CHASE, M. K., N. NUR, AND G. R. GEUPEL. 1997. Survival, productivity, and abundance in a Wilson's Warbler population. Auk 114:354–366.

COOPER, B. A., AND R. J. RITCHIE. 1995. The altitude of bird migration in east-central Alaska: A radar and visual study. Journal of Field Ornithology 66:590–608.

DWIGHT, J., JR. 1900. The sequence of plumages and moults of passerine birds of New York. Annals of the New York Academy of Sciences 13:73–360.

HUSSEL, D. J. T. 1991a. Fall migrations of Alder and Willow flycatchers in southern Ontario. Journal of Field Ornithology 62:260–270.

HUSSEL, D. J. T. 1991b. Spring migrations of Alder and Willow flycatchers in southern Ontario. Journal of Field Ornithology 62:69–77.

JOHNSON, M. D., AND G. R. GEUPEL. 1996. The importance of productivity to the dynamics of a Swainson's Thrush population. Condor 98:133–141.

KESSEL, B. 1984. Migration of Sandhill Cranes, *Grus canadensis,* in east-central Alaska, with routes through Alaska and western Canada. Canadian Field-Naturalist 98:279–282.

MCINTYRE, C. L., AND R. E. AMBROSE. 1999. Raptor migration in autumn through the Upper Tanana River Valley, Alaska. Western Birds 30:33–38.

RAPPOLE, J. H., E. S. MORTON, T. E. LOVEJOY III, AND J. L. RUOS. 1983. Nearctic Avian Migrants in the Neotropics. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.

RIMMER, C. C. 1988. Timing of the definitive prebasic molt in Yellow Warblers at James Bay, Ontario. Condor 90:141–156.

SOGGE, M. K., W. M. GILBERT, AND C. VAN RIPER III 1994. Orange-crowned Warbler (*Vermivora celata*). *In* The Birds of North America, no. 101 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992. Migration of woodland birds at fragmented inland stopover site. Wilson Bulletin 104:580–598.

WOODREY, M. S., AND C. RAY CHANDLER. 1997. Age-related timing of migration: Geographic and interspecific patterns. Wilson Bulletin 109:52–67.

Received 31 January 2000, accepted 27 November 2000.
Associate Editor: F. Moore

The Auk 118(2):519–524, 2001

Growth Rate and Energetics of Arabian Babbler (*Turdoides squamiceps*) Nestlings

AVNER ANAVA,[1,2] MICHAEL KAM,[2] AMIRAM SHKOLNIK,[3] AND A. ALLAN DEGEN[2,4]
[1]*Department of Life Sciences, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel;*
[2]*Desert Animal Adaptations and Husbandry, Wyler Department of Dryland Agriculture,*
Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel; and
[3]*Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel-Aviv 69978, Israel*

ABSTRACT.—Arabian Babblers (*Turdoides squamiceps*) are territorial, cooperative breeding passerines that inhabit extreme deserts and live in groups all year round. All members of the group feed nestlings in a single nest, and all group members provision at similar rates. Nestlings are altricial and fledge at about 12 to 14 days, which is short for a passerine of its body mass. Because parents and helpers feed nestlings, we hypothesized that the growth rate of nestlings is fast and that they fledge at a body mass similar to other passerine fledglings. Using a logistic growth curve, the growth rate constant (*k*) of nestlings was 0.450, which was 18% higher than that predicted for a passerine of its body mass. Asymptotic body mass of fledglings was 46 g, which was only 63% of adult body mass, a low percentage compared to other passerines. Energy intake retained as energy accumulated in tissue decreased with age in babbler nestlings and amounted to 0.29 of the total metabolizable energy intake over the nestling period. However, energy content per gram of body mass increased with age and averaged 4.48 kJ/g body mass. We concluded that our hypothesis was partially confirmed. Growth rate of babbler nestlings was relatively fast compared to other passerine species, but fledgling mass was relatively low.

