

Chapter 14

Variation in the timing of breeding between suburban and wildland Florida Scrub-Jays: Do physiologic measures reflect different environments?

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Abstract: Evidence exists that access to anthropogenic food by birds in urban areas can result in earlier laying dates and larger clutch sizes, both of which have the potential to increase the relative fecundity of urban bird populations. Several mechanisms exist by which supplemental food can advance laying. Supplemental food may provide additional energy, essential nutrients, or an environmental cue that the resources necessary for breeding are available. We examined several physiologic measures of pre-breeding female Florida Scrub-Jays (*Aphelocoma coerulescens*) from a suburban and a wildland population to assess these alternative hypotheses. Plasma protein levels were higher in females from the suburban scrub-jay population, but the difference was absent when we controlled for the number of days prior to laying that we sampled the bird. However, plasma protein levels during the earliest sampling period, long before protein mobilization as a result of vitellogenesis should be occurring in either population, were higher in the suburban population. We found no differences in plasma calcium levels or in the total body lipids between suburban and wildland populations. In both populations, total body lipids declined as laying neared, suggesting that Florida Scrub-Jays may use some endogenous resources to fuel reproduction. From other studies, we know that suburban scrub-jays increase food intake rates relative to jays in wildland populations. However, this strategy does not appear to result in improved body condition. We suggest that the readily available proteins in anthropogenic foods may provide essential nutrients and high intake rates may serve as an

environmental cue, both resulting in earlier laying in suburban jay populations. However, evidence exists suggesting that this may not increase, but rather decrease fecundity because breeding is out of synch with the seasonally fluctuating foods, such as arthropods, necessary to rear nestlings.

1. INTRODUCTION

The impacts of urbanization on avian demography and community structure often have been considered but, with the notable exception of the effects of industrial contaminants such as DDT and its metabolites, relatively little is known about the effects of human settlement on the physiology of individuals. Consideration at this level of analysis may reveal mechanisms producing negative or positive affects on demographic measures. For example, work by Wasser et al. (1997) revealed that endangered Northern Spotted Owls (*Strix occidentalis*) that live close to roads have higher plasma levels of corticosterone than owls farther from roads. High levels of adrenal glucocorticoids (corticosterone and cortisol) have been shown to negatively influence reproduction in reptiles (Moore and Miller 1984, Moore and Zoeller 1985), birds (Wilson and Follett 1975, Siegel 1980, Wingfield 1988, 1994), and mammals (review in Sapolsky 1992). It is clear that an analysis at a physiologic level may reveal mechanisms that effect demographic patterns that may not be readily evident through standard techniques of assessing human impact.

The effects of urbanization on animals can vary and are likely species- and development-specific. Urbanization is likely to decrease essential resources for some species and increase resources for others. This process affects individuals as they compete for these essential and sometimes limited resources, which in turn affects species-specific demographic rates, and ultimately community structure. One resource essential to birds that may vary in different directions with urbanization is food. Natural foods important to birds, such as arthropods, often decline with urbanization (Blair and Launer 1997, Deny and Schmidt 1998, Bolger et al. 2000); however, anthropogenic sources of food often are plentiful and may be readily available to birds (see Pierotti and Annett 2001). Bottom-up (food and productivity) influences on population regulation have received far less attention than top-down (predation and parasitism) influences (see Bolger 2001), and yet food has important implications to species-specific demographic rates.

For many bird species, access to supplemental food often increases clutch size and advances laying date (for a review see Boutin 1991). Early-laying birds often enjoy a reproductive advantage, thus anthropogenic foods may directly benefit some species by increasing their potential fecundity. In

Florida Scrub-Jays (*Aphelocoma coerulescens*) experimentally provisioned supplemental food increased clutch size and advanced laying date (Schoech 1996) and in a suburban population of scrub-jays, where virtually all birds have access to anthropogenic sources of food, the jays lay earlier and have larger clutches than jays in natural habitats without access to extra food (Bowman et al. 1998).

Supplemental food may advance laying via several different mechanisms. If food is limiting, supplemental food may provide additional energy that improves the relative condition of birds so that additional endogenous resources are available for breeding. Alternatively, supplemental foods may provide essential nutrients, such as protein and calcium, necessary for oogenesis, which also may be limited in natural habitats. The relatively acidic scrub-oak habitats frequented by the Florida Scrub-Jay (see Abrahamson et al. 1984) might limit uptake of these nutrients. Finally, birds may use the relative availability of food or intake rates as a cue that resources are adequate for breeding.

Each of these hypotheses generates different predictions regarding the physiological state of adult females during the weeks preceding breeding. To assess each of these hypotheses, we compared (1) total body lipids as a measure of overall body condition and (2) plasma levels of total protein and calcium in breeding female Florida Scrub-Jays during the several weeks prior to breeding between a population in wildlands without access to anthropogenic foods with a population in a suburban matrix where all birds have such access (see Bowman and Woolfenden 2001 for a description and aerial photograph of the two study sites).

