RAPTOR ENERGETICS: A REVIEW

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Ecological energetics, as a discipline, has grown rapidly in recent years. In the broadest sense, it is the study of energy transfers within an ecosystem; however, most research involves only the determination of energy requirements for various categories of activity for a range of organisms. Much interest has focused on thermoregulatory adaptations by endotherms to desert and arctic environments (Schmidt-Nielsen 1964, Scholander 1955, Scholander et al. 1950 a, b, and c, and Irving et al. 1955).

This review is not intended to deal with the enormous volume of literature on endotherm or even avian energetics. I will confine the discussion to work which has examined energy transfers involving raptorial species (orders Falconiformes and Strigiformes). These are heterogeneous orders of birds with regard to size, behavior, and habitat, making them interesting but difficult groups to work with both in the laboratory and in the field.

The ease with which such standard data as body temperature, oxygen consumption, carbon dioxide production, food consumption, and excreta production can be collected varies considerably with the species. Thus technical problems account, in part, for the deficiency in our understanding of raptor energetics which will become apparent in this review. Since 1927 only 28 species have been studied by 20 workers with sample sizes ranging from 1 to 29 (table 1). Ignoring the largest study, the upper limit drops to 10. These facts point to a serious problem with the data base: small sample sizes. Most studies consider only minimum energy requirements (under quite variable conditions) and, sometimes, metabolic rate responses to several environmental temperatures. Very few studies have focused on specific ecological adaptations or the energetic costs associated with factors such as flight, growth, incubation, or molt.

Review of Methods Employed

In his monograph on ecological energetics, Gessaman (1974) provides an extensive and complete review of methods employed in this discipline. These methods will be mentioned only briefly here.

Food Consumption. By measuring the amount of food consumed and excreta produced, the energy metabolized by an animal can be estimated if constant weight of the animal over the period of measurement is assumed. Such data also permit the calculation of digestive efficiency which is of ecological interest.

Respiratory Gas Exchange. The rate at which an animal uses oxygen or produces carbon dioxide is an indirect estimate of metabolic rate. Given both these measurements simultaneously, we may calculate the respiratory quotient which is an indication of the proportion of protein, carbohydrate, and fat that is being metabolized, provided uric acid content of excreta is also known. Such information permits a more accurate estimate of heat production (metabolic rate) than does oxygen consumption or carbon dioxide production alone.

Review of Results

This review is divided into three parts. The first deals with the relationship between body weight and metabolic rate. The second discusses work dealing with the energy cost of productive work (e.g., flight). The third reviews studies which examined responses to varying ambient temperatures and other environmental variables.

Body Size and Metabolic Rate. The relationship between body size and metabolic rate for endotherms has received considerable attention beginning with the work of Brody (1942), Klieber (1961), and Scholander et al. (1950 a, b, and c). This work, for birds, has been reviewed thoroughly in *Avian Energetics* by Calder (1974).

Considerable discussion has surrounded the question of how best to describe (mathematically) the relationship which take the general form: $M = aW^b$, where M is metabolic rate, W is body mass, a is constant, and the exponent b describes the effect of size (Lasiewski and Dawson 1967, 1969; Zar 1968, 1970). The pertinent formulas with respect to raptors were presented by Zar (1968).

The regression formula for standard metabolic rate on body weight was determined empirically based on five species of falconiforms ranging in weight from 0.108 kg to 10.320 kg. The equivalent equation for strigiforms was based on 6 species over a weight range from 0.0377 kg to 1.450 kg. Collins et al. (in prep.) have calculated a revised equation with the addition of new data.

More data will undoubtedly improve the accuracy of these regression equations although the interesting problem will be to uncover the causes of significant inter- and intraspecific deviations from the regression line.

Energy Costs of Productive Work. With respect to the energetic cost of productive work, nothing has been published except for the works of Tucker (1970, 1971, and 1973) and Pennycuick (1968) on the cost of flight. Pennycuick's work is primarily theoretical but includes some observations on African vultures. The empirical work of Tucker was carried out on nonraptorial species.

Tucker (1974:306) presents an approximation formula: $P_i = (6.43 \times 10^{-3} h + 94.15) m^{0.974}$ which may be used to calculate the power requirements of flight given a number of assumptions concerning the bird's mass, altitude of flight, airspeed, wind conditions, wingspan, and basal metabolic rate. In this formula h = altitude, m = mass (of bird), P_i = power output (watts). For a complete discussion of the effect of these factors see Tucker's review in Paynter (1974).

I have included this material relating to nonraptorial species because the equation developed by Tucker and Pennycuick can be applied with reasonable confidence in the development of energetic models from field data. Bartholomew (in Paynter 1974:329) sums it up nicely, "Knowing these things, any one of us . . . can, by using the tertiary formulae, get values as accurate or more accurate than one could obtain by direct physiological measurement."

Response to Climatological Factors. **Cold Environments.** Data for metabolic rates at controlled temperatures outside the thermoneutral zone are available for only five species (Ligon 1969, Coulombe 1970, Gessaman 1972). These data, all for owls, are summarized in figure 1.

The values given for the lower critical temperature are of particular ecological interest. They are commonly accepted as an indication of an animal's tolerance of cold and reflect the insulative quality of the plumage (Scholander et al. 1950 c). This relationship is readily observed in figure 1, which shows a much lower critical temperature and a shallower slope for the Snowy Owl (*Nyctea scandiaca*) than for the other four species. There are no comparable data for falconiforms.

Hot Environments. At ambient temperatures approaching or exceeding normal body temperature, an animal is faced with the problem of dissipating excess heat and/or reducing the absorption of heat from the environment. This can be accomplished both behaviorally and physiologically.

