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RESEARCH ARTICLE

Natal territory size, group size, and body mass affect lifetime fitness in the cooperatively breeding Florida Scrub-Jay

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ABSTRACT

Early rearing conditions can have profound short- and long-term effects on survival and reproduction of vertebrates. In cooperatively breeding birds, where variable social conditions interact with other sources of environmental variation, fitness consequences of the natal environment are of particular interest. We used data from a long-term study of the Florida Scrub-Jay (*Aphelocoma coerulescens*) to examine how characteristics of the natal brood, territory, and social group interacted to influence future survival and reproduction. Nestling and juvenile body mass were significant positive predictors of survival from fledging through the first year of life. The area of oak scrub in the natal territory correlated positively with nestling and juvenile body mass and had two long-term consequences: it was positively related to the probability of becoming a breeder and negatively related to age at first breeding, particularly for males. Effects of natal group size were complex and partially dependent on territory size. Although positively associated with nestling mass and postfledging survival, the presence of helpers was negatively related to juvenile body mass, but only in territories with <8 ha of oak scrub, suggesting that helpers become competitors for food as juveniles in small territories reach independence. Although early-life environmental conditions had strong effects on nestling and juvenile body mass, survival to yearling stage, and acquisition of a breeding territory, early conditions were not significant predictors of survival or reproduction once breeding status was obtained. This result suggests that low-quality jays from poor natal environments are winnowed out of the pool of potential breeders by intense intraspecific competition, ultimately leading to low heterogeneity in breeder quality. Our findings help to resolve the long-standing question of why Florida Scrub-Jays defend such unusually large territories for their body size, revealing a key selective advantage for cooperative territorial defense in the evolution of cooperative breeding.

Keywords: age at fledging, brood size, group size, territory size, helpers, nestling body condition, postfledging survival, silver spoon effects

El tamaño del territorio natal, el tamaño del grupo y la masa corporal afectan el desempeño reproductivo de por vida en la especie de cría cooperativa *Aphelocoma coerulescens*

RESUMEN

Las condiciones iniciales de cría pueden tener profundos efectos de corto y largo plazo en la supervivencia y la reproducción de los vertebrados. En las aves con cría cooperativa, donde distintas condiciones sociales interactúan con otras fuentes de variación ambiental, resultan de gran interés las consecuencias del ambiente natal sobre el desempeño biológico. Usamos datos de un estudio de largo plazo de *Aphelocoma coerulescens* para examinar cómo las características de cría natal, del territorio y del grupo social interactúan para influenciar la supervivencia y la reproducción futura. La masa corporal de los pichones y de los juveniles fueron predictores positivos significativos de la supervivencia desde el emplumamiento hasta el primer año de vida. El área de matorral de roble en el territorio natal se correlacionó positivamente con la masa corporal de los pichones y de los juveniles, y tuvo dos consecuencias de largo plazo; se relacionó positivamente con la probabilidad de convertirse en un ave reproductiva y negativamente con la edad del primer período reproductivo, particularmente para los machos. Los efectos del tamaño de grupo natal fueron complejos y dependieron parcialmente del tamaño del territorio. Aunque se asociaron positivamente con la masa de los pichones y con la supervivencia posterior al emplumamiento, la presencia de los ayudantes se relacionó negativamente con la masa corporal de los juveniles, pero sólo en los territorios con matorrales de roble de <8 ha, sugiriendo que los ayudantes se vuelven competidores por el alimento en los territorios pequeños. Aunque las condiciones ambientales al inicio de la vida tienen fuertes efectos en la masa corporal de los pichones y de los juveniles, en la supervivencia hasta la etapa añal y en la adquisición de un territorio reproductivo, las condiciones iniciales no predijeron significativamente la supervivencia o la reproducción una vez que se obtuvo el estatus reproductivo. Este resultado sugiere que los individuos de baja calidad *A. coerulescens* provenientes de ambientes

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natales pobres son apartados del pool de reproductores potenciales por competencia intraespecífica intensa, trayendo como consecuencia una baja heterogeneidad en la calidad de los reproductores. Nuestros hallazgos ayudan a resolver el interrogante de larga data de por qué *A. coerulescens* defiende estos territorios inusualmente grandes en relación a su tamaño corporal, revelando una ventaja de selección clave para la defensa territorial cooperativa en la evolución de la cría cooperativa.

Palabras clave: ayudantes, condición corporal del pichón, edad de emplumamiento, efectos de la cuchara de plata, éxito reproductivo de por vida, tamaño de grupo, tamaño de la nidada, tamaño del territorio

INTRODUCTION

The environmental conditions that are experienced by vertebrates early in development can have profound fitness consequences (Lindström 1999). Poor-quality natal environments frequently have negative short-term effects on fitness components such as juvenile body condition and juvenile survival (Magrath 1991, van der Jeugd and Larsson 1998, van de Pol et al. 2006). In recent years, however, a growing body of literature has indicated that favorable conditions in the natal environment can have significant long-term fitness benefits (Lindström 1999, Cam and Aubry 2011). These delayed "silver spoon" effects (Grafen 1988) are manifested in later life stages and can affect an array of fitness components, including dispersal and habitat selection (Stamps 2006, van de Pol et al. 2006, Tilgar et al. 2010, Tarwater and Beissinger 2012), phenotypic characters under sexual selection (Scandolara et al. 2014), clutch and litter size (Tilgar et al. 2010, Rödel et al. 2009), and lifetime reproductive performance (Cam et al. 2003). Because residual natal effects on fitness may differ between the sexes (Wilkin and Sheldon 2009), early environmental and social conditions can interact in complex ways.

Questions about the short- and long-term consequences of variation in the early natal environment are of particular interest in cooperatively breeding birds and mammals (Stacey and Koenig 1990, Solomon and French 1997, Koenig and Dickinson 2004). In addition to being exposed to spatiotemporal variation in the physical and biological environment, offspring of cooperative breeders also experience highly variable social conditions. Some individuals in a population may be raised by a single breeding pair, while others are reared cooperatively by a complex social unit consisting of parents and helpers of differing sex, age, relatedness, and social status (Stacey and Koenig 1990). Furthermore, because sexually mature cooperative breeders often show delayed reproduction and compete vigorously for limited breeding vacancies (Koenig et al. 1992), modest social and environmental variation in early rearing conditions has the potential to produce large differences in competitive ability and lifetime fitness.

Strong evidence exists that the presence of helpers during the natal rearing period can enhance the growth, development, and condition of young, leading to higher juvenile survival (Hatchwell et al. 2004, Hodge 2005, Ridley 2007, Sparkman et al. 2010), earlier age at first breeding (Hodge 2005, Russell et al. 2007), and higher adult survival later in life (Sparkman et al. 2010, Brouwer et al. 2012). Collectively, these studies suggest that variation in the early social environment of cooperative breeders can influence the lifetime reproductive fitness of individuals. However, only one previous study (Brouwer et al. 2012) has examined how variation in the natal social environment interacts with other important variables, such as territory quality and brood size, to influence an individual's prospects for long-term survival and reproduction.

