

THE EFFECT OF SUPPLEMENTAL FOOD ON BODY CONDITION AND THE TIMING OF REPRODUCTION IN A COOPERATIVE BREEDER, THE FLORIDA SCRUB-JAY¹

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Abstract. I examined the importance of food availability on when or whether to breed in cooperatively breeding Florida Scrub-Jays (*Aphelocoma coerulescens*). Two of the major factors known to influence the timing of reproduction are adequate food for offspring and sufficient available food for breeding females to produce a clutch. If the nutritive needs of a breeding female affect the timing of clutch initiation, food supplemented females should lay before controls. Supplemented female breeders initiated clutches earlier and produced larger clutches than unsupplemented birds. If food abundance declines as the breeding season progresses to the point where fewer young can be fed, clutch size should also decline. Florida Scrub-Jay females laid smaller clutches as the season progressed. Additionally, female breeders given supplemental food had higher levels of body lipids than controls prior to clutch initiation.

The food supplementation protocol also allows the testing of the hypothesis that non-breeder Florida Scrub-Jays forgo breeding because they are food limited. If food limitation were the only factor in the 'decision' by nonbreeders to forgo breeding, individuals provided with food would become breeders at a higher frequency than unsupplemented birds. However, equal frequencies of control and supplemented nonbreeders became breeders. I also compared body mass and body lipid of breeders and nonbreeders and found that breeders were heavier and had higher percentages of body lipids than nonbreeders. However, these differences probably do not cause them to be nonbreeders but rather are a result of their being nonbreeders.

Key words: Florida Scrub-Jay; *Aphelocoma*; food supplementation; body condition; clutch initiation.

INTRODUCTION

Lack (1950, 1968) postulated that clutch initiation is timed so that nestlings are present when food is most abundant, thereby increasing survival of offspring. Perrins (1965, 1966, 1970) subsequently pointed out that the nutritive needs of a laying female also can affect the timing of a clutch. A sufficient food supply is critical for a breeding female and her body condition must be adequate for her to reactivate her ovaries and associated structures as well as produce eggs. If an inadequate food supply early in the breeding season renders a female incapable of producing a clutch at the time when a clutch should be initiated to assure that food supplies are at their highest when nestlings are being fed, food availability could be simultaneously delaying and accelerating the timing of reproduction (Perrins

1970). The two hypotheses that explain the timing of clutch initiation are not mutually exclusive and are often difficult to separate clearly. Further complicating comparisons and evaluations is the dual nature of food, which can act at both the proximate and ultimate levels. Food acts as an ultimate factor in Lack's hypothesis whereas in Perrins' hypothesis it is a proximate factor (for a discussion of levels of analysis, see Sherman 1988).

Food supplementation studies have proven invaluable in evaluating both Lack's and Perrins' hypotheses. Supplemental food provided when parents were feeding nestling Cactus Wrens (*Campylorhynchus brunneicapillus*), Eurasian Oystercatchers (*Haemaphysalis ostralegus*), and Pied Flycatchers (*Ficedula hypoleuca*) resulted in increased reproductive success, i.e., growth rates, survivorship, or number of young fledged, demonstrating the importance of food when nestlings are being cared for (Simons and Martin 1990, Ens et al. 1992, Verhulst 1994). Similarly, providing supplemental food has advanced the date

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of clutch initiation in numerous species (Daan et al. 1986, Svensson 1995, Wimberger 1988, Hörnfeldt and Eklund 1990, Källander and Karlsson 1993, for exceptions see Högstedt 1981, Simmons 1993, Nakamura 1995).

The importance of food availability in the timing of reproduction in the cooperatively breeding Florida Scrub-Jay was suggested by my observations during an exceptionally late breeding season. During the last 25 years, breeding has nearly always begun between 1 and 15 March (Woolfenden and Fitzpatrick 1984, Woolfenden, pers. comm.); however in 1992, only two females in my study tract initiated clutches during March. Interestingly, members of both of the early-breeding groups were seen with food from outside the station's boundaries. One breeding male was seen carrying dried dog food to his mate, and members of the other group were frequently observed carrying corn from a feeder that a neighboring landowner used to attract game birds. The remaining groups which resided on territories that were isolated from human influences and were not observed with supplemental food did not initiate clutches until April and May. By providing supplemental food to a subset of the population in a subsequent year I was able to determine the importance of food on the timing of reproduction in this species.

