

# BREEDING ENERGETICS AND THERMAL ECOLOGY OF THE ACORN WOODPECKER IN CENTRAL COASTAL CALIFORNIA<sup>1</sup>

WESLEY W. WEATHERS

Department of Avian Sciences, University of California, Davis, CA 95616

WALTER D. KOENIG AND MARK T. STANBACK

Hastings Natural History Reservation and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720

**Abstract.** We used the doubly labeled water (DLW) technique to measure the field metabolic rate (FMR) of adult ( $n = 4$ ) and nestling ( $n = 30$ ) Acorn Woodpeckers (*Melanerpes formicivorus*). Resting metabolic rate (RMR) of adults and nestlings was calculated from  $O_2$  consumption. We constructed the nestlings' energy budget from measurements of the growth rate, FMR, and RMR of different aged nestlings. We measured the body temperature ( $T_b$ ) of two nestlings in the field using implanted radiotelemeters, assessed the nestlings' thermal environment in terms of the air temperature ( $T_a$ ) experienced inside and outside of nest cavities, and studied the ontogeny of nestling homeothermy in the laboratory.

Adult FMR averaged 195 kJ/day, which is 30% lower than predicted from adult mass (82 g) and 2.7 times the measured basal metabolic rate. Nestling FMR (kJ/day) increased with mass ( $m$  in grams) according to the relation:  $FMR = -27.1 + 2.4m$ . Nestling FMR stabilized at about 160 kJ/day (82% of the adult level) by 3 weeks of age.

Nestlings, which are adult sized when they fledge 30–32 days after hatching, grow relatively slowly. Their logistic growth rate constant ( $K = 0.226$ ) is 30% lower than predicted from their mass and is equivalent to that of a tropical species of their size. Nestlings also develop endothermy much more slowly than expected and are unable to maintain adult  $T_b$  when exposed to 15°C for 30 min until they are 3 weeks old. In the field, nestling  $T_b$  fluctuated until about 3 weeks of age, apparently due to intermittent brooding by the adults.

Nestlings metabolized an average of 3,853 kJ/bird over the nestling period (age: 0–31 days). Of the total, RMR comprised 46.8%, whereas activity, thermoregulation, and the heat increment of feeding combined accounted for 40.2%. The energy accumulated in growth amounted to 501 kJ, or 13% of the total. Gross growth efficiency (ratio of energy accumulated in tissue to total metabolized energy) is the lowest reported for any bird. Two factors contribute to low growth efficiency: (1) a slow growth rate, which may result in part from tannins contained in the nestling's partially acorn diet, and (2) thermostatic costs associated with a low nest-cavity  $T_a$ . These unusual physiological features indicate that energetic constraints may play an important role in influencing the costs and benefits of group living in this cooperatively breeding species.

**Key words:** Acorn Woodpecker; doubly labeled water; reproduction; thermoregulation; growth; nestling; body temperature; energy metabolism; *Melanerpes formicivorus*.

## INTRODUCTION

Acorn Woodpeckers (*Melanerpes formicivorus*) are unusual for at least two reasons. First, they are cooperative breeders that live in family groups of up to 15 adults, all of which cooperate in rearing young at a single nest (Koenig and Mumme 1987). Second, they depend upon acorns, which they eat as fresh mast in the autumn and store, often by the thousands, in specialized storage trees called granaries. Stored acorns are critically important to overwinter sur-

vival and reproductive success in both California (Koenig and Mumme 1987) and New Mexico (Stacey and Koenig 1984), and are an important constraint leading to cooperative breeding in this species. Koenig and Mumme (1987) proposed that granary stores constitute a limited resource whose importance to survival and reproduction makes nondispersal by offspring virtually obligatory until such time, if any, that they acquire a breeding position in the population.

Although food resources may have thus played a central role in the evolution of cooperative breeding in this species, we lack basic information concerning the energy requirements of Acorn Woodpeckers or how they allocate energy to re-

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production. To fill this gap, we report here the results of a study of the breeding energetics and thermal ecology of the Acorn Woodpecker. This work reveals several highly unusual features of the physiological ecology of this species, including extremely slow nestling growth and remarkably low growth efficiency. These characteristics reinforce the impression gained from demographic studies of marked individuals (Koenig and Mumme 1987) that Acorn Woodpeckers are adapted to conditions of extreme food or nutrient limitation, which are only partly mitigated by group living and acorn storage.

#### METHODS, STUDY SITE, AND SPECIES

We studied the energetics and thermal ecology of adult and nestling Acorn Woodpeckers during the 1985 and 1986 breeding seasons. To accomplish this we (1) monitored the body mass of nestlings growing in the field, (2) measured the resting oxygen consumption of adults and young in the laboratory, (3) assessed the birds' thermal environment under field conditions in terms of the air temperature ( $T_a$ ) experienced inside and outside of nest cavities, (4) used the doubly labeled water (DLW) technique to measure total daily energy expenditure and water flux of adults and nestlings, (5) measured the body temperature of nestlings in the field using implanted radiotelemeters, and (6) quantified the ontogeny of nestling endothermy under laboratory conditions.

Our study site was on and adjacent to Hastings Natural History Reservation, a 900-ha reserve in the upper Carmel Valley, Monterey County, California, where a color-marked population of Acorn Woodpeckers has been under continuous study since 1971 (Koenig and Mumme 1987). A description of the reserve, its plant communities, and climate are available in MacRoberts and MacRoberts (1976) and Koenig and Mumme (1987).

#### ENERGY TERMS AND CONCEPTS

Efforts to standardize usage of energy terms and concepts (e.g., NRC 1981, Calder 1982) have not met with universal acceptance, owing in part to differing requirements among subdisciplines. Accordingly, we herein describe the terms and concepts used in our study.

Field metabolic rate (FMR) is the rate of  $\text{CO}_2$  production of free-living animals as measured by the DLW technique. When converted to units

of energy (kJ/day), it represents total heat production (or loss). FMR equals metabolized energy (ME) when there is no net synthesis of body tissue (fat, protein, or carbohydrate), or other production (e.g., crop milk, or ova). The sum of FMR and energy retained as growth or production constitutes total metabolized energy (TME). Resting metabolic rate (RMR) is the rate of heat production (calculated from  $\text{O}_2$  consumption in this study) of a fasted animal measured at rest and in the dark during the active phase of its daily cycle. RMR increases at temperatures below the lower critical temperature due to thermoregulatory costs. Basal metabolic rate (BMR) is the rate of heat production of resting, fasted animals measured in the dark within the thermal neutral zone during the rest phase of their daily cycle. In the absence of direct measurements, the BMR of adult birds can be estimated as 0.75 times the thermoneutral RMR (Aschoff and Pohl 1970). Tissue energy (TE) is the total gain (or loss) of gross energy contained in body tissue of an animal. Gross energy (E) is the energy released as heat when an organic substance is completely oxidized to  $\text{CO}_2$  and water.

#### NESTLING GROWTH AND DEVELOPMENT

Growth rate of nestlings was determined by weighing known-aged nestlings between 1975 and 1988. Nestlings were weighed at irregular intervals depending on accessibility of nests. Many nestlings were weighed at intervals of 2 to 3 days, whereas others were only weighed two or three times during the entire nestling period. Measurements were made from day 0 (hatching day) to day 29, 1 to 3 days prior to fledging. Sample sizes for particular ages varied, but in all, 3,660 measurements were made on over 300 different individuals. Only masses of individuals that survived to 22 days of age, when birds were permanently banded, were included. We photographed nestlings at different ages to provide a pictorial record of their development.

#### RESTING METABOLIC RATE (RMR)

*Adults.* We determined adult basal and thermoregulatory energy requirements (maintenance metabolism) by measuring fasting oxygen consumption ( $\dot{V}\text{O}_2$ ) of four woodpeckers (mean mass: 73.1 g) that rested in the dark at stable ambient temperatures between 0 and 38°C during the active phase of their daily cycle. Measurements were also made on fasted birds at night at 36°C.

Between measurements, which were made from 17 May–9 August 1985 and 3–26 May 1986, the birds were housed in outdoor flight aviaries and were provided ad libitum with water and kibble-type, dry, dog food (Purina Hi-Pro). All four adults maintained mass and vigor throughout the measurements.

$\dot{V}O_2$  was determined with an open-circuit respirometry system. Details of the methods, apparatus, and calibration procedures used in these measurements are presented elsewhere (Weathers et al. 1980). For these determinations, birds were placed in either 4-l metal metabolism chambers lined with paper towels or in a hardware cloth (wire) cage contained within a 14-l Plexiglas metabolism chamber. In the latter chambers, birds clung to the wire in a normal upright posture. During the day, lower and more stable oxygen consumption rates were obtained for birds clinging to the wire cages than for birds resting on the floor of the 4-l chambers, and hence we report only the former values. At night both chambers gave comparable values. Body temperature ( $T_b$ ) was determined at the end of each run by inserting a polyethylene-sheathed thermocouple into the cloaca to a depth such that no decrease in  $T_b$  occurred upon slight withdrawal. The thermocouple was calibrated against a mercury thermometer certified by the National Bureau of Standards.

