et al. 2000; Hunt et al. 2002; Prosser et al. 2006). Effects of habitat modification on habitat specialists remain largely unquantified (but see Goodman et al. 2005).

Florida Scrub-Jays (*Aphelocoma coerulescens*) are model subjects for exploring patterns of reproduction and food availability in the context of human-modified habitats. The only bird species restricted entirely to peninsular Florida, the federally threatened Florida Scrub-Jay is an extreme habitat specialist limited to xeric sand ridges dominated by stunted, fire-maintained scrub oaks (*Quercus* spp.) (Woolfenden & Fitzpatrick 1984; Fitzpatrick et al. 1991; Woolfenden & Fitzpatrick 1991, 1996). Numerous studies of Florida Scrub-Jays have suggested that they rarely use other natural habitat (Cox 1984; Woolfenden & Fitzpatrick 1984; Breininger 1989, 1990, 1992; Breininger & Smith 1992), but that they do use elements of human-modified landscapes when they occur near native scrub habitat (Breininger 1999; Mumme et al. 2000; Woolfenden & Fitzpatrick, unpublished data). As a result of increasing human development pressures throughout their range, most extant Florida Scrub-Jay territories exist in the midst of agricultural, suburban and urban landscapes (Woolfenden & Fitzpatrick 1991; Stith et al. 1996; Thaxton & Hingtgen 1996). Research on Florida Scrub-Jays involving human-modified habitats has largely

focused on suburban and urban areas (Thaxton & Hingtgen 1992, 1996; Bowman & Woolfenden 2002; Fleischer et al. 2003; Shawkey et al. 2004). Little attention has been paid to the effect of agricultural habitats on the species. The dominant agricultural practices in Florida involve citrus production and cattle ranching (in the form of improved and semi-improved pastures), both of which generally occur on soils that historically supported scrub. Regenerating pasture (i.e. pasture that is no longer grazed) with some shrub vegetation has been suggested as suitable habitat for Florida Scrub-Jays when in close proximity to native scrub, but initial research suggested that reproductive success in this habitat type is low (Breininger et al. 1995; Duncan et al. 1995; Breininger et al. 1998). However, in many areas across their range, Florida Scrub-Jays continually use regenerating pasture and defend it as a portion of their territories. Given this apparent inconsistency, the factors that influence a Scrub-Jay's decision to use pasture must be examined in order to determine whether certain successional stages of previously grazed pasture can maintain Florida Scrub-Jays indefinitely.

I studied habitat use of Florida Scrub-Jays in relation to reproductive success and foraging efficiency along a pasture-scrub interface in south-central Florida. I tested the hypothesis that when regenerating pasture is located near native scrub, it can serve as a suitable habitat type for supporting Florida Scrub-Jays, by providing adequate nesting and foraging grounds. Support for this hypothesis requires that (1) reproductive success and (2) foraging efficiency in pasture be equivalent to – or better than – those measures in native scrub. Because similar food availability could explain patterns of Florida Scrub-Jay use along this habitat interface, I also examined prey abundance at foraging grounds in each habitat type. As native scrub habitat is disappearing rapidly, and Florida Scrub-Jays use certain types of pasture extensively, long-term management and recovery of this threatened species might be aided by

incorporating regenerating pasture into conservation plans, preserve designs, and habitat buffers.

METHODS

Study Species

Florida Scrub-Jays are non-migratory and live in small family groups (averaging three birds) that are usually focused around a single monogamous breeding pair (Woofenden & Fitzpatrick 1984, 1991, 1996; Quinn et al. 1999). Individual birds remain in their natal territory for at least one year (often longer), during which time they usually act as helpers at the nest (Woofenden & Fitzpatrick 1984). These nonbreeding helpers assist in territory defense, scanning for predators, and feeding nestlings and fledglings (Woofenden 1975); moreover, nonbreeding helpers may increase survival rates and lifespan of breeders (McGowan & Woofenden 1989), nestlings, and fledglings (Mumme 1992). Florida Scrub-Jays defend all-purpose, year-round territories (averaging 9 ha in area) and rarely move outside of them (Woofenden & Fitzpatrick 1996). In south-central Florida, the breeding season extends from late February through late June (Woofenden & Fitzpatrick 1984, 1991).

Study Area

I conducted fieldwork at Archbold Biological Station (ABS), a 2100-hectare private natural scrub preserve in Highlands County, Florida, USA (27° 10' N, 81° 21' W, elevation 38-68 m). My research focused on jays at the site of an ongoing study of Florida Scrub-Jay demography that was initiated in 1969 (Woofenden and Fitzpatrick 1984, 1996), heretofore referred to as the “demography tract.”

The western boundary of the demography tract borders an extensive area of regenerating pasture that differs structurally from the native scrub directly adjacent to it. In particular, the vegetation is dominated by exotic grass species, especially bahia grass (*Paspalum notatum*), and mesic shrubs such as St. John's wort (*Hypericum* spp.). Scattered scrub oaks (mostly sand live oak, *Quercus geminata*) and clumps of

palmettos (*Serenoa repens* and *Sabal etonia*) were probably allowed to remain when the area was converted for cattle ranchland around the turn of the 20th century, but have increased in density since the pasture area has been allowed to regenerate in the last 25 years. In addition, other shrubs typical of native scrub (such as fetterbush, *Lyonia lucida*) have recolonized the area. Florida Scrub-Jays have historically included large portions of the pasture area in their territories and used this habitat type as a nesting site (Woolfenden & Fitzpatrick, unpublished data). I studied all territories along the pasture-scrub interface that had at least 5% pasture habitat, hereafter named ‘interface’ territories. Data on territories that did not occur along this interface (hereafter named ‘native’ territories) were also included in analyses for comparative purposes.