2. METHODS

2.1 Study Population

The two populations of Florida Scrub-Jays reside within Highlands County, Florida. Scrub-jays at Archbold Biological Station (27°10'N, 81°21'W, elevation 38 - 68 m) and a nearby suburban development were studied from mid-January through April of 1998. The suburban population is located approximately 10 km NNW of Archbold (see Bowman and Woolfenden 2001). All jays in both populations were banded with a unique combination of United States Fish and Wildlife Service aluminum bands and plastic color bands. The sex, breeding status (breeder or non-breeding helper), and group association of all jays in both populations was known from ongoing long-term studies. All nests were located during the nest building stage or incubation and, therefore, clutch initiation dates were

known or could be estimated accurately (see Schoech et al. 1991, 1996; Mumme 1992; and Schoech 1996 for further details on the Archbold population).

2.2 Capture and Blood Sampling

Beginning in mid-January, six to eight weeks before the typical onset of breeding, all jays were captured in Potter traps that were baited with peanuts. Only female breeders were trapped and individuals were sampled only once. To assure that we were measuring baseline values of blood chemistry, each trap was monitored continuously, the jay was removed within seconds of capture, and a blood sample collected immediately. To control for possible diel fluctuations in plasma protein and calcium levels, all jays were captured between 0700 and 1100 h. Blood samples were collected in heparinized micro-haematocrit tubes from the ulnar vein following venipuncture with a 26 g needle, stored on ice until return to the laboratory (within 1 - 3 hours), centrifuged, and the plasma harvested for assay. A small volume (20 μ l) of plasma was used for immediate evaluation of plasma protein (see below). The remaining volume was frozen and stored at -20°C until shipped to Indiana University for assay of plasma calcium levels.

Immediately following collection of a blood sample, jays were anaesthetized and total body lipids were determined (see below for details). While recovering from the anaesthetic, individuals were weighed and a standard set of morphometric data were taken, e. g., body mass, tail and wing-chord length, a series of bill measurements, head-breadth, and overall head plus bill length. From the time of capture until release at the capture site birds were held for approximately 0.5 h, thus allowing sufficient time for full recovery from the anaesthetic. All procedures were sanctioned by the Bloomington Institutional Animal Care Use Committee of Indiana University.

2.3 Total Body Lipids

Immediately following collection of a blood sample, body lipids were assessed using total body electrical conductivity (TOBEC). This allows determination of an animal's lean mass and from this, one can estimate total body lipids (Walsberg 1988, Kenagy and Barnes 1988, Roby 1991, Schoech 1996). Accurate use of the instrument requires that subjects are positioned uniformly and kept in the same position for the duration of the scanning procedure. Therefore, all jays were anaesthetized with Metophane (inhaled) and held in a nylon stocking during the procedure.

When calibrated for a species this method is useful for within species comparisons of relative body lipid content, although the technique has come under some criticism (see Morton et al. 1991, Asch and Roby 1995). Calibration of the instrument for a given species necessitates that on one occasion a number of individuals be scanned, killed, and total body fat content measured directly with a lipid extraction technique (e. g., chloroform in a Soxhlet apparatus). For this study, the previously derived linear regression equation (Schoech 1996) from the congeneric Western Scrub-Jay (*A. californica*) was used to estimate total body lipid in Florida Scrub-Jays (for calibration, validation, and methodological details see Schoech 1996).

2.4 Plasma Protein and Calcium

Plasma protein concentration was measured with a hand-held clinical refractometer (Atago Company, Ltd., Model A 300 CL). This allows determination of dissolved solute in a small volume of plasma (20 μ l), based upon the degree to which light passing through the sample is 'bent' or refracted.

Plasma calcium concentration was determined with a kit obtained from Sigma Diagnostics (Procedure No. 587). Calcium reacts in a dose-dependent fashion with o-cresolphthalein complexone to produce a red complex, the intensity of which is directly proportional to the calcium concentration in the plasma sample. Color intensity was subsequently determined with a spectrophotometer set at 575 nm absorbency .

2.5 Data Analyses

Because birds mobilize endogenous reserves of certain nutrients when preparing to breed, we compared physiological attributes between populations relative to calendar date (# of days from the onset of sampling) and relative to laying date (# of days sampling occurred prior to the laying of the first egg of the first clutch). To analyze the data by calendar date, beginning on 21 January, the date sampling began, samples were grouped into 14-day periods. For example, all samples collected between 21 January and 3 February or between 4 and 17 February were combined. Therefore, there were 5 collection periods between 21 January and the termination of data collection on 31 March. To compare females from the two populations that were sampled at equivalent points in their reproductive cycle, samples were grouped by the number of days prior to clutch initiation that they were collected. The number of days within each category was 10, e. g., 10 to 1 days or 40 to 31 days before clutch initiation date. We predicted that if physiological differences were the cause of differences in the timing of

breeding, those differences should exist for both calendar date and laying date analyses. If the differences were the result rather than the cause of differences in the timing of breeding, then we predicted those differences would be significant only for calendar date analyses and not for laying date analyses.

Because not all females that were paired with a male and occupying a territory initiated clutches, sample sizes are less for the analyses that are based upon clutch initiation date. However, for the analyses conducted by calendar date, we found no difference in the results whether these females were included or excluded, thus for the analyses based upon calendar date, we report data from all females sampled whether they subsequently initiated a clutch or not.

