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ENERGETICS OF ACTIVITY AND FREE LIVING IN BIRDS

DAVID L. GOLDSTEIN

Abstract. Knowledge of the energy costs of avian activities, based on studies in both laboratory and field, can be applied to understanding daily energy expenditure (DEE) by free-living birds through the use of time-energy budgets (TEB). In TEB analysis, a compendium of activities is made, and the energy costs are summed. Comparisons of TEB estimates of DEE with those measured directly using doubly-labeled water suggest that the former technique can give accurate results, but can also be misleading. Energy costs of resting and activity should be known for the population under study, and thermoregulatory costs must be properly quantified. Under some conditions energy expenditure by birds reaches a maximum sustainable level. Behavioral flexibility may then be critical to the maintenance of energy balance in the face of changing physical environments and resource availability. Measurements of DEE may provide a quantitative link between foraging ecology (patterns of behavior) and fitness (the ability to survive and reproduce).

Key Words: Foraging energetics; activity costs; time-energy budget; doubly-labeled water; daily energy expenditure.

The costs and benefits of avian foraging can be measured in a variety of currencies. Among these, estimates of energy balance are attractive because of the ability to quantify the energy spent and gained, and because of the fundamental link in which energy gained while foraging can be converted to activity, growth, storage, or reproduction. As such, studies of energy expenditure may provide quantitative tests of a variety of ecological theories regarding such phenomena as foraging strategies, resource competition, or parental investment. Our confidence in these tests rests largely in our ability to assess energy expenditure accurately. In this paper I will address the techniques used to assess rates of energy use, and will discuss some of the implications of the results gained.

THE ENERGY COSTS OF AVIAN ACTIVITIES

The energy costs of avian activities have been estimated in both laboratory and field using a variety of techniques. In the laboratory, analyses of oxygen consumption have been made during resting, alert perching, bipedal locomotion, hovering, gliding, flapping flight, and eating. Such studies provide the bulk of the data available on energy costs of activities.

The cost of a particular activity can be arrived at under certain circumstances (reviewed by Goldstein 1988) using doubly-labeled water (Nagy 1980), which provides a measure of carbon dioxide production (convertible to energy consumption) over an extended (typically several day) period. Such analyses are most applicable to activities with high energy costs; they have been used to calculate the cost of flight in several species (Hails 1979, Turner 1983b, Flint and Nagy 1984, Tatner and Bryant 1986, Masman and Klaasen 1987) and the cost of swimming in Jackass Penguins (*Spheniscus demersus*; Nagy et al. 1984).

Activity costs in unrestrained birds have also been estimated from telemetered heart rates, which may, in well-defined circumstances (see Johnson and Gessaman 1973), provide a reliable index to the rate of oxygen consumption. This approach has been applied rarely to birds, but has yielded estimates of the energy costs of eating and several other activities (Wooley and Owen 1978).

Finally, the energy cost of flight has been estimated for a number of species based on the loss of mass of fat used to fuel the activity (see, e.g., Dolnik and Gavrilov 1973).

Measures of the energy cost of the same activity in the same species using different techniques are few. However, both they and interspecific comparisons reveal consistent ranges of estimates (Table 1), and suggest that each technique is capable of yielding accurate measures of the energy costs of activities.

Our knowledge of the energy costs of some types of activities, such as resting and flight, is now quite good. Flight costs in those aerial species, such as swallows and swifts, that forage in flight are typically 2.5 to 5 times resting energy expenditure (reviewed in Masman and Klaasen 1987). However, sustained flight in other birds is more costly, approximately 11 times resting (Masman and Klaasen 1987), and short flights such as might be used to move between foraging substrates may cost in excess of 20 times resting (Tatner and Bryant 1986).

