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### Abstract

Urbanization alters ecological systems, disturbance regimes, food webs, and a variety of other processes that can influence local flora and fauna. In birds, most studies have focused on behavioral or demographic responses to altered conditions; however, the physiological mechanisms associated with these responses have been understudied. We have previously documented shifts in foraging behavior because of the availability of human-provided food; we sought to see if this was driven by or associated with a change in field metabolic rates. We measured field metabolic rates (FMR), a measure of daily energy expenditure (DEE), of Florida Scrub-Jays (*Aphelocoma coerulescens*) in 2 habitats using doubly labeled water (DLW). One population of jays lived in wildland habitat, the other in a suburban area where the habitat was badly degraded. During the breeding season FMR of suburban males exceeded that of wildland males by over 100%. Female FMR did not differ between sites but increased following incubation. In the wildlands, FMRs of females were barely lower than those of males, but in the suburban landscape, female FMRs were much lower than in males. For both sexes in the wildlands, FMRs were about 3.53 basal rates of metabolism (BMR) during breeding; in the suburbs female FMR exceeded BMR by 43 but did not differ from that of wildland females. Suburban male FMRs exceeded BMR by 7.13. During the nonbreeding seasons of fall and winter, FMR did not differ between habitats, ranging from 1.73 to 2.13 BMR, thus it is the breeding season that separated wildland and suburban jays energetically. In both habitats, a low water economy index (mL/kJ) and low water fluxes indicated that these jays are well adapted to their xeric habitat, but their FMRs distinguished them from desert birds. The very high energetic cost associated with breeding for suburban males may help explain why in the metapopulation of Florida Scrub-Jays, suburban jay populations are sinks. This study underscores the value of physiology in the conservation of listed species.

### Keywords

Conservation physiology, Field metabolic rates, Landscape changes, Seasonal effects, Urbanization, Water economy

### Disciplines

Animal Sciences | Biology | Ornithology

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## Daily energy expenditure of Florida Scrub-Jays (*Aphelocoma coerulescens*) in suburban and wildland landscapes

Hugh I. Ellis<sup>1\*</sup> and Reed Bowman<sup>2</sup>

**ABSTRACT**—Urbanization alters ecological systems, disturbance regimes, food webs, and a variety of other processes that can influence local flora and fauna. In birds, most studies have focused on behavioral or demographic responses to altered conditions; however, the physiological mechanisms associated with these responses have been understudied. We have previously documented shifts in foraging behavior because of the availability of human-provided food; we sought to see if this was driven by or associated with a change in field metabolic rates. We measured field metabolic rates (FMR), a measure of daily energy expenditure (DEE), of Florida Scrub-Jays (*Aphelocoma coerulescens*) in 2 habitats using doubly labeled water (DLW). One population of jays lived in wildland habitat, the other in a suburban area where the habitat was badly degraded. During the breeding season FMR of suburban males exceeded that of wildland males by over 100%. Female FMR did not differ between sites but increased following incubation. In the wildlands, FMRs of females were barely lower than those of males, but in the suburban landscape, female FMRs were much lower than in males. For both sexes in the wildlands, FMRs were about 3.5× basal rates of metabolism (BMR) during breeding; in the suburbs female FMR exceeded BMR by 4× but did not differ from that of wildland females. Suburban male FMRs exceeded BMR by 7.1×. During the nonbreeding seasons of fall and winter, FMR did not differ between habitats, ranging from 1.7× to 2.1× BMR, thus it is the breeding season that separated wildland and suburban jays energetically. In both habitats, a low water economy index (mL/kJ) and low water fluxes indicated that these jays are well adapted to their xeric habitat, but their FMRs distinguished them from desert birds. The very high energetic cost associated with breeding for suburban males may help explain why in the metapopulation of Florida Scrub-Jays, suburban jay populations are sinks. This study underscores the value of physiology in the conservation of listed species. Received 22 May 2019. Accepted 30 July 2020.

Key words: conservation physiology, field metabolic rates, landscape changes, seasonal effects, urbanization, water economy.