In addition to its use as a tool to explore underlying mechanisms in the decision of *when* to breed, food supplementation experiments can be used to investigate the importance of nutritional plane in the decision *whether* to breed. Based on their study of Brown-and-yellow Marshbirds (*Pseudoleistes virescens*), Bay-winged Cowbirds (*Molothrus badius*), and Austral Blackbirds (*Curaeus curaeus*) in Argentina, Orians et al. (1977) hypothesized that insufficient food resources might be responsible for the high numbers of nonbreeding helpers in these species. They further postulate that limited food might be a general factor that causes nonbreeders to forgo breeding in cooperative breeding species.

Considerable evidence exists that younger birds are less adept foragers than their elders (Orians 1969, Greig et al. 1988, Desrochers 1992). Brown (1985) postulated that nonbreeders in cooperatively breeding species (nonbreeders are typically younger birds) might forgo breeding because they have yet to develop adequate foraging skills, and as a result their nutritional plane is relatively poor. Because most Florida Scrub-Jay nonbreed-

ers are first year birds, they may not possess the foraging skills of older birds and consequently their condition may be too poor for them to undertake the rigors of breeding i.e., establish and defend a territory, enlarge their gonads, produce eggs, provision themselves, a mate, and offspring. Despite the subtle differences between the hypotheses of Orians et al. (1977) and Brown (1985), their common ground is that nonbreeding helpers are food-limited. By comparing food-supplemented and control nonbreeders and breeders, I assessed the importance of food availability on the decision of *whether* and *when* to breed in Florida Scrub-Jays.

MATERIALS AND METHODS

STUDY SITE AND GENERAL METHODS

I studied Florida Scrub-Jays at Archbold Biological Station in south-central Florida (27°10'N, 81°21'W, elevation 38–68 m). My research focused on birds in the 'experimental' tract that is adjacent to the population followed by Woolfenden, Fitzpatrick and colleagues for 25 years (Woolfenden and Fitzpatrick 1977, 1984, 1990). The 'experimental' population has been monitored since 1987 (Schoech et al. 1991, Mumme 1992, Schoech 1995). I collected data during three years: 1992 (1 March–27 May), 1993 (25 January–5 May), and 1994 (25 January–13 May).

All birds were readily identifiable by a unique combination of aluminum (USF&WS) and colored plastic bands. Group affiliation, within-group relatedness, breeding status, and nest stage were known from previous years or determined by observation. Each group consisted of one breeding pair and from zero to five nonbreeders. I determined sex by: (1) sex-specific vocalization and stereotypic posture during territorial displays (Woolfenden and Fitzpatrick 1984), (2) observation of brood patches or incubation behavior of females (Woolfenden and Fitzpatrick 1984), (3) dominance of females by males, and of same-sex nonbreeders by breeders (Woolfenden and Fitzpatrick 1977), and (4) direct observation of the gonads with unilateral laparotomy (Wingfield and Farner 1976).

Because I observed most breeding pairs building their nests, the exact timing and duration of the nesting process was known. Every two to three days I checked nests to monitor the number of eggs or chicks present. I divided the breeding season into the following nest stages: (1) pre-

nesting, (2) nest building, (3) egg laying (because I collected few data during this period, I combined these data with those from the nest building stage), (4) incubating, and (5) feeding nestlings.

As part of a concurrent study on the reproductive endocrinology of Florida Scrub-Jays I captured birds throughout the breeding seasons of 1992, 1993, and 1994 (see Schoech 1995, Schoech et al. 1996a). The vast majority of birds were captured in Potter traps, however a few were caught in Japanese mist nets. I monitored traps and nets continuously and removed most birds and collected a blood sample within one minute. As a routine part of the process, I weighed all individuals to the nearest 0.1 gram. Because body condition i.e., fat stores, is often positively correlated with body mass, comparisons of the seasonal profiles of breeders and non-breeders provide insight into whether the nutritional plane is correlated with breeding status.

FOOD SUPPLEMENTATION

To determine the effect of food abundance on body condition, clutch initiation date, and clutch size, I provided supplemental food (dried dog food, peanuts, and mealworms) twice daily to 10 breeding groups (10 breeding pairs with 23 non-breeders) in 1993. The supplemented groups were compared with 32 control (unsupplemented) groups (32 breeding pairs with 23 nonbreeders). Although some control groups had no nonbreeders this is considered unimportant for purposes of this study. Supplementation began in late January and was continued until the supplemented breeding female had finished laying. I minimized the exploitation of this resource by neighboring groups by placing one feeding station per group in the middle of the supplemented group's territory. Although there is some tolerance of non-breeders, neighboring jays are generally vigorously excluded from one another's territories (Woolfenden and Fitzpatrick 1984, pers. observ.). Group members readily learned the location of the feeding station and if not waiting upon my arrival, rapidly responded to my whistle. Although I did not quantify food consumption of the individuals within a territory, I noted that all treatment individuals used the supplemental food and after delivering the food I made certain that all group members had arrived before I departed. To minimize the possibility that any group members could be excluded from

sharing the supplemental food, I supplied food in excess. Additionally, I frequently observed several group members on a feeding station at the same time.