Reproductive History

The long-term demographic study of Florida Scrub-Jays at Archbold Biological Station has generated among the most extensive data on reproductive success, survival, and habitat use available for any imperiled species (Woolfenden and Fitzpatrick 1984, 1996). All individuals are color-banded and virtually all nests are monitored, providing data on both a per-pair and per-nest basis. Locations of territory boundaries and nest placement sites are digitized using ArcGIS (Environmental Systems Research Institute, Inc.), and are available from ABS for each year of this ongoing study (1969-present). Use of regenerating pastures by Florida Scrub-Jays was first documented in 1985 (Woolfenden & Fitzpatrick, unpublished data), and has occurred in every year thereafter, thereby providing data on reproductive success for interface and native territories over 19 consecutive years from 1985-2003. For all territories in all years, I analyzed only nest attempts in which at least 1 egg was laid. Because pairs with nonbreeders have been shown to produce significantly more young

than those without nonbreeders (Woofenden & Fitzpatrick 1984; McGowan & Woofenden 1990; Mumme 1992), I evaluated reproductive success separately for pairs with and without nonbreeders.

Scrub-Jay Observations

Florida Scrub-Jays are excellent subjects for studying behavior, since they acclimate easily to human presence, thereby allowing close observation. From 1 February to 31 July 2003, I conducted one-hour focal observations on the activities of breeding males in five interface territories and a subset of five native territories chosen at random from the core study territories occupying high quality, contiguous scrub. I focused on breeding males because they experienced the highest foraging pressures during the study period, since they were often feeding incubating females or nestlings. Individuals were pre-selected for observations to avoid any possible bias in observing the first bird encountered. The observation sequence was randomized prior to the start of the study period, and all observations occurred between 07:00 and 11:30, and 15:00 and 19:00 EST, because Florida Scrub-Jays are typically active during those times only (DeGange 1976).

I performed a total of 250 focal observations (n=25 observations on each of 5 breeding males in interface territories and each of 5 breeding males in native territories), following a standardized protocol used to quantify habitat use, behavior, and energy budgets of Florida Scrub-Jays (Fleischer et al. 2003; Valligny 2003). Each one-hour observation period was divided into 60 one-minute sampling units, with behavior and locations (pasture or scrub) of focal males recorded as instantaneous samples at the end of each one-minute sample unit. I lumped activity definitions previously described (DeGange 1976; Valligny 2003) and recorded activities in the following four categories: foraging (actively searching for food or eating), sentinel

(scanning the horizon for predators), resting (perching without sentinel scanning and preening), and other (a broad category of various infrequent activities). Periods in which I was not able to follow the focal male during the 60-minute period were excluded. All analyses incorporate only the total time each male was in sight, to avoid any bias potentially introduced by the behavior of jays while out of sight. Total observation time of each focal male in native and interface territories is summarized in Appendix A.

I recorded prey items captured by focal jays during each observation period. Only arthropod prey were included in analyses, as Florida Scrub-Jays forage almost exclusively on arthropods during the breeding season (Stallcup & Woolfenden 1978). Exact prey identification was often impossible, but all prey items could be divided into three size classes: small (<5mm), medium (6-20mm), and large (>20mm). To standardize the data and control for differences between individual males in the amount of time spent foraging, I calculated capture rate as the number of prey items captured per foraging hour (i.e. per 60 minutes of foraging). This approach also controls for time budget differences among habitat types, thereby potentially revealing differences in foraging efficiency among habitats (Fleischer et al. 2003).

Prey Availability

To evaluate differences in arthropod abundances among habitat types, I collected data on relative availability of arthropods known to be eaten by Florida Scrub-Jays (Woolfenden & Fitzpatrick, unpublished data) in both pasture and native scrub. Only prey items in the orders Araneae, Orthoptera, Hemiptera, and Coleoptera (hereafter referred to as “edible” prey) were considered in analyses of prey availability, since these items are biologically the most relevant to Florida Scrub-Jays. I used a protocol previously developed to measure food availability in native scrub at

ABS, by visually searching vegetation around a focal “bugpost” fixed in place in various habitat types (Curry, Riopelle and others, unpublished data). I conducted arthropod searches only within the ten territories selected for the investigation of activity budgets. I used existing bugposts where available, and established new bugposts at random points throughout the interface study area. I conducted ten searches at each of 10 bugposts (5 in pasture, 5 in scrub) throughout the entire study period. During each one-hour search period, I recorded the total number of arthropods encountered and the number of stems searched for each vegetation type in the vicinity of the bugpost. Prey items were divided into the same size classes designated in the foraging efficiency analysis (small, medium and large). To estimate average abundance for each size class in pasture and scrub, I averaged the number of individuals encountered per search hour over all observation periods.

Terminology

Pairs in interface territories had the option of using either the native scrub side or the pasture side of their territory for nesting and daily activities. In contrast, pairs in native territories only had the option of using native scrub. I refer to this distinction as the *habitat context* of nests and activities; habitat contexts are classified as “interface in pasture,” “interface in scrub,” or “native.”

Data Analyses

For analyses of historical reproductive success, I used generalized linear mixed models (GLMM, SPSS 12.0) to test for differences in production of nestlings, fledglings, independent young, and yearlings between interface and native territories, both overall and on a per-habitat context basis. Because multiple comparisons were

performed, I used Bonferroni-adjusted alpha levels of 0.01. When testing for differences between habitat contexts, pairwise comparisons were performed if the tests were significant; Tukey's tests were used when variance was homogenous, and Games-Howell tests were used when variance was unequal. I also used logistic regression models (SAS 9.1.2) to evaluate differences in overall nest success, defined as the proportion of nests producing at least one fledgling. Again, these tests were performed overall (i.e. between native territories and interface territories) and on a per-habitat context basis (i.e. between native territories, interface territories in scrub, interface territories in pasture). Because the presence of nonbreeding helpers and breeder experience can confound comparisons of reproductive success between two habitat types (Woofenden & Fitzpatrick 1984; Mumme 1992; Mumme et al. 2000), I included these variables as factors in all models. Thus, the three main factors in all models were habitat context, the presence of nonbreeding helpers (present or absent), and breeder experience (no experienced breeders present, at least one experienced breeder present). To control for annual variation, year was included as a random factor in each model. For each habitat context category, measures of reproductive success are reported as annual means per nest across all territories, with the exception of nest success, which is reported as the mean number of nests producing at least one fledgling divided by the total number of nests in each habitat context category for each year.

