

VARIATION IN FORAGING BEHAVIOR, DIET, AND TIME OF BREEDING OF FLORIDA SCRUB-JAYS IN SUBURBAN AND WILDLAND HABITATS

ARTHUR L. FLEISCHER JR.¹, REED BOWMAN² AND GLEN E. WOOLFENDEN
Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33862

Abstract. Supplemental food enables some birds to lay eggs earlier, perhaps by allowing birds to increase their energy intake or allocate energy from other activities to reproduction. We examined the relationships between prelaying behavior, food handling and consumption rates, and the timing of breeding of female Florida Scrub-Jays (*Aphelocoma coerulescens*) in suburban and wildland habitats. Scrub-jays in suburban habitats had access to *ad libitum* human-provided foods; wildland jays did not. During both years of this study, suburban scrub-jays bred earlier than their wildland counterparts. Wildland scrub-jays bred earlier in 1997 than in 1996, but the timing of breeding by suburban scrub-jays did not vary between years. Suburban scrub-jays spent less time foraging and more time perching than wildland jays. They handled more food per hour and per foraging hour, suggesting their foraging was more efficient. Despite this, food consumption rates did not differ between the two habitats. Neither time spent foraging or perching nor food consumption rates significantly influenced variation in time of breeding among individuals. Time of breeding was significantly influenced by site, year, and rate of food handling. Individuals that handled more food items per foraging hour, that is, those individuals that were most efficient, were the earliest breeders in both habitats. These results suggest that foraging efficiency increases with access to human-provided food and that resource predictability may be a perceptual cue for the appropriate timing of breeding.

Key words: *Aphelocoma coerulescens*, behavior, foraging, suburban, supplemental food, timing of breeding.

Variación en el Comportamiento de Forrajeo, la Dieta y la Época de Reproducción de *Aphelocoma coerulescens* en Ambientes Suburbanos y Silvestres

Resumen. El alimento suplementario le permite a algunas aves poner huevos más temprano, quizás aumentando su ingestión de energía o permitiendo cambiar la asignación de energía de otras actividades a la reproducción. En este estudio examinamos las relaciones entre el comportamiento pre-postura, la manipulación de alimento y la tasa de consumo con la época de reproducción de hembras de la especie *Aphelocoma coerulescens* en ambientes suburbanos y silvestres. Las aves en ambientes suburbanos tenían acceso a alimento provisto *ad libitum* por humanos, mientras que las aves de las áreas silvestres no. Durante los dos años de estudio, las aves suburbanas se reprodujeron más temprano que las de las áreas silvestres. Las aves de áreas silvestres se reprodujeron más temprano en 1997 que en 1996, pero la época reproductiva de las aves de áreas suburbanas no varió entre años. Las aves suburbanas pasaron menos tiempo forrajeando y más tiempo perchadas que las de áreas silvestres, y además manipularon más alimento por hora y por hora de forrajeo, lo que sugiere que forrajearon más eficientemente. Sin embargo, las tasas de consumo de alimento no difirieron entre los dos ambientes. La variación entre individuos en el momento de la reproducción no fue influenciada significativamente por el tiempo invertido en forrajeo o descanso ni por la tasa de consumo de alimento, pero sí por el sitio, el año y la tasa de manipulación de alimento. Los individuos que manipularon más ítems alimenticios por sesión de forrajeo (los más eficientes), fueron los que se reprodujeron más temprano en ambos ambientes. Estos resultados sugieren que la eficiencia de forrajeo aumenta con el acceso a alimentos provistos por humanos y que la predecibilidad de los recursos podría ser percibida como una señal indicadora del momento de reproducción adecuado.

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¹ Present address: 49 Greenwood Tr., Apt. 4A, Montpelier, VT 05602.

² Corresponding author. E-mail: rbowman@archbold-station.org

INTRODUCTION

The mechanism by which birds time breeding to coincide with favorable resource levels remains an active area of research. Lack (1954) proposed that birds use environmental cues to time egg-laying so that nestlings are present during seasonal peaks in food availability. However, Perrins (1970) noted a paradox in avian reproductive ecology: although a selective advantage exists for early breeding, most birds do not breed as early as selection would predict. Consequently, Perrins proposed a constraint on Lack's model, that low food availability early in a season may limit the ability of a female to produce eggs.

A variety of cues, such as photoperiod and temperature, initiate endocrine changes that precede reproduction (Wingfield and Farner 1993). However, birds also may depend on local resource availability to time breeding, either as a supplementary cue (Wingfield 1983) or to alleviate a physiological constraint (Perrins 1970). Food-supplementation experiments have frequently been used to assess the influence of food availability on timing of breeding (Boutin 1990). Of 26 studies, 15 have demonstrated significant advances in laying dates by food-supplemented individuals (Daan et al. 1989, Meijer et al. 1990, Winkler and Allen 1996, Meijer and Drent 1999). The variation that exists among these studies could be attributed to differences in the methods used, especially the duration and timing of food supplementation, and to variation in natural food abundance at the time of the experiments (Boutin 1990). However, the mechanisms by which food abundance influences laying date are poorly understood, in part because most studies focus on the average response of the experimental group to supplemental food, effectively ignoring the individual.