Here, we capitalize on a unique 33-year dataset to present a comprehensive analysis of the effects of variation in the early natal environment on postfledging survival and lifetime reproductive success in the cooperatively breeding Florida Scrub-Jay (*Aphelocoma coerulescens*). The Florida Scrub-Jay is a habitat specialist that is restricted to oak scrub that grows on sandy, well-drained soils in peninsular Florida. These jays live in permanently territorial family groups centered on a single, permanently bonded, socially and genetically monogamous breeding pair. At any given time, about half of all pairs reside with 1–6 nonbreeders of both sexes, usually the prebreeding offspring of one or both breeders. Most nonbreeders act as helpers by aiding in year-round territory defense and sentinel behavior. During the breeding season, many also feed nestlings and fledglings produced by the breeding adults. Removal experiments have shown that helpers enhance the reproductive success of breeders in two ways: by reducing predation during the nestling stage and by provisioning young. Nestlings receive significantly more food, achieve significantly higher body mass, and have significantly higher postfledging survival when helpers are present (Mumme 1992). Young fledge 15–20 days after hatching, and become nutritionally independent ~90 days after hatching. Disappearance of the male or female breeder in a group results in a breeding vacancy that is filled either by a nearby widow or by a dispersing prebreeder, most often from a nearby territory. However, some males first obtain breeding status by direct inheritance of their natal territory, and others by territorial budding, in which they begin to defend part of their natal territory and pair with

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a dispersing nonbreeder or a nearby widowed female. Dispersal is female-biased, but juveniles less than a year old are extremely sedentary and only rarely disperse (Woolfenden and Fitzpatrick 1984, 1996, Mumme 1992, Townsend et al. 2011).

Our analysis focused on the fitness consequences of variation in 3 aspects of the natal environment of Florida Scrub-Jays: (1) characteristics of the natal brood, including brood size, hatching date, nestling body mass, and age at fledging; (2) characteristics of the natal group, including group size and the ages of the resident breeders; and (3) characteristics of the natal territory, including size and habitat composition. We examined the effects of these early-environment variables on 6 key postfledging components of lifetime fitness in jays: (1) survival from fledging to day 30 posthatching, the age at which fledglings typically become capable of sustained level flight; (2) survival from day 30 to day 90 posthatching, the age at which young jays become nutritionally independent (McGowan and Woolfenden 1990); (3) survival from day 90 to the yearling stage (day 300), the age at which young jays become physiologically capable of breeding (Woolfenden and Fitzpatrick 1984, Schoech et al. 1996); (4) the transition from the yearling stage to establishment of a breeding territory and initial nesting, a transition that varies from a few weeks to several years; (5) age at first nesting; and (6) lifetime reproductive output once breeding status was achieved.

For the Florida Scrub-Jay, questions about the role of the natal territory in shaping an individual's prospects for long-term survival and future reproduction have particular relevance. Mean territory size for this species is ~9 ha (Woolfenden and Fitzpatrick 1984, 1996), much larger than the territories of similarly sized jays (Shank 1986). Previous work has suggested that the exceptionally large and vigorously defended territories of Florida Scrub-Jays constitute an unusual form of parental investment that enhances survival and recruitment of offspring into the breeding population (Woolfenden and Fitzpatrick 1984, 1990). Our analysis provides a critical test of this hypothesis, while controlling for the effects of group size and other potentially confounding variables.

METHODS

Study Area and General Methods

All data were derived from a long-term study of the Florida Scrub-Jay at Archbold Biological Station (hereafter, "Archbold") in Highlands County, Florida (27.10°N, 81.21°W), where a color-banded population has been under continuous study since 1969 (Woolfenden and Fitzpatrick 1984). Because supplemental feeding at Archbold affected certain life-history components during the first decade of the study, our analyses focused on the 33-year period from 1980 to 2012.

Our standard field methods are described in detail in Woolfenden and Fitzpatrick (1984). Briefly, virtually all nests in the study area were found during building, laying, or incubation, and were checked regularly until failure or fledging. All nestlings were banded, measured, and weighed prior to fledging, usually on day 11 (11 days after hatching). Juveniles were recaptured and measured during their first summer, typically when 50–100 days old. All jays in territories within the study area were censused near the middle of each calendar month. In addition, we conducted periodic searches of surrounding areas of suitable habitat to locate and identify banded jays that had dispersed from the study area. Because breeders and jays less than a year old are extremely sedentary, disappearance of birds in these categories from the study area nearly always corresponded with death.

Until 1999, the sex of juvenile and yearling jays was determined using behavioral methods, primarily female-specific "hiccup" vocalizations (Woolfenden and Fitzpatrick 1996). As a result, a significant fraction of the juveniles and yearlings that hatched prior to 1999 died or dispersed before sex could reliably be assigned; these are treated as unknown-sex jays in our analyses. Beginning in 1999, the sex of all nestlings was determined by molecular analysis of blood samples obtained at the time of banding, following the protocol of Fridolfsson and Ellegren (1999).

During April and May of each breeding season, territory boundaries were mapped in detail on an aerial photograph of the study area using methods described by Woolfenden and Fitzpatrick (1984). The resulting maps were then digitized and archived at Archbold via a geographic information system (GIS), using regularly updated ArcGIS for Desktop Advanced software (ESRI, Redlands, California, USA). Detailed habitat maps for most of the study area were completed in 1990, providing data for fine-scale analyses of annual territory characteristics and composition at 3-m^2 resolution. Of particular relevance to the Florida Scrub-Jay and the present study was the distribution and total area of oak-dominated scrub habitats within each territory. These habitats are associated with underlying sandy soils, and their distribution within the study area does not vary over time.

Data Analysis and Statistical Methods

Our analyses focused primarily on 2,025 Florida Scrub-Jays with complete data that were banded as nestlings and fledged successfully between 1980 and 2012. We explicitly considered 6 postfledging components of fitness as dependent variables: (1) survival from fledging (day 15–20 posthatching) to day 30 posthatching; (2) survival from day 30 to day 90; (3) survival from day 90 to day 300; (4) the probability of a 300-day-old yearling successfully acquiring breeding status and nesting; (5) the age at first nesting for jays that became breeders; and (6) lifetime

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reproductive success (total number of young fledged) for jays that became breeders. For some analyses of acquisition of breeding status, we further classified individuals as having either (a) inherited or budded part of the natal territory, (b) dispersed to or established de novo an adjacent territory that shared a territorial boundary with the natal territory, or (c) dispersed to or established a nonadjacent territory.