TOTAL BODY ELECTRICAL CONDUCTIVITY

Total body electrical conductivity (TOBEC) allows estimation of a live animal's lean mass in the field or laboratory (Walsberg 1988, Kenagy and Barnes 1988, Roby 1991). The total body lipid mass of a bird can be computed by subtracting the estimated lean mass from its total live mass (Walsberg 1988, Castro et al. 1990, Roby 1991, Scott et al. 1991). Despite recent papers questioning the accuracy and precision of TOBEC for estimating lipid content (Morton et al. 1991, Asch and Roby 1995), when calibrated for a species the technique is useful for within-species comparisons of relative amounts of body lipids. During 1993 and 1994, I used a Dickey-john (DjME100) Ground Meat Tester to determine the lean body mass of 187 Florida Scrub-Jays. To assure that all individuals were positioned uniformly within the instrument, subjects were anaesthetized with Metofane (inhaled) and further restrained within a nylon stocking. I verified previous findings that the USF&WS aluminum bands had no effect upon TOBEC measurements (Castro et al. 1990, Roby 1991), by measuring the initial 18 birds captured with and without their aluminum bands. There was no difference (paired *t*-test, $T = 0.763$, $P = 0.456$). Therefore, for the remainder of the study I did not remove the aluminum bands prior to using TOBEC. To minimize potential daily variations in total body lipids, I collected all samples between 07:00 and 12:00 hours.

In brief, the field procedure is as follows: (1) read the calibration number from the instrument, (2) read the data number with the sample chamber empty, (3) read the data number with the bird in the sample chamber, (4) repeat steps 2 and 3 approximately 4 times to obtain an average value, and (5) read the calibration number again. Lean body mass (live mass - total lipid content) is closely correlated with the TOBEC number obtained through the formula: $\text{TOBEC number} = 2(N_1 - N_2) \div (\text{CAL}_1 + \text{CAL}_2)$ where N_1 is the average of the readings taken with the chamber empty, N_2 is the average of the data taken with the bird in the chamber, and CAL_1 and CAL_2 are the two calibration numbers.

Derivation of the regression equation that al-

lows determination of lean body mass by TOBEC requires that on one occasion a number of animals (of the species of interest) be scanned, killed, and directly analyzed for fat content. Because Florida Scrub-Jays are a threatened species, I derived the equation with 17 congeneric Western Scrub-Jays (*A. californica*). After killing and weighing the birds, I dried the whole animal until they reached constant mass (three to four days). I then reweighed, homogenized, and placed each whole dried carcass into an extraction filter of known weight. I extracted lipids from the homogenate with chloroform in a Soxhlet apparatus for 48 hours. I then dried and reweighed the filter and lipid-free carcass and calculated the mass of the total body lipids by subtracting the post-extraction mass from the pre-extraction mass. The lipid percentage of the whole animal (% of live mass) can be calculated by the following: Total body lipid (% of live mass) = $(TBL \div TLM) \times 100$ where TBL is the mass of total body lipids, TLM is the total live mass of the subject immediately prior to determination of the TOBEC number. These methods are described in detail by Kenagy and Barnes (1988), Walsberg (1988), and Roby (1991). TOBEC number was significantly correlated with lean body mass ($r = 0.828$, $F_{1,15} = 32.747$, $P < 0.001$). The regression equation ($y = -218.47 + 4.44x$) was used to estimate lean body mass and subsequently, percent body fat in 187 Florida Scrub-Jays during 1993 and 1994. Additionally, the total body mass of the 17 jays sampled was significantly correlated with their total body lipids ($r = 0.560$, $F_{1,15} = 6.860$, $P = 0.019$).

STATISTICAL ANALYSES

I used multi-factor analysis of variance (ANOVA) to determine whether body mass, total body lipid, and clutch initiation dates varied due to year, sex, breeding status (i.e., breeder or non-breeder) and nest stage. I also used analysis of covariance (ANCOVA) to determine the relationship between year, clutch initiation date, and calendar date. Multiple pairwise comparisons were made with Tukey's post hoc test. In all cases significance was set at the $P \leq 0.05$ level.