### Gasto energético diario de la urraca *Aphelocoma coerulescens* en paisajes suburbanos y silvestres

**RESUMEN** (Spanish)—La urbanización altera los sistemas ecológicos, regímenes de perturbación, redes alimenticias y una variedad de otros procesos que pueden influenciar la flora y fauna local. En las aves, la mayoría de los estudios se han enfocado en las respuestas conductuales o demográficas a condiciones alteradas; sin embargo, los mecanismos asociados con estas respuestas han sido subestudiadas. Hemos documentado previamente los cambios en el comportamiento de forrajeo debido a la disponibilidad de alimento provisto por humanos; buscamos dilucidar si esto fue en respuesta o asociado a cambios en las tasas metabólicas en el campo. Cuantificamos las tasas metabólicas de campo (FMR), una medida del gasto energético diario de la urraca *Aphelocoma coerulescens* en 2 hábitats, usando agua doblemente marcada. Una población de urracas vivía en hábitat silvestre y la otra en un área suburbana donde el hábitat estaba sustancialmente degradado. Durante la estación reproductiva, el FMR de los machos suburbanos excedía por más del 100% el de los machos de hábitats silvestres. En hembras, la FMR no difirió entre sitios pero se incrementó después de la incubación. En hábitats silvestres, las FMR de las hembras fueron apenas más bajas que las de los machos, aunque en el paisaje suburbano, las FMR de las hembras fueron mucho más bajas que las de los machos. Para ambos sexos en hábitats silvestres, las FMR fueron cerca de 3.5× las tasas basales de metabolismo (BMR) durante la reproducción; en los suburbios, la FMR de las hembras excedió la BMR por 4× pero no difirió de aquella de hembras en hábitat silvestres. Las FMR de machos suburbanos excedió 7.1× la BMR. Durante las estaciones no-reproductivas de otoño e invierno, la FMR no difirió entre hábitats y tuvo BMR con un rango de 1.7–2.1×, con lo que inferimos que la estación reproductiva separa energéticamente a las urracas de hábitats silvestres de las suburbanas. En ambos hábitats, un bajo índice de economía de agua (mL/kJ) y bajos flujos de agua indicaron que estas urracas están bien adaptadas a sus hábitats xéricos, si bien sus FMR les distinguen de aves del desierto. El muy alto costo energético asociado con la reproducción de machos suburbanos podría explicar por qué en la metapoblación de esta urraca las poblaciones suburbanas están en declive. Este estudio subraya el valor de la fisiología en la conservación de especies enlistadas en alguna categoría de riesgo.

Palabras clave: cambios en el paisaje, economía del agua, efectos estacionales, fisiología de la conservación, tasas metabólicas de campo, urbanización.

Florida's only endemic bird, the Florida Scrub-Jay (*Aphelocoma coerulescens*), a sedentary, cooperative-breeding bird, exists across its extant range in a number of distinct metapopulations and genetic units (Stith et al. 1996, Coulon et al. 2010).

It is restricted to pyrogenic oak-dominated scrubs on well-drained soils (Woolfenden and Fitzpatrick 1984), home to many xeric-adapted species in a paradoxically high rainfall area. Its habitat has been degraded and lost to agricultural and urban development and to changes in the fire regime, resulting in large population declines and its listing as federally Threatened (US Fish and Wildlife Service 1987).

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The Florida Scrub-Jay has been well studied at Archbold Biological Station in south-central Florida for over 4 decades. Its social structure, demography, behavior, and population dynamics have all been investigated (Woolfenden and Fitzpatrick 1984, 1990, 1996, among many other references). In 1991, another long-term study of scrub-jays began on a population that occupied scrub rapidly being suburbanized. A variety of human-associated changes, such as access to supplemental foods, fire suppression, introduction of novel predators, and changes in nighttime light exposure, all affect scrub-jay behavior and demography through various direct and indirect influences (Bowman 1998, Bowman and Woolfenden 2001, Schoech and Bowman 2001, Fleischer et al. 2003, Sauter et al. 2006, Aldredge et al. 2012). Ultimately, these changes are negative for the persistence of scrub-jays in these habitats; recruitment is not sufficient to offset mortality (Bowman 1998).

The many anthropogenic changes associated with urbanization can have complex and interactive effects. For example, arthropod abundance is much lower in the suburbs, likely as a result of changes in habitat and frequent applications of various pesticides (Shawkey et al. 2004). As a result, peanuts and other anthropogenic foods are common in the jay's diet (Fleischer et al. 2003). Peanuts are of relatively high quality (high in protein and fats) for adults and are both spatially and temporally predictable, thus potentially affecting energetic costs associated with foraging (Fleischer et al. 2003). However, because peanuts are plant foods, a much longer digestive time is required to fully metabolize the proteins (Karasov 1990) and thus peanuts may be inadequate for fueling the rapid growth of nestlings. The diet of nestling scrub-jays is dominated by arthropods, especially lepidopteran larvae (Stalcup and Woolfenden 1978). In wildlands, 100% of the nestling diet is animal foods, but in the suburbs 15–30% of their diet is peanuts or other plant foods. This leads to lighter fledgling masses and dehydration, greater rates of brood reduction (Shawkey et al. 2004), and lower post-fledging survival (Bowman 1998). However, despite the reduced abundance of arthropods, neither the time spent foraging nor arthropod capture rates per foraging time differ between suburban and wildland birds nor do significant differences exist in other behaviors in

their overall time budgets (Sauter 2005). The only detectable difference is that suburban birds have higher capture rates when feeding on plant foods, virtually all of which come from human sources. Wildland birds rarely feed on plant foods, with the exception of cached acorns, but all plant foods require a substantial search time to exploit. Suburban females spend a greater proportion of their time during incubation on the nest, in part because the duration of off-bouts is much shorter (Aldredge et al. 2012). This is likely because human-provided foods are spatiotemporally predictable and thus do not require searching time to exploit.