Analyses of habitat preference were performed for nest sites from 1985 to 2003 and for activity budgets in the 2003 breeding season. In order to determine whether Florida Scrub-Jays preferentially used pasture as a site for nesting, daily activities, or foraging, I used the Savage selectivity index (described in Manly et al. 1993), which has been applied for similar studies on Lesser Kestrels (*Falco naumanni*) (Tella & Forero 2000; Garcia et al. 2006).. The index value is defined as:

$$(i) \quad \omega_i = U_i/p_i$$

where U_i is the proportion of observations (number of nests/total nests or number of minutes/total minutes) recorded in pasture and p_i is the proportion of pasture included in the study area. The index values range from 0 (maximum avoidance) to infinity (maximum positive selection), with a value of 1 indicating no selection (Manly et al. 1993). The null hypothesis in this analysis was that Florida Scrub-Jays use pasture in proportion to its availability, and statistical significance was based on comparing the statistic $(\omega_i - 1)/SE(\omega_i)^2$ with the corresponding critical value of a chi-square distribution with one degree of freedom. The standard error of the index (SE) is calculated as:

$$(ii) \quad \sqrt{(1 - p_i)/(u \times p_i)}$$

where u is the total number of observations sampled. I used this index to evaluate nesting habitat preferences, habitat preferences for daily activities, and foraging habitat preferences for breeding males in interface territories. The proportion of pasture in the study area was calculated from historical territory maps using ArcView 3.2 (ESRI). For analyses on activity budgets, I used individual focal males as the sampling unit to avoid pseudoreplication of sequential observations on the same bird.

To examine variations in foraging efficiency in relation to habitat type, I used a generalized linear mixed model (GLMM) with habitat context as a categorical factor and capture rate in each size class as a dependent variable with Poisson error. Capture rate was defined as the number of prey items captured per hour of foraging. Date, time of day, and focal bird ID's were used as random effects. Unless otherwise noted, data reported are means \pm SE of all observations per male.

Differences in food availability between pasture and scrub were tested using Mann Whitney U tests (SPSS 12.0). Data reported are means \pm SE of the number of prey items encountered per search hour for each size class.

RESULTS

Reproductive Success in Regenerating Pasture

From 1985 to 2003, overall reproductive success between pairs in native territories and pairs in interface territories was similar for all stages of the reproductive cycle (Table 1) (GLMM: eggs: $F_{1,31} = 1.55$, $p = 0.22$; nestlings: $F_{1,28} = 0.33$, $p = 0.57$; fledglings: $F_{1,25} = 0.94$, $p = 0.34$; yearlings: $F_{1,25} = 0.01$, $p = 0.95$). During this time, there were 119 nest attempts in which at least 1 egg was laid, by 79 territorial pairs in interface territories. Of these, 38 nests (31.9%) were placed in pasture. When testing on a per-habitat context basis, nests in native territories and on the scrub side of interface territories produced comparable numbers of young at all stages of the reproductive cycle (Table 2). However, nests in pasture consistently produced more young than nests in scrub (Table 2). Despite this trend, the overall effect of nest habitat context was not significant as a main effect (GLMM: eggs: $F_{2,24} = 2.71$, $p = 0.08$; nestlings: $F_{2,60} = 2.69$, $p = 0.08$; fledglings: $F_{2,50} = 1.33$, $p = 0.27$; juveniles: $F_{2,47} = 0.76$, $p = 0.47$; yearlings: $F_{2,47} = 0.17$, $p = 0.85$) or in interaction with other factors (GLMM, all interaction terms $p > 0.01$). Habitat context had the strongest effect during the nestling phase, with nests in pasture producing a mean of 2.64 ± 0.28 nestlings for nests aided by nonbreeding helpers and 2.08 ± 0.40 for nests with no helpers. In contrast, nests in native territories produced a mean of 1.95 ± 0.065 for nests aided by nonbreeders and 1.76 ± 0.06 for nests with no helpers. For nests in scrub, the presence of nonbreeders significantly increased reproductive success, which is consistent with previous studies (Woolfenden and Fitzpatrick 1984; Mumme 1992). Help from nonbreeders was especially important during the fledgling and yearling stages (GLMM: fledglings: $F_{1,147} = 7.76$, $p = 0.01$ and yearlings: $F_{1,122} = 7.25$, $p = 0.01$); however, presence of nonbreeders did not have a significant effect on any measure of reproductive success for nests in pasture (GLMM: eggs : $F_{1,5} = 0.68$, $p =$

0.45; nestlings: $F_{1,5} = 0.45$, $p = 0.53$; fledglings: $F_{1,5} = 2.60$, $p = 0.17$; juveniles: $F_{1,5} = 0.43$, $p = 0.54$; yearlings: $F_{1,5} = 1.17$, $p = 0.33$). The trend of nonbreeding helpers increasing reproductive success holds for nests in pasture during the egg, nestling, and fledgling phases, but is reversed for the juvenile and yearling phases (Table 2).

Overall nest success between pairs in native territories and pairs in interface territories did not differ significantly (Table 1) (Logistic regression: $\beta = 0.15$, $p = 0.43$). However, when evaluating on a per-habitat context basis, 57.9% of nests on the pasture side of interface territories produced at least 1 fledgling, compared to 38.3% of nests on the scrub side of interface territories and 39.9% of nests in native territories. Nest success therefore varied among habitat contexts and also was influenced by the presence of nonbreeding helpers (Table 2). For nests with nonbreeders, mean nest success was 0.56 ± 0.101 , 0.47 ± 0.505 , and 0.44 ± 0.20 for nests of interface territories in pasture, interface territories in scrub, and native territories, respectively. Mean nest success for nests without nonbreeders for these same habitat context categories was 0.62 ± 0.140 , 0.29 ± 0.075 , and 0.37 ± 0.018 . The presence of helpers increased nest success for nests placed in scrub, but did not affect nest success for nests placed in pasture (Figure 1). Furthermore, nests in pasture were consistently more successful than those in scrub, regardless of the presence of nonbreeding helpers (Figure 1); however this trend was only significant when nonbreeding helpers were absent (Logistic regression: $\beta = 0.67$, $p = 0.05$).