*Nestlings.* The  $\dot{V}O_2$  of fasted, nestling woodpeckers resting in the dark during the day was determined between 4 May to 3 June 1986 at Hastings Reservation. For these measurements, nestlings were removed from their nest in the late morning, taken immediately to the laboratory, and placed in an incubator maintained at 36–37°C. They were syringe-fed a semiliquid diet (Gerber's baby food), returned to the incubator for 30 min, and then their thermoregulatory index (TI) was determined (see below). Following the TI determinations, they were placed in individual felt-lined plastic nest bowls housed within a 4-l metal metabolism chamber maintained at 36–37°C. After a 1-hr equilibration period, nestling  $\dot{V}O_2$  was determined using the open-circuit apparatus described above.  $T_b$  was determined at the end of the run as for adults.  $\dot{V}O_2$  measurements began no sooner than 3 hr following the last feeding. For both adults and nestlings, we converted  $\dot{V}O_2$  to metabolic heat production assuming that 20.1 kJ of heat were produced per liter of  $O_2$  consumed.

#### FIELD METABOLIC RATE (FMR)

We used the DLW technique to measure FMR of four adult and 30 nestling woodpeckers. All of the adults were feeding nestlings. Birds were captured on their territory, weighed to the nearest 0.05 g (K-Tron model DS-10 balance) and given an intramuscular injection of water (2.5  $\mu$ l/g body mass) containing 97 atoms-percent  $^{18}O$  and ca. 12 MBq  $^3H$  per ml. Following injection, nestlings were immediately returned to their nest for isotopic equilibration, whereas adults were held in cloth bags. After allowing 1 hr for the labeled water to reach equilibrium with body water, we obtained duplicate 50- $\mu$ l blood samples from a brachial vein and stored them at 4°C in flame-sealed glass microhematocrit tubes for later analysis. The adults were then released back onto their territory and the nestlings returned to their nest. Approximately 1 or 2 days later, the birds were recaptured, reweighed, and a second set of duplicate blood samples obtained. The elapsed time between initial and final blood samples averaged  $24.1 \pm 0.29$  hr (range = 23.9–25.5 hr) for "1-day" samples ( $n = 30$ ), and  $49.0 \pm 1.81$  hr (range = 47.7–51.7 hr) for "2-day" samples ( $n = 4$ ; three of them adults). For nestlings, the time of initial capture ranged from 10:50 to 18:10. Because all nestlings had time to feed before capture or recapture, errors due to diurnal variation in gut-fill should be minimal. All nestlings within a given brood were given the same dose of DLW to minimize error due to their breathing exogenous  $CO_2$  having a different isotopic ratio than that of their body.

Adult woodpeckers proved to be difficult study subjects. Two of the four adults were initially captured at their nests before they fed in the morning. One of these (No. 9) was recaptured the following morning at about 06:40, the other (No. 10) was recaptured 2 days later at 11:27. The other two individuals were initially captured at around 13:00 and 17:00 as they came to their nests to feed nestlings. These two individuals were recaptured approximately 2 days later. Thus, for one of the four adults, gut-fill may have resulted in a slight overestimate of mass change and perhaps a 5% error in FMR. Two of the four adults that we measured (a male and female from the same nest) were fitted with radio transmitters (Biotrack Pty.) to aid in tracking them. A 2-g transmitter was glued to the feathers of the female's back, while a 4-g transmitter was similarly

attached to the male's back. The time budget of the female was determined after her release with the aid of a Radio Shack model TRS100 micro-computer (P. Hooge, unpubl. data).

Blood samples were microdistilled (Wood et al. 1975, Nagy 1983) 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  $^{18}\text{O}$  to fluorine-18 with subsequent counting of the positron-emitting  $^{18}\text{F}$  in a Packard Gamma-Rotomatic counting system (Wood et al. 1975: analyses performed at Crocker Nuclear Laboratory, University of California, Davis by W.W.W. or at University of California, Los Angeles by K. Nagy). Using the equations of Lifson and McClintock (1966) as modified by Nagy (1975), we calculated rates of water flux and  $\text{CO}_2$  production from the isotope measurements.

#### POTENTIAL ERRORS

Errors in calculated rates of  $\text{CO}_2$  production using the DLW technique can result from analytical errors in the isotope measurements or insufficient isotope turnover (Nagy 1980). Although we did not validate the DLW method specifically for woodpeckers, in an earlier validation of our technique using Budgerigars, *Melopsittacus undulatus* (Buttemer et al. 1986), DLW measurements of  $\text{CO}_2$  production differed by less than 6% from values determined simultaneously by the Haldane method (mean difference,  $-0.04\%$ ). The amount of isotope turnover which occurred in our woodpeckers was consistent with minimal measurement error (Nagy 1980). Final  $^{18}\text{O}$  concentration averaged 51% of initial  $^{18}\text{O}$  (range = 20–71%), whereas tritium turnover averaged 83% of  $^{18}\text{O}$  turnover (range = 60–89%).

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 Acorn Woodpeckers, Klaassen et al. (1989) validated use of DLW for rapidly growing Arctic Tern chicks (*Sterna paradisaea*). They found that the DLW technique underestimated  $\text{CO}_2$  production (measured by indirect calorimetry) by 4% during the first 24-hr measurement period. The underestimation increased to 16% during the second day. Because Acorn Woodpeckers grow more slowly than Arctic Terns, and

because most of our DLW measurements were based on 1-day samples, the error attributable to incorporation of isotopes into tissue is probably small.

If nestlings breathed  $\text{CO}_2$  exhaled by unlabeled birds, which shared the nest cavity with them (e.g., adults or helpers), our DLW estimates of  $\text{CO}_2$  production could be in error. In a test of this effect, the DLW method was found to overestimate  $\text{CO}_2$  production by 18–81% when kangaroo rats (*Dipodomys merriami*) breathed air containing 3.4% unlabeled  $\text{CO}_2$  (Nagy 1980). The error varied inversely with absolute humidity and directly with ambient  $\text{CO}_2$  concentration. Although we are unable to discount the possibility of a similar error in our study, Howe et al. (1987) found a mean  $\text{CO}_2$  concentration of only 0.37% in Northern Flicker (*Colaptes auratus*) nests. Assuming a similar  $\text{CO}_2$  level in Acorn Woodpecker nests, little error should attend our measurements. Overall, we believe our DLW measurements of  $\text{CO}_2$  production for individuals to be within  $\pm 10\%$  of actual values.

*Energy equivalent of  $\text{CO}_2$ .* Calculating energy expenditure from  $\text{CO}_2$  production is problematic because "animals are periodic eaters but continuous metabolizers" (Baldwin 1968). One must know not only the animal's diet, because the energy equivalent per liter  $\text{CO}_2$  varies by up to 32% of the minimal value (21.14 kJ/l) depending on the substrate being catabolized (see Gessaman and Nagy 1988a, Weathers and Sullivan 1989), but also whether the animal is in material and energy balance. We estimated the diet of woodpeckers in our study by observing what foraging birds ate, by examining stomach contents, and by neck-collaring nestlings. Based on the first two methods, the diet of adult woodpeckers consisted of 31% acorns and 69% insects; whereas the diet of neck-collared nestlings was approximately 25% acorns and 75% insects (Koenig, unpubl. data). For both groups, we assumed an energy equivalent of 25.5 kJ/l  $\text{CO}_2$ , which was calculated from the fractional diet composition assuming an energy equivalent of approximately 26.5 kJ/l  $\text{CO}_2$  for insects (Weathers and Sullivan 1989) and 23.0 kJ/l  $\text{CO}_2$  for acorns. The latter value was calculated following the methods of Weathers and Nagy (1984) based on the composition of dry acorns (5.5% protein, 15.5% fat, and 74.0% carbohydrate; average of *Q. lobata*, *Q. chrysolepis*, and *Q. agrifolia*; Koenig and Heck 1988; Koenig, unpubl. data).

Animals that fail to eat enough to meet their

energy needs will metabolize body substance. When the chemical composition of the animal's diet differs from that of the catabolized body tissue, an error will result if the energy equivalent for CO<sub>2</sub> based on the diet is used to calculate FMR. The magnitude of the error depends upon the proportion of total CO<sub>2</sub> that is produced from body tissue vs. dietary sources. In our study, three older nestlings lost between 9.1–12.7% of their initial mass during the measurement period. All other individuals gained or maintained their mass. The fastest growing nestlings exhibited mass increases of 9–18% per day. What CO<sub>2</sub> energy equivalent to use for growing nestlings is unclear (for discussion, see Weathers and Sullivan 1989). Accordingly, we assumed a value of 25.5 kJ/l CO<sub>2</sub> for all birds. If the three nestlings that lost mass metabolized exclusively body fat (as is typical of older nestlings undergoing weight recession) their calculated FMR would be about 9% too low.

#### ONTOGENY OF THERMOREGULATION

We examined the developmental change in nestling thermoregulatory ability by calculating the thermoregulatory index (TI):

$$TI = 100 (T_n - T_a)/(T_{ad} - T_a) \quad (1)$$

where  $T_n$  and  $T_{ad}$  are the body temperature of nestling and adults, respectively, and  $T_a$  is the ambient temperature to which both are exposed (see O'Connor 1984, Ricklefs 1987). TI, the percentage of the adult temperature gradient achieved by young exposed to a cold challenge, was determined for individual nestlings and for nestlings in broods of four. For these determinations, nestlings were syringe-fed a semiliquid diet (Gerber's baby food), placed in an incubator at 36–37°C for 30 min, and then placed in an artificial nest (felt-lined plastic bowl) housed within a 15°C chamber. After 30 min elapsed, the nestling's  $T_b$  was determined to within 0.1°C with a Cu-Cn thermocouple connected to a Bailey/Sensortek model Bat-12 thermocouple thermometer, and TI was calculated assuming adult  $T_b = 41.2^\circ\text{C}$ .