Because many jays that hatched after 2003 were still alive and breeding in the study area at the end of the study period (2012), including those cohorts in an analysis of lifetime reproductive success would systematically underestimate true lifetime reproduction. We therefore excluded all jays that hatched after 2003 from our analysis of lifetime reproductive success. Similarly, because some jays do not become breeders until they are 3 yr old, all jays that hatched after 2010 were excluded from analyses of acquisition of breeding status and age at first nesting. Jays that were known to have dispersed and bred out of the primary study area were included in our analysis of acquisition of breeding status; however, only jays that nested within the study area were used in analyses of age at first breeding and lifetime reproductive success. Because some prebreeders that emigrated and bred out of the study area escaped detection during our periodic surveys of surrounding areas, our calculated probability of a yearling acquiring breeding status underestimates the true probability, especially for females (Woolfenden and Fitzpatrick 1984, Fitzpatrick et al. 1999, Coulon et al. 2010).

As independent variables, we explicitly considered 4 aspects of the natal brood: hatching date (day of year), brood size (number of eggs hatched), age at fledging (days since hatching), and nestling body mass at day 11. A few nestlings were banded and weighed at day 9–10 or day 12–13; we estimated day 11 body mass for these individuals from the linear regression equation relating nestling body mass to nestling age.

Three group composition variables were used as independent variables in our analyses: natal group size (breeding pair plus any nonbreeding helpers) resident during the nesting season, and the ages of the breeding female and male. Because preliminary analyses revealed no significant effect of helper sex on any of our measures of survival or future reproductive success, helper sex was not considered in the analyses presented here.

Two characteristics of the natal territory were included as independent variables. The total area of scrub habitat included all oak-dominated habitats on sandy, well-drained soil, but excluded other habitats (e.g., seasonal ponds and wiregrass-palmetto flats) on less well-drained soils. Because Florida Scrub-Jays forage primarily in these well-drained, sandy, scrub habitats, and because the total area of scrub is strongly correlated with overall territory size ($r = 0.71$), the area of scrub served as a composite index of both territory size and quality. Because 8 ha approximated the observed median (7.6 ha) and mean (8.2 ha) area of oak scrub habitat in the dataset, for some analyses we compared individuals from small, low-quality natal territories (<8 ha of scrub) to those from large, high-quality territories (>8 ha of scrub). The proportion of the natal territory consisting of sand roads and open sand fire lanes also was included as an independent variable because of the importance of these areas for foraging (Davison and Fitzpatrick 2010, Morgan et al. 2010).

For our analyses of survival from day 90 to day 300, the probability of becoming a breeder, age at first nesting, and lifetime reproductive success, we included 2 additional variables, sex and juvenile body mass, as independent predictor variables. Because the regression of juvenile body mass on juvenile age was not statistically significant, we did not standardize juvenile mass to a particular age.

We used general and generalized linear mixed models (GLMMs) to analyze the effects of the independent variables on each dependent variable (Zuur et al. 2009). Nest year and identity of the natal nest were included as random effects. All analyses were conducted using JMP version 10.0 (SAS Institute 2012) and R version 3.02 (R Development Core Team 2013) with package 'lme4' version 15 (Bates et al. 2013). Our general modeling approach was to include the same set of 9 (or 11) independent predictor variables (described above) in all statistical models, thereby testing the importance of each predictor variable while simultaneously controlling for the effects of other potentially confounding variables. The predictor variables were only weakly intercorrelated (mean ± SD absolute value of correlation coefficients: $r = 0.08 \pm 0.06$), with the strongest correlation ($r = -0.23$) occurring between brood size and nestling body mass. For each model we also tested the effects of additional interaction or polynomial terms, but included these higher-order effects in the final models only when they were significant ($P < 0.05$). We scrutinized the residuals of all models and checked for potentially spurious findings by comparing model results with simpler exploratory analyses. Data presented in figures represent actual observed values, not model estimates.

RESULTS

Survival from Fledging (Day 15–20) to Day 30

Bivariate logistic regression showed that several brood, group, and territory variables were strongly associated with the survival of juveniles from fledging to day 30. Day 11 body mass, age at fledging, natal group size, and the area of oak scrub in the natal territory were all positively associated with postfledging survival to day 30, while the relationships with hatching date, brood size, and the proportion of the territory comprising sand roads and fire lanes were negative (Figure 1). Age of the breeding adults

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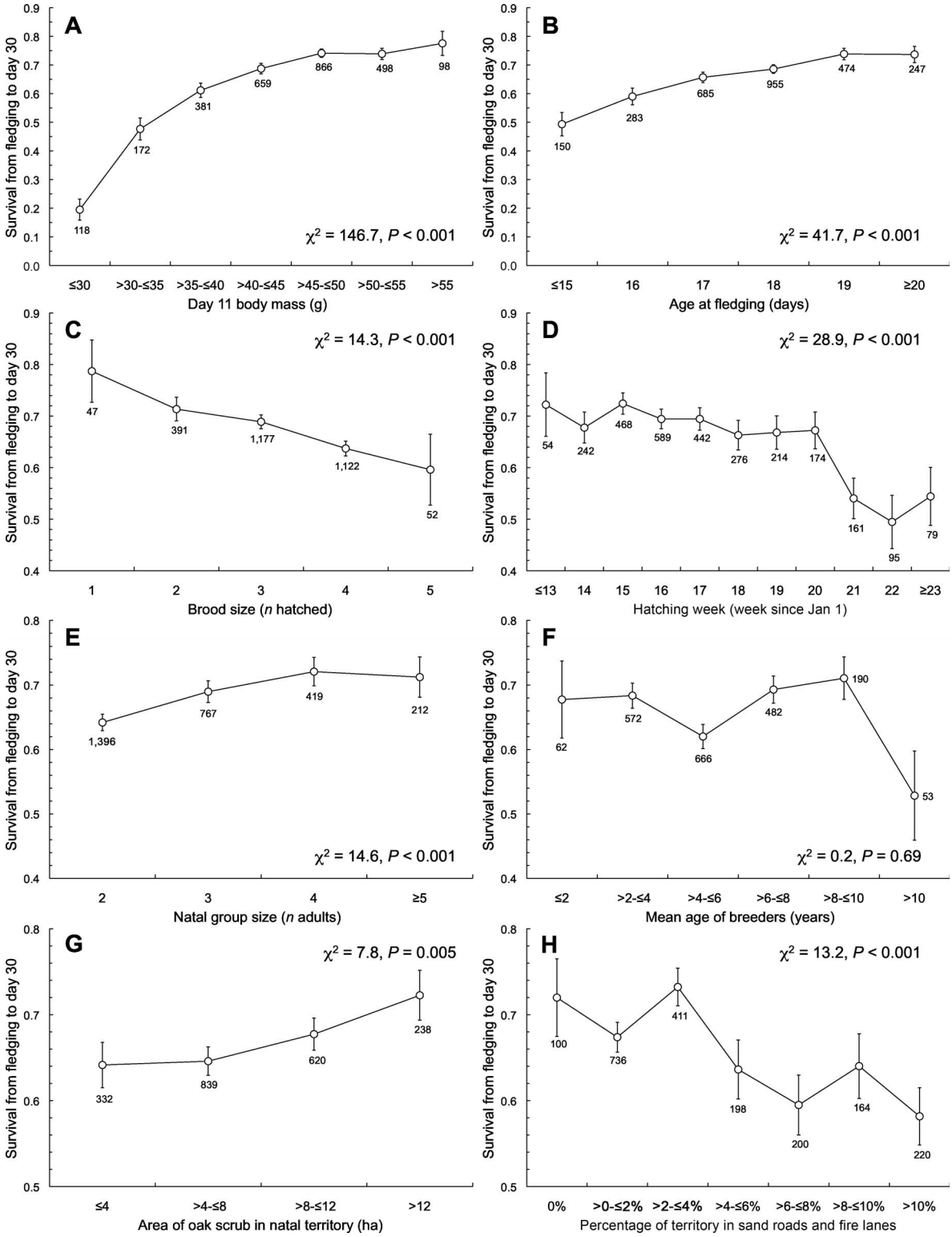