3. RESULTS

3.1 Timing of Reproduction

As in previous years, suburban jays nested earlier than wildland jays ($t = -6.52$, $DF = 66$, $P < 0.001$, Fig. 14.1). The mean laying date of first eggs by the 32 females in the suburbs that laid clutches was 24 March (± 2.3 days SE) and clutch initiation date ranged from 5 March through 23 April. In contrast, the 36 wildland females that initiated clutches had a mean clutch initiation date of 13 April (± 1.95 days SE). The earliest clutch in the wildland population was initiated on 25 March and the latest on 11 May.

3.2 Total Body Lipids

We found no differences between populations in total body lipids by calendar date ($F_{1,81} = 0.34$, $P = 0.56$; Fig. 14.2a) nor did total body lipids vary with calendar date ($F_{4,81} = 1.84$, $P = 0.13$), nor was there an interaction between habitat and calendar date ($F_{1,4} = 0.77$, $P = 0.55$). We found no difference between populations in total body lipids by laying date ($F_{1,57} = 0.43$, $P = 0.51$); however, when the difference in timing of clutch initiation between the two populations was controlled, total body lipids declined as females approached laying ($F_{5,57} = 5.20$, $P = 0.001$; Fig. 14.2b). No interaction existed between habitat and laying date ($F_{1,5} = 0.51$, $P = 0.77$). Post hoc pairwise comparisons found that total body lipids of females sampled within 10 days of clutch initiation were lower than for females sampled 60 - 51 days and 30 - 21 days before laying.

3.3 Plasma Protein

When compared by calendar date, females in the suburban population had higher plasma levels of protein than did females in the wildland population (ANOVA: $F_{1,81} = 6.38$, $P = 0.014$; Fig. 14.3a). In both populations, plasma protein increased with calendar date ($F_{4,81} = 11.06$, $P < 0.001$), but no

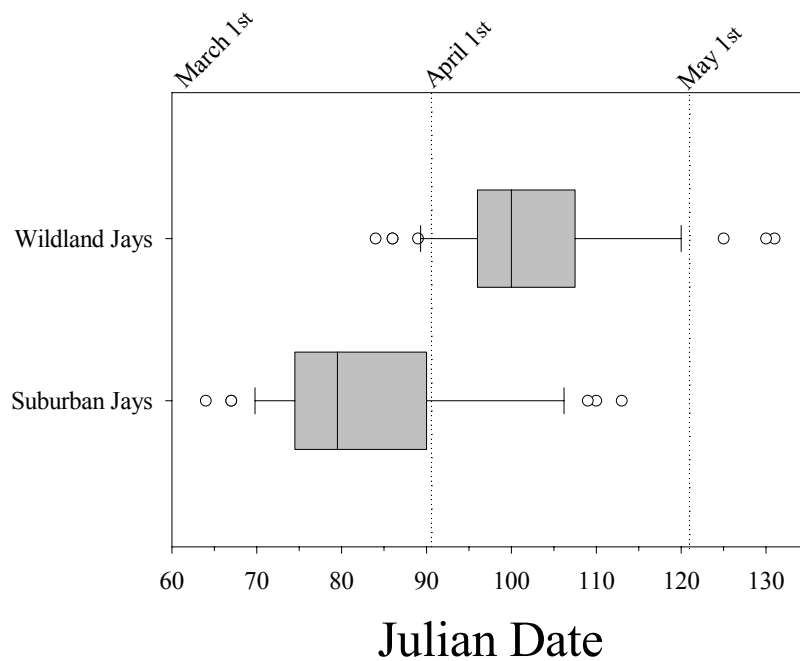


Figure 14.1. A comparison of first clutch initiation dates of Florida Scrub-Jays in a wildland and a suburban population. Suburban females lay significantly earlier than females in natural scrub habitat at Archbold Biological Station. In this horizontal box plot the shaded box represents the middle 50% of each population, the vertical lines within the boxes represent the median laying date, the error bars represent the first 10% and latest 90% of the population, and the circles represent statistical outliers.

interaction existed between date and habitat ($F_{1,4} = 1.04$, $P = 0.39$). Post hoc pairwise comparisons using the Bonferroni adjustment found that plasma protein levels in females from the suburban population during the last sampling period, 18 - 31 March, were significantly higher than suburban females sampled during all three periods between 21 January and 3 March. Additionally, suburban females during this sampling period had levels that were higher than wildland females over the four sampling periods beginning 21 January and ending 17 March. Wildland females sampled during the last period (18 - 31 March) had higher plasma protein levels than females in the wildland population sampled during the first two periods (i.e., from 21 January - 13 February).

Based on our *a priori* hypothesis that suburban jays initiate reproduction earlier than wildland jays because they are in better condition and an expectation that this might be best reflected early in the sampling period, we also compared plasma protein levels during the earliest sampling period (i.e., during the first two periods, between 21 January and 13 February). At this time, suburban females had significantly higher plasma protein levels than wildland females ($F = 4.90$, $P = 0.034$).