If, as Perrins (1970) suggested, additional food alleviates energetic constraints on reproduction, then supplemental food could advance laying by providing energy for reproduction that is not available through local resources. Walsberg (1983) proposed three models by which birds obtain energy for reproduction: increase energy intake, reduce energy allocation to other activities, or use somatic stores. Experimentally supplemented foods are highly predictable in time and space, and thus may require less searching and handling times than natural food

sources. Because foraging behavior often depends on the distribution of food in time and space (King 1974), supplemental food may enable birds to increase their food intake rate or spend less time in energy-intensive behaviors, such as foraging. Either strategy could increase the amount of energy that could be allocated to reproduction, and could thereby influence timing of breeding. Few studies have examined the influence of supplemental food on behavior or food intake rates and the subsequent effects these may have on the timing of breeding of birds (Davies and Lundberg 1985).

We studied two populations of Florida Scrub-Jays (*Aphelocoma coerulescens*) that exhibit differences in timing of breeding. We recorded the behavioral time budgets and rates of food intake of prelaying female Florida Scrub-Jays. One population occurred in a wildland scrub preserve, the other in scrub patches within a suburban residential matrix that offered *ad libitum* sources of human-provided foods. Suburban scrub-jays consistently initiate clutches earlier than wildland scrub-jays (Bowman et al. 1998); however, females in the two populations show few differences in body condition just prior to breeding (Schoech and Bowman 2001). This suggests that the difference in timing of breeding between the two populations is not related to differences in somatic stores, but to differences in the rate of food intake or the time spent foraging, either of which could influence the net rate of energy gain. Food-supplemented females in the suburbs could increase food intake, thereby obtaining more energy to allocate to reproduction. A prediction of this hypothesis is that food intake rate should influence laying date between sites and among individuals. Food-supplemented females also could decrease foraging time, thereby enabling them to allocate more energy to reproduction. A prediction of this hypothesis is that the proportion of time spent foraging should influence laying date. These two hypotheses are not mutually exclusive; if supplemental food is abundant enough to increase foraging efficiency (i.e., the amount of intake per time spent foraging), birds could both reduce foraging time and increase intake rates.

METHODS

STUDY AREAS

We conducted our research in Highlands County, Florida, at Archbold Biological Station

(27°10'N, 81°21'W), a natural scrub preserve (wildlands), and at Placid Lakes Estates (27°16'N, 81°24'W), a residential, suburban development (suburbs) less than 8 km north of the wildland site. Ongoing, long-term demographic studies have been conducted on color-marked populations of Florida Scrub-Jays at both sites (Woolfenden and Fitzpatrick 1984, 1996, Bowman et al. 1998, Bowman and Woolfenden 2001). Wildland scrub-jays may vary their timing of breeding between years from early March to mid-April (Woolfenden and Fitzpatrick 1984, 1996), presumably in response to between-year fluctuations in food supply. However, scrub-jays can be induced to lay earlier when provided with supplemental food (Schoech 1996). Human-provided food is available only in the suburbs (Shawkey 2001). Wildland scrub-jays occasionally receive peanut bits by researchers and visitors, but we consider the amounts they receive inconsequential to their energy budget (Woolfenden and Fitzpatrick 1996).

SCRUB-JAY OBSERVATIONS

In 1996 and 1997, we observed breeder female scrub-jays from mid-January until nest building and egg laying began in March. We observed all birds between 07:00 and 11:30 EST. We selected these times because during the prebreeding period jay foraging activity peaks and then declines during this interval (DeGange 1976). Females that participated in courtship activities with a breeder male were considered breeders, but most had bred during a previous year. We observed different females in each year of the study.

We recorded behavior of focal females using a combination of instantaneous sampling and one-zero sampling (Altmann 1974). Each 20-min observation period was divided into 15-sec sample units. The behavior occurring at the end of each 15-sec period was recorded as an instantaneous sample. We recorded foraging, perching, territory defense, interspecific interactions, nest building, and unknown activity as instantaneous behaviors. Flight, which often occurred during a 15-sec period, but not at the instantaneous sample, was recorded as having occurred (1) or not (0) during a sample period.

DeGange (1976) described the activities of the Florida Scrub-Jay. We followed his definitions with slight modification. We recorded foraging, perching, nest building, and territory de-

fense as defined by DeGange; however, we did not consider flight as mutually exclusive from other behaviors. For example, if a jay flew to a territorial dispute, we recorded territory defense for each instantaneous sample and flight during the intervals between each 15-sec sample. We added interspecific interactions, which included chases and aggressive encounters with other bird species and mobbing terrestrial predators (Francis et al. 1989).

Only females under observation for 15 min or more of the 20-min sampling period were included in the analysis. For each female we divided the number of observations in which a behavior occurred by the total number of observations and standardized each as the proportion of time spent in each behavior. We recorded each interval during which flight occurred and calculated the percentage of intervals between sample points spent in flight.

We recorded all food items handled by the jays. Jays regularly handled natural foods (arthropods, acorns, and small vertebrates) and human-provided foods (cracked corn, birdseed, bread, pet foods, and shelled and unshelled peanuts). In most cases, we recorded each item handled by a jay with its bill as one item handled. However, when jays handled peanuts in the shell, which usually contained two peanut seeds, we considered it as two items handled. When the jays took birdseed at a feeder, we scored each visit as one item of birdseed handled, even though individuals took many small seeds. We estimated the mass of each "item" of birdseed handled as 1 g. We attempted to record whether each food item was consumed or cached. The total number of items consumed by a female included those provided by her mate. We standardized the food handling and consumption data as the number of items handled hr^{-1} or consumed hr^{-1} .