The energy costs of other activities are less well studied. The energetics of treadmill running are well characterized (Taylor et al. 1982). However, the energy cost of terrestrial foraging and locomotion is complex, and depends on the speed of

TABLE 1. ENERGY COSTS OF AVIAN ACTIVITIES MEASURED USING DIFFERENT TECHNIQUES

Activity	Species	Cost	Method	Reference
		Same activity in same species		
Flight	Barn Swallow (*Hirundo rustica*)	1.34[a] 1.30[a]	Mass loss over long flight Doubly-labeled water	Masman and Klaasen (1987)
Flight	House Martin (*Delichon urbica*)	1.01–1.26[a] 0.95–1.08[a]	Doubly-labeled water Mass loss over long flight	Masman and Klaasen (1987)
Flight	Starling (*Sturnus vulgaris*)	9.15[a] 9.0[a]	Oxygen consumption in wind tunnel Doubly-labeled water	Masman and Klaasen (1987)
		Same activity in different species		
Feeding	Loggerhead Shrike (*Lanius ludovicianus*)	2.2[b]	Oxygen consumption	Weathers et al. (1984)
	Black Duck (*Anas rubripes*)	1.7[b]	Heart rate telemetry	Wooley and Owen (1978)
Alert perching	Budgerigar (*Melopsittacus undulatus*)	2.0[b]	Oxygen consumption	Buttemer et al. (1986)
	Black Duck	2.1[b]	Heart rate telemetry	Wooley and Owen (1978)

[a] Cost (watts).

[b] Cost (multiple of basal metabolic rate, the metabolic rate in a resting, post-absorptive animal).

locomotion, slope and evenness of the terrain, and foraging activities that accompany locomotion. The cost of terrestrial foraging has been estimated for just one bird species (Gambel's Quail [*Callipepla gambelii*]: cost was approximately two times predicted resting levels, or 3.5 times actually measured resting energy expenditure [Goldstein and Nagy 1985]).

A number of other activities, including alert perching and food manipulation-eating, have energy costs two to three times resting (Table 2).

THE ENERGY COST OF FREE LIVING

Daily energy expenditure in birds (DEE, the sum of all energy costs incurred in a 24-hour period) has been measured in a number of ways (reviewed by Goldstein 1988), including predominantly the construction of time-energy budgets and the use of doubly-labeled water. Other techniques to measure DEE, such as analysis of sodium turnover or the quantitative collection of excreta, may be applicable to some species or situations (see Nagy 1989), but have been used infrequently or not at all for free-living birds.

In time-energy budget (TEB) analysis, a compendium of activities is made for an animal, and the energy costs of these activities are summed; costs of thermoregulation and production must be added to this. This technique is time consuming, and requires that activities be categorized and accurately timed, that activity costs be estimated, and that thermoregulatory costs be accurately assessed. Yet it requires a minimum of equipment and is inexpensive, and so has been most commonly used to measure DEE in birds.

The doubly-labeled water (DLW) technique provides a more direct and quite accurate (±8%) measure of DEE. However, it provides only a single integrated measure of energy expenditure, and the analyses can be costly. In recent years a number of studies have employed this technique, and its use simultaneously with time-energy budget analysis has provided much insight into the limitations of the TEB technique.

Two particular caveats have emerged from these comparisons. First, resting costs of the study animal must be well known; even subtle seasonal (Goldstein and Nagy 1985) or geographical (Hudson and Kimzey 1966) variation in resting costs can result in significant inaccuracy in calculated energy budgets. Second, a robust analysis of thermoregulatory costs, including accurate assessment of radiative and convective inputs, must be used; again, inattention to these factors can produce significant inaccuracies in the energy budget.

These requirements have been particularly elucidated by a series of comparisons between TEB and DLW analyses of aviary-housed Loggerhead Shrikes (*Lanius ludovicianus*; Weathers et al. 1984) and Budgerigars (*Melopsittacus undulatus*; Buttemer et al. 1986). For the shrikes, substitution into time-energy budgets of metabolic data from a separate population—differing by only 12% in thermal conductance from the study population—produced a 22% increase (inaccuracy) in the calculated rate of energy expenditure. This large effect occurred because the shrikes spent much of their time at temperatures below thermoneutrality. For Budgerigars, ignoring the effects of wind resulted in a similar (15%) underestimate of DEE.