Table 1. Overall reproductive success of Florida Scrub-Jays in all-scrub territories (native) and territories with a mixture of scrub and regenerating pasture (interface). Values reported are means \pm SE per nest, with the exception of nest success, which is reported as the mean \pm SE proportion of nests that fledged at least one young.

Measure of reproductive success	Native territories		Interface territories	
	helpers (N=600)	no helpers (N=700)	helpers (N=68)	no helpers (N=51)
Eggs/nest	3.20 \pm 0.03	3.14 \pm 0.03	3.22 \pm 0.09	3.02 \pm 0.14
Nestlings/nest	1.95 \pm 0.07	1.75 \pm 0.06	2.21 \pm 0.18	1.80 \pm 0.22
Fledglings/nest	1.22 \pm 0.06	0.95 \pm 0.05	1.38 \pm 0.19	0.92 \pm 0.18
Independent young/nest	0.79 \pm 0.05	0.57 \pm 0.04	0.76 \pm 0.12	0.65 \pm 0.15
Yearlings/nest	0.44 \pm 0.03	0.36 \pm 0.03	0.43 \pm 0.09	0.29 \pm 0.10
Nest success	0.44 \pm 0.02	0.37 \pm 0.02	0.50 \pm 0.06	0.37 \pm 0.07

Table 2. Reproductive success of Florida Scrub-Jays with and without nonbreeding helpers in different habitat contexts from 1985 to 2003. Values reported are means \pm SE per nest, with the exception of nest success, which is reported as the mean \pm SE proportion of nests that fledged at least one young.

Measure of reproductive success	Native territories		Interface territories in Scrub		Interface territories in Pasture	
	helpers (N=606)	no helpers (N=700)	helpers (N=43)	no helpers (N=38)	helpers (N=25)	no helpers (N=13)
Eggs/nest	3.20 \pm 0.03	3.14 \pm 0.03	3.08 \pm 0.12	3.00 \pm 0.18	3.48 \pm 0.14	3.08 \pm 0.18
Nestlings/nest	1.95 \pm 0.07	1.76 \pm 0.06	1.95 \pm 0.23	1.71 \pm 0.27	2.64 \pm 0.28	2.08 \pm 0.40
Fledglings/nest	1.22 \pm 0.06	0.96 \pm 0.05	1.26 \pm 0.23	0.79 \pm 0.21	1.60 \pm 0.32	1.31 \pm 0.33
Independent young/nest	0.79 \pm 0.05	0.56 \pm 0.04	0.74 \pm 0.15	0.55 \pm 0.18	0.80 \pm 0.22	0.92 \pm 0.29
Yearlings/nest	0.44 \pm 0.03	0.37 \pm 0.03	0.35 \pm 0.10	0.24 \pm 0.12	0.56 \pm 0.18	0.46 \pm 0.22
Nest success	0.44 \pm 0.02	0.37 \pm 0.02	0.47 \pm 0.08	0.30 \pm 0.08	0.56 \pm 0.10	0.62 \pm 0.14

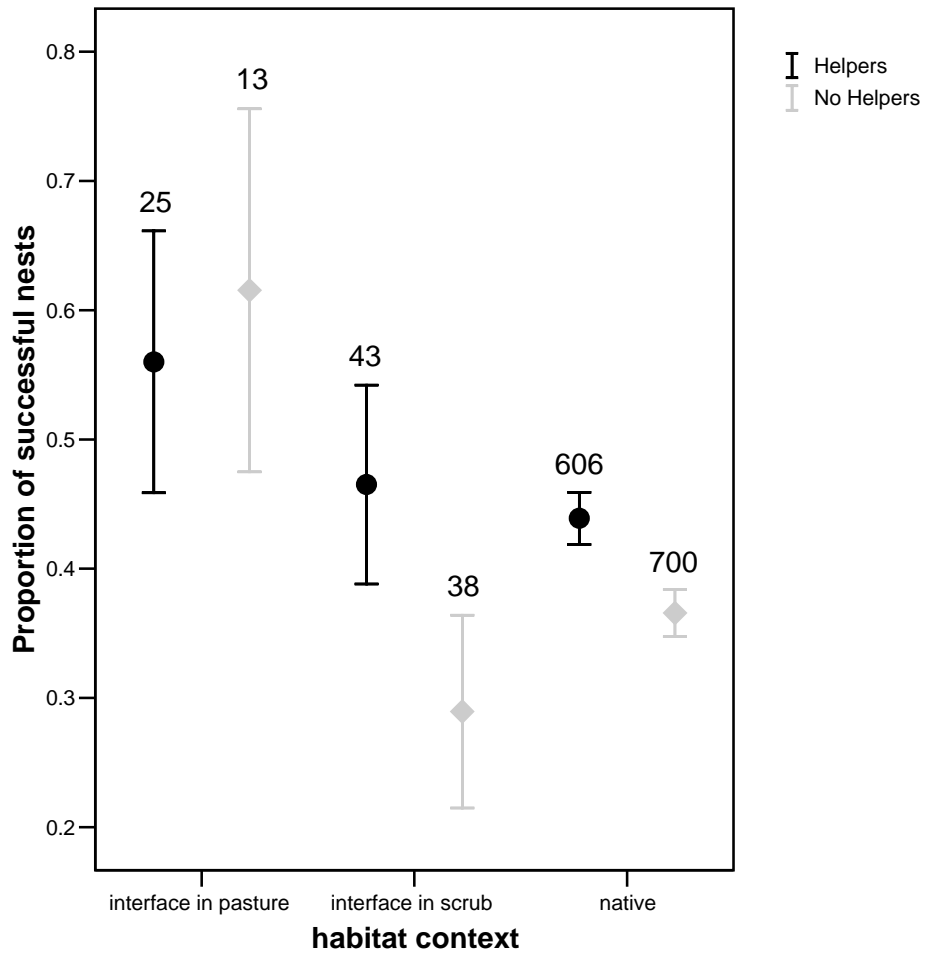


Figure 1. Mean (\pm SE) annual nest success (defined as the proportion of nests producing at least one fledgling) of Florida Scrub-Jays with and without nonbreeding helpers in different habitat contexts. Sample sizes are reported above each plot.