Almost nothing is known on the impacts of urbanization on energy budgets and metabolism. Several studies have suggested a phenotypic divergence in pace-of-life life histories between urban and rural populations of the same species (Charmantier et al. 2017, Sepp et al. 2018) and pace-of-life has also been associated with metabolic rates (Londoño et al. 2015). Hope et al. (2016) showed that urbanization can have an effect on the timing of molt, which has energetic implications (Dietz et al. 1992). An intriguing study (Welbers et al. 2017) has suggested that exposure to artificial light at night reduces the daily energy expenditure (DEE) of breeding Great Tits (*Parus major*), which could have implications for suburban scrub-jays.

Because suburban scrub-jays exploit predictable, human-provided foods, which influence their foraging and incubation behavior, we hypothesized that this would influence field metabolic rates (FMR), a measure of DEE, during their breeding season. Because field metabolic rates are influenced by an animal's behavioral response to its environment, we predicted that FMR would be lower in both breeding males and females in the suburban habitat than in the wildlands.

We used the doubly labeled water method to measure FMR, which also allowed to us to measure total body water (TBW) influx and efflux in both habitats. Urbanization and other human-mediated alterations of natural habitats, such as agriculture, often have profound effects on water availability (Green and Baker 2003, Shochat et al. 2004). For example, increased water availability via agricultural development in the arid Imperial Valley of California has facilitated invasion of nonnative species less adapted to desert conditions

(Monson 1944, 1949). Although Florida oak scrub is a xeric habitat, water is not in short supply. Dew is heavy, scrub is sprinkled with seasonal ponds, and some insects, such as lepidopteran larvae, are high in water content. However, urbanization offers irrigation, bird baths, pools, pet water bowls, etc. for birds to exploit during periods of natural water shortages. We predicted that human-associated water sources would alter TBW in the suburban birds, increasing water flux. The use of energetics and other physiological attributes can shed light on basic questions about how animals adapt to urban environments and demonstrates their value to conservationists studying environmental changes, an application previously suggested by McNab (2006) and Tomlinson et al. (2014) and here applied to the conservation of a listed species.

## Methods

### Experimental sites

Archbold Biological Station (ABS) is at the southern end of the Lake Wales Ridge (Weekley et al. 2008), near Lake Placid, Florida. It encompasses 2,100 ha of mostly oak scrub. We refer to this habitat as “wildland” in that the otherwise natural scrub is fire-maintained by prescribed burning. At the time of the study (1997–1999), the long-term demography tract at ABS comprised 50–60 scrub-jay family groups. Within the demography tract all birds were uniquely banded, all nests were found and monitored until their fate was known, and censuses of all banded birds were conducted monthly. Mean group size averaged 3 birds but ranged from single pairs to groups with 5 or more helpers. About 7–8 km north of ABS, the suburban development of Placid Lake Estates (PLE) supported 60–70 groups of scrub-jays, occurring in patches of scrub surrounded by suburban development (Bowman 1998).

Human housing density ranged from less than 20 houses to over 120 houses per 40.5 ha (100 acres). However, unlike the fire-maintained scrub of the natural landscape at ABS, the suburban scrub did not burn and tended to be overgrown. Scrub-jays depend on fire-maintained scrub and tend to disappear when the habitat becomes structurally complex (Woolfenden and Fitzpatrick 1984, Breininger and Carter 2003). As at ABS, all birds at PLE were banded, all nests found, but

censuses were conducted quarterly instead of monthly.

### Scrub-jay metabolic rates

To measure field metabolic rates, birds were caught twice within ~24 h. Typically, birds could be caught in small Potter traps the first time, but often second trappings were by drop trap or mist net. In general, birds were caught with peanut baits, but occasionally in the spring, crickets were used. We used only breeding adults in this study; however, one ABS male that was the putative breeder at a territory disappeared not long after it was sampled without having bred. Birds used for FMR studies were processed entirely in the field.

Because Florida Scrub-Jays are listed as Threatened, our sample sizes were sometimes constrained by our concern for possible negative effects of sampling and bleeding. This concern also prevented us from holding scrub-jays after the doubly labeled water (DLW) measurement to measure basal metabolic rate (BMR) in the same individuals. BMR was measured in different individual scrub-jays in a separate study (HIE, unpubl. data). Sample size in the fall was further limited by a lack of success with baited traps when jays were busy caching the annual acorn crop; thus, sample sizes among trapping periods varied. Spring refers to April and May during the breeding season; winter to late January to early February; and fall to September. Spring phenology differed slightly between the 2 sites—breeding at PLE began 2–3 weeks earlier than at ABS (Schoech and Bowman 2003). A total of 29 birds were measured in this study. All fall birds were measured in 1997 and all winter birds were measured in 1999. Most spring birds were measured in 1997, but 4 jays were measured in 1998: 2 females in ABS and 2 males in PLE. A *t*-test comparing the 2 1998 ABS females with the 3 ABS females from 1997 showed no difference ( $t = 0.205$ ,  $df = 3$ ,  $P = 0.851$ ). A similar comparison for PLE showed no difference ( $P = 0.506$ ) between the 2 males from 1998 with the 3 from 1997. Consequently, 1997 and 1998 spring scrub-jays were pooled by sex in our analyses.