#### NESTLING BODY TEMPERATURE

Between 4–24 May 1986, we remotely monitored the  $T_b$  of two nestlings in the field using abdominally implanted Mini-mitter model X transmitters. Both nestlings were from nests containing five nestlings and were 9 days old (and approximately 36 g) when implanted. Nestling

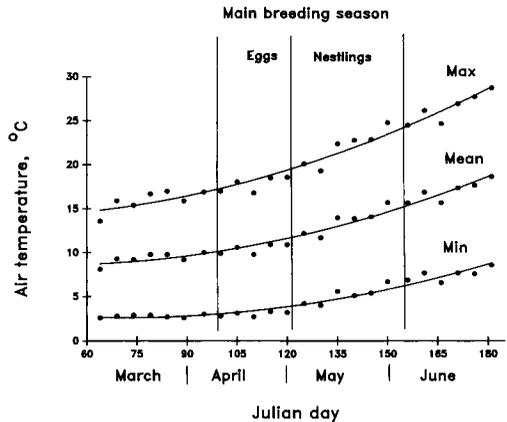


FIGURE 1. Air temperature at the study site in relation to time of year (Julian day 120 is 30 April). Each datum depicts the average value for the preceding 5–6 days based on 17 years of records (1969–1985, inclusive). The second order polynomial curves represent least squares fits described by equations 2, 3, and 4 for maximum (Max), mean, and minimum (Min) temperatures, respectively.

A's nest was located 3.6 m above ground in a 0.29-m diameter oak limb. Nestling B's nest was located 7.9 m above ground in a 0.30-m diameter oak limb. A small AM radio receiver taped to the tree limb outside the nest chamber received the Minimitter signal. The pulse signal was conditioned with a comparator circuit and recorded with a Campbell 21 × micrologger. Air temperature within the nest cavity was measured with a Cu-Cn thermocouple that was placed high enough above the nestlings to avoid contact with the brooding adult(s). Air temperature outside the nest was measured with a shaded thermocouple placed about 1 m away from the nest. A 21 × micrologger monitored the temperatures once every 10 sec and calculated the average every 10 min. The Mini-mitter transmitters were calibrated against a thermometer certified by the National Bureau of Standards immediately before they were implanted and again after they were removed from the birds.

#### STATISTICS

Unless indicated otherwise, data are presented as mean ± 1 SD. Other statistical procedures used are described below.

#### RESULTS

Figure 1 summarizes 17 years of air temperature measurements at Hastings Reservation for the period 1 March–29 June (Julian days 60–180),

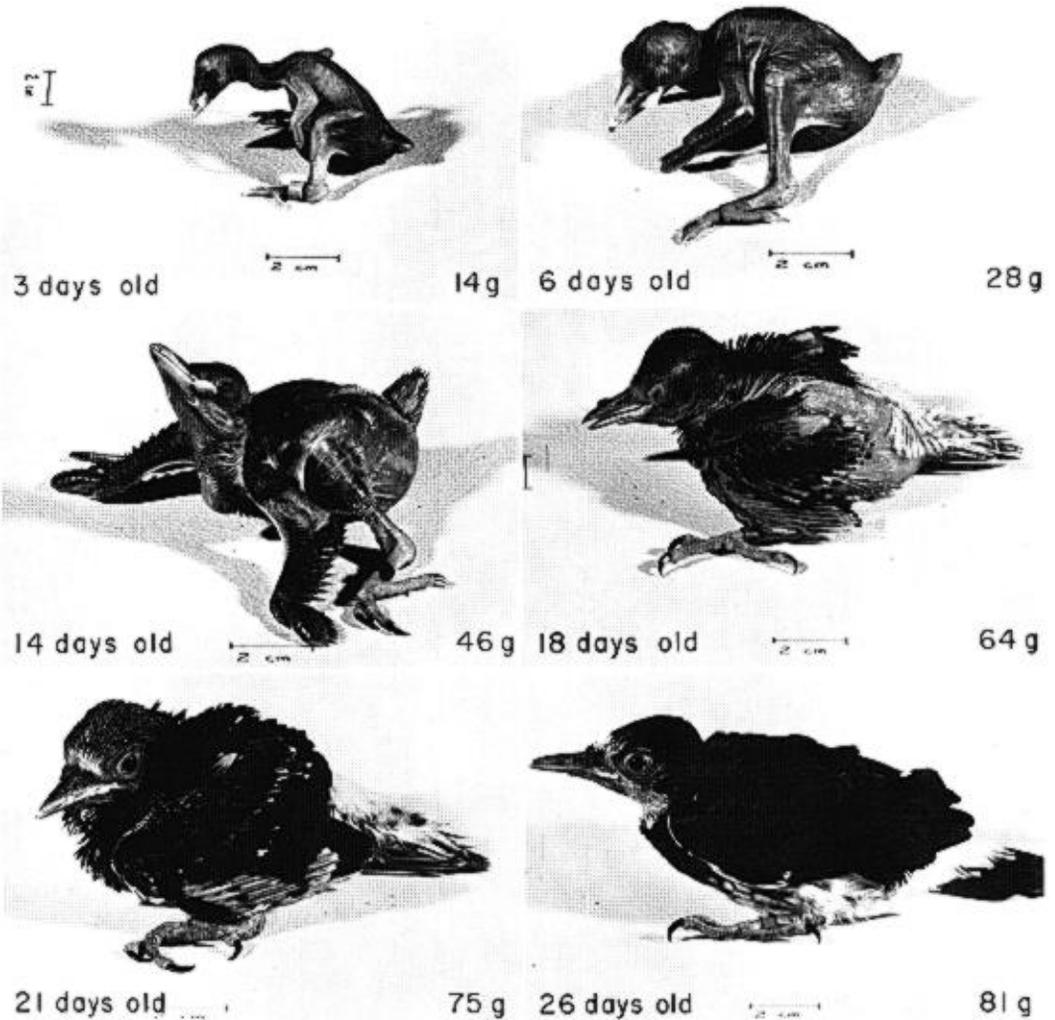


FIGURE 2. Growth and development of nestling Acorn Woodpeckers. Each photograph is of a different individual.

which encompasses the main breeding season. The least squares polynomial lines fitted to the data are as follows:

$$\text{Max } T_a = 15.0 - 0.036X + 0.0006X^2, \quad (2)$$

$$r^2 = 0.964$$

$$\text{Mean } T_a = 9.8 - 0.054X + 0.0006X^2, \quad (3)$$

$$r^2 = 0.966$$

$$\text{Min } T_a = 5.2 - 0.072X + 0.005X^2, \quad (4)$$

$$r^2 = 0.946$$

where  $X$  is Julian day.

#### NESTLING GROWTH AND DEVELOPMENT

Brood size is generally three to five, and hatchlings weigh an average of  $4.7 \pm 0.84$  g ( $n = 187$ ), or 5.9% of adult mass (80 g). Hatchling Acorn Woodpeckers are very altricial—completely naked and eyelids fused. Their eyes do not open until they are about 10 days old and by 2 weeks of age they are still essentially featherless (Fig. 2). By 3 weeks of age, nestlings are adult-sized and covered with feathers, although the feathers are still in sheaths. Fledging occurs in 30–32 days

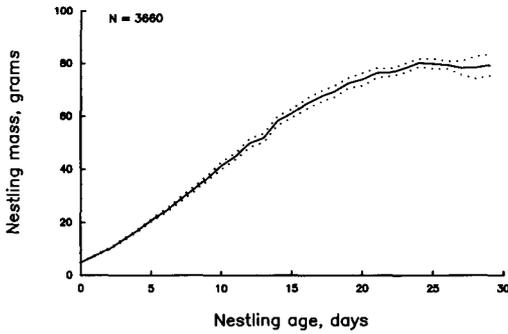


FIGURE 3. Nestling Acorn Woodpecker mass in relation to age. The solid line connects the means (not shown) of a total of 3,660 measurements on over 300 individual nestlings. The dotted lines enclose the 95% confidence interval.

at a mass of about 80 g. Sexual size dimorphism is slight (Stanback, unpubl. data).

For descriptive purposes, and to facilitate comparison of woodpeckers with other kinds of birds, we fit the nestling mass data (Fig. 3) for ages 0–26 days, by three equations: Gompertz, logistic, and Richards (Ricklefs 1983). The mass data are better fit by the Gompertz equation than the logistic equation, as indicated by the former's lower residual mean square (Table 1), although, as is often the case, the Gompertz fit overestimated the asymptote. The shape parameter ( $M$ ) of the Richard's equation indicates that the Gompertz equation is a somewhat better fit (Table 1). Nonetheless, all three equations provide good fits and for comparative purposes we will use the logistic equation to describe Acorn Woodpecker growth:

$$m(t) = \frac{82.19}{1 + 9.79(e^{-0.226t})} \quad (5)$$

TABLE 1. Growth curve parameters for the Acorn Woodpecker.  $A$  = asymptote (g),  $K$  = growth rate constant ( $\text{days}^{-1}$ ),  $I$  = age (days) at the inflection point of the growth curve,  $MS$  = residual mean squares (squared deviations). The shape factor  $M = 1.35$  for the Richards equation, 2 for the logistic, and 1 for the Gompertz.