Deserts are characterized by unpredictable rainfall and unpredictable, often sparse, food availability

---

[4] Address correspondence to this author. E-mail: degen@bgumail.bgu.ac.il

(Evenari et al. 1982), which can lead to a relatively slow growth rate of nestlings. The Arabian Babbler (*Turdoides squamiceps*) inhabits extreme deserts, which suggests that the growth rate of babbler nestlings would be slow. However, that does not appear to be the case because nestlings fledge at 12 to 14 days (Zahavi 1990), which is short compared to passerines of similar body mass (Ricklefs 1968). Consequently, nestlings have either a fast growth rate or they fledge at a low body mass, or both.

Arabian Babblers are cooperative breeders and parents and helpers participate in the feeding of nestlings. All group members provision at similar rates, irrespective of sex or dominance rank within the group (Wright 1997, 1998) and, therefore, we hypothesized that the growth rate of nestlings is fast. To test that hypothesis, we determined growth rate of babbler nestlings using a logistic growth curve and compared results with other passerines. We also measured energy use in babbler nestlings and estimated body-energy accumulation during growth.

Materials and Methods.—Study species and study site.—The Arabian Babbler (65 to 85 g) is a passerine species distributed in Saudi Arabia, Sinai, and in some of the extreme deserts of Israel, and is the only bird species in Israel that lives in groups year round. Those groups are territorial with the number of birds per group generally between 3 and 5 individuals, but the range is between 2 and 22 (Zahavi 1990).

Egg laying in each group of babblers takes place in one nest usually between February and August. Three clutches are possible. Breeding females lay between 3 and 5 eggs during each clutch and, where more than one female lays, the total number of eggs can reach 13. Maximum number of fledglings from one nest is about six. All members of the group participate in all phases of nesting and rearing young (Zahavi 1989, 1990).

All birds, including nestlings, were color banded. To determine growth rate of nestlings, 77 chicks from 24 nests were used; all nests were attended by parents and helpers. Five nests had a brood of two, 10 had a brood of three, 8 had a brood of four, and 1 had a brood of five. All nests were observed daily, and time of hatching was determined in each. Age of nestlings was measured in days. Changes in body mass of nestlings were followed by periodically weighing them over the nesting period and pooling the total of 547 measurements that were made (Degen et al. 1992).

The study was done at the Nature Reserve at Hatzeva (30°45′N; 35°15′E) in the Arava, ~30 km south of the Dead Sea. That site is characterized by long, hot, dry summers. It has a winter rainfall that averages 35 mm annually, but there are large variations in total rainfall and in its temporal and spatial distribution. Average daily air temperature for the hottest (August) and coldest (January) months are 30°C and 15°C, respectively (Stern et al. 1986).

Doubly labelled water measurements.—Field metabolic rate (FMR) and water flux of babbler nestlings were measured from February to August, 1996. Nestlings ($n = 65$) were injected subcutaneously with 70 μl/g water whose oxygen was 95% ^{18}O and whose tritium produced 1.85 MBq/mL. Injections were done between 0900 and 1100 (GMT + 2 h). One hour was allowed for equilibration of the isotopes with body fluids (Degen et al. 1981), after which time a blood sample was collected from a brachial vein and the nestling was weighed on an electronic balance (± 0.2 g). Further blood samples were taken daily for the next one to two days at the same hour.

Blood samples were microdistilled under vacuum until dryness to obtain pure water. Specific activity of tritium in the water was measured by liquid scintillation spectrometry (Nagy 1983). Level of ^{18}O specific activity was measured by an autogamma counting system (Packard) after converting ^{18}O to gamma-emitting ^{18}F by cyclotron-generated proton activation (Wood et al. 1975). Blood samples from three noninjected nestlings from different nests were treated similarly to measure background levels of ^{18}O and tritium.