### Field procedures

Birds were caught, weighed with a Pesola scale, and injected in their breast muscle with 0.25 mL

DLW, using a 26-gauge needle. The syringe and needle were calibrated for each field season and the coefficient of variation was under 0.5% in all cases. The injection solution was  $^{18}\text{O}$  water enriched with 83  $\mu\text{Ci}$  of  $^3\text{HHO}$  per 25 mL.

Following injection, we held each bird in a darkened box for half an hour while the solution equilibrated in its body water. A small amount of blood was drawn from a brachial vein and immediately flame-sealed in heparinized glass hematocrit tubes and tagged for identification. We then released the bird to its territory. Twenty-four hours after the first blood draw, we re-trapped the bird and bled it for a second sample. If a bird could not be caught within a 23–25 h window, we waited until the next day in order to get a close approximation of a 48 h period. The time error as a percentage from an ideal 24 h window for our sample groups varied only 1–3%. We also bled scrub-jays that had not been injected for background samples. Blood samples were brought to the laboratory of Ken Nagy at the University of California at Los Angeles, where  $^{18}\text{O}$  was analyzed using proton activation (Wood et al. 1975). Tritium was measured with a scintillation counter.

### Water analyses

We calculated TBW and water influx and efflux using equations from Nagy and Costa (1980). We compared TBW using both  $^3\text{H}$  and  $^{18}\text{O}$  and found that the averages were within 1% of each other. However, we used  $^{18}\text{O}$  to estimate water flux and TBW. Both Nagy (1987) and Williams et al. (1993) summarized validation studies that have been done to demonstrate the efficacy of the DLW method for FMR, and Williams et al. (1993) noted studies validating the use of tritiated water to measure water flux.

We converted our measurements (in mL  $\text{CO}_2/\text{g}\cdot\text{h}$ ) into energy equivalents (kJ/d) utilizing conversion factors of 21.9 kJ/L  $\text{CO}_2$  for granivores and 25.7 kJ/L  $\text{CO}_2$  for insectivores as suggested by Nagy et al. (1999). We adjusted those numbers to 22.66 kJ/L  $\text{CO}_2$  for the winter, 24.94 kJ/L  $\text{CO}_2$  for the spring, and 23.42 kJ/L  $\text{CO}_2$  for the fall, based on the diet of the scrub-jays in different seasons (approximately 80% acorns and 20% insects in the winter, 20% acorns and 80% insects during the spring breeding season and summer, and 60%

acorns and 40% insects in the fall; R. Bowman, pers. obs.).

### Statistical analyses

All measures of central tendency and dispersion are means and standard deviations, respectively, unless otherwise noted. Comparisons were made using standard *t*-tests and analyses of variance, including 2-way ANOVA. ANOVA tests are specifically noted in Results; all others are *t*-tests. These tests were accomplished using R 3.4.0 (R Core Team 2017). Following Hurlbert and Lombardi (2009) and Wasserstein et al. (2019), we have not used  $\alpha$ -values to determine arbitrary levels of significance of our statistics. Instead, we provide *P*-values for all our tests, allowing readers to evaluate our interpretation of them.

## Results

### Body mass

During the breeding season, body mass of scrub-jays did not differ by site ( $t = 1.259$ ,  $df = 17$ ,  $P = 0.225$ ). Although body mass in this species is known to fluctuate throughout the day (Brand and Bowman 2012, Cucco and Bowman 2018), average mass change in our birds during the periods over which we measured FMR was minimal. For example, during the spring (breeding season) about half of the birds lost weight and half gained (Table 1). At no time were these changes particularly large compared to body masses (Table 2).

### Field metabolic rates

We found FMR to vary by season and, during breeding, by site for males but not females. FMR during breeding (spring) and nonbreeding (fall and winter) seasons are summarized in Fig. 1.

*Breeding season*—Diet-corrected FMR values (kJ/d) during the breeding season varied (2-way ANOVA) by site ( $F = 15.28$ ,  $df = 1, 15$ ,  $P = 0.001$ ), sex ( $F = 5.01$ ,  $df = 1, 15$ ,  $P = 0.041$ ), and the interaction of site and sex ( $F = 4.39$ ,  $df = 1, 15$ ,  $P = 0.054$ ) (Table 2). Only 4 individuals were sampled in 1998 (2 females from ABS, 2 males from PLE), and after removing those 4 individuals, the effects of site ( $F = 9.19$ ,  $df = 1, 11$ ,  $P = 0.011$ ), sex ( $F = 5.06$ ,  $df = 1, 11$ ,  $P = 0.046$ ), and their interaction ( $F = 3.80$ ,  $df = 1, 11$ ,  $P = 0.077$ )



**Table 1.** Body mass changes in Florida Scrub-Jays in wildlands (ABS) and suburbs (PLE) of Florida in 3 seasons.

Season	Location	Mass loss (g)	Mass gain (g)
Spring (Breeding)	ABS	1.04 ± 0.75 ( <i>N</i> = 5)	1.12 ± 1.15 ( <i>N</i> = 6)
	PLE	1.06 ± 0.58 ( <i>N</i> = 5)	1.33 ± 2.14 ( <i>N</i> = 3)
Winter	ABS	2.28 ± 1.24 ( <i>N</i> = 3) <sup>a</sup>	N/A ( <i>N</i> = 0)
	PLE	4.10 ( <i>N</i> = 1) <sup>a</sup>	N/A ( <i>N</i> = 0)
Fall	PLE	N/A ( <i>N</i> = 0)	2.20 ± 1.98 ( <i>N</i> = 2)

<sup>a</sup> One bird each from ABS and PLE showed no change in mass.

changed little. We therefore assumed that FMR did not vary by year and pooled all years for subsequent analyses.