Equation	$A$	$K$	$I$	$MS$
Logistic	82.19	0.226	10.10	1.23
Gompertz	89.19	0.135	7.93	0.90
Richards	85.74	0.167	2.66	0.67

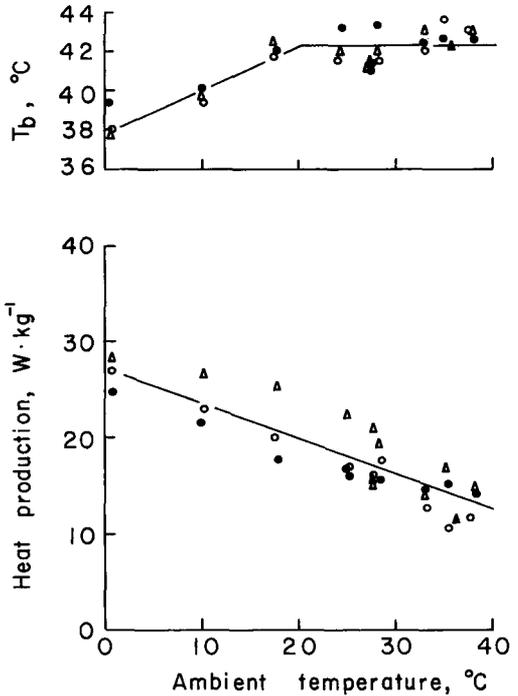


FIGURE 4. Body temperature (top) and metabolic heat production (bottom) of four fasted, adult Acorn Woodpeckers (mean mass = 73.1 g) measured in the dark during the day in relation to ambient temperature. Sloping lines are least squares regression lines described by equation 7 for  $T_b$  below 20°C and equation 6a for heat production. Different symbols denote different individuals.

where  $m(t)$  is nestling mass at  $t$  days of age (hatching = day 0) and  $e$  is the base of natural logarithms.

#### RESTING METABOLIC RATE (RMR)

*Adults.* The metabolic heat production (calculated from  $\dot{V}O_2$ ) of fasted adult woodpeckers resting in the dark during the day is shown in Figure 4. This plot differs from the typical endotherm pattern in lacking a clearly defined thermoneutral zone. Furthermore, the least squares regression line relating metabolism to  $T_a$  extrapolates to zero metabolism at  $T_a = 75^\circ\text{C}$ , far above the woodpeckers measured  $T_b$ . RMR ( $\text{W/kg}$ ) increased linearly with decreasing  $T_a$  ( $^\circ\text{C}$ ) as follows:

$$\text{RMR (W/kg)} = 27.3 - 0.365T_a \quad (6a)$$

Converting RMR to units of  $\text{kJ/day}$ , we have:

TABLE 2. Metabolic rate of adult Acorn Woodpeckers.

Condition <sup>a</sup>	Metabolic rate (W/kg) <sup>b</sup>		
	Observed	Predicted <sup>c</sup>	% predicted
Active ( $\alpha$ ) phase			
Clinging	13.79 $\pm$ 2.07 (10)	8.97	154
Rest ( $\rho$ ) phase			
Clinging	10.63 $\pm$ 1.05 (4)	7.15	148
Standing	9.83 $\pm$ 0.54 (9)	7.15	137

<sup>a</sup> Mean  $T_a$  = 35.6°C; range = 33.2–38.2°C.

<sup>b</sup> Values are reported as  $\bar{x} \pm$  SD.

<sup>c</sup> Predicted for a 73.1-g nonpasserine bird by the appropriate equation of Aschoff and Pohl (1970).

$$\begin{aligned} \text{RMR (kJ/day)} &= 177 - 2.49T_a \quad (6b) \\ (s_{y,x} &= 11.32, s_b = 0.184, \\ r^2 &= 0.871, n = 30). \end{aligned}$$

At  $T_a$ 's between 33–38°C,  $\dot{V}O_2$  was minimal and equivalent to 13.8 W/kg during the day and about 10.1 W/kg at night (Table 2). During the day,  $T_b$  of adults remained constant ( $\bar{x} = 42.4 \pm 0.81$ ;  $n = 17$ ) at  $T_a > 20^\circ\text{C}$ , and varied directly with  $T_a$  between 0 to 20°C (Fig. 4). The equation relating  $T_b$  to  $T_a$  below 20°C is:

$$\begin{aligned} T_b &= 38.0 + 0.22T_a \quad (7) \\ (r &= 0.921, n = 9). \end{aligned}$$

*Nestlings.* The resting metabolic rate (RMR; kJ/day) of fasted nestlings measured at  $T_a = 36$ –37°C during the day (Fig. 5) increased linearly with body mass ( $m$ ; grams) as follows:

$$\begin{aligned} \text{RMR (kJ/day)} &= 2.25 + 1.00m \quad (8) \\ (s_{y,x} &= 6.10, s_b = 0.039, \\ r^2 &= 0.927, n = 55). \end{aligned}$$

#### FIELD METABOLIC RATE (FMR)

Nestling FMR increased linearly with body mass ( $m$ ; grams) (Fig. 5) according to:

$$\begin{aligned} \text{NESTLING FMR (kJ/day)} \\ &= -27.1 + 2.40m \quad (9) \\ (s_{y,x} &= 21.61, s_b = 0.241, \\ r^2 &= 0.780, n = 30). \end{aligned}$$

Four of the older nestlings depicted in Figure 5 had FMR's that lie considerably above the regression line. Three of these birds, depicted by shaded circles, were nest mates whose nest tree was located on an exposed ridge top. The FMR of these three birds was measured during a period of especially cold and windy weather, and it seems likely that increased thermoregulatory costs con-

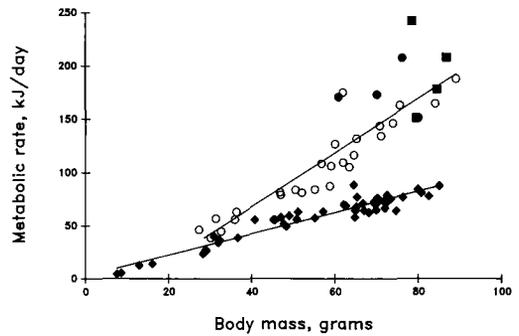


FIGURE 5. Field metabolic rate (FMR) of nestling (circles) and adult (filled squares) Acorn Woodpeckers, and resting metabolic rate (RMR) of nestlings (filled diamonds) in relation to mass. Lines are least squares regression lines fitted to the nestling data and described by equation 9 for FMR and equation 8 for RMR. Filled circles denote FMR of three nestlings measured during an especially cool period.

tributed to their high FMR. We have no explanation for the fourth nestling's high FMR.

Adult FMR (Fig. 5; shaded squares) ranged from 151 to 242 kJ/day ( $\bar{x} = 195 \pm 39.2$  kJ/day;  $n = 4$ ), and overlapped the FMR of adult-sized nestlings.

#### WATER CONTENT AND FLUX

The fraction of body mass consisting of water (TBW) was determined by oxygen-18 dilution. Adult TBW averaged 0.670. Nestling TBW decreased with mass ( $m$ , grams) (Fig. 6) according to:

$$\begin{aligned} \text{TBW} &= 0.924 - 0.0024m, \quad (10) \\ (s_{y,x} &= 0.0214, s_b = 0.0003, \\ r^2 &= 0.782, n = 26). \end{aligned}$$

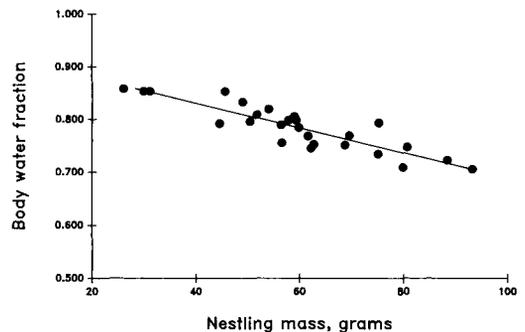


FIGURE 6. Fraction of nestling Acorn Woodpecker body mass consisting of water in relation to age. Line is the least squares regression line described by equation 10.

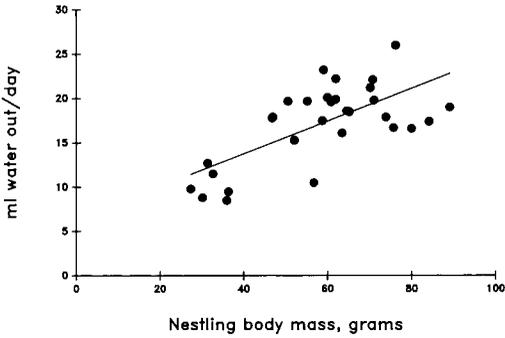


FIGURE 7. Field water efflux of nestling Acorn Woodpeckers in relation to mass. Solid line is the least squares regression line described by equation 11.

Total water efflux (TWE, ml/day) of nestlings measured in the field with DLW increased with mass ( $m$ , grams) (Fig. 7) according to:

$$TWE = 6.40 + 0.18m \quad (11)$$

$(s_{y-x} = 3.37, s_b = 0.038, r^2 = 0.463, n = 30).$

TWE of four adult woodpeckers (mean mass = 82.25 g) averaged  $29.3 \pm 4.27$  ml/day, which is 1.38 times the value predicted by equation 11.