Total body water (TBW) of each nestling was calculated from the initial dilution volume of isotopic water, and water fluxes were calculated from the subsequent decline in specific activity of tritium over time (Degen et al. 1981). We were suspect of the exact injection volume in some nestlings and, therefore, there were 48 TBW measurements of the 65 injected nestlings. In nestlings without TBW measurement, TBW values from the regression analysis of TBW on body mass was used (see results) to calculate water flux and FMR (Anava et al. 2001). Total body solids were calculated as the difference between body mass and total body water. Rates of CO_2 production were estimated from the declines in specific activities in tritium and ^{18}O over time (Nagy 1980). Eight samples could not be measured for ^{18}O and, therefore, there were 57 FMR measurements.

Treatment of data.—A logistic equation was used to describe the growth curve of nestlings (Ricklefs 1968). We calculated the age of maximum growth rate (in days) and maximum growth rate (in grams per day) at the inflection point. To compare the growth rate of Arabian Babbler nestlings with other bird species, we determined the time required to grow from 10 to 90% (t_{10-90}) of asymptotic body mass (Ricklefs 1968).

Rates of CO_2 production of babbler nestlings were converted to rates of heat production and energy intake on the basis of an insect diet: 25.7 J were expended per milliliter of CO_2 produced (Nagy 1983) and metabolizable energy was 0.75 of gross energy (Robbins 1983). We assumed water influx equalled metabolic and preformed water from food. For insects, a volume of 0.660 μl of metabolic water was generated per milliliter of CO_2 produced (Nagy

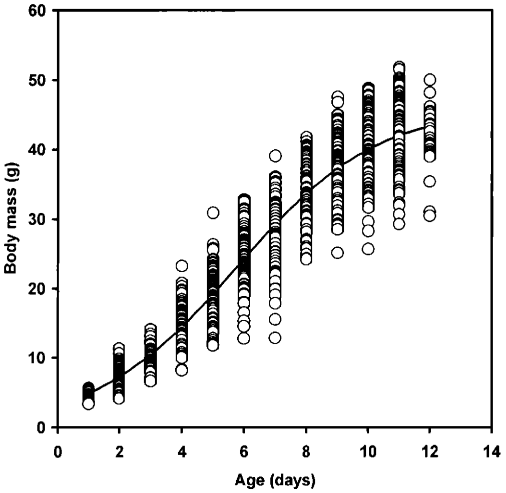

FIG. 1. Body mass of Arabian Babbler nestlings in relation to age. The line represents the logistic growth curve (see text).

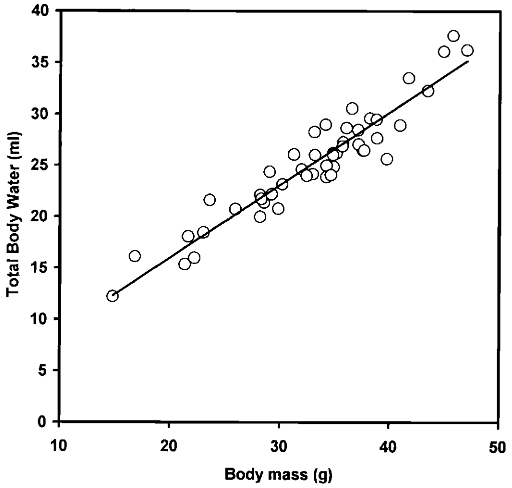

FIG. 2. Total body water volume of Arabian Babbler nestlings in relation to body mass.

1983). Preformed water intake was calculated as the difference between water influx and metabolic water.

We used FMR, growth rate, and changes in total body solids to calculate the energy budget of nestlings. Metabolizable energy intake (MEI) of the growing Arabian Babbler nestlings was expressed in terms of heat production (HP) plus or minus energy retention (ER) accumulated in new tissue. HP was estimated from the DLW measurements and ER from the changes in body solids of the growing nestlings, assuming that 21.3 kJ were accumulated as body energy per gram of body solid gain (Weathers and Sullivan 1991). Dry-matter intake was calculated from the MEI, assuming 20.3 kJ of metabolizable energy were yielded per gram dry matter (Nagy 1983). Fresh-matter intake was the sum of dry matter and preformed water of the diet. Total ER as a fraction of total MEI was determined on a daily basis and over the whole nestling period.