To determine whether food-supplemented nonbreeders became breeders more frequently than unsupplemented birds, I used 2×2 contingency tables to derive the Pearson χ^2 statistic. I also use a 2×3 contingency table to test whether the frequency of breeding pairs that bred with-

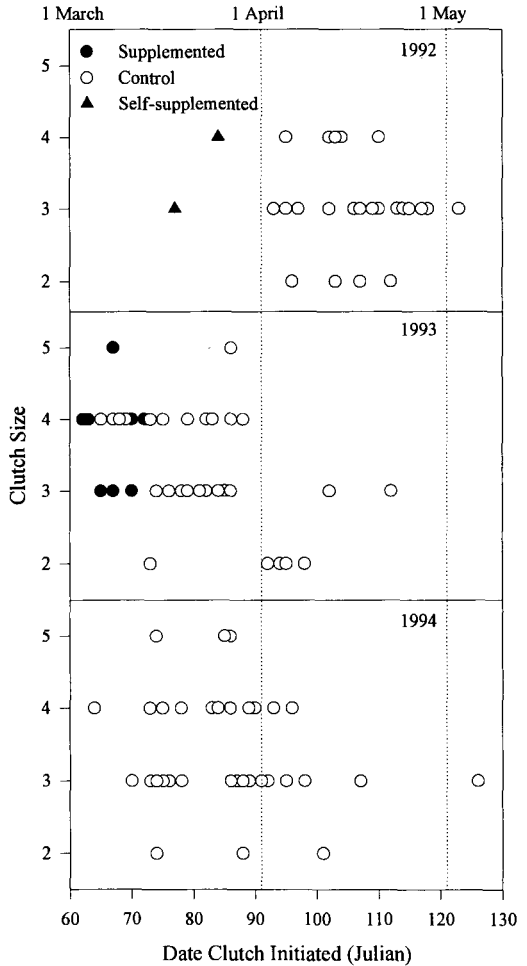


FIGURE 1. The relationship between clutch initiation date and clutch size for each of the three years of the study. Filled circles in 1993 represent clutches laid by females in food supplemented groups. Filled triangles in 1992 represent the self-supplemented groups that obtained food from off-station sources.

in a given year differed between the years of the study.

RESULTS

TIMING OF REPRODUCTION

Even though 1993 was an extremely early breeding season, food supplemented groups advanced laying an average of 16 days when compared with unsupplemented groups. Breeder females in supplemented groups initiated clutches earlier than control females ($t_{40} = -4.483$, $P < 0.001$, see Fig. 1).

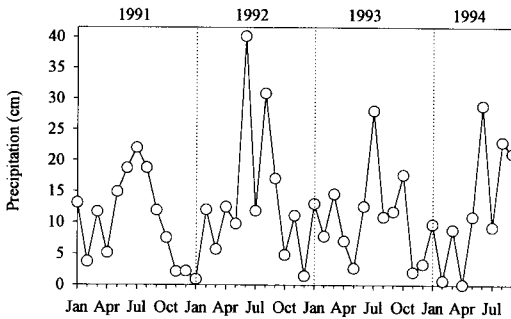


FIGURE 2. Rainfall recorded at Archbold Biological Station from January 1991 through January of 1994. Note the low rainfall during the late fall–early winter of 1991–1992.

In 1992, nesting began later than in any of the 25 years in which the adjacent population of Florida Scrub-Jays has been monitored (Woolfenden and Fitzpatrick, pers. comm.). Clutch initiation in 1992 was also the latest of the three years of my study ($F_{2,96} = 53.967$, $P < 0.001$, I deleted the food-supplemented groups from 1992 and 1993 for this analysis). Post hoc pairwise comparisons confirmed that nesting began later in 1992 than in 1993 or 1994 ($P < 0.001$ for both comparisons).

I examined weather records from the study site to ascertain whether year-to-year variations in rainfall might explain the lateness of the 1992 breeding season (Fig. 2). Woolfenden and Fitzpatrick (1984) noted that rainfall totals during the months preceding a breeding season were correlated with some measures of reproductive success. Because the effects of weather are frequently delayed and may primarily influence subsequent breeding seasons, I limited the years tested to 1991, 1992, and 1993. The three-month period (November–January) that preceded the 1992 breeding season had less rainfall than the same period in the other two years of the study ($F_{2,273} = 3.404$, $P = 0.035$, Fig. 2). Rainfall during this period that immediately precedes the initiation of courtship and breeding may be essential for production of the food resources needed by the jays (see Discussion). However, if the entire year was considered, precipitation did not differ between years ($F_{2,1093} = 0.587$, $P = 0.556$).

