

BROOD SIZE AND THERMAL ENVIRONMENT INFLUENCE FIELD METABOLISM OF NESTLING YELLOW-EYED JUNCOS

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ABSTRACT.—We used the doubly-labeled-water method to examine the effect of thermal environment (mean shade air temperature) and brood size (two to six young) on field metabolic rate of nestling Yellow-eyed Juncos (*Junco phaeonotus*). The relationship between brood size and nestling field metabolic rate was curvilinear, such that nestling energy expenditure was lowest in broods of four (the most common clutch size) and highest in broods of two (the smallest brood size). Mean air temperature accounted for 21.0% of the variation in nestling field metabolic rate, whereas brood size accounted for 17.5% of the variation. Although brood reduction would decrease the brood's field metabolic rate, the reduction is not proportional to the decrease in brood size. Received 15 November 1990, accepted 27 June 1991.

LACK (1947) proposed that clutch size in altricial birds is determined by the maximum number of young that parents can feed adequately. Whereas some studies have supported this contention by documenting increased nestling mortality or decreased nestling mass in enlarged broods, in many species the most productive clutch size exceeds the most common clutch size (reviewed in Martin 1987). To accommodate such findings, Lack's hypothesis was refined to incorporate costs to parents that raise enlarged broods, such as increased energy demand or decreased survival (Williams 1966, Charnov and Krebs 1974). The existence of such costs, which are assumed to create a tradeoff between current and future reproductive success, is basic to life-history theory and to predictions concerning optimal clutch size in birds (Fisher 1930, Williams 1966, Charnov and Krebs 1974, Stearns 1976, Lindén and Møller 1989). The relationship between brood size and parental cost has proven difficult to quantify, however, because of variation in individual foraging ability, territory quality, within- and between-season effects, and the potential for bet-hedging strategies (Bryant 1988, Lindén and Møller 1989, Frank and Slatkin 1990). This is unfortunate, because predictions of optimal clutch size depend upon the nature of this relationship (Bryant 1988). Evaluating the effect of brood size on parental costs becomes even more problematical if brood energy requirement is a nonlinear function of brood size, as is suggested by several indirect measures of brood energy demand (Royama 1966, Mertens 1969, O'Connor 1975, Dunn 1976, Crossner 1977, Westerterp et al. 1982).

Most previous studies of the relationship between brood size and nestling energy requirements have weighed nestlings (Royama 1966, Crossner 1977, van Balen and Cavé 1970, Mertens 1977), estimated food consumption and feces production (Westerterp 1973, Royama 1966, Bryant and Gardiner 1979, Westerterp et al. 1982), or extrapolated laboratory measurements of nestling oxygen consumption to the field (O'Connor 1975, Mertens 1969, 1977, Westerterp 1973). Each of these indirect measures has inherent limitations. The first method, determining nestling growth curves, does not distinguish effects of brood size from those of weather on food availability or parental effort. The second method is unreliable because of the difficulty in accurately quantifying food delivery and feces production (Hubbard 1978). The third method typically underestimates nestling energy requirements by neglecting the costs of activity and thermoregulation (Gettinger et al. 1985, but see Bryant and Gardiner 1979, Westerterp 1973). In Savannah Sparrows (*Passerculus sandwichensis*), for example, this latter method underestimated nestling energy requirements by 25% (Williams and Prints 1986). As an alternative to these indirect methods, nestling energy demand can be determined directly using the doubly-labeled-water (DLW) technique. The DLW method measures energy expended on basal metabolism, thermoregulation, activity, the heat increment of feeding, and biosynthesis, but not the energy accumulated as new tissue. Only a few such measurements have been made, however (Gettinger et al. 1985, Williams and Nagy 1985, Williams and Prints 1986, Klaassen et al. 1989, Weathers and

Sullivan 1989, 1991, Weathers et al. 1990, Mock et al. 1991). Only Williams and Nagy (1985) have examined the effect of brood size on daily energy expenditure, and found no significant difference between Savannah Sparrow nestlings in broods of two or three. To better understand the relationships between brood size and brood energy requirements, we used the DLW technique to measure directly nestling Yellow-eyed Junco (*Junco phaeonotus*) energy requirements (exclusive of the energy incorporated into new tissue) in broods of two to six young.