Understanding these details of energetics can significantly affect the interpretation of field observations, as seen in studies of desert phasianids (Goldstein and Nagy 1985, Kam et al. 1987). These birds survive the rigors of the desert summer in part by reducing their activity during the hottest midday hours. This in turn is made possible by the birds' very low resting metabolic rates, which result in low overall energy requirements and hence reduced foraging requirements. Together these factors produce levels of DEE markedly lower than those of other similar-sized birds (Nagy 1987). Time-energy budgets constructed using allometrically predicted, rather than measured, metabolic rates would have significantly over-estimated DEE, and would not have yielded a proper understanding of the forces shaping these birds' activity budgets. Similarly, allometric predictions of DEE have substantial uncertainty (Nagy 1987) and may provide estimates of DEE significantly at variance with actual values.

Accurate continuous assessment of the microclimates occupied by free-living birds is a significant challenge, but has been successfully approached in a number of studies (Mugaas and King 1981, Biedenweg 1983, Goldstein 1984, Stalmaster and Gessaman 1984, Masman 1986). Accurate time-energy budgets also require that time budgets be constructed for individual birds, rather than being compiled from data on many individuals, whose activity patterns may vary considerably (Rijnsdorp et al. 1981). Finally, TEB's require that activities be categorized and recorded; even activities with quite different energy costs, such as restful vs. alert perching, may be difficult to distinguish in the field. Despite these seeming pitfalls, rigorous TEB analyses can yield results very similar to DLW (Goldstein 1988, Nagy 1989). The overall level of accuracy required depends, of course, on the questions being asked by the researcher.

TABLE 2. ENERGY COSTS OF AVIAN ACTIVITIES

Activity	Energy cost (multiple of BMR)[a]
Flight	
Aerial species	2.7–5.7
Other birds, sustained flight	~11
European robin, short flights	23
Gliding	2
Terrestrial locomotion	Varies with speed and form of locomotion
Perch	
Rest	1.0
Alert	1.9–2.1
Preen	1.6–2.3
Eat	1.7–2.2
Sing-call	2.9
Bathe	2.9

[a] See Hails (1979), Taylor et al. (1982), Masman and Klaasen (1987), and Goldstein (1988) for reviews with complete references.

IMPLICATIONS FOR FORAGING ECOLOGY

A foraging bird must choose among behaviors with different energy costs, and must acquire sufficient energy to meet both these costs and the costs of other activities, maintenance, thermoregulation, storage, and production. Studies have demonstrated that a changing physical environment may strongly influence a bird's pattern of time use. Changing weather may alter food availability, thereby necessitating a change in foraging strategies (e.g., Murphy 1987). In more extreme situations, the physical environment imposes such a strenuous thermal load on the bird that foraging is either impossible (excessive heat load; Goldstein 1984) or energetically too expensive (in extreme cold) to be profitable (Evans 1976). In these cases, foraging may cease altogether. An understanding of the energy costs of activities provides a means for evaluating the costs and benefits of these changing behavioral strategies. However, studies of avian daily energy expenditure have demonstrated that more subtle influences, such as convective heat loss and acclimatization of resting metabolic rate, can also have important impacts on overall energy expenditure. It is this overall level of expenditure which must be balanced by the energy gained during foraging.

Under some circumstances, the rate of daily energy expenditure by birds apparently reaches a maximum sustainable level, estimated to be approximately four times the resting (basal) metabolic rate for a variety of species (Drent and Daan 1980, Kirkwood 1983; see also Karasov, this volume). This level may be a consequence of energy processing constraints, such as the ability to transport nutrients through and across the alimentary tract (Karasov et al. 1986). Behavioral responses to changes in weather or resource availability must be critical to balancing the energy budget during such periods of maximal energy expenditure. Studies of these potentially stressful portions of the annual cycle should provide fruitful testing grounds for understanding interactions between behavior and energetics.

Studies of DEE provide a potential link between foraging ecology, energetics, and measures of fitness. Fulfillment of this promise will require accurate assessment of energy expenditure by individual birds. Time-energy budgets can achieve such accuracy, but only if rigorously applied. Energy expenditure depends both on the types of activities employed and on subtle patterns of acclimatization of metabolic rates and thermal balance with the environment. During certain portions of the annual cycle, or in response to changing climatic conditions, behavioral flexibility may be essential to balancing the energy budget. Careful studies of the energetics of individual animals in different circumstances, and of species with similar diets but different behavior patterns (see Goldstein 1988), should help to illuminate the forces governing the patterns of time use by birds.

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