Looking only at wildland birds (Table 2), we found no difference in FMR between sexes, with male and female values overlapping considerably ( $t = 0.716$ ,  $df = 9$ ,  $P = 0.492$ ). However, within the suburbs, FMRs differed more between males and females whose data sets had almost no overlap ( $t = 2.117$ ,  $df = 6$ ,  $P = 0.079$ ). The difference in sites was ascribable to the PLE males whose FMR ( $502.70 \pm 165.29$  kJ/d) exceeded males at ABS ( $238.93 \pm 47.02$  kJ/d) by over 100% ( $t = 3.767$ ,  $df = 9$ ,  $P = 0.0044$ ). But not all breeding males had active nests when they were measured. When the analysis was limited to males with active nests, breeding males at PLE had still higher FMRs ( $518.11 \pm 186.66$  kJ/d,  $n = 4$ ) than males at ABS ( $242.35 \pm 50.04$  kJ/d,  $n = 4$ ) by 114% ( $t = 2.854$ ,  $df = 6$ ,  $P = 0.029$ ). In all male–male comparisons between sites, the ranges of data values were non-overlapping. Unlike breeding males, female FMR did not differ between the 2 sites ( $t = 0.954$ ,  $df = 6$ ,  $P = 0.377$ ) during the breeding season.

We also compared FMR in females pre- and post-hatching. We had no measurements for females at PLE on eggs, but at ABS we found a

difference ( $t = 4.550$ ,  $df = 3$ ,  $P = 0.0199$ ) between females on eggs ( $169.99 \pm 32.74$  kJ/d,  $n = 3$ ) and females after hatching ( $281.71 \pm 5.15$  kJ/d,  $n = 2$ , where one nest was 2 d and the other 13 d post-hatch). Pooling both sites, we found, with one exception, that breeding female FMRs increased following hatching (Fig. 2). Since both sexes feed older nestlings and fledglings, we also compared FMRs for males and females pooled for each site following hatching. Despite non-overlapping FMR values between the 2 sites and FMR values for PLE adults feeding young 80% higher than at ABS ( $481.77 \pm 180.98$  kJ/d,  $n = 5$ : 3 male, 2 female; vs.  $268.02 \pm 23.99$  kJ/d,  $n = 3$ : 1 male, 2 female), the differences were not strong ( $t = 1.972$ ,  $df = 6$ ,  $P = 0.096$ ), potentially reflecting the large range in FMR at PLE (330–772 kJ/d) as opposed to ABS (241–285 kJ/d).

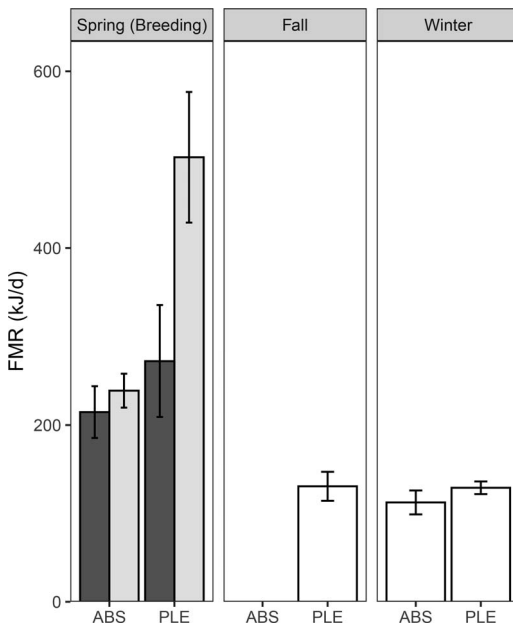
*Nonbreeding seasons*—Our sample size in winter did not allow a reliable comparison of sex, so Table 2 combines sex for winter birds. No real difference ( $t = 0.798$ ,  $df = 4$ ,  $P = 0.469$ ) existed for diet-corrected FMR between ABS birds and PLE birds. Our sample in the fall was even more limited with only 2 birds of unknown sex from PLE. Their diet-corrected FMR was  $130.70 \pm 23.20$  kJ/d. To determine if there was a

**Table 2.** Field metabolic rates (FMR) of Florida Scrub-Jays in wildlands (ABS) and suburbs (PLE) during 3 seasons compared to predicted values. All values for mass are in g, for FMR are in kJ/d.