METHODS

Our study site in the Chiricahua Mountains of southeastern Arizona (Rustler Park, elevation 2,560 m) is a forest containing little understory and areas of short grass meadow and bracken fern (*Pteridium* sp.). The predominant tree species are *Pinus ponderosa*, *P. strobiformis* and *Pseudotsuga menziesii* (for a detailed site description, see Balda 1967).

We recorded clutch size for 239 nesting attempts during the 1984–1988 breeding seasons. Nests that failed prior to incubation or within two days of the onset of incubation were classified as incomplete and were not included in our analysis.

We used the DLW technique to determine the field metabolic rate (FMR) of nestling juncos in broods of two to six between 14 June and 2 July 1985 ($n = 22$ nestlings), and 6 June and 13 July 1988 ($n = 43$ nestlings). Seventeen nestlings were not included in the analysis for the following reasons: sample lost in processing ($n = 2$), nestling disappeared ($n = 3$), and nestling fledged ($n = 12$).

Because the vast majority of Yellow-eyed Junco nests contain either three or four young, we manipulated brood size at eight nests during the 1988 field season to produce different-sized broods. Nestlings were exchanged either at the time they were injected with DLW or 24 h prior to injection. We matched nestlings to be transferred as closely as possible for size and age to achieve a range in nestling weights within augmented clutches that was not significantly different from that of naturally occurring clutches (augmented nests, 2.6 ± 1.2 g [$\bar{x} \pm SD$], $n = 5$ vs. natural nests, 2.2 ± 0.9 g, $n = 20$; $t = 0.84$, $df = 23$, $P > 0.05$). To accommodate potential weather effects on metabolic rate, we simultaneously measured FMR in an enlarged brood (5–6 nestlings), a normal brood (3–4 nestlings), and a reduced brood (2 nestlings). After the second DLW measurement, we returned nestlings to their original nest.

The nestling stage typically lasts 10 to 13 days in Yellow-eyed Juncos. We injected nestlings with DLW four to eight days after hatching (85% were either five or six days post-hatching). At this age, nestlings are

partially feathered and are brooded for only 9% of the daylight hours (unpubl. data). Nestlings were given an intramuscular injection of water containing 97 atom% ^{18}O and about 0.6 MBq ^3H ; they were returned to their nest to allow the labeled water to reach equilibrium with body water. After 1 h, we weighed the nestlings to the nearest 0.05 g with a portable electronic balance, obtained duplicate 0.05-ml blood samples from the brachial vein, and replaced the nestlings in their nests. The blood samples were stored in flame-sealed glass microhematocrit tubes at 4°C for later analysis. Approximately 24 h later (range 23.8–24.3 h) the nestlings were reweighed and a second set of duplicate blood samples was obtained. As the time of injection ranged from 0730 to 1430, all nestlings were fed before blood sampling, and errors due to diurnal variation in gut-fill should be minimal.

Blood samples were micro-distilled (Wood et al. 1975) to obtain pure water, which was assayed for tritium activity (Searle model Mark III liquid scintillation counter, toluene-Triton X100-PPO scintillation cocktail) and for oxygen-18 content by cyclotron-generated proton activation of ^{18}O to fluorine-18 with subsequent counting of the positron-emitting ^{18}F in a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Using the equations of Lifson and McClintock (1966), as modified by Nagy (1975), we calculated rates of CO_2 production from the isotope measurements.

Concurrent with the DLW measurements, we monitored shade air temperature (T_a) 1 m above the ground at a central location in Rustler Park (copper-constantan thermocouple, Campbell Scientific 21X microdata logger). Most nests were located within 200 m of the site at which T_a was measured. The T_a was measured at 60-s intervals and averaged every hour in 1985, and measured at 10-s intervals and averaged every 10 min in 1988. Yellow-eyed Juncos typically place their nests in shaded locations on the ground, such as under rocks or fallen logs, or in vegetation. The T_a at such sites is close to shade temperature measured 1 m above ground (Weathers and Sullivan, unpubl. data). Thus, T_a as we measured it approximates the nest's thermal environment.