Panting is commonly used by raptors under heat stress. It has the effect of moving relatively large quantities of air over the moist respiratory surfaces thereby removing water vapor. Since water has a high heat of vaporization, it is an effective mechanism for heat dissipation, providing the animal can efficiently replace the lost water and maintain proper blood gas concentrations. Panting also adds to the heat burden because of the associated muscular activity.

Ligon (1969) and Coulombe (1970) have reported respiratory water loss (RWL) for three species of owls (*Athene cunicularia, Otus trichopsis,* and *Micrathene whitneyi*). These data show a rapid and substantial rise in RWL commencing at an ambient temperature approximately equal to body temperature. The sharp jump in RWL was associated with the onset of gular fluttering in owls (a mechanism unavailable to the falconiforms). Here again no data on RWL are available for the falconiforms.

Countercurrent vascularizaton in appendages has been demonstrated for a variety of endotherms (e.g., Irving and Krog 1955, Scholander et al. 1950). Bartholomew and Cade (1957) have reported the only study of this mechanism in raptors. They demonstrated in American Kestrels (*Falco sparvarius*) a rise in tarsal temperature associated with increasing ambient temperature, thereby reducing the gradients between tarsal and core temperature, and ambient and tarsal temperature. As ambient temperature approached normal body temperature, so also did tarsal temperature, and this corresponded to a rise in body temperature. Presumably, the rise in tarsal temperature was caused by increased blood flow due to vasodilation (Bartholomew and Cade 1957). A similar response has been demonstrated in several large falcons (Mosher and White 1978).

Sun Bathing. Several avian studies have pointed out the value of sunbathing as a supplement to endogenous heat production (Hamilton and Heppner 1967, Lustick 1969). Other studies have discussed the relationship of a spread-wing posture observed in Ciconidae (Kahl 1971) and raptors (Cade 1973). While sunbathing apparently provides a supplementary source of heat under some conditions, the spread-wing posture of some raptors appears not to be correlated with control of body temperature (Cade 1973).

Circadian Rhythms in Metabolic Rate. Daily cycles in metabolic rate and body temperature have been recorded for raptors associated with their nocturnal or diurnal habits (Bartholomew and Cade 1957, Graber 1962, Coulombe 1970, Gatehouse and Markham 1970).

The most striking of these studies compared two species of owls with a small falcon (Gatehouse and Markham 1970). The owls had higher nighttime standard metabolic rates (SMR), and the falcon had a higher daytime SMR. Such variation in SMR has not always been considered in studies which report this parameter.

Other Factors Affecting Metabolic Rate. There may be sexual differences in metabolic rate unrelated to differences in body size. Although female Broad-winged Hawks (*Buteo platypterus*) are about 15 percent heavier than males, they have the same weight specific metabolic rate (Mosher and Matray 1974).

Wind is a significant factor in an animal's thermal environment and can have a considerable impact on the rate of heat loss. Gessaman (1974) is the only worker to report the effects of wind velocity on metabolic rate for a raptor. He found oxygen consumption of Snowy Owls to be a linear function of the square root of airspeed at -20° and -30° C.

Plumage color, unrelated to absorption of radiant energy, may also be related to metabolic rate. Red phase Screech Owls have higher metabolic rates at low ambient temperatures than do gray phase birds (Mosher and Henny 1976). This difference may be due to differences in plumage conductance.

Future Research Directions

This review has been undertaken for the purpose of pointing out gaps in our knowledge of raptor energetics and to encourage research designed to close these gaps.

Basic data are needed in the following areas: (1) energy cost for productive work, especially molt, incubation, growth, and flight; (2) metabolic response to wind and humidity; (3) seasonal metabolic acclimation; (4) energetic efficiencies—metabolized energy/gross energy intake and efficiency of prey capture, i.e., energy value of captured prey/energy cost of hunting; and (5) sexual differences, unrelated to body weight, in metabolic responses.

Besides these basic data, there are several other problems of broader ecological interest. The thermal environment of the nest is crucial to the young and can affect adults by requiring a greater investment of energy in the form of brooding or shading behavior. Direction of exposure of cliff nests is one factor controlling their thermal environment (Mosher and White 1976). A detailed study including nest temperature, radiation regimen, reflectivity of nest background, and nest success would be significant. How the desert-nesting Ferruginous Hawk (*Buteo regalis*) is adapted to the extremes of temperature it faces would be an equally interesting problem. The solution is likely to be both behavioral and physiological. For example, there may be a relationship between respiratory water loss and the relatively large gapes of the Ferruginous Hawk (Niel Woffinden pers. comm).

Differences in plumage coloration may be correlated with differences in thermal conductances (Mosher and Henny 1976). In addition, there may be regional metabolic adaptations to environmental variation within species as reflected by plumage variation (Blem 1974). Study of plumage thermal conductance is a reasonable starting point.

The ecological importance of predators in community function is generally accepted. A knowledge of their energy requirements and the avenues and efficiencies of energy utilization is equally important.

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A CHEAP METHOD OF DIVIDING LARGE PENS FOR BREEDING RAPTORS

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If you wish to separate a pair of birds over winter or to divide a large pen into smaller ones, we found that inexpensive canvas panels were excellent for this purpose.

The panels can be cut to size and nailed to the ceiling, floor, and walls with narrow strips of plywood and small nails. Small, weighted flaps covered the feed holes, and two 20-inch-long zippers were sewn about 2 feet apart as a door for each pen. These doors were used for changing bath water and entering pens.

These panels are inexpensive and fast to assemble and take down. They can be reused numerous times and are easy to wash and store when not in use. They can be left up as permanent partitions or put up and removed as required.

We have used these panels to winter female Peregrines and Merlins with very satisfactory results.