When compared by laying date, plasma protein levels increased as clutch initiation date neared ($F_{5,58} = 8.82$, $P < 0.001$; Fig. 14.3b) and females in the two populations exhibited the same pattern. However, we found no differences in plasma protein between the two populations ($F_{1,58} = 0.024$, $P = 0.88$) when we controlled for time before laying and no interaction occurred between these factors ($F_{1,5} = 0.73$, $P = 0.60$). Because we found no differences with respect to urbanization, we combined habitats for post hoc pairwise comparisons by days before clutch initiation. Plasma protein levels were highest during the sampling period immediately prior to clutch initiation, i. e., from 10 - 1 days before a female laid her first egg.

3.4 Plasma Calcium

Plasma calcium levels increased with calendar date ($F_{4,80} = 3.29$, $P = 0.02$; Fig. 14.4a), but no differences existed between populations ($F_{1,80} = 1.92$, $P = 0.17$) nor was there any interaction between habitat and calendar date ($F_{1,4} = 0.30$, $P = 0.88$). Calcium in females sampled from 18 - 31 March was higher than that of those females sampled between 4 - 17 February.

Plasma calcium levels increased as laying date neared ($F_{5,58} = 3.89$, $P = 0.005$), but there were no differences between populations ($F_{1,58} = 0.57$, $P = 0.46$; Fig. 14.4b) nor was there any interaction between habitat and laying date ($F_{1,5} = 0.91$, $P = 0.48$). Plasma calcium levels during the period immediately preceding laying (1 - 10 days) were significantly higher than all

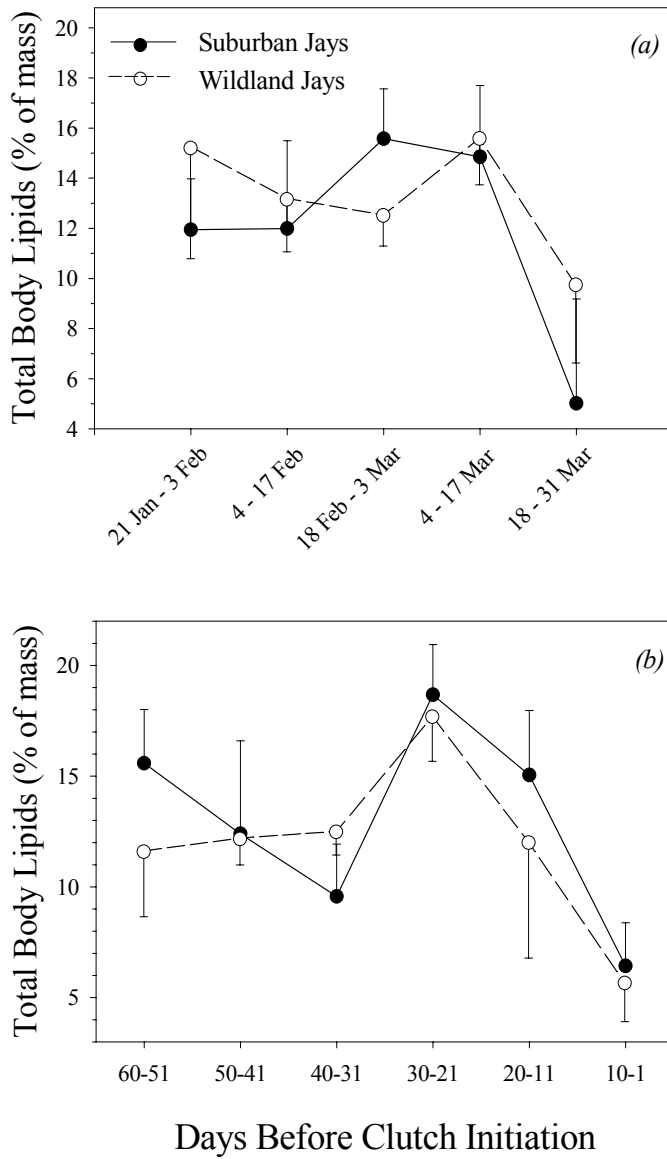


Figure 14.2. A comparison of mean (\pm SE) total body lipid levels in female breeders in two populations of Florida Scrub-Jays, relative to calendar date (a) and relative to time of sampling prior to laying date (b).

