

# ENERGY AND WATER USE BY GREAT GREY SHRIKE NESTLINGS IN UNPREDICTABLE DESERT ENVIRONMENTS

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**ABSTRACT.**—Deserts are characterized by unpredictable food supplies which can lead to a slow growth rate of nestling birds. However, given that Great Grey Shrike (*Lanius excubitor*) males use prey from their caches to augment freshly caught prey in providing food for their mates and nestlings, we hypothesized that their nestlings would not have a slow growth rate, but one that is equivalent to that in other passerine nestlings from temperate areas. To test this hypothesis, we measured growth rates and energy use in Great Grey Shrike nestlings and fledglings, and energy expenditure in two adult males that attended nests. Growth rate of Great Grey Shrike nestlings was similar to that predicted for passerines from temperate areas. However, metabolizable energy available in the cache amounted to only about 7.2% of the total energy requirements of the nestlings or 4.2% of the total energy requirements of parents and nestlings during the nestling period. Hence other factors were also important in determining growth rate. These included an extremely low maintenance energy requirement of nestlings (30% of that predicted for a bird of its body mass when it weighed 10 g which gradually increased to 70% at 50 g). This allowed for more of the energy intake to be used for growth and also reduced foraging costs of males. Another factor was the relatively low amount of retained body energy as a fraction of metabolizable energy intake, 0.15–0.16, indicating more water per unit growth than in other passerines. Energy expenditure of adult males was substantially lower than that predicted for a passerine of similar body mass. Males collected 4.83 times the energy that they consumed in order to provide their mates and offspring with food. Yet, their ratio of field metabolic rate to basal metabolic rate was only 2.33, the lowest reported value for adults feeding altricial young.

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The breeding season of adult birds is the most energy demanding period in their overall annual energy budget. In particular, feeding nestlings is the time of peak energy expenditure of adults, mainly as a result of extra foraging costs (Bryant 1988, Weathers and Sullivan 1989). Deserts are characterized by unpredictable rainfall and consequently unpredictable food availability (Evenari et al. 1982). Nestling birds that are faced with unpredictable food supplies often use a strategy of resource storage, i.e. they store lipid as energy reserves (O'Connor 1978, Bryant and Hails 1983). This can lead to their having relatively slow growth rates. The more unpredictable the food supply, the greater the

lipid storage and consequently the slower their growth rate (Bryant and Hails 1983).

Great Grey Shrikes (*Lanius excubitor*) include extreme deserts in their distribution and males impale prey all year (Yosef 1989). This caching makes their food supply ostensibly more predictable than that afforded other desert birds. Further, the male does all provisioning of his mate and young; he feeds his mate during the nestling period and she feeds the young. Given that food from caches is available to augment freshly caught prey that males feed to their mate and chicks, we hypothesized that desert-dwelling Great Grey Shrike nestlings would have growth rates similar to those found in temperate passerine altricial nestlings hatched to parents of the same size as Great Grey Shrike adults.

To test this hypothesis, we determined the growth rate of Great Grey Shrikes from hatch-

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ing to fledging and compared it with growth rates for temperate passerines. We also used doubly labeled water to estimate energy expenditure and water flux of nestlings and fledglings and of adult males that were raising nestlings.

STUDY AREA AND METHODS

This study was done near Sede Boqer in the Negev Desert Highlands, Israel, from February to June 1987. The area is arid with an annual mean winter rainfall of 104 mm, but there are large annual variations in total rainfall and in its temporal and spatial distribution (Zangvil and Druian 1983). The site is a loess-covered plateau that supports a sparse dwarf shrub community which has been described elsewhere (Yosef and Pinshov 1989).

We determined growth rate by weighing 66 nestlings from 14 nests. We marked the nestlings by painting their claws. Each individual was weighed only a few times and usually over a period of only several days. Because of our disruptions, on a number of occasions, nestlings were moved by their parents (Yosef and Pinshov 1988a) which interrupted our weighings. Thus, we could not establish a complete growth curve for any single individual and pooled the total of 380 measurements that were made. We also captured and recaptured two fledglings and two adult males (that were feeding mates and young) as well, and they provided post-fledging data.