Results.—Nestling development and growth.—Arabian Babblers at hatching weighed 4.47 ± 0.61 g (n = 37) or 6.2% of adult body mass. Hatchlings were completely naked and their eyelids were fused. Their eyes opened between four and six days, during which time feathers emerged. As fledglings, aged 12 to 14 days, their bodies were covered with plumage, but development of wings and tail were not complete and, as a result, they were unable to fly. Tarsus length on day 10 (36.7 ± 1.53 mm, $n = 24$) was 96.6% of adult size (38.8 ± 0.91 mm, $n = 110$).

From the growth curve ($n = 547$) of nestlings ($n = 77$) described by the logistic curve (Fig. 1; Appendix), the asymptotic body mass of the babblers was 46.0 g and the constant parameters B and k were 13.3 and 0.450, respectively. The ratio between asymptote body mass and mean adult mass (72 g) was 0.63. Maximum growth rate of nestlings, 5.17 g/day, was attained at 5.74 days and the time required to grow from 10 to 90% of asymptotic body mass ($t_{10\text{-}90}$) was 9.76 days

Total body water, water flux and field metabolic rate.—Total body water volume (TBW; in milliliters), estimated from ^{18}O space, increased linearly with body mass (m_b; in grams), TBW = 0.711 m_b + 1.781 (n = 48; $S_b = 0.36$; $S_{y.x} = 1.75$; $r^2 = 0.89$; and $P < 0.001$, Fig. 2). However, TBW, as a fraction of body mass, decreased linearly with body mass (in grams), TBW = 0.861−0.0028 m_b ($n = 48$; $S_b = 0.001$; $S_{y.x} = 0.06$; r^2 = 0.11; and $P < 0.05$).

Both water influx and water efflux increased linearly with body mass. The regression equation of water influx (milliliters per day) on body mass (in grams) was Water influx = 0.352 m_b + 5.221 ($n = 65$; $S_b = 0.06$; $S_{y.x} = 3.56$; $r^2 = 0.36$; and $P < 0.001$), and water efflux (milliliters per day) on body mass (in grams) was Water efflux = 0.490 m_b− 2.051 ($n = 65$; $S_b = 0.05$; $S_{y.x} = 2.99$; $r^2 = 0.61$; and $P < 0.001$, Fig. 3). Water efflux at 22.8 ml/day equalled water influx and this occurred at ~50 g body mass. Field metabolic rate (FMR) of the nestlings increased linearly with body mass (Fig. 4). The regression equation of FMR (kilojoules per day) on body mass (in grams) was FMR = 1.52 m_b− 4.35 ($n = 57$; $S_b = 0.37$; $S_{y.x}$ = 19.12; r^2= 0.24; and $P < 0.001$).

Discussion.—Arabian Babblers attain adult body mass between 8 and 12 months of age (A. Anava unpubl. data). The nestling phase (12 to 14 days) is short compared to other passerines of similar body mass and to passerines in general (Ricklefs 1968). Shortening the nestling period can (1) allow adults to produce more clutches per year; (2) reduce the risk

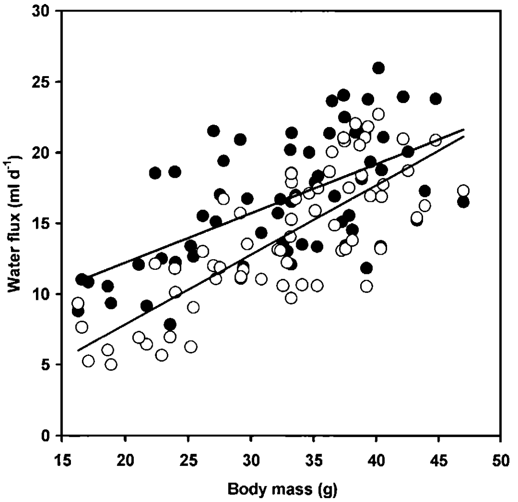

FIG. 3. The effect of body mass on water influx (solid circles) and water efflux (open circles) in Arabian Babbler nestlings.