Season	Location	Sex	<i>N</i>	Mass	FMR	×BMR <sup>a</sup>	% Passerine FMR <sup>b</sup>	% Desert bird FMR <sup>b</sup>
Spring (Breeding)	ABS	Male	6	77.3 ± 3.9	238.93 ± 47.02	3.57	119.51	203.55
		Female	5	74.2 ± 3.6	214.68 ± 65.47	3.35	110.44	188.03
	PLE	Male	5	82.0 ± 7.7	502.70 ± 165.29	7.09	241.59	411.69
		Female	3	74.2 ± 2.5	272.34 ± 109.42	4.25	140.01	238.38
Winter	ABS	Combined	4	74.4 ± 3.1	112.45 ± 27.07	1.75	57.72	98.69
	PLE	Combined	2	70.9 ± 0.6	129.03 ± 10.12	2.11	68.41	116.92
Fall	PLE	Unknown	2	78.8 ± 0.4	130.70 ± 23.20	1.92	64.54	110.41

<sup>a</sup> BMR is basal metabolic rate based on a day/night average 1.856 mL O<sub>2</sub>/g·h (HIE, unpubl. data).

<sup>b</sup> Based on Nagy et al. 1999.

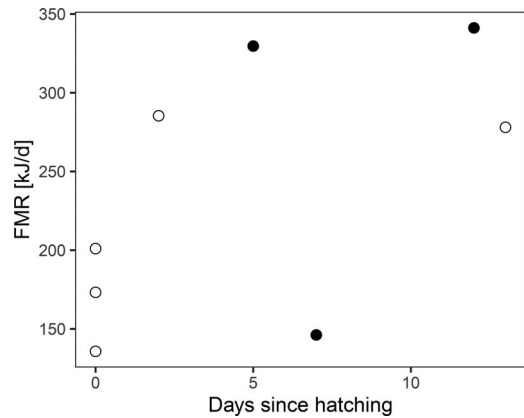


**Figure 1.** Field metabolic rates (FMR) for Florida Scrub-Jays in the wildlands of Archbold Biological Station (ABS) and the suburbs of Placid Lake Estates (PLE), Florida, during breeding (spring) and nonbreeding (fall and winter) seasons. Dark bars indicate females; light bars are males; open bars have combined sexes. Error bars are standard errors.

difference between breeding and nonbreeding seasons, we used an average FMR for all winter and fall scrub-jays ( $121.16 \pm 23.10$  kJ/d,  $n = 8$ ) and compared it with the average for spring ABS birds of both sexes ( $227.91 \pm 58.32$  kJ/d,  $n = 11$ ). We used only ABS birds to keep the comparison conservative. There was a substantial difference ( $t = 4.875$ ,  $df = 17$ ,  $P << 0.001$ ) between the 2 non-overlapping data sets.

### Water relations

Water influx and efflux varied little during DLW measurements, regardless of season or site (Table 3). Water influx did not differ between sexes for all data combined ( $t = 0.898$ ,  $df = 22$ ,  $P = 0.730$ ); thus sexes were pooled for further analyses. Water influx was below that expected for all wild birds and far below that expected for passerine birds as modeled by Nagy and Peterson (1988). Scrub-jay water influx was much closer to that of desert birds from their model.



**Figure 2.** Field metabolic rate of female Florida Scrub-Jays at the nest during the brooding period. FMR is plotted against the number of days post hatching. The highest value shown is 15 d; fledging occurs on day 18. Open circles are wildland birds from ABS; closed circles are suburban birds from PLE. Pearson's correlation  $r = 0.563$  ( $t = 1.668$ ,  $df = 6$ ,  $P = 0.146$ ).

Water influx did not differ between wildland (ABS,  $n = 11$ ) and suburban (PLE,  $n = 8$ ) birds during the breeding season ( $t = 1.641$ ,  $df = 17$ ,  $P = 0.119$ ) and was nearly identical for the 2 sites during winter ( $t = 0.262$ ,  $df = 4$ ,  $P = 0.807$ ). Pooling data for the 2 sites and comparing by season, there was a sharp drop in water influx in winter ( $13.91 \pm 1.07$  mL/d,  $n = 6$ ) compared to spring ( $20.60 \pm 6.10$  mL/d,  $n = 19$ ) ( $t = 2.636$ ,  $df = 23$ ,  $P = 0.0148$ ). Both of our fall birds were from PLE. The water influx for those birds was virtually identical to PLE breeding birds ( $t = 0.211$ ,  $df = 8$ ,  $P = 0.838$ ) but much higher than PLE winter birds ( $t = 5.96$ ,  $df = 2$ ,  $P = 0.0273$ ). TBW did not differ among seasons but within the breeding season ABS scrub-jays had lower TBW than PLE birds ( $t = 2.106$ ,  $df = 17$ ,  $P = 0.0504$ ). Average TBW for all 29 birds was 67.8%.

## Discussion

### Field metabolic rate

Our study explored the daily energy expenditure of Florida Scrub-Jays in 2 different habitats during 3 seasons. We found differences in FMR of scrub-jays based on season, sex, and site. Our most complete data set is during the breeding season during which the FMR of suburban males exceeded that of wildland males by over 100%.



**Table 3.** Water flux and total body water of Florida Scrub-Jays (sexes combined) in wildlands (ABS) and suburbs (PLE) during 3 seasons.