To control for differences in the amount of time spent foraging, we also present the food data as items handled and items consumed per foraging hr. Using handling and consumption rates per foraging hr controls for any differences in time budget between sites and may indicate potential differences in foraging efficiency between sites. For these foraging efficiency comparisons we excluded courtship feedings to minimize any bias in the frequency of feeding by males.

ESTIMATES OF ENERGY EXPENDITURE AND INTAKE

Organisms require time and energy for maintenance and reproduction (King 1974). Without knowing an individual's allocation of time, estimates of energy budgets lack behavioral context. Each behavior and each food item has a different energy value. Using the behavioral data we converted time budgets to estimates of energy expenditure (kJ hr^{-1}). Using the diet data we converted food consumption rates to estimates of energy intake (kJ hr^{-1}).

We combined the time budget data and foraging data from 1996 and 1997 to estimate the energy budget of females at each site. To estimate energy expenditures, we used values from Goldstein (1988) to calculate an average activity cost for each behavior, measured as a multiple above basal metabolic rate (BMR). We used the allometric equation of Lasiewski and Dawson (1967) to estimate BMR for a 75.0-g bird. For each behavior, we multiplied $\text{BMR} (\text{kJ hr}^{-1}) \times \text{activity cost} \times \% \text{ time}$. The jays at both sites flew at similar rates; thus we used DeGange's (1976) estimate of 1% of the total time budget to calculate the energy expense of flight. We calculated the activity cost when jays were out of sight as the average between foraging and perching.

To estimate energy intake, we estimated the total energy values (kJ) for most foods consumed by the jays. We calculated the average mass of food items consumed by the jays and then multiplied the estimated metabolizable energy value of a food item by the number consumed hr^{-1} to estimate energy intake hr^{-1} . Abrahamson and Abrahamson (1989) present data on the energy content (J g^{-1} edible fruit) of acorns found on the Lake Wales Ridge of Florida. We could not identify to species acorns consumed by jays, so we averaged the energy values reported for three oak species common at both sites, scrub oak (*Quercus inopina*), sand live oak (*Q. geminata*), and Chapman's oak (*Q. chapmanii*), to represent the energetic contribution of an acorn. Altman and Dittmer (1968) report energy values for raw peanuts. Orthopterans and lepidopteran larvae are the commonly consumed animal prey of scrub-jays (Stallcup and Woolfenden 1978). We used values reported by Bell (1990) to estimate the energy value of arthropods. We estimated the energy value of miscellaneous human-provided foods by averaging the

values, per gram, of millet, cracked corn, and white bread. Because all energy available in foods may not be assimilated, we used the following sources to estimate metabolizable energy: acorns (Koenig 1991), peanuts (Karasov 1990), and arthropods (Bell 1990).

STATISTICAL ANALYSIS

The sampling unit used in analyses was the individual female because sequential observations of each female were not independent. Values reported in the results are means \pm SE of all observations per female, unless otherwise noted. We used two-way ANOVA to test the effects of site and year on the percent of time spent in each behavior. We arcsine or square-root transformed all proportional data. We used Tukey's multiple comparison procedure to test all significant ANOVAs and Dunn's procedure to test all significant Kruskal-Wallis ANOVAs. We used a forward stepwise linear regression model to test the influence of behavior and food-handling and consumption rates on the dates of clutch initiation. We used only those variables in the regressions that differed between sites in the univariate ANOVAs. We tested for differences in the relationship between food handling rates and breeding date among females between sites using ANCOVA with date of clutch initiation as the dependent variable, site as the independent variable, and the rate of food handling hr^{-1} as the covariate (SPSS Inc. 1999).

RESULTS

CLUTCH INITIATION

In total, we observed 31 wildland and 50 suburban scrub-jays; of these, 28 wildland and 46 suburban females laid eggs. Suburban females initiated first clutches significantly earlier than wildland females ($F_{1,70} = 33.4, P < 0.001$), and this was true in both years (Fig. 1). Females initiated clutches significantly earlier in 1997 than 1996 ($F_{1,70} = 9.9, P < 0.01$); however, we detected no interaction between site and year ($F_{1,70} = 2.4, P = 0.13$). The mean date of clutch initiation for suburban females was 13 March in 1996 and 11 March in 1997, with the earliest clutch starting on 28 February in both years. The mean dates of clutch initiation for wildland females was 2 April in 1996 and 21 March in 1997, with the earliest clutch starting on 22 March in 1996 and 8 March in 1997.

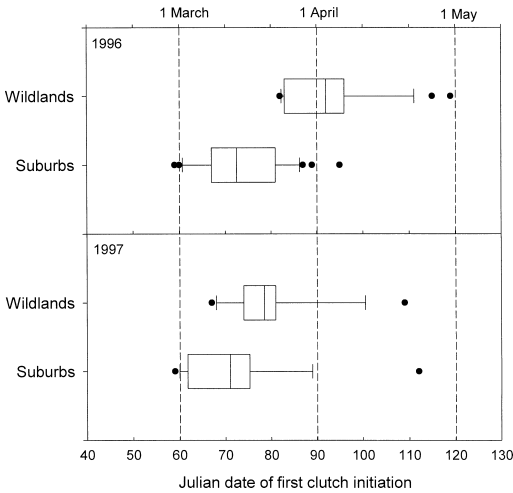


FIGURE 1. Timing of first clutches of focal Florida Scrub-Jays in wildlands and suburbs. Vertical lines within the boxes represent the mean laying date. The boxes represent the time during which the middle 50% of the population initiated laying. Error bars represent the timing of laying for 10% and 90% of the populations. Filled circles represent outliers.