Potential errors.—Errors in calculated rates of CO_2 production using the DLW technique can result both from analytical errors in the isotope measurements and from insufficient isotope turnover (Nagy 1980). Although we did not validate the DLW method specifically for nestling juncos, in earlier validations of our technique using Budgerigars (*Melopsittacus undulatus*; Buttemer et al. 1986) and Verdins (*Auriparus flaviceps*; Webster and Weathers 1989), DLW measurements of CO_2 production of individuals differed by less than 9% from values determined simultaneously by the Haldane method (mean difference <2%). The amount of isotope turnover which occurred in our juncos was consistent with minimal measurement error (Nagy 1980). Final ^{18}O concentra-

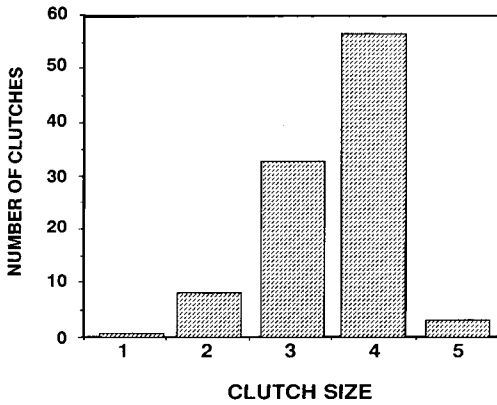


Fig. 1. Frequency of completed clutch sizes in this population of Yellow-eyed Juncos.

tion averaged 51% of initial ^{18}O (range 20 to 71%), whereas tritium turnover averaged 83% of ^{18}O turnover (range 60% to 89%).

Errors may attend DLW measurements of rapidly growing animals owing to irreversible and disproportional incorporation of isotopes into body tissue (Nagy 1980, Williams and Nagy 1985). Although the extent of the error remains uncertain for Yellow-eyed Juncos, Klaassen et al. (1989) validated the DLW method for rapidly growing Arctic Tern chicks (*Sterna paradisaea*). They found that DLW underestimated CO_2 production (measured by indirect calorimetry) by 4% during a first 24-h measurement period and by 16% during a second 24-h period. Presumably the error is a function of the amount of growth that occurred during the measurement period. Mass changes for nestling juncos in our study ranged from -4.0% to $+22\%$ (mean = $9.3 \pm 2.1\%$). Seventeen nestlings gained or lost less than 5% of their initial mass, whereas 31 gained more than 5% of their initial mass during the one-day measurement period. Because all of our DLW measurements were based on one-day samples, and growth was moderate, the error attributable to incorporation of isotopes into tissue is probably small (perhaps $<5\%$). Furthermore, because change in body mass during the DLW measurements was unrelated to brood size ($r = 0.076$), any observed pattern be-

TABLE 1. Stepwise regression of mean shade air temperature, brood size, and nestling mass on nestling CO_2 production (df = 2 and 45, $r^2 = 0.41$, $F = 15.69$, $P < 0.01$).

Factor	Coefficient	SE
Intercept	9.46	
Mean air temperature	-0.235	0.056
Brood size	-0.254	0.066
Mass	ns ($P > 0.05$)	

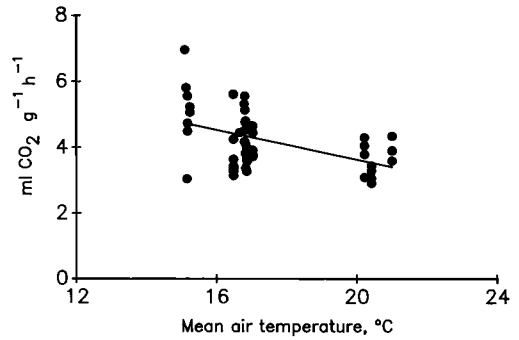


Fig. 2. Relationship between mean air temperature and CO_2 production of nestling juncos.

tween metabolic rate and brood size is uncomplicated by systematic bias.

Unless indicated otherwise, values are the mean \pm 1 SD.

RESULTS

Completed clutches ranged in size from one to five eggs. Clutches of one, two, and five were rare, and 56% of all nests contained four eggs (Fig. 1).