The lateness of the 1992 breeding season, as well as my observation that several breeding pairs failed to initiate clutches that year, led me to examine whether the percentages of established

breeding pairs that failed to produce a clutch varied between years. In 1992, a lower percentage of established pairs (83.8%) bred than in 1993 (97.7%) or 1994 (95.6%, Pearson's $\chi^2 = 6.542$, $P = 0.038$).

VARIATION IN CLUTCH SIZE

To determine whether food supplementation had an effect on clutch size, I compared supplemented and unsupplemented groups. If I include the self-supplemented groups from 1992 i.e., the two groups that obtained food from off-station, food supplemented females laid larger clutches than control females during 1992 and 1993 ($T_{71} = 2.44$, $P = 0.017$). However, if I consider only 1993, there was no difference in clutch sizes of supplemented and control females ($T_{40} = 1.544$, $P = 0.131$).

Because clutch size appears to decrease as the breeding season progresses (Fig. 1), I examined this trend further. To control for the potential confounding variables of year and the age of the breeding female (see Discussion), I used multiple regression analysis with Julian date, female age, and year as independent variables and clutch size as the dependent variable. This analysis confirmed that early clutches were larger than those laid later in the breeding season ($F_{3,112} = 6.81$, $P < 0.001$). However, only Julian date ($P < 0.001$) is necessary to predict clutch size. Neither female age ($P = 0.559$) nor year ($P = 0.922$) have predictive value.

FOOD SUPPLEMENTATION: EFFECTS ON NONBREEDERS

If the hypothesis that nonbreeders do not breed because they are food limited is correct, nonbreeders that were provided with supplementary food should be more likely to attempt to breed than unsupplemented nonbreeders. During 1993, five of the 23 supplemented nonbreeders became breeders but four of the 23 control nonbreeders did the same. These frequencies are not different ($\chi^2 = 0.138$, $P = 0.710$). Although not all of these new breeders laid eggs or produced young, all paired, courted, and established a territory (or occupied an already established territory) and defended a territory with an opposite-sexed jay. Because females must obtain adequate food to develop their ovaries and ovarian ducts as well as produce eggs, food limitation would be expected to have a greater affect on them. There-

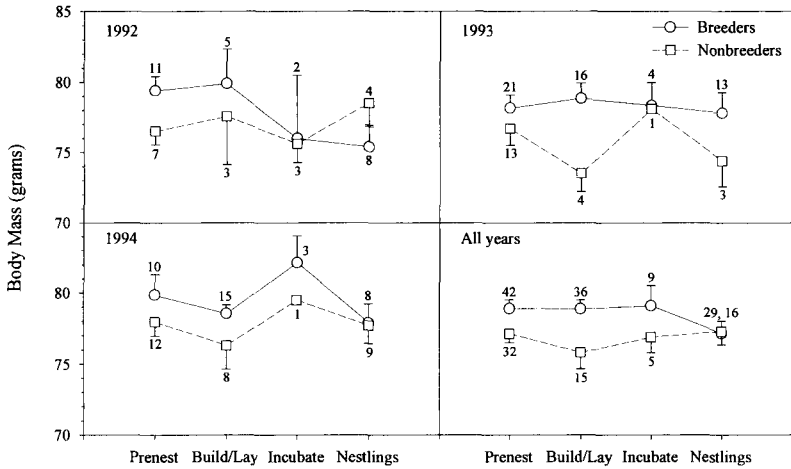


FIGURE 3. Body mass (mean \pm SE) profiles of male breeders and nonbreeders for all three years of the study. Breeders were significantly heavier than nonbreeders but their body masses remained constant throughout the breeding season.

fore, I compared supplemented and unsupplemented females. Although my sample sizes are small, two of the 15 supplemented females changed their breeding status. However, this was not different from the controls, of which one of the 17 became a breeder ($\chi^2 = 0.521, P = 0.471$). Because food supplemented and control nonbreeder Florida Scrub-Jays were equally likely to become breeders, the hypothesis that nonbreeders forgo breeding because they are food limited is not supported.