TIME BUDGETS

We used the 232 focal observations that lasted at least 15 min in our analyses. We collected 160 focal observations in 1996 (48 on 19 wildland

jays; 112 on 34 suburban jays) and 72 focal observations in 1997 (27 on 12 wildland jays; 45 on 16 suburban jays). At both sites during both years, perching, foraging, and territory defense together accounted for nearly 95% of the females' time budgets. Overall, time budgets of females differed significantly between wildland and suburban sites ($\chi^2_1 = 345.3, P < 0.001$).

Overall, females spent about 60% of their time perching, with suburban females spending 11% more time perching than wildland females ($F_{1,77} = 14.2, P < 0.001$). Overall, females spent more time perching in 1996 than 1997 ($F_{1,77} = 11.1, P < 0.001$; Fig. 2a). The interaction between site and year was significant ($F_{1,77} = 6.5, P < 0.05$). Wildland females spent significantly less time perching in 1997 (41%) than in 1996 (61%; Tukey's test, $P < 0.05$), but suburban females spent similar time perching in both years (65%, 1996; 63%, 1997).

Overall, females spent less than 40% of their time foraging, with suburban females spending 12% less time foraging than wildland females ($F_{1,77} = 16.0, P < 0.001$). Overall, females spent more time foraging in 1997 than 1996 ($F_{1,77} = 12.1, P < 0.001$; Fig. 2b). The interaction between site and year was not significant ($F_{1,77} = 3.5, P = 0.07$), but the proportion of time spent

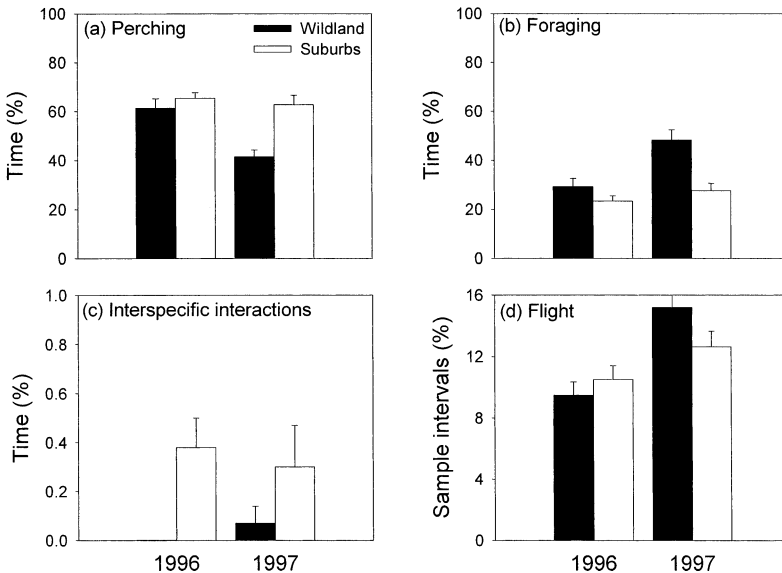


FIGURE 2. Activity budgets of prelaying female Florida Scrub-Jays in wildlands and suburbs. Instantaneous behaviors are (a) perching, (b) foraging, and (c) interspecific interactions. Flight (d) is measured as the percentage of 15-sec intervals in which flight occurred between behavioral samples. Sample size (in females), wildlands: 1996, $n = 19$; 1997, $n = 12$; suburbs: 1996, $n = 34$; 1997, $n = 16$. Note differences in y-axis scales.

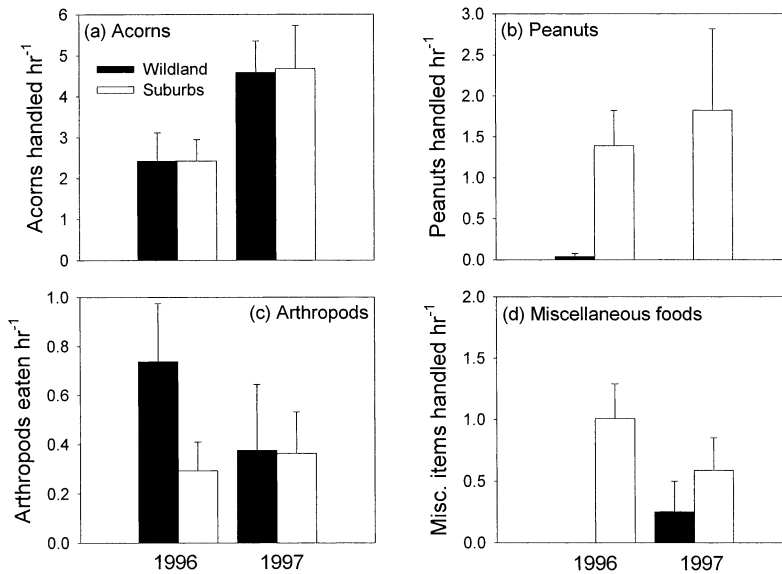


FIGURE 3. Mean \pm SE number of food items handled hr^{-1} by prelaying female Florida Scrub-Jays in wildlands and suburbs. Items handled are (a) acorns, (b) peanuts, (c) arthropods, and (d) miscellaneous foods. "Miscellaneous foods" combines vertebrates that jays caught as well as birdseed, bread, and cracked corn provided by humans. Sample size (in females), wildlands: 1996, $n = 19$; 1997, $n = 12$; suburbs: 1996, $n = 33$; 1997, $n = 16$. Note differences in y-axis scales.

foraging by suburban females varied less between years (23%, 1996; 27%, 1997) than by wildland females (29%, 1996; 48%, 1997).