Season	Location	N	Mass <sup>a</sup> (g)	TBW <sup>b</sup> (%)	H <sub>2</sub> O flux <sub>in</sub> (mL/d)	H <sub>2</sub> O flux <sub>out</sub> (mL/d)	H <sub>2</sub> O flux <sub>in</sub> /predicted H <sub>2</sub> O flux <sup>c</sup>			Water economy index (mL/kJ)
							All	Passerine	Desert	
Spring (Breeding)	ABS	11	75.8 ± 4.0	65.6 ± 3.3	18.7 ± 5.7	18.8 ± 5.2	0.67 ± 0.19	0.36 ± 0.10	1.06 ± 0.30	0.083
	PLE	8	79.1 ± 7.3	70.7 ± 7.1	23.2 ± 6.1	23.4 ± 6.0	0.81 ± 0.21	0.43 ± 0.11	1.28 ± 0.33	0.070
Winter	ABS	4	73.8 ± 2.8	67.0 ± 3.0	13.8 ± 1.3	13.2 ± 0.9	0.51 ± 0.05	0.27 ± 0.03	0.80 ± 0.08	0.129
	PLE	2	69.9 ± 0.8	66.6 ± 0.4	14.1 ± 0.7	13.4 ± 1.6	0.53 ± 0.03	0.29 ± 0.02	0.84 ± 0.04	0.084
Fall	PLE	2	78.8 ± 0.4	67.8 ± 3.0	22.2 ± 1.8	20.8 ± 0.6	0.78 ± 0.07	0.41 ± 0.04	1.11 ± 0.09	0.172

<sup>a</sup> Mass is average of capture and recapture values.

<sup>b</sup> TBW is average total body water of capture and recapture values; variation <0.5% for each bird.

<sup>c</sup> Predictions based on equations from Nagy and Peterson (1988).

Average FMRs did not differ between wildland and suburban female birds, but female values increased notably after hatching, because most females begin foraging after hatching (Fig. 2). Males, by contrast, are always actively foraging and defending their territories. Their FMR values are high throughout the breeding season. However, differing local environmental conditions between our 2 sites may result in profound differences in FMR. Despite previous studies that found the amount of time foraging and foraging success did not differ between suburban and wildland populations (Sauter 2005), the preferred foods for feeding nestlings (lepidopteran larvae) are much reduced in the suburbs (Shawkey et al. 2004). Although plant foods are common in the average suburban nestling diet, almost 50% of suburban pairs fed animal foods to their nestlings exclusively, suggesting that some birds may expend much more energy searching for scarce arthropods, rather than feed a low-quality food to their nestlings (Sauter et al. 2006). How much more energy is expended by these males is unclear, because previous studies could not separate those that fed exclusively animal foods versus those that included human-provided plant foods in the nestling diet. However, the FMR value of every sampled male at PLE exceeds the FMRs of all males at ABS.

Because nesting phenology is earlier in the suburbs, suburban jays may begin feeding nestlings before peak arthropod availability (Bowman 1998, Schoech and Bowman 2003), which may influence both energy expenditure and nesting success. Peak foraging demand occurs during the fledgling stage, beginning about 18 d post-hatch (McGowan and Woolfenden 1990), but since none

of our birds was measured during that period of peak demand, it is possible that the site effect we documented could be even larger.

The significance of these higher male FMR values in the suburbs is put in perspective by the FMR/BMR ratios (Table 2). We have separately measured BMR of Florida Scrub-Jays and found nighttime values to be 13.8% lower than daytime values; the mean for night and day was 1.856 mL O<sub>2</sub>/g·h (HIE, unpubl. data). BMR was the same in both habitats. Ellis and Gabrielsen (2019) advised that in computing FMR/BMR ratios, BMR be adjusted for the relevant number of hours of daytime and nighttime. Because of the relatively low latitude of our study area (27.3°N), such adjustments of BMR had minimal effect (<1%), so we used our average value for all our ratios. Drent and Daan (1980) proposed a range of FMR/BMR values that might reasonably be expected in breeding birds. The maximum they suggested was 4.0. Since that time, a few species (primarily seabirds that forage long distances from their nests) have been recorded with ratios approaching 5.0 (Ellis and Gabrielsen 2002). Both male and female scrub-jays from wildlands and females (mostly on nests) from the suburbs have ratios between about 3.0 and 4.0, thus falling within the expected range of Drent and Daan (1980). But male scrub-jays from the suburbs average 7.09, a ratio that is extraordinarily high. Two of these 5 birds have ratios of 8.39 and 9.58; the lowest is 4.60. Male birds from the suburbs appear to be working harder than any other birds reported in the literature.

Because breeding females forage less than breeding males (Stallcup and Woolfenden 1978)

during the time period over which we sampled in the breeding season, it is not surprising that their FMRs were lower. The lowest FMRs for breeding birds came from the 3 incubating females (all from ABS). Their mean FMR ( $169.99 \pm 32.74$  kJ/d) is  $2.67 \times$  BMR. To the extent that FMR can be partitioned (Williams and Dwinell 1990), the difference between BMR and FMR of 106 kJ/d may estimate the increment for the cost of incubation, including the cost of maintaining eggs at the proper temperature, various maintenance activities, and even the rare but occasional feeding foray a female might make. After hatching, FMRs of females at both sites increased over time (Fig. 2) as does the relative proportion of their time spent provisioning older nestlings and fledglings (McGowan and Woolfenden 1990).