Habitat Preferences

From the period between 1985 and 2003, Florida Scrub-Jays in interface territories placed 31.9% of their nests in pasture and the yearly amount of pasture included in these territories averaged 29.4%. Thus, Florida Scrub-Jays neither positively selected for pasture nor avoided pasture as a nesting site (Savage selectivity index, $\omega_i \pm SE = 1.086 \pm 0.375$, $p > 0.05$). As expected from this overall trend, the proportion of nests placed in pasture increased as the proportion of pasture included in interface territories increased (Figure 2). Over the period from 1985 to 2003, the proportion of nests placed in pasture ranged from 0 to 0.75 and the proportion of pasture included in interface territories ranged from 0.09 to 0.39 (Table 3). No nests were placed in pasture among those territories containing less than 20% pasture (Figure 2).

Despite considerable variation in the proportion of each territory comprised of pasture and the proportion of time each bird spent in pasture, breeding males in interface territories consistently preferred pasture for their daily activities in 2003 (Figure 3). However, preference for pasture as a foraging site was not consistent, with some breeding males positively selecting pasture for foraging (i.e. MARI and SWAL) and others avoiding pasture – thereby positively selecting for scrub – as a foraging site (i.e. CACT, FENC, JERE) (Figure 3). Breeding males in interface territories significantly selected for pasture in their overall time budgets ($\omega_i \pm SE = 1.49 \pm 0.139$, $p < 0.01$); but they did not show any selection (or avoidance) of pasture when only considering foraging time.

Table 3. Nesting trends of Florida Scrub-Jays in regenerating pasture from 1985 to 2003 at Archbold Biological Station. Proportions and Savage selectivity index are reported as annual means; the percentage of successful nests is reported as the percent of all nests that fledged at least one young in each year.

Year	Total number of territories	Total number of nests	Proportion of nests in pasture	Proportion of pasture in territories	ω_i	% successful nests in pasture
1985	3	4	0.25	0.26	0.96	100
1986	4	5	0.40	0.37	1.08	50
1987	4	5	0	0.09	0	0
1988	5	6	0.33	0.30	1.10	0
1989	7	12	0.25	0.30	0.83	100
1990	5	9	0.44	0.29	1.52	50
1991	4	7	0.29	0.37	0.78	50
1992	4	6	0	0.32	0	0
1993	5	10	0.30	0.34	0.88	33
1994	4	5	0.60	0.28	2.14	67
1995	3	3	0.67	0.30	2.23	100
1996	4	4	0.75	0.39	1.92	67
1997	5	10	0.20	0.24	0.83	50
1998	4	6	0.17	0.23	0.74	100
1999	3	5	0.20	0.29	0.69	100
2000	4	6	0	0.15	0	0
2001	3	5	0.60	0.20	3.00	33
2002	4	6	0.67	0.30	2.23	50
2003	5	5	0.40	0.34	1.18	50

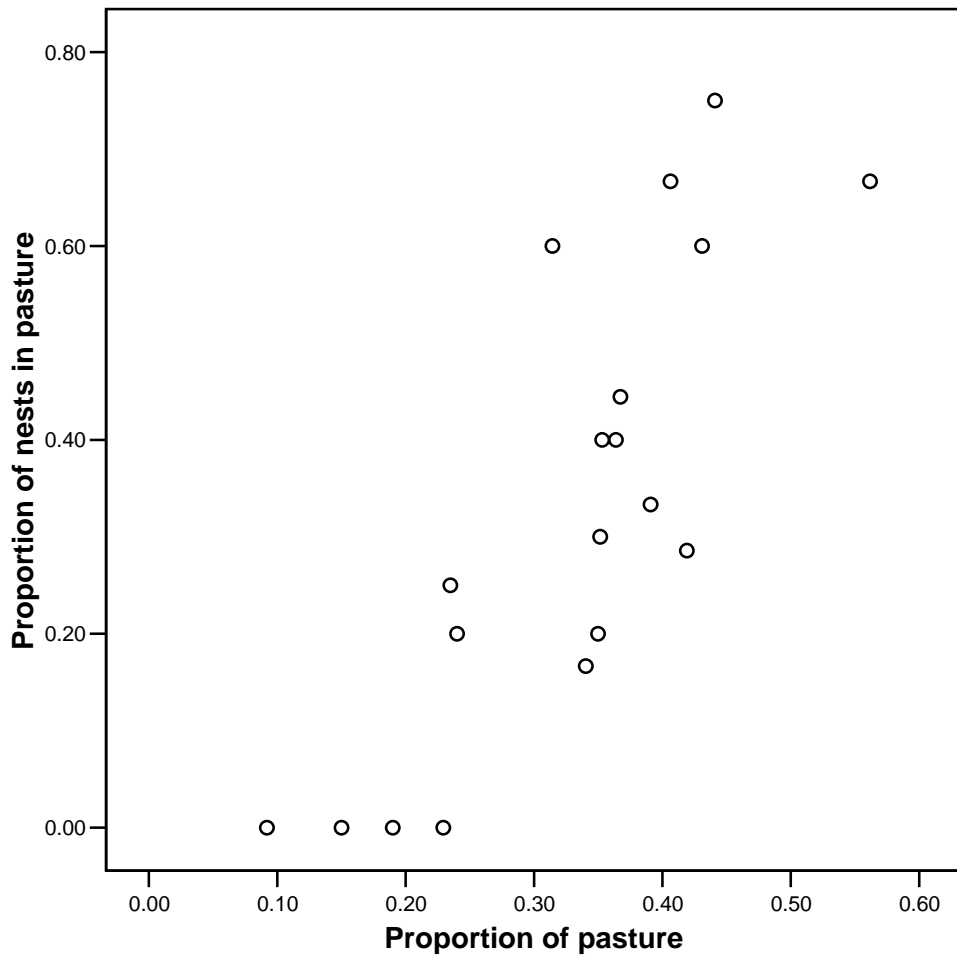


Figure 2. The relationship between the proportion of Florida Scrub-Jay nests placed in pasture and the proportion of pasture included in interface territories at Archbold Biological Station (1985-2003).