Simultaneously with the mass measurements, we used doubly labeled water to measure energy and water use in the shrikes. These data allowed us to resolve, in part, how Great Grey Shrike nestlings grow at the rates we found. Details of the methods may be found in Degen et al. (1992).

Total body water (TBW) volumes were estimated from the initial dilution of isotopes, and water fluxes were calculated from the subsequent decline in specific activity of tritium over time (Nagy and Costa 1980). Water influx equaled total water intake, that is, metabolic water and water from food (preformed water). Water vapor diffusional exchange across permeable surfaces was considered negligible. Water efflux was calculated as  $-water\ influx - \Delta TBW$ .

The separation of total energy into its components

(metabolizable energy intake, heat production, energy for maintenance and energy retention) is based on several assumptions about energy and water content of food and efficiency of energy utilization. These are described in detail by Degen et al. (1992)

RESULTS AND DISCUSSION

The growth curve of the Great Grey Shrike nestlings was sigmoidal as is generally the case for birds and mammals (Degen et al. 1992). From the logistic growth equation fitted to the data, we calculated that the time it took Great Grey Shrikes to grow from 10% to 90% of their asymptotic body mass was 11.5 days which is just 1.5% greater than the values predicted for a temperate passerine of the same asymptotic body mass by Ricklefs' allometric equation (Ricklefs 1968). The slope of the linearized logistic curve, *k*, which is an indication of the average growth rate of the nestlings was 0.381. This is in the range measured for mesic passerines in general and 101.9% of that predicted for a bird with an asymptotic body mass of 50g. By contrast, *k* values for desert species in the same area, at the same time of year, as our shrikes are only one-third of the value for shrike nestlings (Table 1).

Thus, our original hypothesis is superficially supported by the data. Great Grey Shrike nestlings raised in the desert have growth rates equivalent to those of temperate passerines and greater than those of typical desert ones. However, we based our hypothesis on the assumption that the cache collected by adult males provided a predictable food supply. This might, to some extent, be true, but simple arithmetic, based on the number of insects found in shrike caches by Yosef (1989), suggests that the stored food could not account for more than a small fraction of the total energy needed. Indeed, as we show below, the metabolizable energy in an average cache could supply only 7% or less of the needs of the chicks.

TABLE 1. Comparison of logistic growth curve slope (*k*) values among nestlings of two desert-breeding altricial passerines, Great Grey Shrike nestlings, and the value predicted by the allometric equation of Ricklefs (1968) for a temperate altricial passerine of the same asymptotic body mass (*m<sub>t</sub>*) as the Great Grey Shrike.

Species	<i>k</i>	
Great Grey Shrike	0.381	Degen et al. 1992
Desert Lark ( <i>Ammonomanes deserti</i> )	0.132	Shkedy and Safriel 1992
Crested Lark ( <i>Calerida cristata</i> )	0.134	Shkedy and Safriel 1992
Predicted-50g asymptotic <i>m<sub>t</sub></i>	0.374	Ricklefs (1968)

Total body water increased with age as expected (Degen et al. 1989). Total body water volume as a fraction of body mass decreased from approximately 0.90 in nestlings to 0.62 in mature birds as it does in other species (Degen et al. 1992). This reduction in the fraction of total body water volume is related to an accumulation of body solids and lipid in the growing nestling.

We calculated rates of heat production and energy intake from rates of CO<sub>2</sub> production. Throughout the study, total heat production of the Great Grey Shrike nestlings, fledglings, and adults was lower than the daily energy expenditure predicted by Nagy's equation for free-living birds of the same body mass (Nagy 1987).

Nestlings of 10 g produced only 30% of the heat predicted for a bird of their body mass, and this increased to 70% for fledglings of 50 g.