BODY MASS

All jays combined. I used four-factor ANOVA with year, sex, breeding status, and nest stage as factors to examine variation in body mass (Figs. 3 and 4). At the population level, body mass differed between years ($F_{2,341} = 4.616, P = 0.011$). Jays were heavier during 1994 than in 1993 (Tukey's test; $P = 0.010$). However, mass during 1992 did not differ from 1993 ($P = 0.842$) or 1994 ($P = 0.066$). Males were heavier than females ($F_{1,341} = 41.902, P < 0.001$) and breeders

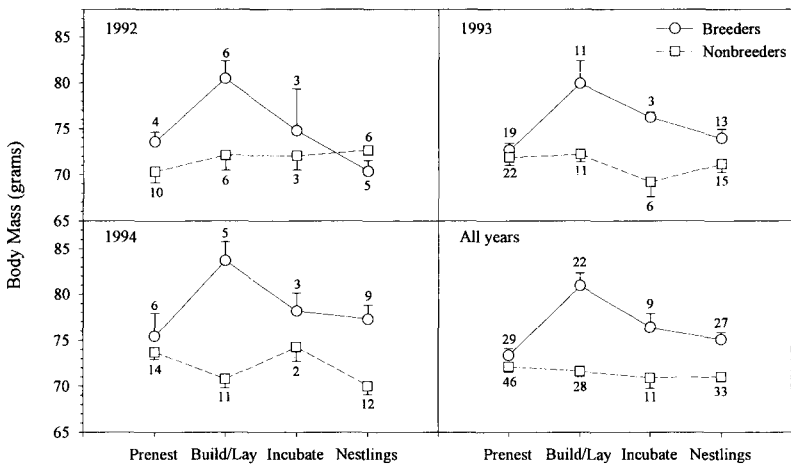


FIGURE 4. Body mass (mean \pm SE) profiles of female breeders and nonbreeders for the three years of the study. Breeders were significantly heavier than nonbreeders and their body masses differed between nest stages.

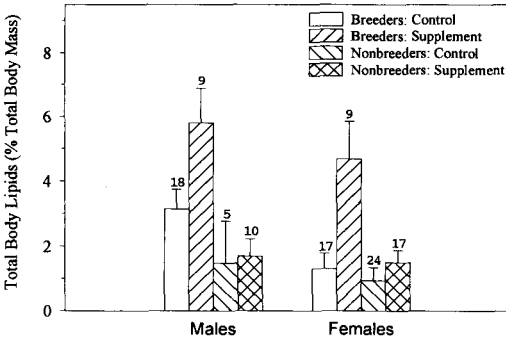


FIGURE 5. Mean values (± SE) of estimated body lipids for supplemented and control birds during 1993. Food supplemented birds had higher percentages of body lipids than controls and breeders were fatter than nonbreeders.

were heavier than nonbreeders ($F_{1,341} = 37.232, P < 0.001$). I found that jays were heavier during the build/lay stage than during care of nestlings (Tukey's test; $P = 0.014$).

Males only. Male breeders were significantly heavier than male nonbreeders ($F_{1,160} = 4.003, P = 0.047$, Fig. 3), but there were no differences in

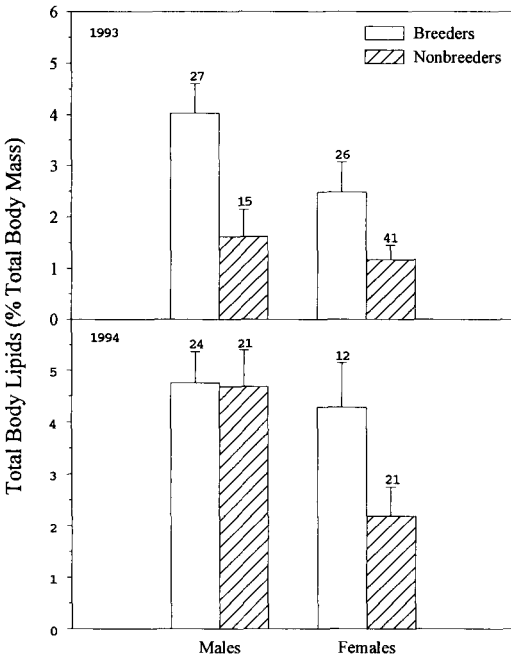


FIGURE 6. Comparisons of estimated body lipids (mean ± SE) between breeders and nonbreeders for 1993 and 1994.

body mass due to year ($F_{2,160} = 1.689, P = 0.188$) or nest stage ($F_{3,160} = 0.743, P = 0.528$).

Females only. Female body mass, in contrast to that of males, differed between years ($F_{2,181} = 3.280, P = 0.040$, Fig. 4). Females were heavier in 1994 than in 1993 (Tukey's test; $P = 0.032$). Additionally, breeders weighed more than nonbreeders ($F_{1,181} = 50.317, P < 0.001$), and body mass differed between nest stages ($F_{3,181} = 7.545, P < 0.001$). Females were heavier during the build/lay stage than during prenesting or while feeding nestlings (Tukey's test; $P < 0.001$ for both comparisons).