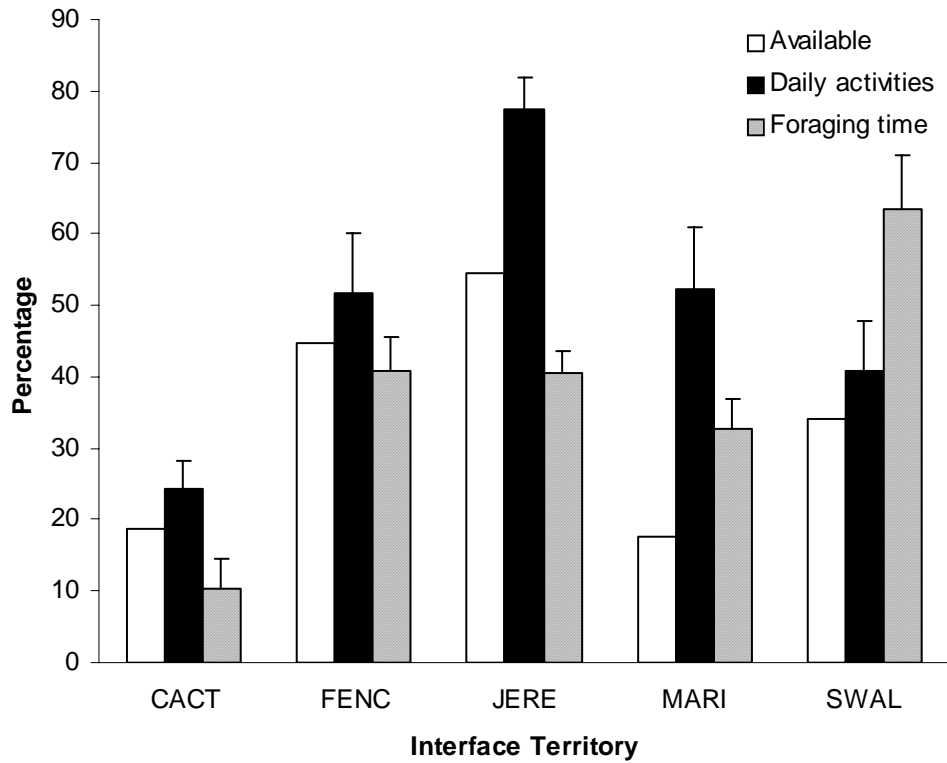


Figure 3. Use of pasture by breeding males in the 5 interface territories studied in 2003. White bars represent the percentage of pasture available; black bars represent the average percentage of time spent for all daily activities (categorized as foraging, sentinel, resting, other); hatched bars represent the average percentage of time spent foraging.

Foraging Efficiency and Prey Availability

Foraging efficiency of interface males in pasture (4.87 prey items/hour of foraging) was comparable to that of breeding males in native territories (5.58 prey items/hour of foraging), but significantly lower (2.53 prey items/hour of foraging) for interface males in scrub (Figure 4). A similar trend of foraging efficiency was observed for small sized prey, with interface males in pasture being the most efficient and interface males in scrub foraging significantly less efficiently (GLMM: $F_{3,512} = 4.836$, $p = 0.003$). Interface males in pasture captured a mean (\pm SE) of 0.352 ± 0.04 small prey items per hour of foraging, whereas interface males in scrub and breeding males in native territories captured 0.137 ± 0.02 and 0.347 ± 0.11 , respectively. For medium and large prey items, breeding males in native territories were significantly more efficient than males in interface territories, regardless of their habitat context (GLMM: medium prey: $F_{3,302} = 1.599$, $p > 0.05$, large prey: $F_{3,119} = 0.826$, $p > 0.05$).

Prey availability between the two habitat types differed significantly only for small prey items (Mann-Whitney test: $U = 2991.5$, $p < 0.01$), with a mean abundance (\pm SE) of 5.31 ± 0.82 small prey items per search hour in pasture compared to 3.09 ± 0.56 small prey items per search hour in scrub (Figure 5). There was no difference in the abundance of medium sized prey (1.47 ± 1.02 items per search hour in pasture and 1.44 ± 0.48 items per search hour in scrub) or large prey items (0.34 ± 0.93 items per search hour in pasture and 0.82 ± 0.51 items per search hour) between habitat types (Figure 5).

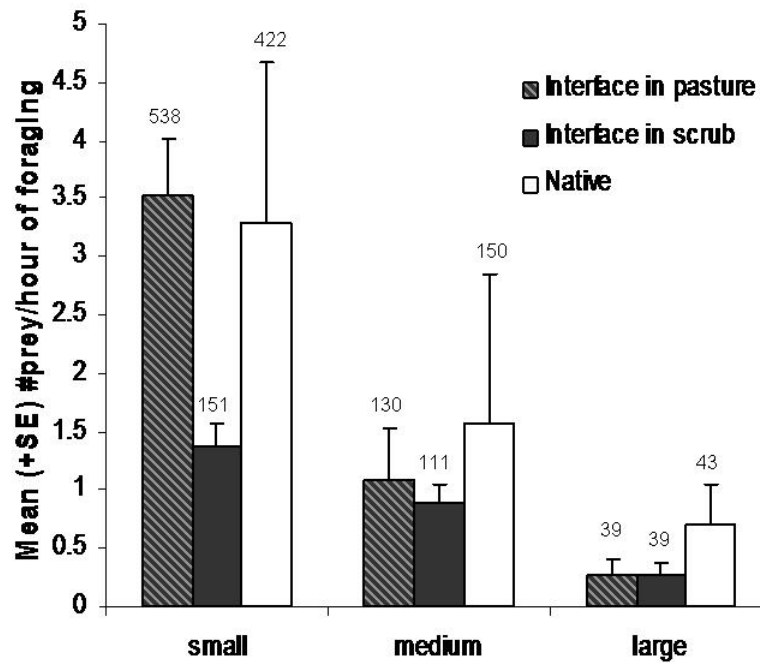


Figure 4. Foraging efficiency of breeding males in different habitat contexts during the 2003 breeding season at Archbold Biological Station. Hatched bars represent the average foraging efficiency of interface territory males when foraging in pasture; black bars represent the average foraging efficiency of interface territory males when foraging in scrub; white bars represent the average foraging efficiency of native territory males. Sample sizes for each habitat context are reported above the bars