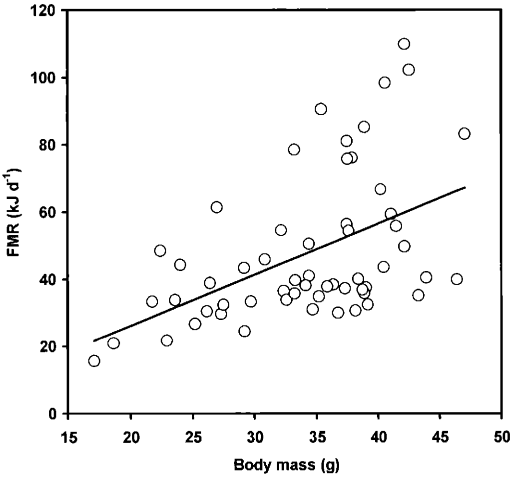

FIG. 4. The effect of body mass on field metabolic rate (FMR) in Arabian Babbler nestlings.

of predation (Lack 1968); and (3) allow adults and fledglings to move from the nesting site to forage new patches. During the nestling period of babblers, skeletal development is fast, which is typical of most passerines. However, that is not the case with the development of feathers and body size and, as a result, fledglings are unable to fly and to forage independently for about two months (A. Anava pers. obs.). They are dependent on their parents and helpers for food. Thus, those fledglings are like nestlings, but are outside the nests.

The growth rate constant (k) was 0.450/day which was 18% higher than that predicted (0.381/day) for a passerine of its body mass (Ricklefs 1968). The time required to grow from 10 to 90% of its body mass ($t_{10\text{–}90}$) was 9.76 days which was 17% faster than that predicted (11.4 days) for a passerine of its body mass (Ricklefs 1968). The ratio between the asymptote and adult mass, 0.63, is one of the lowest in passerine species (Bateman and Balda 1973, Degen et al. 1992, Weathers et al. 1990, Woolfenden 1978).

Water content, as a fraction of body mass, decreased with age in babbler nestlings. A reduction has been reported in other birds (Robbins 1983, Rowe 1990) and is related to an accumulation of body lipid in growing nestlings (O'Connor 1977, Robbins 1983). Water efflux and influx increased with body mass in growing nestlings. Near fledging (46 g), mass specific water influx was 46 ml g^{-1} day^{-1} which was similar to the 41 ml g^{-1} day^{-1} found for adults (Anava 2000) and similar to Northern Shrike (*Lanius excubitor*) nestlings near fledging (Degen et al. 1992).

Metabolizable energy intake followed a sigmoidal curve, as has been reported for Northern Shrikes (Degen et al. 1992). It increased with age (Fig. 5) and reached its peak (72 kJ/day) at 10 days of age. Total metabolizable energy intake (MEI) per chick over the nesting phase of 1 to 14 days was 759.4 kJ. This is only 68.5% of the predicted MEI (kJ/nestling) calculated from an equation generated from fledgling body mass and fledging time (Weathers 1992). The ratio of ER to MEI decreased from 0.62 at 1 day of age to 0.05 at 14 days of age (Appendix). Growing nestlings required more energy for maintenance and

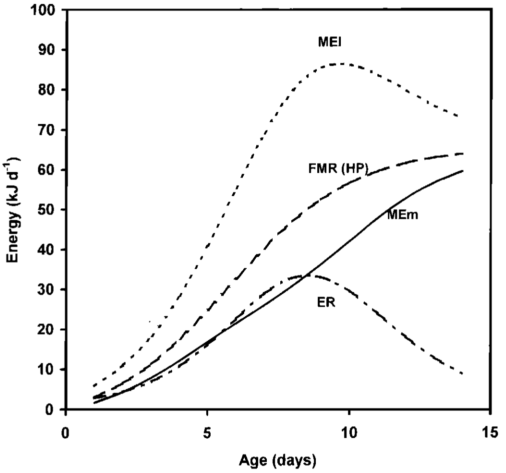

FIG. 5. Metabolizable energy intake (MEI); field metabolic rate (FMR), heat production (HP); metabolizable energy for maintenance (MEm); and energy retention (ER) of Arabian Babbler nestlings. The area between FMR and MEm represents the heat increment of feeding for growth. Values were based on logistic growth curve (see text).