Scrub-jays breeding in wildland habitats had FMRs 10–20% higher than expected for passerines (Nagy et al. 1999), while male scrub-jays breeding in suburban habitats were >140% higher (Table 2). In both habitats FMR values for scrub-jays of both sexes are low in the nonbreeding season (>31% below expectation), in spite of active harvesting of acorns in the fall (DeGange et al. 1989) and the possibility of increased thermoregulatory costs in the winter. Fleischer et al. (2003) proposed higher daily energy expenditure in winter than we found, but their value may have been inflated by estimates of BMR and its multiples taken from the literature. However, their conclusion that there is likely no difference in pre-breeding costs between wildland and suburban scrub-jays is confirmed by our findings. Relatively high FMRs in the breeding season may result in part from more active territorial defense and foraging during that season (Woolfenden and Fitzpatrick 1984), but it is difficult to evaluate the low FMR values we found in scrub-jays outside the breeding season. Few other passerines have FMR data for both breeding and nonbreeding seasons, but 2 desert birds, Arabian Babbler (*Turdoides squamiceps*) and Dune Lark (*Mirafra erythroclamys*), do not show such seasonal differences (Anava et al. 2000 and Williams 2001, respectively).

### Water relations

TBW during the breeding season was higher in suburban PLE birds than in wildland ABS birds.

Since a reduction in TBW may correlate with an increase in fat (Ellis and Jehl 1991), it is possible wildland birds have a slight advantage over suburban jays in energy stores. But the TBW differences were not great and we did not measure fat directly. To the extent that TBW and fat are related, the nearly identical TBWs of PLE and ABS birds in the winter in this study agree with the findings of Schoech and Bowman (2003) of no differences in lipids comparing pre-breeding scrub-jays in wildlands and suburbs. The overall average for all sampled birds (67.78%) is consistent with that of lean birds (Ellis and Jehl 1991). Considering how energetically stressful breeding can be, especially in the suburbs, this species does not seem to prepare for it in advance by laying on fat.

Water flux varied by season, but not site (ABS and PLE; Table 3). Water influx was lower during the winter pre-breeding season than in the combined spring breeding and fall seasons ( $t = 3.016$ ,  $df = 25$ ,  $P = 0.0058$ ). The Lake Wales Ridge is a xeric environment because water percolates rapidly through the sandy soils, making it quickly unavailable following rains, and seasonal ponds are often dry during the winter when rainfall is lowest. However, it is also likely that this difference reflects changes in diet. In winter, the diet is predominantly acorns, which may have relatively less water content than arthropods, large orthopterans, and lepidopteran larvae typical of the spring diet. Compared with all wild birds, and even more dramatically passerine birds (Nagy and Peterson 1988), scrub-jays have a very low water influx rate, especially in the winter (Table 3). Although they do not resemble desert birds energetically (Table 2), they seem very much like desert birds in their water economy. Although a higher TBW and slightly elevated water influx in breeding suburban PLE birds suggest that urban influences and perhaps nearby agriculture may mitigate the xeric conditions of the Lake Wales Ridge, this is a minor compensation.

Nagy and Peterson (1988) suggested using an existing ratio, the “water economy index” (WEI), to determine the relationship between water economy and energy use. WEI is the ratio of water flux (in mL H<sub>2</sub>O/d) to field metabolic rate (kJ/d), hence it is in units of mL H<sub>2</sub>O/kJ. WEI in scrub-jays is lowest for birds during the breeding season and is lower than that of many desert birds

(Nagy and Peterson 1988). This probably reflects their higher energy demands during breeding.

### Conclusion

Field metabolic rates reflect ecological conditions. The greater demands of the breeding season are reflected in higher FMRs than in other seasons for Florida Scrub-Jays. Contrary to our initial prediction, we found males in the breeding season to have very high values of FMR in the suburbs. We believe these values reflect the many changes that accompany the degradation of their habitat. The 7.1 FMR/BMR multiple seen there seems to be at, if not beyond, the upper limit of sustainable energy expenditure. This is important because, as Williams (1993) noted, approaching this limit may incur a fitness cost. Survival of breeding males in the suburbs is lower than males in the wildlands, but so is that of females, even though female FMRs did not differ from those of wildland females. However, it may be difficult to determine the fitness cost of a high FMR in suburban males. In the suburban habitat, most jays are exposed to artificial night light, but that does not appear to depress DEE. Similarly, the anthropogenic availability of water seems to have little or no effect on water flux.

The high FMR values for breeding male scrub-jays in the suburbs suggest these males are working harder than wildland males to provide food for their mates and offspring during the breeding season, but that other behavioral differences that influence DEE of jays in suburban and wildland habitats may also exist. These patterns are consistent with other evidence suggesting that this species is negatively affected by suburban development and that most suburban populations are typically demographic sinks, not sources (Bowman 1998, Boughton and Bowman 2011). This study emphasizes the value of using conservation physiology as a component in deciphering the causes of population decline that accompany increased urbanization in many species of birds.

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