FIGURE 1. Raw data plots showing the survival of young Florida Scrub-Jays from fledging to day 30 in relation to (**A**) body mass as an 11-day-old nestling, (**B**) age (days since hatching) at fledging, (**C**) brood size, (**D**) hatching week, (**E**) natal group size, (**F**) age of the breeding pair, (**G**) area of oak scrub habitat in the natal territory, and (**H**) percentage of the territory consisting of sand roads and firebreaks. Means, standard error bars, and sample sizes are shown. Chi-square statistics were derived from bivariate logistic regressions of survival vs. the independent variables in their original (continuous) forms, not the recoded categories shown for visualization purposes.

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TABLE 1. Generalized linear mixed model (binomial error distribution, logit link function) of factors contributing to the survival of young Florida Scrub-Jays from fledging (day 15–20 posthatching) to day 30 after hatching. Identity of the natal nest and nest year were included in the model as random effects. Because the relationship between day 11 body mass and survival to day 30 was curvilinear (Figure 1A), a significant quadratic term was included for this effect; other polynomial and interaction terms were not significant ($P > 0.05$) and were excluded from the model. Significant effects are denoted with an asterisk. Total sample size was 2,025 fledglings in 1980–2012.

Term	Estimate	SE	*Z*	*P*
Intercept	−2.96	1.03	−2.9	0.004*
Day 11 body mass (g)	30.79	3.03	10.2	<0.001*
[Day 11 body mass (g)]^2	−16.30	3.39	−4.8	<0.001*
Hatching date (day of year)	−0.0095	0.0036	−2.6	0.009*
Age at fledging (days)	0.28	0.05	6.2	<0.001*
Brood size (*n* young hatched)	−0.18	0.08	−2.2	0.03*
Group size (*n* adults)	0.20	0.06	3.3	0.001*
Age of breeding female (yr)	−0.046	0.024	−1.9	0.05
Age of breeding male (yr)	0.013	0.022	0.6	0.56
Area of scrub in natal territory (ha)	0.017	0.016	1.0	0.30
Proportion of territory in roads and firebreaks	−3.23	1.48	−2.2	0.03*

in the group was unrelated to survival to day 30 (Figure 1F). In a generalized linear mixed model (GLMM), all of the factors listed above were significant predictors of survival to day 30 except the area of scrub in the territory and age of the breeders (Table 1). A second GLMM limited to known-sex juveniles that hatched in 1999–2012 produced similar results and is not presented.

Because of the strong effect of nestling body mass on postfledging survival (Table 1, Figure 1A), we also explored factors contributing to variation in nestling mass. In this analysis, group size and the area of oak scrub in the territory were significant positive predictors of nestling

TABLE 2. General linear mixed model (normal error distribution, identity link function) of factors contributing to day 11 nestling body mass of Florida Scrub-Jays. Identity of the natal nest and nest year were included in the model as random effects. Polynomial and interaction terms were not significant ($P > 0.05$) and were excluded from the model. Significant effects are denoted with an asterisk. Total sample size was 2,025 nestlings that fledged in 1980–2012.

Term	Estimate	SE	*Z*	*P*
Intercept	46.02	1.85	24.9	<0.001*
Brood size (*n* young hatched)	−2.07	0.24	−8.5	<0.001*
Hatching date (day of year)	0.010	0.012	0.9	0.39
Group size (*n* adults)	0.54	0.20	2.8	0.006*
Age of breeding female (yr)	0.032	0.078	0.4	0.69
Age of breeding male (yr)	0.060	0.070	0.9	0.39
Area of scrub in natal territory (ha)	0.20	0.05	3.8	<0.001*
Proportion of territory in roads and firebreaks	−2.26	4.95	−0.5	0.65