If heat production in shrikes was relatively lower than in other nestlings with similar growth rate, then the fraction of the metabolizable energy intake used for maintenance must have been low. This low heat production for maintenance in young nestlings will contribute to reduced foraging costs for feeding males. The slow increase in heat production of nestlings with age would suggest slow development of thermoregulation as the birds grow. Thus, energy for thermoregulation is also saved as has been described by for other growing nestlings by O'Connor (1977).

Metabolizable energy intake also followed a sigmoidal curve. The ratio of metabolizable energy intake to average daily energy retention, generally decreased as the nestlings grew. Total metabolizable energy intake over the nestling period averaged 1140 kJ; nestlings retained 172 to 183 kJ in increased body energy, or 15% to 16% of the total metabolizable energy intake.

The mean field metabolic rate (FMR) of two adult males was 112.1 kJ/day which was similar to that of fledglings of similar body mass, but which was only 67.8% of that predicted for a free-living passerine of the same body mass (Nagy 1987). Furthermore, the FMR of the adults was only 54.2% of that predicted for non-erally foraging adults feeding altricial nestlings. We recognize that this is based on only two adult males, but these values are still especially low.

Maximum energy collected per day by males coincided with day 18 of the nestling period, when mean metabolizable energy intake per

nestling was 91 kJ. Mean daily energy expenditure for the adult males was 112 kJ and since they maintained constant body mass during the study, energy intake equaled energy expenditure. If we assume that each male provided food for five nestlings and his mate, and that the energy intake of the female was similar to that of the male, then maximum daily metabolizable energy provided by the male equaled 679 kJ [(91 kJ/nestling × 5 nestlings) - (112 kJ/adult × 2 adults)]. In order to provide this amount of energy, males had to collect 33.4 g dry matter or 133.8 g fresh matter of insects.

By making the same kinds of assumptions as in the above calculation, we also calculated total metabolizable energy collected by a male Great Grey Shrike over the 18-day nestling period. Metabolizable energy intake per nestling over the 18-day period was 1140 kJ and per adult was 2018 (112 kJ/d × 18 d) kJ. Therefore, males had to collect a total of 9736 kJ [(1140 kJ/nestling × 5 nestlings) + (2018 kJ/adult × 2 adults)] metabolizable energy over the nestling period. In order to provide this energy, males had to collect 480 g dry matter or approximately 1918 g of fresh matter of insects. Of the total energy collected, each adult consumed approximately 20.7%; that is the males consumed one fifth of the total energy that they collected, and the nestlings consumed 58.5% or 1,123 g.

Assuming each insect had a mass of one gram (a conservative assumption), 1123 insects were fed to the chicks. As only 80 items, on average, were found in a shrike cache when hatching took place (Yosef 1989), the larder supplied 7.2% or less of the food intake of the nestlings!

O'Connor (1978) described three reproductive strategies for passerines according to food availability. (1) With predictable food available before and during breeding, birds use a clutch adjustment strategy, that is, females lay the optimal number of eggs that the food supply can support. (2) With unpredictable food availability before nesting but stable after, birds use a brood reduction strategy, that is, feed the strongest chicks and, if necessary, let the weakest perish. (3) With unpredictable food availability before and after nesting, a resource storage strategy is used, that is, nestlings accumulate lipid material which can be mobilized if there is a shortage of food.

Because of unpredictable food supplies associated with deserts, the last strategy appears

to suit desert passerines, and because of the high energy value of lipid material, this strategy should be characterized by slow growth rates in nestlings. Great Grey Shrikes, however used the first strategy. That is, the growth rate of the nestlings was equivalent to that of passerines from temperate areas.

This is attributable, in part, to the very low maintenance energy requirements of the young and to the slow development of thermoregulation. In addition, The energy expenditure of males was only half of that predicted for non-aerially foraging adults feeding altricial

nestlings. If we assume that the males can sustain a similar increase in energy expenditure to that sustained by other adult passerines raising their young, then Great Grey Shrike males may have much leeway, even in poor years, to provide their nestlings with food to maintain normal growth rates.

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