The time spent in all other behaviors did not differ significantly between sites or years, with the exception of time spent in interspecific interactions ($F_{1,77} = 8.0$, $P < 0.05$; Fig. 2c). Females in the suburbs spent significantly more time in interspecific interactions than did females in wildlands, but at both sites these interactions accounted for less than 0.5% of their time. Interspecific interactions at both sites involved predominantly birds, of which interactions with Blue Jays (*Cyanocitta cristata*) and Northern Mockingbirds (*Mimus polyglottos*) were most frequent.

Overall, females flew during 11% of the sampling intervals (Fig. 2d). Frequency of flying did not differ between sites ($F_{1,77} = 0.5$, $P = 0.50$), but did vary between years ($F_{1,77} = 12.5$, $P < 0.001$). In 1997, females flew during 13% of the sampling intervals, compared to only 10% in 1996. The interaction between site and year was not significant ($F_{1,77} = 2.6$, $P = 0.11$).

FOOD HANDLING AND CONSUMPTION RATES

Food handling. Females at both sites handled acorns at similar rates ($F_{1,76} < 0.1$, $P = 0.95$).

Females at both sites handled significantly more acorns in 1997 than 1996 ($F_{1,76} = 8.3$, $P < 0.01$). The interaction between site and year was not significant (Fig. 3a).

We observed only one wildland female handle peanuts, on only one occasion. Suburban females handled about 1.5 peanuts hr^{-1} ($F_{1,76} = 7.9$, $P < 0.01$). Peanut handling rate did not differ between years ($F_{1,76} < 0.1$, $P = 0.71$), nor did an interaction exist between site and year (Fig. 3b).

The number of acorns and peanuts, combined, handled hr^{-1} did not differ between sites ($F_{1,76} = 2.4$, $P = 0.13$). Females handled more acorns and peanuts, combined, in 1997 than 1996 ($F_{1,76} = 9.3$, $P < 0.05$), but the interaction between site and year was not significant ($F_{1,76} < 0.1$, $P = 0.94$).

Jays consumed all the arthropods they handled. Therefore we report only the number consumed hr^{-1} . This number did not differ between sites ($F_{1,76} = 1.4$, $P = 0.24$) or years ($F_{1,76} = 0.6$, $P = 0.45$), nor did an interaction exist between site and year (Fig. 3c).

We observed only one female at each site handling vertebrates. One female in the wildlands handled two hylid treefrogs, and one fe-

TABLE 1. Mean number of food items consumed hr^{-1} by prelaying female Florida Scrub-Jays in wildlands and suburbs, 1996–1997. We placed many human-provided foods such as birdseed, bread, and cracked corn into a “miscellaneous” category, along with rare natural food items such as berries and nuts. Sample sizes: 31 wildland birds and 49 suburban birds.

Items consumed	Wildlands	Suburbs	$F_{1,76}$	P
Acorn	1.66 ± 0.28	0.96 ± 0.16	4.1	0.05
Peanut	0.02 ± 0.02	0.22 ± 0.06	5.1	0.03
Arthropod	0.60 ± 0.18	0.32 ± 0.09	1.4	0.24
Vertebrate	0.05 ± 0.05	0.01 ± 0.01		
Miscellaneous	0	0.44 ± 0.13		
Courtship feeding ^a	0.32 ± 0.21	1.09 ± 0.17	7.0	0.01
Total	2.64 ± 0.31	3.04 ± 0.25	0.9	0.34

^a Number of courtship feedings hr^{-1} . We assumed that each courtship feeding consisted of only one food item.

male in the suburbs handled one brown anole (*Anolis sagrei*).

In 1996, we did not observe any wildland females handling miscellaneous food items. In suburbs, miscellaneous foods amounted to 15% of the total items handled. These included only two native foods, greenbrier berries (*Smilax auriculata*; $n = 2$) and scrub hickory nuts (*Carya floridana*; $n = 4$), but many human-provided foods: cracked corn ($n = 25$), birdseed ($n = 11$), pieces of bread ($n = 10$), and pet food ($n = 3$). The number of these food items handled hr^{-1} differed significantly between sites ($F_{1,76} = 8.2$, $P < 0.01$), but not years ($F_{1,76} = 0.5$, $P = 0.46$), and no interaction existed between site and year (Fig. 3d).

For all foods, suburban females handled significantly more items hr^{-1} than wildland females ($F_{1,76} = 3.9$, $P < 0.05$), the bulk of which were human-provided foods. Females handled more items in 1997 than 1996 ($F_{1,76} = 7.2$, $P < 0.01$), largely because acorn handling at both sites was more frequent in 1997. No interaction between site and year was detected ($F_{1,76} < 0.1$, $P = 0.82$).