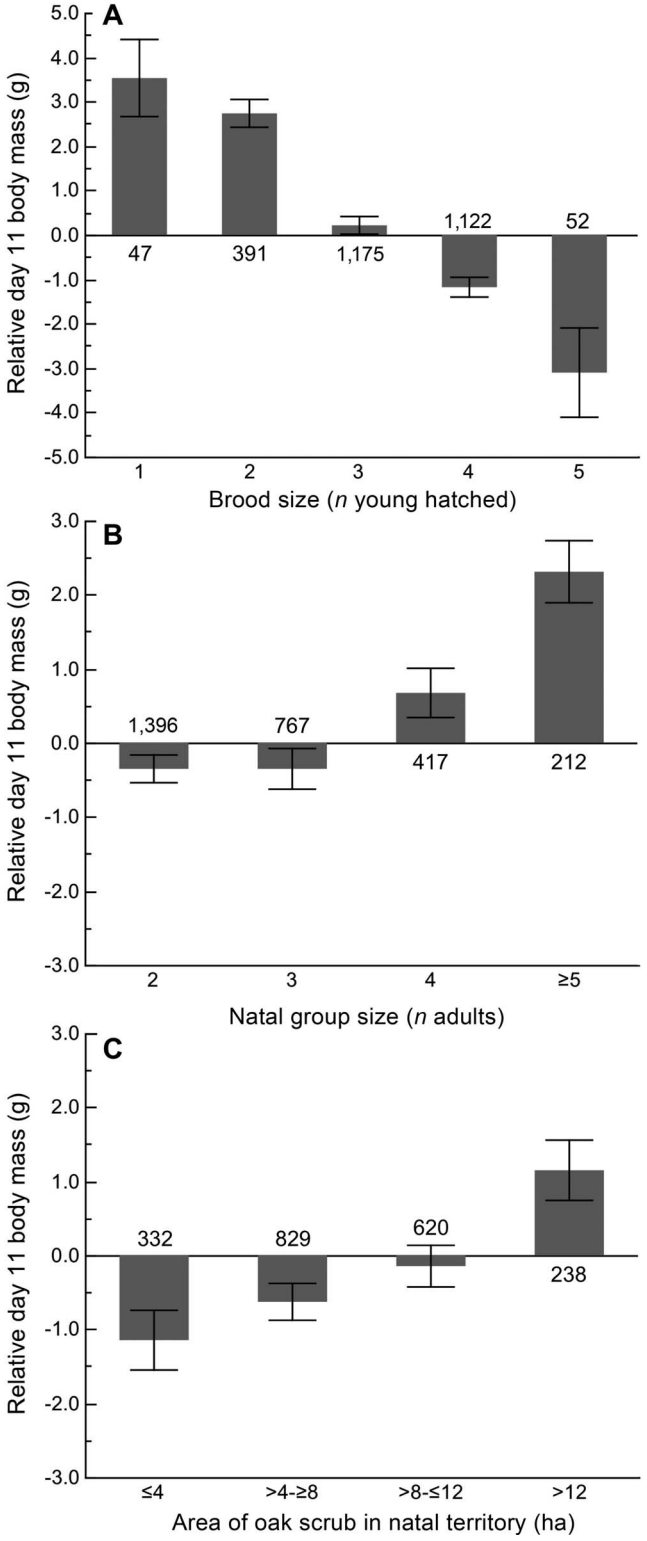


FIGURE 2. Raw data plots showing the relative body mass of 11-day-old Florida Scrub-Jays in relation to (**A**) brood size, (**B**) group size, and (**C**) the area of oak scrub habitat in the natal territory. Means, standard error bars, and sample sizes are shown. Relative day 11 body mass is the difference between the day 11 body mass of a nestling and the mean day 11 body mass for all nestlings from that particular nest year.

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TABLE 3. Generalized linear mixed model (binomial error distribution, logit link function) of factors contributing to the survival of juvenile Florida Scrub-Jays from day 30 to day 90 (nutritional independence). Identity of the natal nest and nest year were included in the model as random effects. Polynomial and interaction terms were not significant ($P > 0.05$) and were excluded from the model. Significant effects are denoted with an asterisk. Total sample size was 1,343 juvenile jays that survived from fledging to day 30 in 1980–2012.

Term	Estimate	SE	*Z*	*P*
Intercept	2.74	1.90	1.4	0.15
Day 11 body mass (g)	0.046	0.015	3.2	0.002*
Hatching date (day of year)	−0.0073	0.0057	−1.3	0.20
Age at fledging (days)	−0.13	0.07	−1.8	0.08
Brood size (*n* young hatched)	0.09	0.12	0.8	0.45
Group size (*n* adults)	0.092	0.093	1.0	0.32
Age of breeding female (yr)	−0.009	0.037	−0.3	0.79
Age of breeding male (yr)	−0.061	0.033	−1.9	0.06
Area of scrub in natal territory (ha)	0.036	0.025	1.4	0.15
Proportion of territory in roads and firebreaks	−4.29	2.26	−1.9	0.06

TABLE 4. Generalized linear mixed model (binomial error distribution, logit link function) of factors contributing to the survival of known-sex juvenile Florida Scrub-Jays from day 90 (nutritional independence) to day 300 (yearling). Identity of the natal nest and nest year were included in the model as random effects. Polynomial and interaction terms were not significant ($P > 0.05$) and were excluded from the model. Significant effects are denoted with an asterisk. Total sample size was 884 known-sex jays that survived to day 90 in 1980–2012.

Term	Estimate	SE	*Z*	*P*
Intercept	−1.42	2.51	−0.6	0.57
Sex (male)	−0.08	0.21	−0.4	0.70
Day 11 body mass (g)	0.001	0.019	0.1	0.94
Juvenile body mass (g)	0.054	0.026	2.1	0.04*
Hatching date (day of year)	−0.0034	0.0069	−0.5	0.63
Age at fledging (days)	0.018	0.084	0.2	0.83
Brood size (*n* young hatched)	−0.00	0.14	−0.0	0.99
Group size (*n* adults)	−0.12	0.10	−1.3	0.21
Age of breeding female (yr)	0.061	0.044	1.4	0.17
Age of breeding male (yr)	−0.001	0.037	−0.1	0.96
Area of scrub in natal territory (ha)	−0.018	0.028	−0.7	0.51
Proportion of territory in roads and firebreaks	0.52	2.76	0.2	0.85

mass, while brood size was a significant negative predictor (Table 2, Figure 2). Limiting the analysis to known-sex nestlings and including sex as a factor in the model produced similar results.

Survival from Day 30 to Day 90 (Independence)

In a GLMM, only nestling body mass was a significant positive predictor of juvenile survival from day 30 to day 90 (Table 3). The proportion of the territory in roads and fire lanes and age of the breeding male had marginally significant negative effects (Table 3).

Survival from Day 90 to Day 300 (Yearling)

We found no significant predictors of survival from day 90 to day 300 among all juveniles that survived to day 90, a sample that included many unknown-sex jays. However, in a separate analysis restricted to known-sex birds, body mass as a juvenile was a significant positive predictor of survival to the yearling stage when sex was included as a factor in the GLMM (Table 4). Body mass as a juvenile, in turn, was significantly greater in males and positively influenced by body mass as a nestling (Figure 3A) and the area of scrub in the natal territory (Table 5). Juvenile body mass was negatively related to natal group size (Table 5), a result that was unexpected given the strong positive relationship between group size and nestling body mass (Table 1, Figure 1E). However, even though the interaction between group size and the area of scrub was not significant in the model ($Z = 1.65$, $P = 0.10$; Table 5), the negative relationship between natal group size and juvenile body mass was pronounced only in small, low-quality territories with <8 ha of oak scrub (Figures 3B, 3C).

Becoming a Breeder and Lifetime Reproductive Success

Of 638 known-sex yearlings with complete data, 368 (163 females, 205 males) eventually became breeders in or near our study area. The smaller number of females known to have become breeders is attributable to female-biased dispersal out of the study area (Woolfenden and Fitzpatrick 1984). Besides sex, the area of oak scrub in the natal territory was the only significant predictor of acquisition of breeding status in the GLMM (Table 6, Figure 4A). A comparison of yearling males from small (<8 ha of scrub) and large (>8 ha of scrub) natal territories showed that large natal territory size was associated with an increased probability of becoming a breeder (64% to 73%, respectively), primarily through a higher probability of budding or inheriting part of the natal territory (20% to 24%) or of acquiring an adjacent territory (23% to 26%). The probability of a yearling male acquiring a nonadjacent territory was identical (22%) for males from small and large natal territories. For yearling females, a large natal territory was associated with a more modest increase in the probability of becoming a breeder (47% vs. 51% for females from small and large natal territories, respectively), and this difference was driven almost entirely by a higher probability of dispersal to a nonadjacent territory (33% vs. 37%).

The area of scrub in the natal territory was also a significant predictor of age at first nesting (Table 7), particularly for males (Figure 4B). Males that were reared in territories containing large areas of oak scrub first bred at younger ages than those reared in territories with less scrub (Figure 4B).