We examined the effect of brood size on nestling CO_2 production ($\dot{V}\text{CO}_2$) along with two other potential determinants of nestling energy expenditure, air temperature and nestling mass. Among nestlings of the same age, $\dot{V}\text{CO}_2$ ($\text{ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) was strongly influenced by both mean air temperature and brood size but not by nestling mass (Table 1). Mean air temperature was the first term entered into the stepwise-regression equation and accounted for 21.4% of the variation in nestling $\dot{V}\text{CO}_2$ (Fig. 2). Brood size, the second and last variable entered, accounted for 17.5% of the variation in $\dot{V}\text{CO}_2$. Statistically holding temperature constant, brood size accounted for 25.9% of the variation in nestling energy expenditure (partial correlation, $P < 0.01$). We designed our experiment to control for potential weather effects by simultaneously measuring a small-, medium-, and large-sized brood. Our experimental design was effective in that brood size showed a low correlation with T_a ($r = 0.55$, df = 47, $P > 0.05$), and there was a very high interaction between brood size and temperature ($r = 0.95$, df = 47, $P < 0.05$). Multicollinearity resulting from our experimental design precluded us from including an interaction term between brood size and tempera-

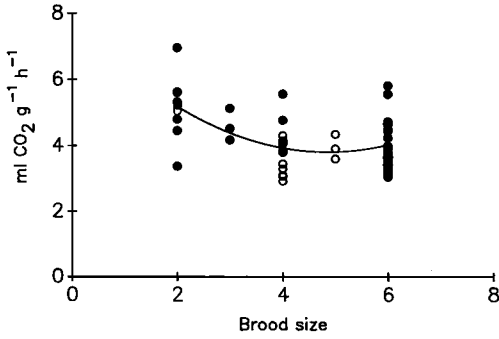


Fig. 3. Relationship between brood size and CO₂ production of nestling juncos.

ture in our stepwise regression analysis (S. Durham, pers comm).

Nestling FMR was lowest in broods of four, the most common brood size. Nestlings in broods of two had significantly higher FMR than nestlings in broods of four or six young (ANOVA, $F = 7.87$, $df = 2$ and 39 , Scheffé F -test, $P < 0.05$). Differences in FMR between broods of four and six were not statistically significant. The relationship between FMR ($\text{ml CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) and brood size (B) is nonlinear (Fig. 3) and is best described by the quadratic equation:

$$\text{FMR} = 7.81 - 1.65B + 0.17B^2$$

($r^2 = 0.287$, $df = 2$ and 45 , $P < 0.01$). The quadratic term provides a significantly better fit than a linear regression ($F = 7.09$, $df = 1$ and 45 , $P < 0.05$).

We used the mean $\dot{V}\text{CO}_2$ of nestlings in broods of two to six to determine the entire brood's $\dot{V}\text{CO}_2$ over this range of brood sizes (Table 2). We then compared the entire brood's $\dot{V}\text{CO}_2$ with that expected if the nestlings had metabolic rates

TABLE 3. Consequences of brood reduction for most common brood sizes found in Yellow-eyed Juncos.

Original brood size	Entire brood cost ^a	Reduced brood size	New-brood cost	Percent decrease in brood	
				Size	Cost
4	15.44	3	13.85	25	10
4	15.44	2	10.34	50	33
3	13.85	1	10.34	33	25

^a Total CO₂ produced ($\text{ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) based on Table 2.

equal to those of nestlings in broods of four (i.e. $3.86 \text{ ml CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$). The $\dot{V}\text{CO}_2$ of entire broods was 102 to 134% of the predicted brood costs based on the energy expenditure of nestlings in broods of four (Table 2). We also used the entire brood $\dot{V}\text{CO}_2$ to examine the effect of brood reduction on brood metabolic rate. Although brood $\dot{V}\text{CO}_2$ decreased when brood size was reduced, the reduction in $\dot{V}\text{CO}_2$ was not proportional to the number of young lost (Table 3).

Augmented broods (one with four young, four with six young) contained both original and introduced nestlings. There was no significant difference in mean $\dot{V}\text{CO}_2$ ($\text{ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) of original versus introduced young (original, $\bar{x} = 4.23 \pm 0.81$, $n = 14$; introduced, $\bar{x} = 3.94 \pm 0.76$, $n = 11$; Student's $t = 0.92$, $df = 23$, $P > 0.05$).

Most nestlings (90%) gained mass during the 24-h period between blood samples. Mass changes ranged from -0.55 g (-4%) to 2.14 g ($+22\%$). Both mass change and percent mass change were independent of brood size (mass change, $r^2 = 0.028$, $df = 47$, $P = 0.26$; percent mass change, $r^2 = 0.006$, $df = 47$, $P = 0.61$).