Food consumption. Wildland females consumed significantly more acorns and fewer peanuts hr^{-1} than suburban females (Table 1). Wildland females handled 3.3 acorns hr^{-1} and consumed 1.7 acorns hr^{-1} , indicating that half were cached or discarded. Suburban females handled 1.5 peanuts hr^{-1} , but consumed only 0.2 peanuts hr^{-1} , indicating that most peanuts were cached or discarded. However, no difference existed in the number of acorns and peanuts combined consumed hr^{-1} between sites ($F_{1,76} = 1.0$, $P = 0.31$) or between years ($F_{1,76} = 3.4$, $P = 0.07$). We did not observe wildland females consuming

miscellaneous food items. Suburban females frequently consumed miscellaneous foods, almost all of which were human provided. The consumption rate of these items did not vary between years ($F_{1,76} = 0.4$, $P = 0.55$).

Suburban females received more feedings from their mate hr^{-1} than wildland females (Table 1). The rate of feedings by mates hr^{-1} did not differ between years ($F_{1,76} = 0.3$, $P = 0.61$) nor did any interaction exist between site and year ($F_{1,76} = 0.4$, $P = 0.55$). Despite the additional consumption of human-provided foods and the additional feedings by mates, we found no difference in the consumption rate of all foods between the two sites (Table 1). The rate of food consumption did not vary between years ($F_{1,76} = 0.1$, $P = 0.72$), nor did any interaction exist between site and year ($F_{1,76} < 0.1$, $P = 0.95$).

Food handling and consumption per foraging hour. Suburban females handled more food items hr^{-1} , but spent less time foraging than wildland females, suggesting that foraging was more efficient in the suburbs. In general, suburban females handled foods, other than arthropods, at higher rates per foraging hr than wildland females. However, these rates were significant only for peanuts ($F_{1,76} = 8.6$, $P < 0.01$) and for miscellaneous food items ($F_{1,76} = 8.4$, $P < 0.01$), which were mostly human provided. Overall, suburban females handled nearly twice the number of food items per foraging hr than did wildland females ($F_{1,76} = 12.8$, $P < 0.001$).

Suburban females consumed more peanuts ($F_{1,76} = 4.2$, $P < 0.05$) and more miscellaneous food items ($F_{1,76} = 4.6$, $P < 0.05$) per foraging hr than wildland females. The ingestion of acorns and arthropods per foraging hr did not

TABLE 2. Estimated energy budget (kJ hr^{-1}) of prelaying female Florida Scrub-Jays in wildlands and suburbs, 1996–1997. Flight was estimated as 1% of the total time budget (see text), but since most territorial interactions consisted of flight, the proportion of time spent in territory defense was reduced by 1% so that time budgets equaled 100%. BMR = Basal metabolic rate (kJ hr^{-1}).

Activity	BMR ^a	Cost ^b	Wildlands		Suburbs	
			% Time	kJ hr^{-1}	% Time	kJ hr^{-1}
Perch	3.5	2	53	3.66	65	4.49
Forage	3.5	5	37	6.38	25	4.31
Territory defense	3.5	6.5	3	0.67	3	0.67
Interspecific interactions	3.5	6.5	<0.1	<0.01	<0.5	<0.1
Nest building	3.5	5	2	0.35	3	0.52
Flight	3.5	11	1	0.38	1	0.38
Out of sight	3.5	3.5	4	0.48	3	0.36
Total energy budget				11.93		10.83

^a From Lasiewski and Dawson 1967.

^b Estimated as a multiple of BMR, from Goldstein 1988.

differ significantly between sites. The total number of food items consumed per foraging hr did not differ significantly between sites ($F_{1,76} = 0.1$, $P = 0.78$).

ENERGY EXPENDITURE AND ENERGY INTAKE

Our behavioral data for both years combined suggested suburban females expended nearly 10% less energy than wildland females (Table 2). Suburban females expended 41% of their energy perching and 40% foraging. In contrast, wildland females expended about 31% of their energy perching and 53% foraging. Based on our time budgets, the total energy expended differed significantly between sites ($F_{1,77} = 11.7$, P

< 0.001) and years ($F_{1,77} = 10.1$, $P < 0.01$). The interaction between site and year was significant ($F_{1,77} = 7.9$, $P < 0.01$); wildland females expended more energy in 1997 than 1996, but energy expended by suburban females did not differ between years (Fig. 4).

The total energy of acorns, peanuts, arthropods, and miscellaneous foods consumed hr^{-1} did not differ between sites ($F_{1,76} = 1.4$, $P = 0.24$; Table 3). At both sites, females derived most of their energy from acorns and little from arthropods. Wildland jays obtained more energy from acorns than suburban jays; suburban jays made up the difference by consuming peanuts and miscellaneous human-provided foods.

The net energy gain (mean energy intake minus the mean energy expended), although not statistically comparable, was slightly higher in the wildland site. The net energy gain of wildland jays was 16.0 kJ hr^{-1} ; the net energy gain of suburban jays was 14.8 kJ hr^{-1} .