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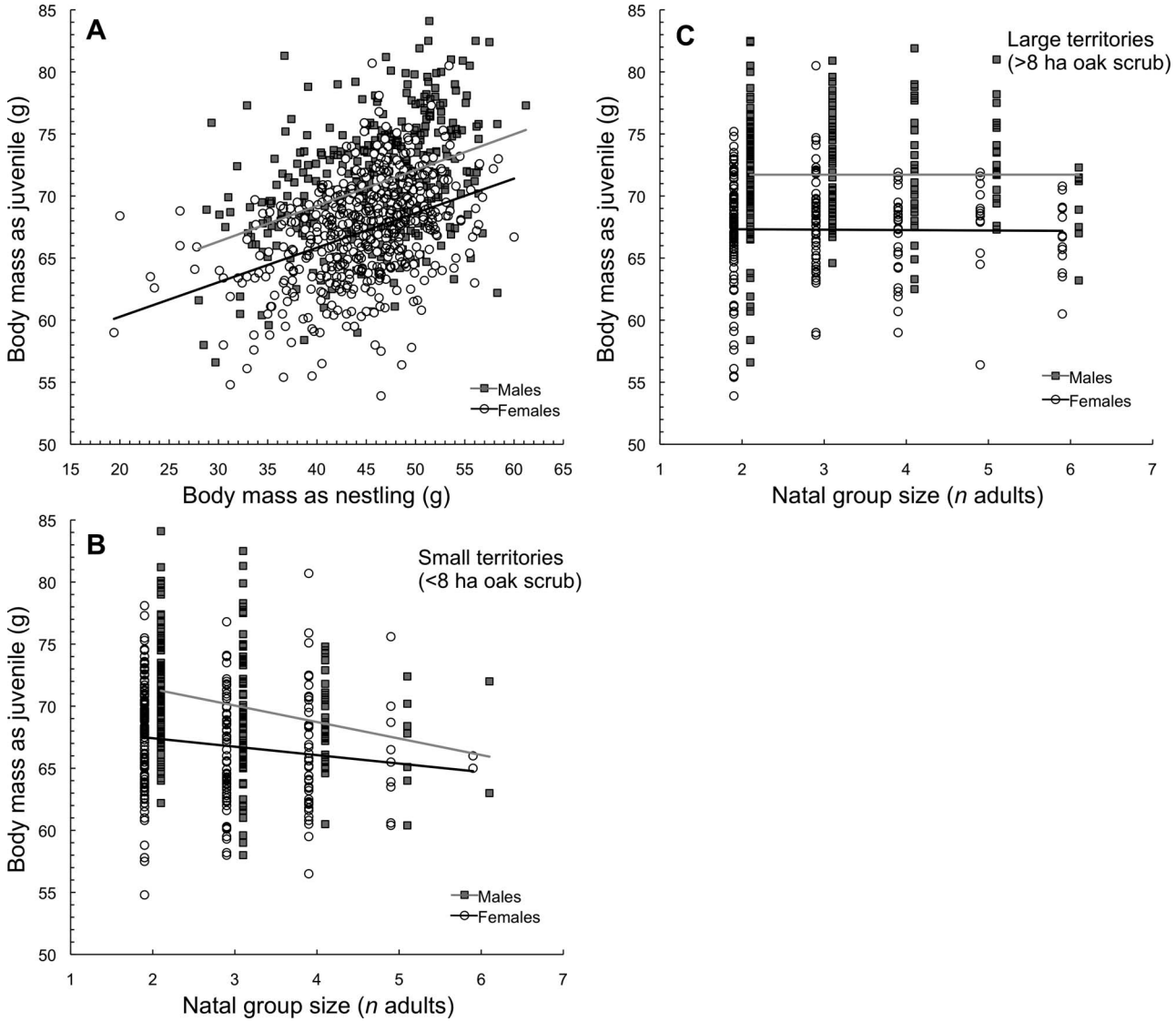


FIGURE 3. Raw data plots showing factors contributing to variation in juvenile body mass in Florida Scrub-Jays. Panel (**A**) shows the relationship between body mass as an 11-day-old nestling and body mass as a juvenile for males and females. In a general linear mixed model ($r^2 = 0.81$) in which nest year and identity of the natal nest were included as random effects, both sex and day 11 body mass were significant predictors of body mass as a juvenile (Table 5). Panels (**B**) and (**C**) show the relationship between juvenile body mass and natal group size in territories with <8 ha of oak scrub ($Z = -3.27$, $P = 0.001$) and >8 ha of oak scrub ($Z = -0.41$, $P = 0.68$), respectively. Total sample size is 884 known-sex juveniles captured and weighed when 45–110 days old.

Despite the many effects of early natal experience on factors influencing fitness up to and through recruitment as a breeder, we found no significant early-life predictors of lifetime reproductive success after becoming a breeder. Similar nonsignificant results were obtained for alternative measures of lifetime reproductive performance, such as duration of reproductive lifespan and lifetime production of young surviving to independence (day 90).

DISCUSSION

For young Florida Scrub-Jays, early-life environmental conditions have significant short- and long-term fitness consequences that are manifested in postfledging survival, the probability of acquiring a breeding territory, and age at first nesting. Three aspects of the natal biological and social environment are especially important: nestling body mass, the area of oak scrub in the natal territory, and natal group size.

Nestling body mass, which was determined largely by natal brood size, group size, and territory size (Figure 2), was positively associated with postfledging survival through nutritional independence (day 90), even when potentially confounding variables were controlled statistically. It was also an important positive predictor of juvenile body mass, which in turn was positively associated with

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TABLE 5. General linear mixed model (normal error distribution, identity link function) of factors contributing to juvenile body mass of Florida Scrub-Jays. Identity of the natal nest and nest year were included in the model as random effects. Polynomial and interaction terms were not significant ($P > 0.05$) and were excluded from the model. Significant effects are denoted with an asterisk. Total sample size was 884 known-sex juveniles that fledged in 1980–2012.

Term	Estimate	SE	*Z*	*P*
Intercept	52.16	3.31	15.8	<0.001*
Sex (male)	1.76	0.11	15.7	<0.001*
Day 11 body mass (g)	0.29	0.02	12.8	<0.001*
Hatching date (day of year)	0.008	0.011	0.8	0.42
Age at fledging (days)	0.12	0.13	0.9	0.34
Brood size (*n* young hatched)	0.13	0.21	0.6	0.53
Group size (*n* adults)	−0.49	0.16	−3.0	0.002*
Age of breeding female (yr)	−0.023	0.068	−0.3	0.73
Age of breeding male (yr)	0.037	0.058	0.6	0.53
Area of scrub in natal territory (ha)	0.14	0.04	3.3	0.001*
Proportion of territory in roads and firebreaks	8.35	4.32	1.9	0.05

juvenile survival to the yearling stage. Although the fitness consequences of nestling body mass were primarily manifested early in a jay's life, they produced long-term cumulative advantages. Jays that achieved 4 postfledging developmental milestones (surviving to day 30, day 90, day 300, and becoming a breeder) were larger as nestlings than jays that failed to achieve these milestones (Figure 5). This result corroborates evidence from other avian and mammalian species that variation in natal body condition can have far-reaching fitness consequences (Magrath 1991, Hatchwell et al. 2004, Hodge 2005, Ridley 2007, Rödel et al. 2009, Sparkman et al. 2010, Tilgar et al. 2010, Brouwer et al. 2012).