ONTOGENY OF THERMOREGULATION

At hatching, Acorn Woodpeckers are ectothermic and they become competent thermoregulators rather slowly. We quantified the development of thermoregulatory capacity in terms of the thermoregulatory index (TI): the percentage of the adult  $T_b - T_a$  gradient attained following a 30-min exposure to 15°C (see Methods). The TI of nestlings tested individually increased ex-

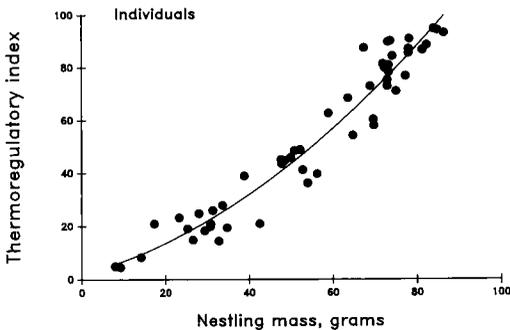


FIGURE 8. Thermoregulatory index of nestling Acorn Woodpeckers exposed individually to 15°C for 30 min in relation to mass. Curved line is the least squares regression line described by equation 12.

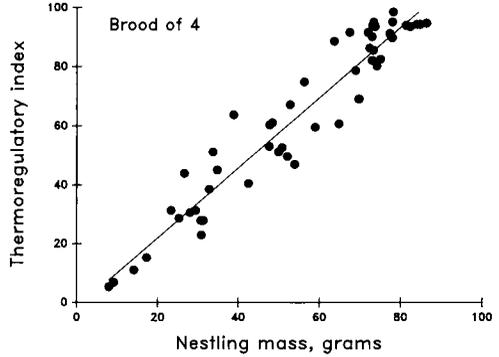


FIGURE 9. Thermoregulatory index of nestling Acorn Woodpeckers exposed as a brood of four individuals to 15°C for 30 min in relation to mass. The least squares regression line is described by equation 13.

ponentially with body mass ( $m$ , grams) (Fig. 8) according to:

$$\log_{10} TI = -0.5664 + 1.307 \log_{10} m, \quad (12)$$

$(\log_{10} s_{y-x} = 0.0891, s_b = 0.0507, r^2 = 0.930, n = 52).$

The above equation predicts a TI of 50% at 54.1 g mass, which would be attained at about 13.5 days of age, or about 44% of fledging age (31 days). A nestling's ability to maintain  $T_b$  during the cold challenge improved if it was tested in a brood of four, such that a TI of 50% was attained about 3 days sooner, at a mass of 43.6 g (Fig. 9). The relation between TI and nestling mass was linear for 52 individuals tested in broods of four and can be described as:

$$TI = -1.86 + 1.19m, \quad (13)$$

$(s_{y-x} = 8.13, s_b = 0.051, r^2 = 0.957).$

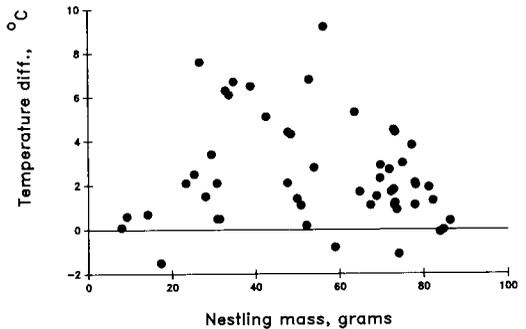


FIGURE 10. Difference in body temperature of nestling Acorn Woodpeckers exposed to 15°C for 30 min when in a brood of four vs. when exposed individually.

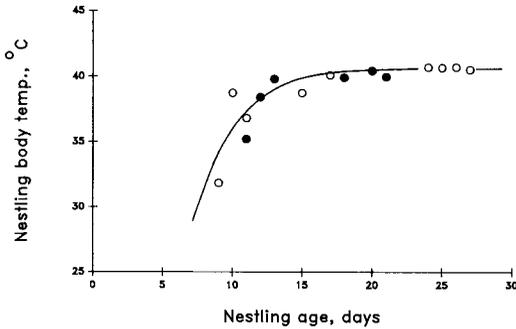


FIGURE 11. Mean 24-hr body temperature (measured by radiotelemetry) of two free-living Acorn Woodpecker nestlings (represented by different symbols) in relation to age. Curved line fitted by eye.

The thermal benefit of being in a brood of four is illustrated by plotting the difference in  $T_b$  observed for each nestling following a 30-min exposure to 15°C either singly or with brood mates (Fig. 10). In four cases,  $T_b$  was higher when cold-exposed singly (negative values in Fig. 10). More typically,  $T_b$ 's were higher for nestlings in broods of four. The thermal advantage of having brood mates was small for nestlings that were less than 40% or more than 60% of fledging age. For nestlings of mid-age,  $T_b$  was as much as 9.2°C higher when cold-exposed with brood mates.

#### NESTLING BODY TEMPERATURE AND NEST TEMPERATURE

The mean 24-hr  $T_b$  of two free-living nestlings, as measured with implanted radiotelemeters, increased with age up to about 3 weeks of age and was constant thereafter (Fig. 11). Lower mean  $T_b$  of younger nestlings was a consequence of their cooling during periods when adults left the nest to forage. This is illustrated in Figure 12, which presents 1 day's  $T_b$  record for one of the two nestlings studied (aged 15 days). At night, when it was being continuously brooded, the nestling's  $T_b$  was stable and averaged  $39.7 \pm 0.39^\circ\text{C}$ . In the morning, the nestling's  $T_b$  fell to about 20°C, presumably because the adults left the nest to forage.  $T_a$  within the nest chamber at this time was about 10°C. The nestling's  $T_b$  returned to near 40°C at around 06:30, following the adult's morning feeding bout. Fluctuations in nestling  $T_b$  between 10:00 and 20:00 probably represent variable brooding behavior by the adults.

Between 4–24 May 1986 we measured  $T_a$  at

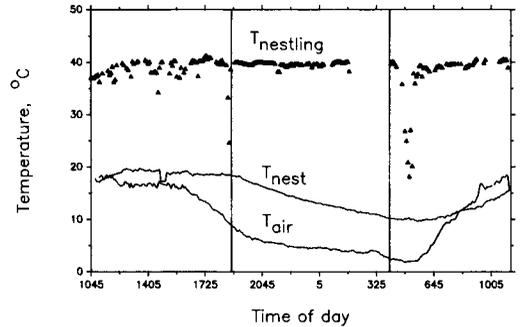


FIGURE 12. Body temperature (measured by radiotelemetry) of a free-living 15-day-old nestling Acorn Woodpecker (triangles), nest temperature (upper solid line), and air temperature (lower solid line) in relation to time of day. Vertical lines denote the times of dusk and dawn.

10-min intervals inside and outside of the two nest cavities that contained telemetered nestlings. Over this time period,  $T_a$  averaged 13.9°C ( $n = 5,016$ ) and nest temperature ( $T_n$ ) averaged 17.9°C ( $n = 4,568$ ). Under these generally cool conditions,  $T_n$  averaged 3.7°C higher than  $T_a$ . The difference between  $T_n$  and  $T_a$  was higher at night than during the day (Fig. 12).

#### DISCUSSION

The main breeding season for Acorn Woodpeckers at Hastings Reservation extends from April through June, with the majority of clutches being initiated between 15 April and 15 May (Koenig and Mumme 1987). Incubation requires 11 days and most nests contain nestlings between 26 April and 26 May (Julian days 116–146). During this period, the weather at Hastings has yet to settle into the uniformly balmy days that characterize California's summer. Minimum air temperatures fall below 5°C at night, daytime high temperatures rarely exceed 20°C (Fig. 1), and cool days with light rain are not uncommon (MacRoberts and MacRoberts 1976, pers. observ.). These generally cool conditions increase both adult and nestling energy requirements and affect several aspects of the species' breeding biology.

#### NESTLING GROWTH

The eggs of woodpeckers are smaller than those of similar-sized birds, with the exception of the (largely) parasitic Cuculiformes (Rahn et al. 1975). The mean weight of 35 freshly laid Acorn Woodpecker eggs (10 different females) was 5.28 g, 90%

of the value predicted by the Piciformes equation of Rahn et al. (1975) based on a mean female mass of 78.1 g (Koenig 1980). Thus, the eggs of Acorn Woodpeckers are small, even by the standards of a taxon that lays extremely small eggs. Acorn Woodpeckers also have one of the shortest incubation periods of any bird (Rahn and Ar 1974), their eggs hatching in just 11 days.

Despite their extreme altriciality at hatching, nestling Acorn Woodpeckers grow relatively slowly. The growth rate constant  $K$ , based on the logistic equation (Table 1), can be compared with that of other altricial species, ranging in size from small passerines to large raptors, using Ricklefs' (1968) regression equation and an asymptotic mass of 82.19 g. Based on Ricklefs' equation, the Acorn Woodpecker's  $K$ -value (0.226) is only 69% of the expected value (0.326), and is close to the value predicted for tropical species (Ricklefs 1976), which are generally regarded as being slow-growing. Slow growth occurs in another member of the genus *Melanerpes* (see below), but it is not a general characteristic of the class Piciformes, as the  $K$ -values of other woodpeckers equal those expected for altricial birds of their size (R. E. Ricklefs, unpubl. data: *Dryocopus pileatus*  $K = 0.29$ – $0.33$ ; *Picoides borealis*  $K = 0.32$ ; and *Picoides pubescens*  $K = 0.33$ ).