TABLE 2. Observed and predicted CO₂ production of Yellow-eyed Junco broods containing different numbers of nestlings.

Brood size	n	Single nestling ($\bar{x} \pm \text{SD}$)	CO ₂ production ($\text{ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$)		Percent increase ^c	Nestling equivalents ^d
			Observed ^a	Predicted ^b		
2	9	5.17 ± 0.97	10.34	7.72	34	2.7
3	3	4.62 ± 0.49	13.86	11.58	20	3.8
4	12	3.86 ± 0.78	15.44	—	—	—
5	3	3.95 ± 0.38	19.75	19.30	2	5.1
6	21	4.03 ± 0.77	24.18	23.16	4	6.3

^a Mean CO₂ production per nestling multiplied by number of nestlings in brood.

^b Predicted CO₂ production of brood this size assuming each nestling's CO₂ production equivalent to that of nestling in brood of 4.

^c $100(\text{observed} - \text{predicted})/\text{predicted}$.

^d Observed brood CO₂ production/CO₂ production of nestling in brood of 4.

DISCUSSION

Among Yellow-eyed Juncos, brood size has a significant, nonlinear effect on nestling field metabolic rate, with the most common clutch size (four young) also being the most efficient brood size. The thermoregulatory benefit of huddling most likely accounts for the decrease in nestling energy expenditure when brood size increases from two to four young. Our direct field measurements thus support the conclusion derived from laboratory studies and indirect field measurements that thermoregulatory advantages experienced by larger broods partially compensate for their increased energy requirements (Royama 1966, Mertens 1969, 1977, O'Connor 1975, Dunn 1976, Crossner 1977, Westerterp et al. 1982).

Nestling Yellow-eyed Juncos in broods of six probably did not have a thermoregulatory advantage over nestlings in broods of four, however. Nestlings in broods of six had difficulty fitting into the nest and some either partially extended beyond the nest rim or formed two layers of nestlings within the nest. This probably increased activity costs in the enlarged broods, which may account for the apparent upturn in metabolism in broods of six (Fig. 3). An increase in per-nestling metabolic rate has been observed in several species as brood size increases beyond the modal level. Westerterp et al. (1982) suggested that European Starlings (*Sturnus vulgaris*) in broods of seven expended more energy than those in broods of five, because of increased activity levels, competition for food, and deterioration of the insulative quality of the nest. In large broods of Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*; Mertens 1969, 1977, van Balen and Cavé 1970, O'Connor 1975), hyperthermia seemed to increase metabolism over that of smaller broods. Hyperthermia is unlikely to occur among nestlings of species like the Yellow-eyed Junco, which have fairly small broods (2-5 young) and build open-cup nests; increased activity costs are likely responsible for the rise in $\dot{V}CO_2$ of enlarged broods.

A nonlinear relationship between brood size and nestling $\dot{V}CO_2$ complicates interpretations of the effect of brood size on parental costs. A 25% reduction in the typical brood size results in only a 10% decrease in the brood metabolic rate (Table 3). This and previous studies indicate that predictions of optimal clutch size need

to take the thermal characteristics of the brood into consideration.

Although brood size was a significant predictor of nestling junco metabolic rate, the thermal environment (based on shade air temperature) accounted for a greater percentage of the variance in nestling $\dot{V}CO_2$. For open-cup nesters with relatively small broods (2-5 young), nest microhabitat and day-to-day variation in weather may have a larger effect on brood energy demand than does variation in brood size. If so, selection on nest site and/or nest structure may be stronger than selection on clutch size. Williams and Prints (1986) found no significant difference in energy expenditure of nestling Savannah Sparrows in broods of two or three young. Over this small range of brood sizes, the thermal environment may be a much larger determinant of energy requirements than is brood size.

Even though the most efficient brood size for Yellow-eyed Juncos is also the most common clutch size, it does not necessarily follow that this is the optimal clutch size for this population. Translating brood energy requirements into parental cost is not a straightforward task. Although we found a significant effect of brood size on nestling metabolic rate, we found no significant effect of brood size on daily energy expenditure among parents raising natural or manipulated clutches (T. Gumbart et al., unpubl. data). Additional studies that examine nestling and fledgling growth, as well as survival and parental survival, in natural and manipulated clutches are needed to determine the optimal clutch size of this and other species.

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