TABLE 6. Generalized linear mixed model (binomial error distribution, logit link function) of factors contributing to the probability that a yearling (day 300) Florida Scrub-Jay later became a breeder. Identity of the natal nest and nest year were included in the model as random effects. Polynomial and interaction terms were not significant ($P > 0.05$) and were excluded from the model. Significant effects are denoted with an asterisk. Total sample size was 638 known-sex jays that survived to day 300 in 1980–2010.

Term	Estimate	SE	*Z*	*P*
Intercept	−0.93	2.29	−0.4	0.68
Sex (male)	0.87	0.19	4.6	<0.001*
Day 11 body mass (g)	0.020	0.017	1.2	0.22
Juvenile body mass (g)	−0.000	0.022	−0.0	0.99
Hatching date (day of year)	−0.0032	0.0058	−0.6	0.58
Age at fledging (days)	0.029	0.072	0.4	0.69
Brood size (*n* young hatched)	0.05	0.11	0.5	0.64
Group size (*n* adults)	−0.097	0.085	−1.2	0.25
Age of breeding female (yr)	−0.065	0.036	−1.8	0.07
Age of breeding male (yr)	0.001	0.031	0.0	0.97
Area of scrub in natal territory (ha)	0.056	0.024	2.4	0.02*
Proportion of territory in roads and firebreaks	−3.62	2.36	−1.5	0.13

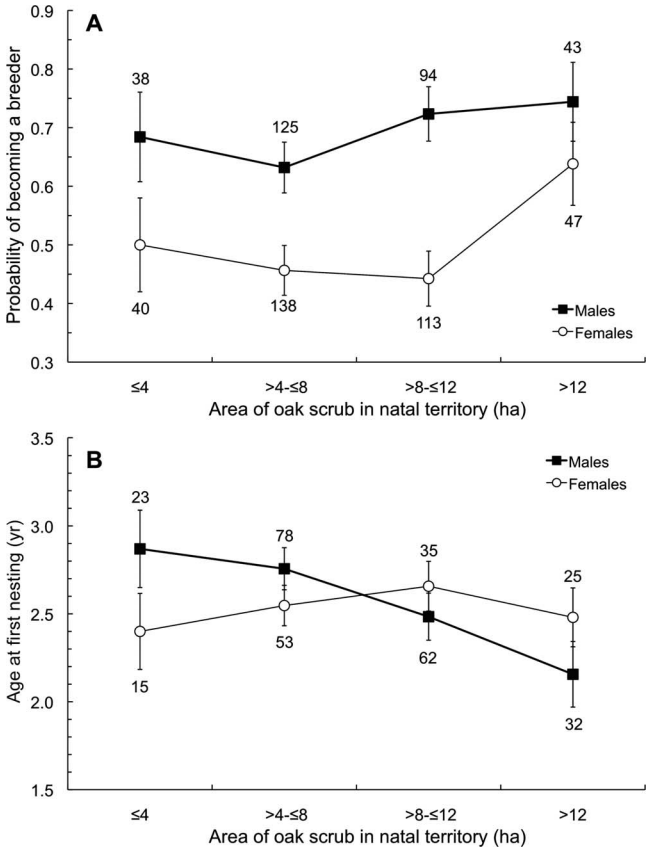


FIGURE 4. Raw data plots showing the relationship between the area of oak scrub in the natal territory and (**A**) probability of yearling Florida Scrub-Jays eventually becoming breeders, and (**B**) age at first breeding. Means, standard error bars, and sample sizes are shown. Although the general linear mixed model for age at first breeding showed no significant interaction between sex and area of oak scrub ($Z = 1.38$, $P = 0.17$; Table 7), the raw data portrayed here suggest a significant effect of scrub area on age at first nesting for males ($F_{1,193} = 8.6$, $P = 0.004$) but not for females ($F_{1,126} = 0.0$, $P = 0.94$).

A novel finding of our study was that the area of oak scrub in the natal territory, a key indicator of territory size and quality, had significant fitness consequences for Florida Scrub-Jays. In the short term, the area of oak scrub was a significant predictor of nestling and juvenile body mass, even when group size and other potentially confounding variables were controlled statistically. Positive relationships between scrub area and body mass suggest that Florida Scrub-Jays significantly reduce the density of the highest-quality food resources in small territories, a possibility that has also been suggested for other cooperatively breeding birds (e.g., Komdeur 1994). In the long term, the area of oak scrub in the natal territory was a significant predictor of the probability of becoming a

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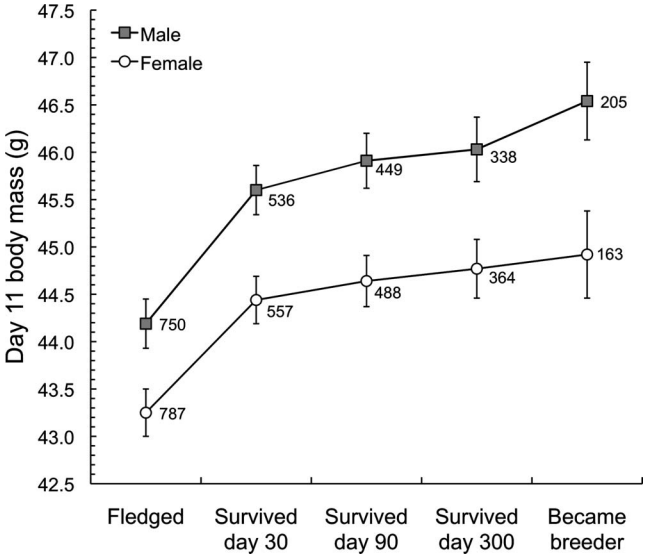


FIGURE 5. Cumulative effects of selection on nestling body mass over the course of development in male and female Florida Scrub-Jays. For both males and females, jays that achieved a particular developmental milestone were larger as nestlings than jays that failed to do so. Means, standard error bars, and sample sizes are shown.

TABLE 7. General linear mixed model (normal error distribution, identity link function) of factors contributing to the age at first nesting (log-transformed) of Florida Scrub-Jays. Identity of the natal nest and nest year were included in the model as random effects. Polynomial and interaction terms were not significant ($P > 0.05$) and were excluded from the model. Significant effects are denoted with an asterisk. Total sample size was 324 jays (128 females, 196 males) that fledged in 1980–2010 and initially nested in the study area.