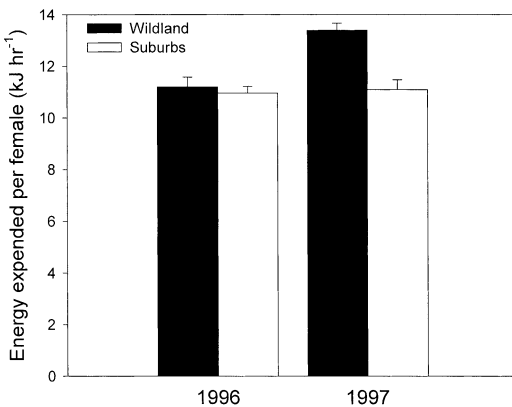


FIGURE 4. Mean \pm SE estimated energy expenditure (kJ hr^{-1}) of prelaying female Florida Scrub-Jays in wildlands and suburbs. Sample size (in females), wildlands: 1996, $n = 19$; 1997, $n = 12$; suburbs: 1996, $n = 34$; 1997, $n = 16$.

INFLUENCE ON INDIVIDUAL VARIATION IN TIMING OF BREEDING

Time spent foraging and time spent perching differed between sites and were inversely related ($r = -0.9$, $P < 0.001$). We tested each separately in the regression model and retained only time perching because it had a greater influence on the overall model. We examined the relationship of site, year, time perching, and food items handled hr^{-1} , on the date of clutch initiation of the focal females that laid eggs. Three variables explained 45% of the variation in laying date (Table 4). Site explained 35% of the variation,

TABLE 3. Estimated energy (kJ) consumed hr⁻¹ by prelaying female Florida Scrub-Jays in wildlands and suburbs, 1996–1997.

Site/Item	Consumption rate ^a (items hr ⁻¹)	Energy (kJ item ⁻¹)	Metabolizable energy ^b (%)	Energy consumed (kJ hr ⁻¹)
Wildlands				
Acorn	1.66	23.05	69	26.4
Peanut	0.02	29.23	82	0.57
Arthropod	0.60	2.20	71	0.94
Total				27.91
Suburbs				
Acorn	0.96	23.05	69	15.27
Peanut	0.22	29.23	82	5.27
Arthropod	0.32	2.20	71	0.5
Miscellaneous	0.44	14.08	74	4.58
Total				25.62

^a Data from Table 1.

^b Acorn data: Koenig 1991; peanut data: average of three studies that used peanuts in Appendix 1 of Karasov 1990; arthropod data: Bell 1990; miscellaneous food data: average of acorn, peanut, and arthropod.

the total number of food items handled hr⁻¹ explained another 6% of the variation, and year explained another 3% of the variation. Neither the rate at which different food items (i.e., acorns, peanuts, arthropods, and miscellaneous food items) were handled hr⁻¹, nor the percent of time perching explained enough variation to enter the model. Females that handled more food hr⁻¹ initiated clutches earlier than females that handled fewer items. The relationship between the rate of food items handled and the date of clutch initiation among females was the same at both sites (ANCOVA $F_{1,69} = 0.12, P = 0.73$).

DISCUSSION

We found that suburban scrub-jays bred earlier and spent less time foraging, but were more ef-

ficient at foraging than were jays in wildland habitats. Despite these differences, their net energy gain was slightly less than that of wildland jays. In wildlands, scrub-jays eat many energy-rich acorns; suburban jays eat many fewer acorns but make up some, but not all of the energy by eating human-provided foods, such as peanuts. Although foraging behavior differed between sites, net energy gain did not appear to explain the difference in timing of breeding between suburban and wildland habitats. However, at both sites birds that handled more food hr⁻¹ tended to breed earliest, suggesting that foraging efficiency itself might be a perceptual cue for breeding.

Supplemental food often advances laying date in birds (Daan et al. 1989, Meijer et al. 1990,

TABLE 4. Results of linear forward stepwise regression to examine the relationship of time perching, food items handled hr⁻¹, site, and year on the date of clutch initiation of Florida Scrub-Jays in wildlands and suburbs, 1996–1997.

Independent variables in model	Coefficient	R ²	Δ	F _{1,69}	P
Site	-0.56	0.35	0.35	37.6	<0.001
Total food items handled hr ⁻¹	-0.20	0.42	0.06	4.3	<0.05
Year	-0.19	0.45	0.03	4.2	<0.05
Variables not in model:					
Acorns handled hr ⁻¹				0.6	0.44
Peanuts handled hr ⁻¹				0.1	0.84
Arthropods handled hr ⁻¹				0.3	0.61
Miscellaneous items handled hr ⁻¹				0.8	0.36
% Time perching				0.1	0.90

Winkler and Allen 1996, Meijer and Drent 1999), including Florida Scrub-Jays (Schoech 1996). In suburban habitats, human-provided foods are predictable resources that birds easily can exploit (Cowie and Hinsley 1988a, 1988b); the effects of such food on laying date are likely to be similar to the effects of experimentally provisioned food. Several studies have found that birds in suburbs breed earlier than their rural counterparts (Cramp 1972, Tatner 1982, Dhondt et al. 1984, Johnson 1994), and this appears to be true for Florida Scrub-Jays (Bowman et al. 1998, this study).

Some birds reduce their daily energetic expenditures during oogenesis by reallocating time spent in various activities rather than by increasing food intake (Ettinger and King 1980, Mugaas and King 1981, Williams and Ternan 1999). Several studies that manipulated food supply and simultaneously measured behavior of birds have observed changes in time budgets (Dunnock [*Prunella modularis*], Davies and Lundberg 1985; Black Redstart [*Phoenicurus ochruros*], Cucco and Malacarne 1997; Rufous Hummingbird [*Selasphorus rufus*], Hixon et al. 1983). Prebreeding female Dunnocks that were food supplemented allocated 26% less time to foraging and 14% more time to perching than control females (Davies and Lundberg 1985). Our results are consistent with these studies; suburban females spent 12% less time foraging and 10% more time perching, than wildland females. They were able to decrease foraging time and yet increase their food handling rates by increasing their foraging efficiency.