Avian growth rates can also be compared in terms of the maximum absolute growth rate (g wet mass/day) calculated at the midpoint of the linear growth phase (i.e., at the inflection point of the growth curve). The inflection point for Acorn Woodpeckers occurs at 10.1 days. At this time, mass = 40.6 g and absolute growth rate = 4.6 wet grams/day. Drent and Daan (1980) summarized absolute growth rate data for altricial and semiprecocial seabirds and raptors. For these groups, which grow much slower than passerines, absolute growth rate is described by the equation: (wet g/day) =  $0.202 m^{0.74}$ ; where  $m$  = adult mass in grams. This equation predicts a growth rate of 5.4 g/day for a bird of the Acorn Woodpecker's size, a value 1.17 times the observed rate. Although it may not be appropriate to compare woodpeckers with seabirds, these calculations serve to emphasize that Acorn Woodpeckers grow more slowly than most other species.

Why do Acorn Woodpeckers grow so slowly? One contributing factor may be the nestlings' diet, which consists of both insects and pieces of acorns. Acorns contain relatively little protein (3.9 to 7.1% of dry weight) and significant

TABLE 3. Food items delivered to Acorn Woodpecker nestlings by adults. Data are based on 1,077 hr of feeding watches at 47 nests of 19 different groups between 1979–1982 (Mumme and Koenig, unpubl. data).

Nestling age (days)	No. nest watches	No. feeds consisting of		% acorns
		acorns	insects	
1–5	50	55	266	17.1
6–10	61	199	735	21.3
11–15	56	267	687	28.0
16–20	156	306	1,087	22.0
21–26	71	386	1,499	20.5
26+	71	402	909	30.7
Total	372	1,615	5,183	23.8

amounts of tannins (see Koenig and Heck 1988). Tannins bind proteins (Bate-Smith 1973, Temple 1981, Martin and Martin 1982) and depress the growth rate of domestic chicks when present in the diet at levels of 0.5% or greater (Vohra et al. 1966). Tannins have also been shown to depress digestibility of acorns by Acorn Woodpeckers (W. D. Koenig, unpubl.). Extensive observations of adults feeding nestlings (R. L. Mumme and W. D. Koenig, unpubl. data) reveal that acorn pieces constitute a sizable proportion of the food items delivered to nestlings (Table 3). Acorns represent a significantly greater proportion of food items delivered to 11- to 15-day-old and  $\geq 26$ -day-old nestlings than to other ages (ANOVA arcsin transformed data:  $F_{5,347} = 2.41$ ;  $P = 0.036$ ). Although these data do not reveal what fraction of nestling TME derives from acorns, they suggest that the fraction is highest when nestlings are growing most rapidly; i.e., at 11–15 days of age.

Data available from other melanerpine woodpeckers suggest that slow growth may be characteristic of this taxon. Jackson (1970) documented growth for a brood of Red-headed Woodpeckers (*Melanerpes erythrocephalus*). Their growth is best described by the logistic equation (R. E. Ricklefs, unpubl. data) with a growth rate constant ( $K = 0.289$ ) that is 88% of predicted (Ricklefs 1968) based on their asymptotic mass of 80.1 g. Thus, Red-headed Woodpeckers also grow slowly, although not as slowly as Acorn Woodpeckers.

Adult Red-headed Woodpeckers average about 90% of the mass of Acorn Woodpeckers (Dunning 1984) and their nestlings fledge 31 days after hatching, the same age as in Acorn Woodpeckers.

Similarly long nestling periods are suggested by the data on other temperate melanerpine species compiled by Jackson (1977) and may be even longer in some tropical species. For example, Skutch (1969) reported that the young of the Golden-naped Woodpecker (*Melanerpes chrys-auchen*), which are only about 70% of the mass of Acorn Woodpeckers in California, fledge at 33–36 days of age.

Melanerpine Woodpeckers frequently feed on low-protein, fruit diets (Short 1982). Thus, slow growth rates may be a more general adaptation found within the genus rather than a trait peculiar to Acorn Woodpeckers and their diet high in acorns. Also worthy of note is the high frequency of unusual social organization within this genus: at least eight of 21 species (38%) recognized by Short (1982), including the Acorn Woodpecker, are known or probable cooperative breeders. Although distinguishing cause from effect is problematical, we believe that low-protein diets, slow growth, and cooperative breeding, three highly unusual traits found regularly within this genus, are interrelated.

#### NESTLING HOMEOTHERMY

The age at which individual altricial nestlings attain effective homeothermy (defined arbitrarily as the ability to maintain 75% of the adult  $T_b - T_a$  gradient upon exposure to 15–25°C for some time period) was summarized for 22 species by Dunn (1975) (for an analysis of the cooling method, see Ricklefs 1987). Based on Dunn's data, the age at which effective homeothermy is attained ( $Y$ ; days) varies inversely with growth rate as follows:

$$Y = 16.6 - 18.8K \quad (14)$$

$$(s_{y,x} = 1.64, s_b = 2.45,$$

$$r^2 = 0.747, n = 22),$$

where  $K$  is the logistic equation growth-rate constant. Although equation 14 is derived from a heterogeneous data set, it describes the data well. For 11 of the species considered by Dunn, the observed age at which effective homeothermy was attained is within 10% of the predicted value, compared with a mean difference from predicted of 16% (range = 0–45%) for all 22 species. Equation 14 predicts that nestling Acorn Woodpeckers ( $K = 0.226$ ) should attain 75% of the adult  $T_b - T_a$  gradient by 12.4 days of age. The observed value, 19.5 days, is 57% greater than predicted; the largest departure from predicted yet observed. Nestling Acorn Woodpeckers thus de-

velop the ability to regulate their  $T_b$  very slowly, even for a slow-growing species. As a consequence, there is a 2-week period, between the time they are 1–3 weeks old, when nestlings are relatively large, poorly feathered, and unable to effectively maintain  $T_b$  when cold-challenged. These characteristics make it theoretically possible for adults to manipulate a nestling's energy requirements by varying the amount of brooding that the chick receives. When insects are limited, adults could brood chicks less, thereby permitting them to become hypothermic, which would decrease their food needs. Because older nestlings undoubtedly respond to low  $T_a$  by increasing their metabolic heat production, lack of continuous brooding coupled with low  $T_a$  would increase their energy expenditure. Thus, withholding brooding to curtail nestling energy demands would be limited to young nestlings incapable of increasing endogenous heat production in response to low  $T_a$ . Such a scenario presupposes low nest-cavity temperatures.

Nest-cavity temperatures during the breeding season at Hastings Reservation are often so low (Fig. 1) that nestlings less than 3 weeks old rapidly become hypothermic unless they are brooded continuously. For birds in general, the age at which brooding ceases tends to coincide with the development of effective endothermy (Dunn 1973). This does not appear to be true for Acorn Woodpeckers, for whom brooding declines almost linearly with time after the first 4–5 days of the nestling period (M. T. Stanback, W. D. Koenig, and R. L. Mumme, unpubl. data). This is supported by our  $T_b$  data for free-living nestlings, which indicate that brooding is intermittent well before nestlings are capable homeotherms. The average daily  $T_b$  of free-living nestlings younger than 2 weeks of age is lower than that of older nestlings (Fig. 11). This is undoubtedly due to episodes of hypothermia resulting from brooding adults leaving the nest to forage, as was clearly the case at dawn for a 15-day-old nestling (Fig. 12). Apparently, the amount of time that adults can devote to brooding is constrained by the adults' foraging and/or other activity requirements. Thus, one important contribution of nest helpers is to aid in brooding nestlings.

#### NESTLING ENERGY BUDGET

In its simplest form, a nestling's energy budget consists of the following components of the total metabolized energy (TME):

$$\text{TME} = \text{BMR} + \text{HI} + \text{TR} + \text{A} + \text{TE} \quad (15)$$

where BMR is the basal metabolic rate (including the cost of biosynthesis), HI is the heat increment of feeding (SDA), TR is the cost of thermoregulation, A is the cost of physical activity, and TE is the energy accumulated in tissue (growth). Gross energy intake can be calculated from TME provided assimilation efficiency is known.

We used our metabolism and growth data to calculate the nestlings' energy budget (see Appendix 1). The increase in TME with age was sigmoidal (Fig. 13), with TME reaching 90% of its asymptotic value (ca. 170 kJ/day) by 15 days of age.

Total metabolized energy per chick over the nestling stage (age 0–31 days) was 3,853 J (Appendix 2). Of the total, RMR comprised about 47%, whereas activity, HI, and thermoregulation combined accounted for about 40%. The energy accumulated in growth (TE) was only 13% of TME, which is the lowest fraction observed yet for any altricial bird. Gross growth efficiency (expressed as TE/TME) averages 0.24 (range = 0.17–0.29) in 13 altricial species (Wijnandts 1984, Klaassen et al. 1989); substantially higher than the Acorn Woodpecker's average of 0.13. Two factors that may contribute to the Acorn Woodpecker's relatively inefficient growth are: (1) the growth depressing effects of tannins contained in the partially acorn diet, and (2) a relatively large maintenance energy requirement. Slow growth prolongs the time that nestlings remain in the nest and thereby increases the total energy required for maintenance (basal metabolism plus thermostatic costs), whereas fast growth decreases the cumulative maintenance energy requirement and thereby increases gross growth efficiency. For example, Arctic Terns *Sterna paradisaea* (Klaassen et al. 1989) produce semi-precocial chicks that weigh 115 g when they fledge at 21 days of age. The nestling terns' TME, 4,442 kJ, is only 16% greater than that of the Acorn Woodpecker, despite the fact that fledgling terns are 44% larger than fledgling woodpeckers. The terns' higher gross growth efficiency (0.23) results partly from their relatively fast growth rate.