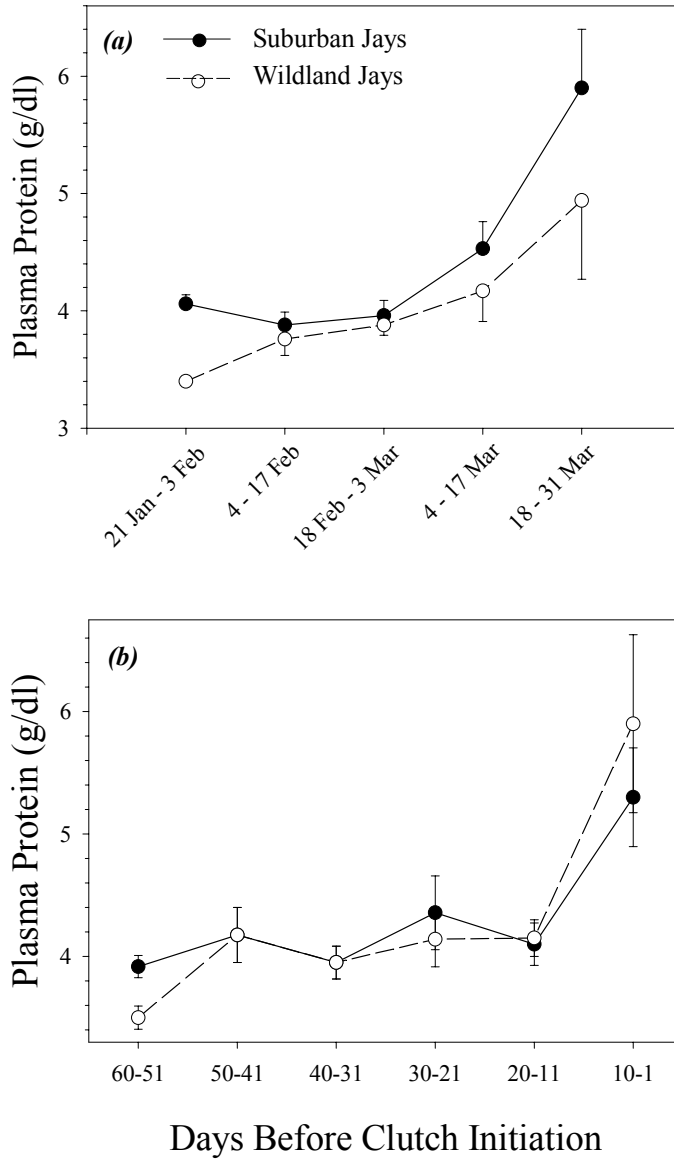


Figure 14.3. A comparison of mean (\pm SE) plasma protein levels in female breeders in two populations of Florida Scrub-Jays, relative to calendar date (a) and relative to time of sampling prior to laying date (b).

periods with the exception of the sampling period that was next closest to laying (i. e., 11 - 20 days before clutch commencement, $P = 0.056$).

4. DISCUSSION

Our results do not appear to support strongly any of the three hypotheses. Although plasma protein levels were higher among suburban scrub-jays, we found no population difference when we controlled for days prior to laying. The pattern in which plasma protein levels become elevated as laying approaches in many avian species has been shown to reflect an increase in blood levels of vitellogenin (White 1991). This protein which is produced in the liver in response to endocrine signals (primarily estradiol and progesterone) and transported to the ovary via the blood stream, is a major component in avian yolk (Jackson et al. 1977, Deeley et al. 1993, Ho 1991, Carey 1996). Therefore, the increases seen after 24 February in the suburban females and 9 March in the wildland females (see Fig. 2a) probably reflect the onset of vitellogenesis. However, we found a significant between-population difference in protein levels in the females that were sampled very early in our study, prior to 13 February (see Fig. 14.3b). This sampling occurred 39 days before most suburban females and nearly 60 days before most wildland females laid eggs, well before the time when jays from either population would be yolking follicles.

We suggest that this difference reflects the protein-rich and anthropogenically supplemented diets of females in the suburbs. Two of the most common food items in the suburbs are shelled peanuts and pet foods, both of which have relatively high amounts of protein (Fleischer 2000). Acorns, a common dietary item of wildland scrub-jays during the winter also are relatively high in proteins, however, they have high concentrations of tannins which tend to decrease the ability of animals to effectively metabolize proteins. Arthropods are relatively scarce in natural scrub during the winter, thus it seems as if the habitat-specific differences in protein availability may influence differences in the timing of breeding between habitats. The readily available proteins (or the essential amino acids that they contain) in supplemental food may allow females to come into full reproductive state earlier or serve as a signal that the time is appropriate to initiate reproduction.

Calcium is essential for somatic growth in young animals, and later, in homeostasis of bodily functions; in birds calcium also is necessary for egg shell deposition. Wildland scrub-jays may obtain calcium by taking small vertebrate prey, such as small reptiles, mammals, and amphibians