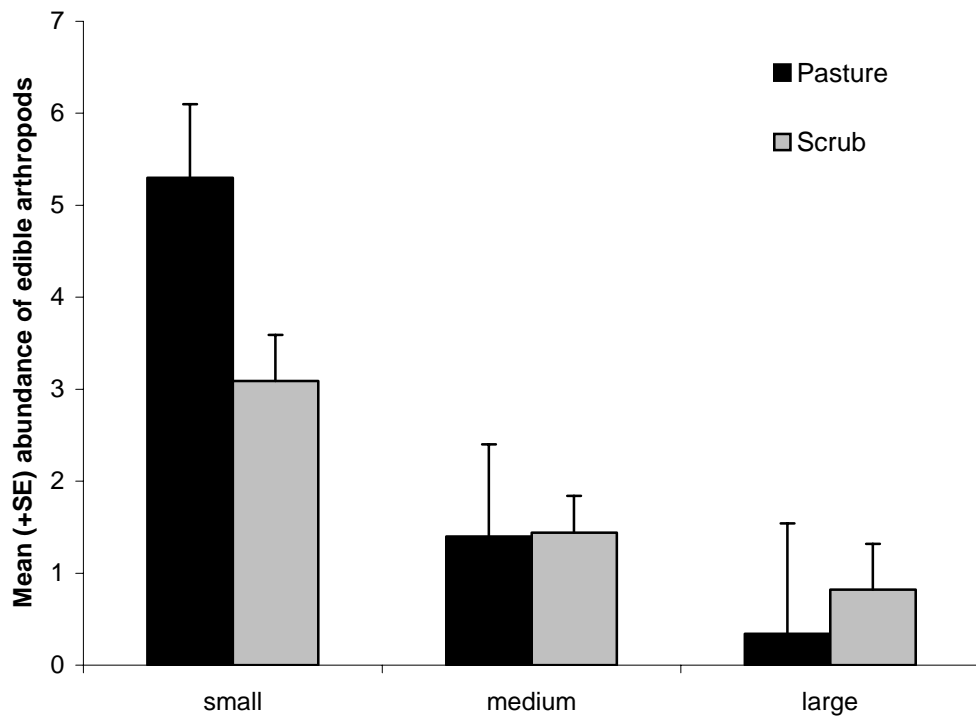


Figure 5. Availability of edible prey items in pasture and scrub at Archbold Biological Station in 2003, presented as mean number of prey items per hour searched. Sample sizes for each habitat type are reported above the bars.

DISCUSSION

Conventional wisdom about imperiled habitat specialists focuses management efforts on intact native habitat for sustaining viable populations, discounting all other habitat types as hostile environments (McIntyre & Barrett 1992). However, this perspective overlooks the fact that individual organisms respond differently in different landscape contexts, and that some non-native habitat types can support sustained populations (Petit et al. 1999; Marzluff & Ewing 2001; Goodman et al. 2005). Such habitats can serve as reservoirs of biodiversity under proper management (Marzluff & Ewing 2001; Pickett et al. 2001). Broadening our definitions of suitable habitat for some habitat specialists has key implications for management of imperiled species, for which habitat protection is of paramount importance.

Recovery and persistence of imperiled species requires knowledge about the land uses that are compatible with their successful reproduction and survival (Morrison & Humphrey 2001). Previous studies have shown that reproductive success of Florida Scrub-Jays can be greatly reduced in human-modified habitats. These reductions in reproductive success have often been linked to differences in food quality and abundance, and involve influences on the timing of reproduction (Fleischer et al. 2003; Schoech et al. 2003, 2004) and reductions in chick survival (Reynolds et al. 2003a, 2003b; Shawkey et al. 2004). However, these studies are limited to evaluations of reproductive success in suburban landscapes (Thaxton & Hingtgen 1996; Fleischer et al. 2003; Schoech et al. 2003; Thorington & Bowman 2003; Schoech et al. 2004), now widely considered to be population sinks for Florida Scrub-Jays. Urban fragments will probably contribute little to long-term population stability of Florida Scrub-Jays throughout their range (Breininger 1999). While urban/suburban development is the land-use type most threatening to the remaining scrub habitat in the Florida peninsula, agricultural land-uses – in particular, clearing

for pastures – still figure prominently in the vicinity of scrub habitat (Davison, unpublished data). However, because of a lucrative real estate market throughout peninsular Florida, these agricultural landscapes are quickly being converted to urban/suburban land-use types (Morrison & Humphrey 2001).

My results suggest that when pasture is located near native scrub, it can serve as a suitable habitat type for supporting Florida Scrub-Jays, in terms of nesting and foraging grounds, especially where it contains elements of structure and composition that are similar to native scrub. Not only did Florida Scrub-Jays not discriminate against pasture as a nesting site, but they actually produced more young per nest in pasture than in native scrub. This trend held at every stage of the reproductive cycle. During the nestling and fledgling phases, when pressure to provide nourishment to young is highest, nests in pasture seemed to do particularly well when compared to their counterparts in native scrub. In addition, survival of nestlings appears to be higher when nests are placed in pasture (Appendix B). As a consequence, nests located in pasture were consistently more successful at fledging young than nests located in native scrub. Therefore, these findings clearly support the hypothesis that pasture provides equivalent nesting grounds (in terms of overall success) when in close proximity to native scrub. Although nonbreeding helpers have been shown to increase reproductive success of pairs nesting in scrub (Woolfenden & Fitzpatrick 1984; McGowan & Woolfenden 1990), a surprising result of this study indicates that nonbreeding helpers did not have the same effect on the reproductive success of pairs when nesting in pasture. Therefore, the dynamics of family groups – especially in terms of the benefits conferred to reproductive success by nonbreeding helpers – may be entirely different along the interface of native scrub and agricultural landscapes.