In addition to slow growth, nestling woodpeckers seem to have an unusually high maintenance energy requirement. Although we did not measure hatchling RMR, the relation of nestling RMR to mass is strictly linear (Fig. 5). The RMR predicted for a 4.7-g hatchling from the Figure 5 data (Equation 8) is 6.95 kJ/day. From

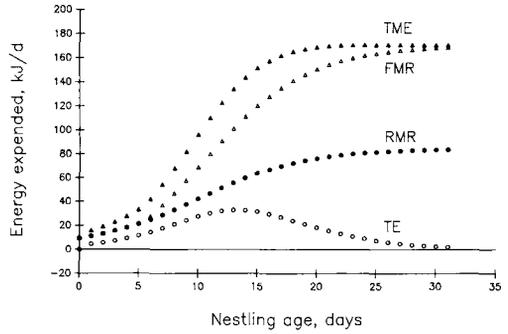


FIGURE 13. Energy expenditure of nestling Acorn Woodpeckers as a function of age. TE = energy accumulated in new tissue (i.e., growth), RMR = resting metabolic rate of fasted young during the day, FMR = field metabolic rate (measured with doubly labeled water), and TME = total metabolized energy (i.e., field metabolic rate + growth). See Appendix for calculation methods.

this we calculate the nestlings' mass-independent metabolic rate as  $2.46 \text{ kJ day}^{-1} \text{ g}^{-0.67}$ . The mass-independent BMR of adults (76 g) is  $3.64 \text{ kJ day}^{-1} \text{ g}^{-0.67}$  for nighttime measurements and  $4.98 \text{ kJ day}^{-1} \text{ g}^{-0.67}$  during the day. Bucher (1987) compared the metabolic intensity of nestling birds by calculating the ratio of hatchling to adult mass-independent metabolism. The ratios for Acorn Woodpeckers are, respectively, 0.68 and 0.50 for nighttime and daytime adult BMR values. These values are the highest reported for any altricial bird (Bucher 1987), and indicate that the metabolic intensity of nestling woodpeckers is comparable with that of precocial species. An inherently high metabolic rate is thus another factor that reduces the woodpecker's gross growth efficiency.

The energy devoted to growth can also be expressed as a fraction of the chick's BMR (Dunn 1980; but see Williams and Prints 1986). For the Acorn Woodpecker, this value (TE/BMR) decreases in a more or less exponential fashion from hatching levels of about 0.9 to 0 at the end of the growth period. Such a pattern is typical of birds in general, and other species that have been studied exhibit initial values between 2.50–0.70 (Ricklefs 1983). Acorn Woodpeckers are thus on the low end of the observed range.

#### ADULT ENERGETICS

The RMR of adult Acorn Woodpeckers is unusual in two respects. First, the plot of RMR vs.  $T_a$  lacks a thermoneutral zone (Fig. 4). This cir-

TABLE 4. Conditions surrounding adult Acorn Woodpecker field metabolic rate (FMR) determinations.

Bird no.	Gender	Mass (g)	Date <sup>a</sup>	Mean $T_a$ (°C)	FMR (kJ/day)	Social group <sup>b</sup>
9	F	78.4	8-9 May	10.2	242	3 breeders, no nonbreeding helpers
10	M	86.7	8-10 May	9.8	208	
42	M	84.5	4-6 June	20.2	178	pair only
43	F	79.4	16-18 June	22.4	151	4 birds; 3 breeders + 1 nonbreeding helper

<sup>a</sup> Date that bird's FMR was determined by doubly labeled water.

<sup>b</sup> Number of birds cooperating in the breeding effort at this bird's nest.

cumstance results partly from an unexpected and progressive hypothermia at  $T_a$ 's below 20°C, which reduces RMR through the  $Q_{10}$  effect. It is very unusual for an 80-g bird to become hypothermic at such relatively high temperatures following only 3 hr of fasting. Whether this represents an adaptive response serving to conserve energy or an inability to regulate  $T_b$  is unclear. In any event, as a consequence of hypothermia, resting energy expenditure is reduced at moderate temperatures. Although a similar hypothermia was reported for the Green Woodhoopoe *Phoeniculus purpureus* (Ligon et al. 1988), which is also a cooperatively breeding, cavity-nesting bird, it apparently resulted from the semistarved condition of the birds used by Ligon et al. (1988), as Green Woodhoopoes in good condition do not become hypothermic (J. B. Williams, M. A. du Plessis, and W. R. Siegfried, pers. comm.).

The second unusual trait is that the Acorn Woodpecker's BMR is much higher than expected for a bird of its size (Table 2). The BMR of the Great Spotted Woodpecker *Dendrocopos major* is also about 40% higher than predicted (Gravrilov, unpubl. data, in Kendeigh et al. 1977), which suggests that a high BMR may characterize the family Picidae. If hypothermia at relatively high  $T_a$  represents an adaptative response serving to conserve energy, then a high BMR would be regarded as counteradaptative. Reconciling this paradox will require additional data on woodpecker metabolism.

The average FMR of the four breeding adults that we studied (195 kJ/day) can be compared with DLW measurements of other species using the predictive equations of Weathers and Sullivan (1989). Based on these equations, our woodpeckers' FMR is 77% of that predicted for an 82.3-g nonpasserine feeding nestlings and 91% of that expected for breeding birds in general. The predictive equations are biased in favor of aerial-foraging insectivores (swifts and swallows)

and seabirds, both of which have relatively high FMR (Nagy 1987, Weathers and Sullivan 1989), and thus they may not apply to relatively non-volant species such as the Acorn Woodpecker.

Parental effort of breeding birds studied with the DLW method has been evaluated in terms of the FMR/BMR ratio (Dijkstra 1988, Weathers and Sullivan 1989). This ratio is highest in adults that are feeding nestlings, for whom it ranges from 2.0 in ground-foraging passerines to 5.2 in some seabirds, and averages 3.6-3.7 in nonpasserine species. The BMR of an 82.3-g Acorn Woodpecker (the mean mass of our FMR birds) is 71.8 kJ/day (Table 2), which gives a FMR/BMR ratio of 2.7. Thus, from this perspective as well, the energy requirements of breeding adult Acorn Woodpeckers seem to be somewhat low. In reality they may be even lower than our estimates, as the radio transmitters worn by two of our birds may have increased their FMR (Gessaman and Nagy 1988b).

The FMR of our four adult Acorn Woodpeckers ranged widely from 151 to 242 kJ/day (Table 4), with two of the adults' FMR overlapping that of older nestlings (Fig. 5). The wide range in FMR can be explained in part as follows. The adults with the highest FMR (Nos. 9 and 10) were the female and one of the males at a nest with three breeding adults (two males, one female; no nonbreeding helpers). Both birds wore radio transmitters and it is likely that this increased their energy expenditure. Gessaman and Nagy (1988b) found a 41-50% increase in the energy expenditure of flying pigeons that wore radio transmitters equal to 2.5-5% of their mass. Although the female wore the smaller of the two transmitters (2 g), her FMR was higher than the male's. Transmitters weighing 4 g have been shown to reduce Acorn Woodpecker activity (P. Hooge, unpubl.) and this may partially account for the male's lower FMR.

Another factor that probably contributed to

TABLE 5. Time budget of adult female Acorn Woodpecker (No. 9) feeding nestlings and her estimated field metabolic rate.

Category	Activity		Energy expended kJ
	Duration, hr/day	Cost factor ×BMR <sup>a</sup>	
Nighttime rest	10.00	1.0	29.0
Daytime perching	9.66	2.0	56.0
Preening	1.06	2.2	6.8
Eating	0.53	2.2	3.4
Flying	1.54	12.0	53.6
Other <sup>a</sup>	1.20	2.3	8.0
Total	23.99		156.8

<sup>a</sup> Includes: feeding young, "moving," displaying, gleening, drilling holes.

<sup>b</sup> BMR = basal metabolic rate.

the high FMR of adults Nos. 9 and 10 was the cooler weather that prevailed during the time that they were studied. The other two adults (Nos. 42 and 43) experienced much warmer conditions, which would have reduced their thermostatic costs (Table 4).

We can estimate adult No. 9's thermostatic costs from our time budget data (Table 5) using metabolic cost assignments for the various activity categories based on our measurements of BMR. The energy cost assignments in Table 5 follow Buttemer et al. (1986), except for flight which was estimated from the female's mass using the nonpasserine equation of Rayner (1982). The nighttime BMR predicted for a bird of No. 9's size is 2.9 kJ/hr (Table 2). FMR calculated from No. 9's time budget is 157 kJ/day, which is 65% of the value measured with DLW. The difference between measured FMR and FMR estimated from the time budget (= 85 kJ/day) represents the energy cost of thermoregulation and equals 35% of the measured FMR. Basal plus thermostatic costs thus equal about 155 kJ/day, or 64% of the female's total FMR, a fraction comparable to that of other birds (Walsberg 1983). We emphasize that the female's actual thermostatic costs are uncertain because our estimate of them relies on assumed activity costs. We are least confident of our flight cost assignment. If the energy cost of flight was 50% higher than we estimate, due to the effect of wearing a radio transmitter, thermostatic costs would be reduced to 58 kJ/day; which, although smaller, is still 24% of FMR. Clearly, thermoregulatory costs are partly responsible for the relatively high FMR of adults Nos. 9 and 10, although the exact magnitude of their contribution is uncertain.