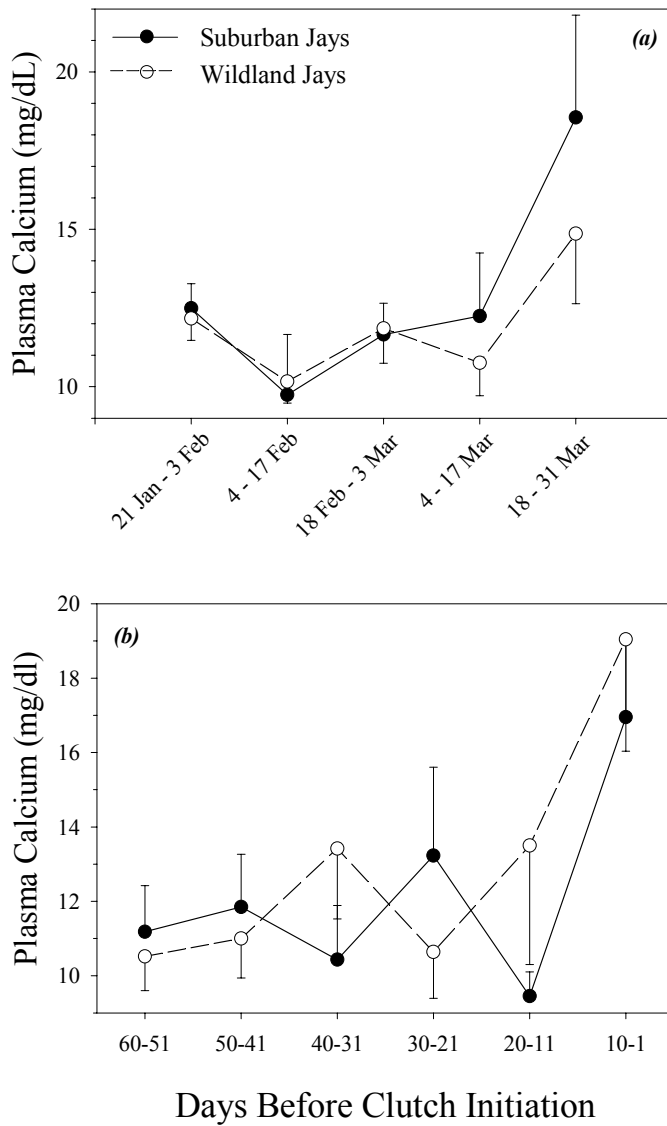


Figure 14.4. A comparison of mean (\pm SE) plasma calcium levels in female breeders in two populations of Florida Scrub-Jays, relative to calendar date (a) and relative to time of sampling prior to laying date (b).

(Woolfenden and Fitzpatrick 1984, 1990, personal observation). However, the relatively acidic environment of oak scrub may decrease the availability of calcium (Klasing 1988). In the suburbs, calcium is likely more abundant, occurring in pet foods and in the calcareous shell fill upon which most roads in the suburban area are constructed; thus calcium is unlikely to be limiting.

Nevertheless, we found no population differences in plasma calcium levels. The marked increase in plasma calcium levels immediately preceding clutch initiation observed in females from both populations (Fig. 14.4b) clearly shows the movement via the blood stream of endogenously and/or exogenously derived calcium to the oviduct for egg shell formation.

We also found no population differences in total body lipids. This is somewhat surprising because Schoech (1996), who provided jays in their natural habitat with supplemental food, found that supplemented female breeders had higher levels of total body lipids than did controls, but birds were not measured during the same pre-breeding period as in this study. In both populations, total body lipids decreased as laying neared. These data suggest that the differences in timing of breeding between the two populations is not a result in differences in energy availability.

The decline in total body lipids as laying neared is interesting, but not from a specifically urban perspective. Although some large species of waterfowl rely mostly on endogenous energy (i.e., lipids) and nutrient reserves for egg production (Ankney and MacInnes 1978, Ankney and Alisauskas 1991), it is commonly assumed that females of smaller species, such as passerines, must increase their food intake for egg production (Perrins 1970, 1996). The comparison between birds that depend on endogenous stores rather than exogenous dietary intake has been termed capital versus income breeders, respectively (see Drent and Daan 1980, Meijer and Drent 1999). However, such a comparison may be overly simplified since it is likely that females use a combination of capital and income during oogenesis. For example, Williams and Ternan (1999) found that female zebra finches reduce locomotor activity rather than increase food intake during oogenesis. If female zebra finches meet part of the increased energetic or nutritional demands of oogenesis by reallocation of their daily energetic expenditures, it is likely that other species may use a similar strategy. Fleischer (2000) found that suburban scrub-jays spent less time foraging and more time perching, yet increased their food intake rate when compared with scrub-jays in wildland habitats. If true, this potential energy savings does not appear to result in improved body condition.

The spatial and temporal predictability of anthropogenic foods may enable scrub-jays to increase their intake rates, while spending less time searching for and handling these foods (Fleischer 2000). In some birds, the

intake rate of certain foods, especially arthropods, appears to be a cue to initiate reproduction (Benkman 1990, Winkler and Allen 1996). In Florida Scrub-Jays, the timing of breeding is not correlated with arthropod availability, but with late winter abundance of herptiles and the size of the previous autumn's acorn crop (Curry, Woolfenden, and Fitzpatrick, unpubl. data). Presumably jays assess the abundance of these foods through intake rates; thus if peanuts, the anthropogenic food most heavily used by jays during this pre-breeding period, serve as an ecological surrogate for acorns, jays may be making breeding decisions based on their availability. Their relatively high quality also may contribute to the earlier breeding by suburban jays.

For many birds early breeding confers a reproductive advantage. Early breeding birds, including Florida Scrub-Jays in natural habitats, often lay larger clutches (Perrins 1965, Boutin 1989, Meijer et al. 1990, Svensson 1995, Schoech 1996, Woolfenden and Fitzpatrick 1984, 1990, 1996, Winkler and Allen 1996). Late-nesting pairs of Florida Scrub-Jays are less likely to produce young and these young are less likely to survive (because of increased predation as the season progresses; see Woolfenden and Fitzpatrick 1984, Schaub et al. 1992). Thus we might expect that access to anthropogenic foods which leads to earlier breeding and larger clutch sizes (Bowman et al. 1998) in suburban scrub-jays might confer a reproductive advantage to these populations. However, scrub-jays almost exclusively feed their nestlings arthropods, so most anthropogenic foods may not be suitable for nestling development. Scrub-jays in wildlands may vary their time of breeding to coincide with seasonally fluctuating arthropod populations. Bowman et al. (1998) found that suburban scrub-jay reproduction was poorest relative to scrub-jays in natural habitats when the difference in laying date between the two populations was greatest. If Florida Scrub-Jays use supplemental food as a cue to initiate breeding, but nest before seasonal resources are available, then supplemental food, rather than mitigating the decrease in availability of natural food (see Bolger 2001), may further reduce its availability.