Term	Estimate	SE	*Z*	*P*
Intercept	1.13	0.57	2.0	0.05
Sex (male)	−0.010	0.022	−0.5	0.64
Day 11 body mass (g)	−0.0008	0.0039	−0.2	0.82
Juvenile body mass (g)	−0.0001	0.0054	−0.0	0.98
Hatching date (day of year)	−0.0003	0.0014	−0.2	0.81
Brood size (*n* young hatched)	−0.006	0.026	−0.3	0.80
Age at fledging (days)	−0.006	0.017	−0.3	0.76
Group size (*n* adults)	0.001	0.020	0.1	0.96
Age of breeding female (yr)	0.011	0.008	1.3	0.21
Age of breeding male (yr)	0.0053	0.0073	0.7	0.47
Area of scrub in natal territory (ha)	−0.013	0.005	−2.7	0.007*
Proportion of territory in roads and firebreaks	−1.14	0.58	−2.0	0.05

breeder and the age at first nesting, particularly for males (Figure 4). These crucial consequences of natal territory size reflect the fact that ~25% of male Florida Scrub-Jays become breeders on part of their natal territory via territorial budding, and that larger territories increase the opportunity for this (Woolfenden and Fitzpatrick 1978, 1984). Larger territories also have more neighboring territories, thereby providing more opportunities for prebreeding jays to compete for adjacent breeding vacancies from the safety of home. These two pathways to local territory acquisition—budding or inheritance of the natal territory and dispersal to an adjacent territory with a shared territorial boundary—occurred more frequently in males from large natal territories. Collectively, our results help to resolve a long-standing question about why Florida Scrub-Jays defend such unusually large territories for their body size (Shank 1986). Vigorous year-round efforts to enlarge the territory represent a form of parental investment that promotes short- and long-term success of offspring.

Natal group size has complex fitness effects that are partially antagonistic. A large group clearly benefits jays early in life, by increasing nestling body mass and by promoting survival from fledging to day 30, even after controlling for potentially confounding variables. These benefits of helpers are consistent with previous experimental and observational data on Florida Scrub-Jays (Mumme 1992, Shawkey et al. 2004, Schoech et al. 2008) and other cooperative breeders (Hatchwell et al. 2004, Hodge 2005, Ridley 2007, Russell et al. 2007, Sparkman et al. 2010). However, we also found a previously unsuspected cost associated with helpers: Juvenile body mass, which was a significant predictor of survival to the yearling stage, was negatively related to natal group size, but only in territories of below-average size (Figures 3B, 3C). We suggest that as juvenile jays begin to forage on their own and are fed less frequently by adults (around day 50 posthatching; McGowan and Woolfenden 1990), helpers transition into competitors for food resources within groups having comparatively little oak scrub for foraging. Body mass as a juvenile is therefore determined by a complex interplay between natal group size and the area of oak scrub available to the group for foraging. This interaction provides evidence of another benefit that Florida Scrub-Jays obtain by defending extremely large territories: reducing the potential for competition with other group members (e.g., Komdeur 1994).

Other characteristics of the natal brood and territory also had significant effects on fitness. Natal brood size had two negative consequences for young Florida Scrub-Jays. First, it had a strong negative effect on nestling body mass, which in turn had many short- and long-term effects on survival (discussed above). Second, natal brood size had a direct negative effect on juvenile survival from fledging to day 30. In addition to underscoring the importance of within-family competition in the Florida Scrub-Jay, these brood size effects provide evidence of life-history tradeoffs among clutch size, offspring quality, and postfledging survival that merit further investigation (e.g., Nur 1984).

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Postfledging survival to day 30 was positively related to age at fledging (Figure 1B). Although it is usually assumed that premature fledging of songbirds has a negative effect on postfledging survival, surprisingly few data are available to support this contention. In fact, the only study that we found that explicitly addressed this issue (Streby et al. 2013) found that premature fledging had no negative effects on short-term survival. Our results, in contrast, provide strong evidence that early fledging can be detrimental to postfledging survival.

The proportion of the natal territory comprising sand roads and fire lanes had a surprising negative effect on postfledging survival. Although high-speed paved roads are known to have pronounced negative impacts on the survival of Florida Scrub-Jays (Mumme et al. 2000), the present association between roads and juvenile mortality cannot be explained by road kill; sand roads and fire lanes within Archbold are private, unpaved, and lightly travelled by low-speed vehicles that pose no threat to jays. Instead, we suspect that roads and fire lanes facilitate patrolling movements by the numerous mammalian and snake predators in this habitat, and that juvenile jays tend to be more conspicuous and vulnerable when foraging or roosting along roads.

Age of the breeding female and male was not a significant predictor of any aspect of the future survival and reproduction of offspring. Most studies of other cooperative breeding systems have similarly found little evidence that prior experience directly affects future reproductive performance (Komdeur 1996, Khan and Walters 1997, Koenig and Walters 2011, DuVal 2013).

Early-life environmental conditions had strong fitness effects on individual Florida Scrub-Jays, playing major roles in juvenile survival, survival to the yearling stage, and acquisition of a breeding territory. However, for those jays that finally did acquire breeding space and breed, natal environment had no lingering relevancy in predicting future survival or reproduction. None of the natal brood, group, or territory variables that we examined significantly affected lifetime reproductive output of jays that had become breeders. This finding contrasts with evidence of a "silver spoon" effect in other studies (Rödel et al. 2009, Sparkman et al. 2010, Tilgar et al. 2010, Brouwer et al. 2012), but is fully consistent with numerous aspects of the Florida Scrub-Jay's social and ecological milieu. Acquiring and permanently defending a territory is a delayed and exceptionally competitive affair in Florida Scrub-Jays, and relatively few individuals ultimately succeed (Woolfenden and Fitzpatrick 1984). Once paired, Florida Scrub-Jays are completely genetically monogamous (Townsend et al. 2011), and even divorce is extremely rare (Woolfenden and Fitzpatrick 1984, Marzluff et al. 1996). In such a system, individuals that survive to adulthood and acquire a breeding territory tend to be the highest-quality birds, and thus may have relatively little interindividual variability in intrinsic attributes that affect fitness. Under such conditions, extra-pair mating strategies and dissolution of pair bonds would yield few reproductive benefits (Townsend et al. 2011). Lifetime reproductive performance once breeding status is obtained therefore likely depends on surviving and responding appropriately to varying environmental conditions, rather than on any lingering effects of the natal environment.

Our analyses portray the Florida Scrub-Jay as a species that exists perilously near the edge of its available food supply. The strong negative effects of brood size on nestling body mass and postfledging survival suggest an extrinsically imposed limit to how much food provisioners can find and deliver to nestlings. Under such conditions, helpers confer a significant fitness advantage, but can become competitors for limited food unless they also help to expand territory size and increase the total area of oak scrub available for foraging. Collectively, these relationships suggest that reliance on habitats in which resources are thinly but evenly dispersed, like Florida's oak scrub, facilitates the evolution of group territoriality and cooperative breeding (Fitzpatrick and Bowman in press).

In summary, our study (1) adds to the growing body of evidence that the early natal environment can have far-reaching consequences for survival and lifetime fitness of long-lived vertebrates; (2) provides insight into the long-standing puzzle of why Florida Scrub-Jays defend exceptionally large territories; and (3) clarifies how natal territory size and group size collectively shape an individual's long-term prospects for survival and reproduction.

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