The adult with the lowest FMR (No. 43) benefited from both warm weather and the presence of helpers at the nest (Table 4). In sum, the FMR of the four adults that we studied varied in accordance with expectations. Namely, it was highest in the two birds wearing radio transmitters that were studied during cool weather and lowest for the two birds without transmitters that were studied during warm weather. Further, among the latter group, FMR was lowest for the adult from the nest with helpers. As emphasized by Nagy (1989), the DLW method is now sufficiently sensitive to detect small differences in FMR between individuals.

#### ECOLOGICAL CONSEQUENCES

The physiological properties of Acorn Woodpeckers documented here are generally consistent with those expected of a species that is severely food- or nutrient-limited. Adults become hypothermic at relatively high ambient temperatures (Fig. 4), as would be expected if the ability to cope with the additional thermoregulatory demands of low temperature was difficult. Nestling growth is slow, and young, like adults, become hypothermic very easily until they are over 2 weeks old (Fig. 11). Older young experience high thermoregulatory demands due to their cool nest microclimate. Because of the nestling's slow growth and high thermoregulatory demands, the total energy cost of reproduction in Acorn Woodpeckers is relatively high. Yet because this cost is spread out over a long nestling phase, the proportion of the adult's daily energy budget devoted to reproduction (parental effort) is fairly low.

Acorn Woodpeckers typically live in foothill and montane areas throughout their range, which extends from southern Oregon to northern Colombia. Given the relatively cold conditions to which nestlings are therefore typically exposed during the spring breeding period, nestling and adult hypothermia is potentially advantageous in reducing energy demands and prolonging life when conditions are poor.

At least three features of the Acorn Woodpecker's life history help mitigate the potentially costly effects of these characteristics. The first is nesting in cavities, which provides an improved thermal environment for breeding birds (Mertens 1977). The second is relatively low predation rates, even compared to other cavity-nesting species (Koenig and Mumme 1987), which re-

duces the potential costs of a lengthy nestling period. The third is cooperative breeding. Because Acorn Woodpeckers typically live in family groups of three to five adult birds (up to as many as 15), all of which participate in brooding and feeding of young, the high cost of reproduction and the time and energy demands of nestlings are typically spread out among several adults.

Why do Acorn Woodpeckers, which breed communally in groups of up to 15 individuals and have substantial food reserves available in the form of stored acorns, have such extremely low nestling growth rates? Such slow growth may have a phylogenetic component and characterize melanerpine woodpeckers in general. Even at this taxonomic level, however, slow growth is probably related to diet, as virtually all species within this genus depend substantially on fruit or other low-protein foods. These unusual features, along with the high frequency of cooperative breeding in this genus, may be related and represent an adaptive complex of life-history characteristics.

In the case of Acorn Woodpeckers, slow growth is probably related to the low protein and high tannin content of the acorns upon which they depend. Koenig and Mumme (1987) have documented that Acorn Woodpeckers at Hastings Reservation generally are unable to breed successfully without access to stored acorns during the spring. This suggests that energetic or nutritional requirements needed to reproduce are simply not provided by the available insects on a territory. Supplemental food is necessary, and this is typically provided by stored acorns. Yet the low-protein content of acorns, compounded by the high level of tannins, which are known to bind proteins and reduce their availability to animals (e.g., Robbins et al. 1987), may produce conditions of protein limitation in breeding Acorn Woodpeckers.

Physiological constraints appear to alter costs and benefits in ways that influence the functional consequences of behaviors. In this case, protein limitation is consistent with many of the unusual physiological characteristics of Acorn Woodpeckers documented here. Protein limitation may also be an important factor influencing the costs and benefits of cooperative breeding. The additional brooding and feeding capabilities provided by group members beyond a pair (both additional breeders and nonbreeding helpers) may be particularly valuable as a consequence of the

slow development of nestlings and their extended vulnerability to external conditions. Thus, the Acorn Woodpeckers' unusual social behavior may be related to their unusual physiology.

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## APPENDIX 1

We based our nestling energy budget calculations (Fig. 13; Appendix 2) on nestling mass predicted by the logistic equation (Equation 5) rather than on actual mass, because day-to-day variations in observed mean nestling mass tended to obscure the central trend with respect to the energy accumulated in body tissue (TE). Total metabolized energy (TME) was calculated as the sum of the field metabolic rate (FMR), as measured

with DLW, and TE. Resting metabolic rate (RMR) and FMR were estimated from Equations 8 and 9, respectively, and the mean nestling mass predicted for each day. For nestlings 5 days old and younger, FMR was assumed to equal RMR, since Equation 9 predicts  $FMR < RMR$  for this age group. RMR calculated from Equation 8 does not account for possible reductions in RMR due to nestling hypothermia and thus may overestimate the actual value. Such an error would result in an underestimation of the proportion of FMR attributable to HI, activity, and thermoregulation. The energy content of nestlings (EC; kJ) was calculated by multiplying the dry mass predicted (Equation 10) for each age by the assumed energy density of nestling tissue (23.4 kJ/g dry mass). The daily increment in TE (kJ/day) was obtained by subtracting the previous day's EC (kJ) from the current day's value.

The energy density of lean, dry, nestling tissue averages a fairly constant 20.1 kJ/g for most species (Dunn 1973). Nestling fat content varies widely among species, however, ranging from about 8–50% of dry mass (reviewed by Ricklefs 1983). Because avian body fat contains about 37.7 kJ/g (Ricklefs 1974), the energy density of nestling tissue is fairly sensitive to variation in its fat content. Although we did not measure the fat content of woodpecker nestlings, our impression is that it is rather low and we can estimate it with sufficient accuracy as follows. Species with unreliable food supplies (e.g., some seabirds and aerial-feeding passerines and swifts) tend to accumulate relatively large amounts of fat—up to 50% of dry mass (O'Connor 1978, Bryant and Hails 1983, Ricklefs 1983). In most species, lipid content is much lower; on the order of 8.6 to 25% of dry mass (calculated from Ricklefs 1983). Given the latter range in fat content, the energy density of typical nestlings is 21.6 to 24.5 kJ/g dry mass. For our calculations, we assumed an intermediate value of 23.4 kJ/g dry mass, equivalent to a fat content of 17.6%. Assuming the fat content of Acorn Woodpeckers is within the usual range of 8–25%, our estimated TE values should be within 7% of the true value.

## APPENDIX 2. Parameters of the nestling Acorn Woodpecker's energy budget.

Age (days)	Mass <sup>a</sup> (g)	EC <sup>b</sup> (kJ)	TE <sup>c</sup> (kJ/day)	RMR <sup>d</sup> (kJ/day)	FMR <sup>e</sup> (kJ/day)	TME <sup>e</sup> (kJ/day)
0	7.6	16.8	0.0	9.9	9.9	9.9
1	9.3	21.5	4.7	11.6	11.6	16.3
2	11.4	27.5	6.0	13.6	13.6	19.6
3	13.8	35.1	7.7	16.0	16.0	23.7
4	16.6	44.8	9.7	18.8	18.8	28.5
5	19.7	57.0	12.2	22.0	22.0	34.2
6	23.3	72.1	15.1	25.6	28.9	43.9
7	27.3	90.3	18.3	29.5	38.4	56.6
8	31.5	112.0	21.7	33.8	48.6	70.3
9	36.0	137.0	25.0	38.3	59.4	84.4
10	40.7	165.1	28.1	42.9	70.5	98.6
11	45.3	195.7	30.6	47.5	81.6	112.2
12	49.8	227.9	32.2	52.1	92.4	124.7
13	54.1	260.8	32.8	56.4	102.8	135.6
14	58.1	293.2	32.5	60.4	112.4	144.9
15	61.8	324.4	31.1	64.0	121.2	152.4
16	65.1	353.4	29.1	67.3	129.0	158.1
17	67.9	379.9	26.5	70.2	135.9	162.4
18	70.4	403.5	23.6	72.6	141.9	165.4
19	72.5	424.1	20.6	74.8	146.9	167.5
20	74.3	441.9	17.7	76.5	151.2	168.9
21	75.7	456.9	15.1	78.0	154.7	169.8
22	77.0	469.6	12.6	79.2	157.6	170.3
23	78.0	480.1	10.5	80.2	160.0	170.5
24	78.8	488.7	8.7	81.0	162.0	170.7
25	79.5	495.8	7.1	81.7	163.6	170.7
26	80.0	501.6	5.8	82.2	164.9	170.7
27	80.4	506.3	4.7	82.7	165.9	170.6
28	80.8	510.1	3.8	83.0	166.8	170.6
29	81.1	513.2	3.1	83.3	167.4	170.5
30	81.3	515.6	2.5	83.5	168.0	170.4
31	81.5	517.6	2.0	83.7	168.4	170.4
Sum			501	1,802	3,352	3,853

<sup>a</sup> Calculated as:  $\text{mass (g)} = 82.19 / (1 + 9.79e^{-0.226t})$ , where  $t$  = days of age.

<sup>b</sup> Nestling energy content (EC) calculated as:  $\text{kJ} = [1 - (0.924 - 0.0024 \times m)] \times 23.4 \times m$ , where  $m$  = mass in grams.

<sup>c</sup> Daily increment in tissue energy (TE) calculated by subtracting the previous day's EC from the current day's EC.

<sup>d</sup> Resting metabolic rate (RMR) of fasted nestling calculated as:  $\text{kJ/day} = 2.25 + m$ .

<sup>e</sup> Field metabolic rate calculated as:  $\text{kJ/day} = -27.1 + 2.40m$ , except for days 0-5, for which FMR was assumed to equal RMR.