Female Dunnocks that spent more time perching laid earlier than females that perched less (Davies and Lundberg 1985). We found no similar correlation. Although suburban scrub-jays spent more time perching and expended less energy, their net energy gain was slightly lower than that of wildland jays. When natural foods are abundant, birds may be able to forage less, but maintain their food intake by becoming more efficient. However, in suburban habitats scrub-jays are able to maintain their intake rate only by feeding on human-provided foods, which may be less energetically valuable than natural foods. Peanuts, which comprised ca. 30% of the human-provided foods consumed by scrub-jays, are energetically similar to acorns, but miscellaneous human-provided foods provide less energy. Jays consuming these foods did

not take in enough energy to maintain the energy they saved by reducing foraging time. These patterns suggest that the timing of breeding in jays was not constrained by energy.

Egg production may not be as costly as previously thought (van Noordwijk et al. 1995, Perrins 1996). In Barn Swallows (*Hirundo rustica*), the period of egg formation is not particularly costly relative to routine energy demands, suggesting that energy should not constrain egg formation in this species (Ward 1996). Other recent studies have found no evidence of energy constraints on the timing of breeding (van Noordwijk et al. 1995, Winkler and Allen 1995, 1996); but if energy does not constrain breeding in scrub-jays, why do jays decrease foraging and increase perching when food availability is higher?

Florida Scrub-Jays have a sentinel system (McGowan and Woolfenden 1989) whereby one member scans the sky from an exposed perch and alerts other group members to the presence of predators. In some birds, a cooperative sentinel system may result from state-dependent, individually selfish patterns of behavior (Wright, Berg, et al. 2001). Vigilance may be a trade-off between foraging efficiency and predation risk (Bednekoff 1997). Suburban jays spent most of the increased perching time as sentinels; even wildland jays provided with just a few peanuts reduce foraging time and increase vigilance (Bednekoff and Woolfenden, unpubl. data). Arabian Babblers (*Turdoides squamiceps*) provided with supplemental food increase sentinel effort (Wright et al. 2001). Because suburban scrub-jays forage more efficiently than wildland jays, they can shift time from foraging to vigilance and still maintain their food consumption rates. Even though human-provided foods may not be the energy equivalent of natural foods, jays may be able to decrease their risk of predation without incurring an energy cost; thus the differences we observed in behavior between suburban and wildland scrub-jays may have been driven more by predation risk than by an energy optimization strategy for reproduction.

Our results suggest food may be linked to the timing of breeding through a perceptual cue rather than through a release from energy constraints. At both sites, jays that foraged most efficiently bred the earliest. Food availability and foraging success may cue birds' breeding decisions. Great Tits (*Parus major*) appear to use

foraging success early in the season to time breeding to coincide with the emergence of caterpillars (Perrins 1991, van Noordwijk et al. 1995, Seki and Takano 1998). Various measures of foraging success also appear to influence timing of breeding in other species, including White-winged Crossbills (*Loxia leucoptera*), and Red Crossbills (*L. curvirostra*, Benkman 1990), and Tree Swallows (*Tachycineta bicolor*, Winkler and Allen 1996). We suggest that Florida Scrub-Jays also use foraging success or efficiency, in part, to time breeding.

Site explained the most variation in timing of breeding among individual scrub-jays. Because food handling rates differed between sites, this could explain some of the difference; however, other variables could account for the differences in timing of breeding between sites. Human-provided food differs in quality from natural foods, and food quality can influence timing of breeding (Ramsay and Houston 1997, Nager et al. 1997; Schoech and Bowman, unpubl. data). In Florida Scrub-Jays, food quality affects egg quality (Reynolds et al. 2003a) and nestling growth and survival (Reynolds et al. 2003b). However, the suburban environment differs from the wildlands in other respects that could influence timing of breeding. Suburban light pollution and heat-island effects could influence the cues used for timing breeding. We have little evidence that temperature differences exist between the suburban and wildland study sites. The phenology of oak leaf-out does not appear to differ between sites (RB, unpubl. data). Suburban habitats are lighter at night than the wildlands. Constant dim light can affect biological rhythms in birds (Kumar et al. 2000), but few data exist on whether exposure to some nighttime light influences the photoperiodic effect on breeding in birds. However, with respect to both temperature and light, we believe that the predicted effects on timing of breeding are inconsistent with our observation. We believe that both should advance timing of breeding relative to the wildland population by a consistent amount, but should not necessarily reduce between-year variation, as we have observed (Bowman et al. 1998).

The results of this study suggest that foraging efficiency, measured as the rate of food handling, has a measurable effect on the timing of reproduction of Florida Scrub-Jays. Future manipulative studies should attempt to discriminate

between the effects of food predictability and nutritional quality on timing of breeding, to better understand the physiological mechanisms underlying various cues and the behavioral responses to resource variation. Human-provided foods in suburban habitats appear to alter the behavior and reproductive strategies of birds; whether that is beneficial or not remains to be tested.

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