BODY CONDITION

To determine whether food supplementation increased total body lipids, I used three-factor ANOVA with sex, breeding status, and treatment (food supplemented or control) as factors (Fig. 5). Food supplemented birds had greater lipid levels than controls ($F_{1,101} = 11.800, P = 0.001$), and breeders had higher lipid levels than nonbreeders ($F_{1,101} = 22.200, P < 0.001$). However, body condition did not differ between males and females ($F_{1,101} = 3.446, P = 0.066$).

Overall, the jays had a higher percentage of body lipids in 1994 than in 1993 ($F_{1,179} = 15.539, P < 0.001$). Similarly, males had a higher percentage of body lipid than females ($F_{1,179} = 8.772, P = 0.003$) and breeders had higher levels than nonbreeders ($F_{1,179} = 12.356, P = 0.001$, Fig. 6).

DISCUSSION

The pronounced effect of supplemental food upon the timing of clutch initiation in Florida Scrub-Jays supports Perrins' (1965, 1970) hypothesis that the nutritive requirements of the breeding female can affect clutch initiation dates. However, these data do not refute Lack's (1950, 1968) hypothesis (see Introduction). The effect of experimental feeding is evident during the 1993 breeding season when all 10 supplemented groups began breeding exceptionally early and within 11 days of one another. The small variance in laying date demonstrates the importance of food at this period in the breeding cycle. Laying date in supplemented groups was advanced even though 1993 was the earliest breeding season on record during the 25 years that the adjacent population at Archbold Biological Station has been under study (Woelfenden, pers. comm.). Additional support for the effect of food upon breeding comes from an ongoing study of Florida Scrub-Jays at

two sites in a nearby suburban development (Placid Lakes, Florida) 7 and 12 km northwest of my study site. In each of the three years of my study, the nearby suburban jays began nesting one to two weeks earlier and, the nesting season persisted one to two weeks longer than the jays at my site at Archbold Biological Station. Additionally, in 1995 the suburban population began nesting almost one month before the Archbold jays. At the suburban sites supplemental food is readily available from bird feeders, dog and cat bowls, and by people feeding peanuts to the relatively tame jays (R. Bowman, pers. comm.).

Further evidence of the importance of food and its effect upon the nutritional plane of a female can be inferred from the body mass and lipid data. On average, female breeders increased their body mass $10.13 \pm 0.46\%$ (7.49 ± 0.41 g, mean \pm SE) between prenesting and the build/lay stage (Fig. 4). Additionally, in the year that I manipulated food, supplemented female breeders weighed more ($t = -3.283$, $P = 0.003$) and had higher lipid levels than control female breeders (Fig. 5). The body mass profiles during this transitional period are very consistent from year-to-year and this marked increase likely reflects gains in reproductive somatic tissue, ovarian follicle, and subsequent egg synthesis. Clearly, sufficient food is required to 'fuel' the growth (Daan et al. 1986, Masman et al. 1988, Meijer et al. 1988).

The evidence from the experimentally and opportunistically self-supplemented birds that increased food resources advance laying dates led me to hypothesize that food availability might also explain the observed between-year differences in the timing of clutch initiation. I was especially interested in factors that might explain the extreme lateness of the 1992 breeding season (see Fig. 1). There is considerable information that environmental fluctuations such as rainfall, temperature, food abundance experienced by an organism can influence when it breeds (Wingfield 1980, 1983, Wingfield and Kenagy 1991, Hahn et al. 1995). Wingfield and Kenagy (1991) classify the numerous environmental factors that a cyclic breeder might use to time its reproductive activities as "initial predictive" (i.e., long-term cues such as day length) or "supplementary" information (i.e., short-term cues such as local conditions). They postulate that species that breed at low latitudes experience favorable conditions

for a relatively long period and as a result are likely to use supplementary information to delay or accelerate their reproductive effort as local conditions dictate (see also Wingfield et al. 1992, Wingfield et al. 1993).

Could environmental factors explain the inter-year variation in the timing of breeding of the subtropical dwelling Florida Scrub-Jay? The unusually low rainfall during the late fall and early winter of 1991–1992 (November–January) may be indirectly responsible for the lateness of the subsequent breeding season of 1992 (see Figs. 1 and 2). Abundant evidence has shown that rainfall affects food resources and that the timing of precipitation can be critical for growth, reproduction, and survival of plants and animals (Pianka 1988, Wingfield and Kenagy 1991). In 1992, the low rainfall preceding the breeding season may have slowed or delayed the emergence of insects and subsequently, the small vertebrates that prey upon them. The lack of sufficient insect and vertebrate prey when the omnivorous jays begin to regrow their gonads and initiate pre-breeding courtship behaviors may have caused females to be unable to meet their nutritive requirements to begin breeding. My observations of the two early-breeding groups that obtained food from off-station support the hypothesis that food limitation caused the delayed season of 1992.