Regenerating pasture clearly provided suitable foraging habitat for Florida Scrub-Jays. Jays used pasture as a foraging ground exactly in proportion to its

availability in the landscape; therefore, as predicted, they did not spend less time foraging in pasture than in the native scrub directly adjacent to it. They are more successful at capturing small prey in pasture, perhaps because small prey items are more locally abundant in pasture; but it appears that their ability to capture medium and large sized prey items is reduced. This suggests that Florida Scrub-Jays may be focusing their foraging efforts on capturing small prey at the expense of capturing larger, more energetically important prey items that are equally abundant as in native scrub. Since food intake is one of the major determinants of successful reproduction in birds (Reynolds et al. 2003a, 2003b; Nagy & Holmes 2004), it is possible that the higher foraging efficiency exhibited by Florida Scrub-Jays on small prey items in pasture compensates for their reduced efficiency on larger prey items, thereby accounting for the high rates of reproductive success observed in this modified habitat type. Knowledge of the energetic contribution of these prey items is necessary to determine whether the differences in foraging efficiencies and abundance of small arthropods between pasture and scrub influence patterns of reproductive success, but is beyond the scope of this study.

Conservation Implications

Habitat management of Florida Scrub-Jays must address the suitability of different habitat types at the territory scale, because territories are the essential demographic units within the landscape (Breininger & Carter 2003). Territories must contain the habitat components needed by Florida Scrub-Jays (Breininger et al. 1995); however, managers tend to consider only patches of oak large enough to sustain a territory when identifying suitable habitat. When Florida Scrub-Jay territories are located at the edge of human-modified habitat, certain pastures may serve as essential habitat for population persistence, especially if open oak habitat is too small or

fragmented to allow jays to persist. Preserve design for Florida Scrub-Jays should therefore include pasture habitat if it occurs alongside native or near-native scrub, an addition that could potentially allow for a population that is larger than would be maintained by scrub alone. Larger populations are less susceptible to inbreeding, epidemics, and catastrophic events (Soule 1987), therefore any effort that increases population sizes of Florida Scrub-Jays will contribute to their long-term persistence in Florida.

Although large scrub-oak communities are the best indicators of a site's suitability for Florida Scrub-Jays (Cox 1984; Woolfenden & Fitzpatrick 1984) and must remain the priority for Florida Scrub-Jay habitat protection, acquiring and restoring pasture areas near native scrub can be an alternative management strategy when large tracts of scrub are not available. Florida Scrub-Jays clearly tolerate pasture, and pasture areas can act quickly as buffers to encroaching residential and commercial development. Furthermore, pasture areas are more flammable than scrub habitat, and may therefore enhance the opportunity for fires to burn into native scrub (Breininger et al. 1991, 1995). Since prescribed burning is the preferred management tool for maintaining scrub within an adequate successional state for Florida Scrub-Jays, pasture buffers may consequently facilitate prescribed burning efforts. Corridors of regenerating pasture habitat can also be important in preserve designs – by providing nesting and foraging grounds – especially given the poor dispersal abilities of Florida Scrub-Jays (Woolfenden 1970; Woolfenden & Fitzpatrick 1984; Breininger et al. 1991). Given the prominence of pasture habitat near scrub habitat throughout peninsular Florida, acquisition and gradual restoration of pasture areas can greatly contribute to management efforts for Florida Scrub-Jays across their range.

Human alterations have disrupted natural habitats on a broad scale and at an unprecedented rate (Vitousek et al. 1997), and protecting large tracts of natural

habitats has become unrealistic (Morrison & Humphrey 2001). As a result, we are forced to revisit our conventional notions of what “suitable” habitat means for species faced with mounting human-pressures on their habitat. Conservation of species that differ in their tolerance of habitat alterations and human activities presents a challenge requiring varied – and perhaps unconventional – management approaches (Morrison & Humphrey 2001). Biologically speaking, human-modified habitats, while perhaps not optimal in our conventional conception of suitable habitat, can offer opportunities to maintain and even enhance populations of species in decline. These habitats can serve as buffers around native habitat, corridors between fragmented habitat tracts and, as suggested in this study, a potentially suitable alternative when the management of large tracts of native habitat is no longer possible. As we run out of options for managing imperiled species – particularly those that are habitat specialists – this revision in our definition of suitable habitat offers an unexpected opportunity for meeting our conservation goals.

APPENDIX A

Total observation time of each focal male.

Territory Type	Territory Name	Jay ID	Minutes observed	Minutes “out of sight”
Interface	CACT	W-FM	1363	137
Interface	FENC	LGC-	1413	87
Interface	JERE	-PPC	1406	94
Interface	MARI	YYC-	1354	146
		U		
Interface	SWAL	AP-CU	1367	133
Native	BIGL	Z-OG	1320	180
Native	EBAY	ZY-B	1256	244
Native	N18E	ZL-R	1384	116
Native	PLAZ	ZOG-	1296	204
Native	XRDS	G-PM	1240	260

APPENDIX B

Survival ratios of Florida Scrub-Jays with and without nonbreeding helpers in different habitat contexts at Archbold Biological Station from 1985 to 2003. Totals are reported in parentheses.

	Native territories		Interface territories in scrub		Interface territories in pasture	
	helpers (N=606)	no helpers (N=700)	helpers (N=43)	No helpers (N=38)	helpers (N=25)	no helpers (N=13)
Nestlings/eggs	0.61 (1179/1940)	0.56 (1222/2201)	0.64 (84/132)	0.57 (65/114)	0.76 (66/87)	0.68 (27/40)
Fledglings/nestlings	0.63 (737/1179)	0.55 (667/1222)	0.64 (54/84)	0.46 (30/65)	0.61 (40/66)	0.63 (17/27)
Independent young/fledglings	0.65 (476/737)	0.59 (396/667)	0.59 (32/54)	0.70 (21/30)	0.50 (20/40)	0.71 (12/17)
Yearlings/independent young	0.57 (269/476)	0.64 (253/396)	0.47 (15/32)	0.43 (9/21)	0.70 (14/20)	0.50 (6/12)

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