4.1 Policy and Management Recommendations

Clearly anthropogenic sources of food have an effect on the timing of breeding and clutch size of suburban populations of Florida Scrub-Jays, but the net effect of this influence may be negative rather than positive. The bulk of this food (peanuts and bird seed) is purposely provided for the birds by the human population. Bird feeding is likely to have a variety of direct and indirect benefits to wildlife, including but not limited to increased appreciation for wildlife. Suggesting that bird feeding be prohibited is

unwarranted, but perhaps the public should be more aware of the changing seasonal resource needs of birds and provide food appropriate to the life history cycle of birds. Before and during the breeding season, food with readily available proteins might be appropriate, such as several new commercially available bird foods mixed with dehydrated lepidopteran larvae.

Other sources of anthropogenic foods, such as waste, may be of relatively poor quality for birds (see Pierotti and Annett 2001) and their utilization by birds also may have deleterious consequences. In addition, the attraction of mesopredators to such waste foods may have additional negative impacts on bird communities in urban areas. Urban communities should be planned so that wastes are made less available to wild birds and other animals.

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REFERENCES

- Abrahamson, W. G., A. F. Johnson, J. N. Layne, and P. A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Fla. Sci.* 47:209-250.
- Ankney, C. D., and C. D. McInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459-471.
- Ankney, C. D. and R. T. Alisauskas. 1991. The use of nutrient reserves by breeding waterfowl, p. 2170-2176. *In* B. D. Bell, R. O. Cossee, J. E. C. Flux, B. D. Heather, R. A. Hitchmough, C. R. Robertson, and M. J. Williams [EDS.], *Acta XX Congressus Internationalis Ornithologici*. New Zealand Ornithological Congress Trust Board, Wellington, New Zealand.
- Asch, A., and D. D. Roby. 1995. Some factors affecting precision of the total body electrical conductivity technique for measuring body composition in live birds. *Wilson Bull.* 107:306-316.
- Benkman, C. W. 1990. Intake rates and the timing of crossbill reproduction. *Auk* 107:376-386.
- Blair, R. B., and A. E. Launer. 1997. Butterfly diversity and human land use: species assemblages along an urban gradient. *Biol. Conserv.* 80:113-125.

- Bolger, D. 2001. Urban birds: populations, community, and landscape approaches, p. 155-177. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.
- Bolger, D. T., A. V. Suarez, K. Crooks, and S. A. Morrison. 2000. Arthropods in habitat fragments: effects of area, edge and Argentine ants. *Ecol. Appl.* 10:1230-1248.
- Boutin, S. 1989. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* 68:203-220.
- Bowman, R. and G. E. Woolfenden. 2001. Nest success and the timing of nest failure of Florida Scrub-Jays in suburban and wildland habitats, p. 385-404. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.
- Bowman, R., G. E. Woolfenden, and J. W. Fitzpatrick. 1998. Timing of breeding and clutch size in the Florida Scrub-Jay, *Aphelocoma coerulescens*. *Ostrich* 69:316.
- Carey, C. 1996. Female reproductive energetic, p. 324-374 *In* C. Carey [ED.]. Avian energetics and nutritional ecology. Chapman and Hall, New York.
- Deeley, R. G., R. A. Burtch-Wright, C. E. Grant, P. A. Hoodless, A. K. Ryan, and T. J. Schrader. 1993. Synthesis and deposition of egg proteins, p. 205-222 *In* R. J. Etches and A. M. Verrinder [EDS.]. Manipulation of the avian genome. CRC Press, Boca Raton.
- Deny, C., and H. Schmidt. 1998. Insect communities on experimental mugwort (*artemisia vulgaris* L.) Plots along an urban gradient. *Oecologia* 113:269-277.
- Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.
- Fleischer, A. L. Jr. 2000. The influence of time budget and rate of food handling and consumption on the timing of breeding of female Florida Scrub-Jays (*Aphelocoma coerulescens*): A comparison between populations in natural and suburban habitats. MS thesis, University of South Florida, Tampa, FL.
- Ho, S-M. 1991. Vitellogenesis, p. 91-126 *In* P. K. T. Pang and M. P. Schreibman [EDS.]. Vertebrate endocrinology: Fundamentals and biomedical implications, Vol. 4. Academic Press, Orlando.
- Jackson, R. L., H. Y. Lin, J. T. S. Chan, and A. R. Means. 1977. Estrogen induction of plasma vitellogenin in the cockerel: studies with phosvitin antibody. *Endocrinology* 101:849-857.
- Kenagy, G. J., and B. M. Barnes. 1988. Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington. *J. Mammol.* 69:274-292.
- Klasing, K. C. 1998. Comparative Avian Nutrition. Cab International, New York.
- Meijer, T., S. Daan, and M. Hall. 1990. Family planning in the kestrel (*Falco tinnunculus*): The proximate control of covariation of laying date and clutch size. *Behaviour* 114:117-136.
- Meijer, T. S., and R. Drent. 1999. Re-examination of the capital and income dichotomy in breeding birds. *Ibis* 141:399-414.
- Moore, F. L., and L. J. Miller. 1984. Stress-induced inhibition of sexual behavior: corticosterone inhibits courtship behaviors of a male amphibian (*Taricha granulosa*). *Horm. Behav.* 18:400-410.
- Moore, F. L., and R. T. Zoeller. 1985. Stress-induced inhibition of reproduction: evidence of suppressed secretion of LH-RH in an amphibian. *Gen. Comp. Endocrinol.* 60:252-258.
- Morton, J. M., R. L. Kirkpatrick, and E. P. Smith. 1991. Comments on estimating total body lipids from measures of lean mass. *Condor* 93:463-465.
- Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behav. Ecol. Sociobiol.* 31:319-328.