In addition to having profound effects on the decision of when to breed, the quantity of food and its effects upon the body condition of a bird can also affect the decision of whether or not to breed. It is intuitively clear that if a factor (e.g., rainfall, temperature, social conditions) that caused an individual to delay breeding continues for the duration of the breeding season, the individual might forgo breeding that year. Evidence that this is the case comes from Galapagos Finches (*Geospiza* spp.) and cooperatively breeding White-browed Sparrow Weavers (*Plocepasser mahali*), which forgo breeding during periods of drought (Grant and Grant 1980, Curry and Grant 1991, Wingfield, unpubl. data). The factor, assumedly lack of food due to low precipitation, that probably caused the generally late breeding in 1992, may also have been responsible for the relatively low percentage of established breeding pairs (84%) that 'chose' to breed that year. In contrast, virtually all breeders built nests and initiated clutches in the other two years of the study (98% in 1993 and 96% in 1994).

The role of food availability and body con-

dition in the 'decision' by Florida Scrub-Jay nonbreeding helpers to forgo breeding remains less clear. Food supplemented nonbreeders did not become breeders more frequently than control nonbreeders, although nonbreeders of both sexes had lower body masses and lipids than breeders (see Figs. 3–6). Even though female breeders outweighed nonbreeders, their masses were equivalent during the prenesting period (Fig. 4). This suggests that nonbreeders foraged as efficiently as breeders throughout the winter months. Does the rapid increase in the body mass of breeders following the prenesting period, while nonbreeders' mass remained unchanged reflect a superior foraging ability? It is conceivable that the types of food that were available changed, and as a result, a difference in the foraging abilities of breeders and nonbreeders became evident. A more likely alternate explanation is that nonbreeding females are physiologically able to gain weight but in the absence of intra-pair stimulation and courtship feeding from a mate, the physiological 'machinery' is not activated (Schoech 1995). This might also explain the differences in body lipid of breeders and nonbreeders (Fig. 5).

Schoech et al. (1996b) found that nonbreeders have activated ovaries (i.e., their ovaries are not regressed as they are in winter); however they have smaller ovarian follicles than breeders. They suggest that nonbreeder females are reproductively competent, but because they lack the opportunity in terms of a territory and stimulation from a male they fail to fully express breeding behaviors and physiology (for discussion of the effects of habitat-constraint on cooperative breeders see Selander 1964, Brown 1969, and Emlen 1982). Unfortunately, I have no body mass data from females that changed breeding status from nonbreeder to breeder. However, five of the nine nonbreeders that became breeders in 1993 and 1994 produced clutches. All laid three-egg clutches and these new breeder females probably underwent body mass changes similar to that seen for all other breeders (see above, Fig. 4).

My findings suggest that the within- and between-year variation in the timing of reproduction in the Florida Scrub-Jay are attributable to variable food availability and its effects upon breeding females' nutritional plane. Breeders provided with supplemental food initiated clutches earlier, laid larger clutches (if the 1992 birds are included), and were in better condition

than controls. These findings support the hypothesis that the energy requirements of a breeding female affect the annual timing of avian reproduction (Perrins 1965, 1970). At the same time, if the assumption that food supplies dwindle as the season advances are valid, my finding of a reduction in clutch size as the season progresses indirectly supports Lack's (1950, 1968) hypothesis. If future conditions when nestlings are present are important and it is less likely that nestlings hatched later in the season will survive, there will be selection to commence breeding as early as possible and to reduce clutch size later in the season (Perrins 1965, Daan et al. 1986, Svensson 1995). In the face of a dwindling food supply or an increase in nest predators, it makes biological sense to reduce the number of mouths to feed.

The data on nonbreeders do not support the contention that nonbreeders forgo breeding because they are food constrained (Orians et al. 1977). If a lack of food was the sole factor causing nonbreeders to remain reproductively quiescent, then food supplemented nonbreeders might be expected to attempt to become breeders or be more likely to become a breeder when a territory had a vacancy. However, supplemented nonbreeders did not become breeders more frequently than controls. Neither do the body mass data (see above) support the hypothesis that nonbreeders' inefficiency as foragers results in their remaining reproductively inactive (Brown 1985). Although nonbreeders are characterized by relatively low body mass and body lipids, this is probably not the reason they are nonbreeders. Rather, I suggest that they have low body mass because they are nonbreeders. Given the opportunity, a nonbreeder will readily become breeder.

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