thermoregulation and, therefore, a smaller proportion of MEI was available for growth. Thus, even if the efficiency of utilization of energy for growth remained constant, that is, the relative proportions of heat increment of feeding for growth and of ER stayed constant, the ratio of ER to MEI would decrease. However, concomittantly, as nestlings grew, the ratio of ER per change in body mass increased from 3.18 kJ per g body mass in nestlings of 1 day to 5.65 kJ per g body mass in nestlings of 14 days. The nestlings were putting on proportionately more body solid and more lipid as they grew, and thus the energy content per change in body mass increased with age. Average energy content per gram of body mass over the whole nestling period was 4.48 kJ per gram.

Calculated total dry matter and fresh matter intakes of each young over the 14 day nestling period was 35.8 and 202.3 g, respectively. Mass-specific daily dry matter intake generally decreased with age and ranged between 0.07 and 0.11 per gram of body mass. Lowest fresh-matter intake per day as a fraction of body mass was 0.52 at 12 to 14 days of age and highest fresh-matter intake as a fraction of body mass per day was 1.49 on the day after hatching. Red-backed Shrikes (*Lanius collurio*) had an overall fresh-matter intake per day of 0.56 body mass with a daily range of 0.40 to 0.78 (Diehl 1971) and Northern Shrikes had a daily intake of 0.38 to 0.85 of body mass.

We concluded that our hypothesis was partially confirmed. Growth rate of Arabian Babbler nestlings was relatively fast compared to other passerine species, but fledging mass was relatively low. A consequence of early fledging could be that predation is reduced and foraging area in a harsh environment is increased.

Acknowledgments.—We thank Amotz Zahavi for his helpful discussions, Ron Mumme, Carlos Bosque, and an anonymous reviewer for constructive suggestions and personnel at Hatzeva Field School for their help and hospitality. This research was supported by the Israel Science Foundation administered by the Israel Academy of Sciences and Humanities.

LITERATURE CITED

ANAVA, A., M. KAM, A. SHKOLNIK, AND A. A. DEGEN. 2000. Seasonal field metabolic rate and dietary intake in Arabian Babblers (*Turdoides squamiceps*) inhabiting extreme deserts. Functional Ecology 14:607–613.

BATEMAN, G. C., AND R. P. BALDA. 1973. Growth, development, and food habits of young Pinon Jays. Auk 90:39–61.

DEGEN, A. A., B. PINSHOW, P. U. ALKON, AND H. ARNON. 1981. Tritiated water for estimating total body water and water turnover rate in birds. Journal of Applied Physiology: Respiratory, Environmental and Exercise Physiology 51:1183–1188.

DEGEN, A. A., B. PINSHOW, R. YOSEF, M. KAM, AND K. A. NAGY. 1992. Energetics and growth rate of Northern Shrike (*Lanius excubitor*) nestlings Ecology 73:2273–2283.

DIEHL, B. 1971. Productivity investigation of two types of meadows in the Vistula Valley. XII. Energy requirement in nestling and fledgling Red-backed Shrike (*Lanius collurio* L.). Ekologia Polska 19:235–248.

EVENARI, M., L. SHANAN, AND N. TADMOR. 1982. The Negev: The Challenge of a Desert, 2nd ed. Harvard University Press, Cambridge, Massachusetts.

LACK, D. 1968. Ecological Adaptation for Breeding in Birds. Methuen, London.

NAGY, K. A. 1980. CO_2 production in animals: Analysis of potential errors in the doubly labeled water method. American Journal of Physiology 238· R466–R473.

NAGY, K. A. 1983. The doubly labeled water ($^3HH^{18}O$) method: A guide to its use. UCLA Publication Number 12-1417, University of California at Los Angeles, Los Angeles.