- Perrins, C. M. 1965. Population fluctuations and clutch size in the great tit (*Parus major*). *J. Anim. Ecol.* 34:601-647.
- Perrins, C. 1970. The timing of birds' breeding seasons. *Ibis* 112:242-255.
- Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. *Ibis* 138:2-15.
- Pierotti, R., and C. Annett. 2001. The ecology of Western Gulls in habitats varying in degree of urban influence, p. 309-331. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic, Norwell, MA.
- Roby, D. 1991. A comparison of two noninvasive techniques to measure total body lipid in live birds. *Auk* 108:509-518.
- Sapolsky, R. M. 1987. Stress, social status, and reproductive physiology in free-living baboons, p. 291-321 *In* D. Crews [ED.], *Psychobiology of reproductive behavior: An evolutionary perspective*. Prentice-Hall, New Jersey.
- Schaub, R., R. L. Mumme, and G. E. Woolfenden. 1992. Predation on the eggs and nestlings of Florida scrub jays. *Auk* 109:585-593.
- Schoech, S. J. 1996. The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida scrub-jay (*Aphelocoma coerulescens*). *Condor* 98:234-244.
- Schoech, S.J., R. L. Mumme, and M.C. Moore. 1991. Reproductive endocrinology and mechanisms of breeding inhibition in cooperatively breeding Florida scrub jays (*Aphelocoma c. coerulescens*). *Condor* 93:354-364.
- Schoech, S. J., R. L. Mumme, and J. C. Wingfield. 1996. Delayed breeding in the cooperatively breeding Florida scrub-jay (*Aphelocoma coerulescens*): inhibition or the absence of stimulation. *Behav. Ecol. Sociobiol.* 39:77-90.
- Siegel, H. S. 1980. Physiological stress in birds. *Bioscience* 30:529-534.
- Svensson, E. 1995. Avian reproductive timing: when should parents be prudent? *Anim. Behav.* 49:1569-1575.
- Wasser, S. K., K. Bevis, G. King, and E. Hanson. 1997. Noninvasive physiological measures of disturbance in the northern spotted owl. *Cons. Biol.* 11:1019-1022.
- Walsberg, G. E. 1988. Evaluation of a nondestructive method for determining fat stores in small birds and mammals. *Physiol. Zool.* 61:153-159.
- White, H. B., III. 1991. Maternal diet, maternal proteins and egg quality. p. 1-15 *In* D. C. Deeming and M. W. J. Ferguson [EDS.], *Egg incubation: Its effects on embryonic development in birds and reptiles*. Cambridge University Press, Cambridge.
- Williams, T. D., and S. P. Ternan. 1999. Food intake, locomotor activity, and egg laying in Zebra finches: Contribution to reproductive energy demand? *Physiol. Biochem. Zool.* 72:19-27.
- Wilson, F. E., and B. K. Follett. 1975. Corticosterone-induced gonadosuppression in photostimulated tree sparrows. *Life Sci.* 17:1451-1456.
- Wingfield, J. C. 1988. Changes in reproductive function of free-living birds in direct response to environmental perturbations, p. 121-148 *In* M. H. Stetson [ED.], *Processing of environmental information in vertebrates*, Springer-Verlag, Berlin.
- Wingfield, J. C. 1994. Modulation of the adrenocortical response to stress in birds, p. 520-528 *In* K. G. Davey, R. E. Peter, and S. S. Tobe [EDS.], *Perspectives in comparative endocrinology*. Natl. Res. Council of Canada.
- Winkler, D. W., and P. E. Allen. 1996. The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment? *Ecology* 77:922-932.
- Woolfenden, G. E., and J. W. Fitzpatrick. 1984. *The Florida Scrub Jay: Demography of a Cooperative-breeding Bird*. Princeton University Press, New Jersey.

- Woolfenden, G. E., and J. W. Fitzpatrick. 1990. Florida scrub jays: a synopsis after 18 years of study, p. 241-266 *In* P. B. Stacy and W. D. Koenig [EDS.], *Cooperative breeding in birds: Long-term studies of ecology and behavior*. Cambridge University Press, Cambridge.
- Woolfenden, G. E., and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*), p. 1-28 *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 228. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D. C.