O'CONNOR, R. J. 1977. Differential growth and body composition in altricial passerines. Ibis 119:147–166.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.

ROBBINS, C. R. 1983. Wildlife Feeding and Nutrition Academic Press, New York.

ROWE, R. A. 1990. Tritiated water measurements of water flux in nestling and adult Zebra Finches (*Poephila guttata*). Comparative Biochemistry and Physiology 95A:253–257.

STERN, E., Y. GRADUS, A. MEIR, S. KRAKOVER, AND H. TSOAR. 1986. Atlas of the Negev. Keterpress Enterprises, Jerusalem, Israel.

UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION. 1977. Map of the world distribution of arid lands. MAB, Technical Note 7. UNESCO, Paris.

WEATHERS, W. W. 1992. Scaling nestling energy requirements. Ibis 134:142–153.

WEATHERS, W. W., M. T. STANBACK, AND W. D. KOENIG. 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. Condor 92:341–359.

WEATHERS, W. W., AND K. A. SULLIVAN. 1991 Growth and energetics of nestling Yellow-eyed Juncos. Condor 93:138–146.

WOOD, R. A., K. A. NAGY, S. T. MACDONALD, S. I. WAKAKUWA, R. J. BECKMAN, AND H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. Analytical Chemistry 47:646–650.

WOOLFENDEN, G. E. 1978. Growth and survival of young Florida Scrub Jays. Wilson Bulletin 90:1–18.

WRIGHT, J. 1997. Helping-at-the-nest in Arabian Babblers: Signalling social status or sensible investment in chicks? Animal Behaviour 54:1439–1448.

WRIGHT, J. 1998. Helping-at-the-nest and group size in the Arabian Babblers (*Turdoides squamiceps*). Journal of Avian Biology 29:105–112.

ZAHAVI, A. 1989. Arabian Babbler. Pages 253–275 *in* Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

ZAHAVI, A. 1990. Arabian Babblers: The quest for social status in a cooperative breeder. Pages 105–130 *in* Cooperative Breeding in Birds (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.

Received 30 August 1999, accepted 15 February 2001.
Associate Editor: C. Bosque

APPENDIX. Parameters of the nestling Arabian Babbler's energy budget.

Age (d)	m_b[a] (g)	Δm_b (g)	ER[b] (kJ/day)	FMR[c] (kJ/day)	MEI[d] (kJ/day)	ER/MEI
0	3.22	0.00	0.00	3.14		
1	4.86	1.64	5.21	3.16	8.37	0.622
2	7.19	2.33	7.74	6.58	14.32	0.540
3	10.36	3.17	11.13	11.40	22.53	0.494
4	14.40	4.04	15.23	17.54	32.77	0.465
5	19.18	4.77	19.38	24.80	44.18	0.439
6	24.32	5.14	22.49	32.61	55.10	0.408
7	29.32	5.01	23.48	40.22	63.70	0.369
8	33.76	4.43	22.00	46.96	68.96	0.319
9	37.36	3.60	18.67	52.44	71.11	0.263
10	40.09	2.73	14.60	56.59	71.19	0.205
11	42.05	1.96	10.71	59.56	70.28	0.152
12	43.40	1.35	7.51	61.62	69.12	0.109
13	44.31	0.91	5.10	63.00	68.09	0.075
14	44.91	0.60	3.38	63.91	67.29	0.050
Total		41.7	219.1	543.5	759.4	0.289

[a] Mean body mass (m_b; gram) = $46/[(1 + 13.27) \times e^{-0.45 \times t}]$.

[b] Daily energy retention (ER) calculated as: ER = fraction of body solids × Δm_b × energy yield. ER = $(1 - (0.865–0.0029 \times m_b)) \times \Delta m_b \times 21.3$.

[c] Field metabolic rate calculated from the equation: FMR = $1.52 \times m_b^{-4.35}$.

[d] Metabolizable energy intake: MEI = FMR + ER.