# Energetics

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Studies of raptor energetics are extremely important in understanding the natural history of birds of prey. As terminal predators and sometimes keystone organisms, raptors are important components of many ecosystems. Because they are at the apex of the food pyramid, potentially they are the final repository of heavy metals, pesticides, and other stable compounds, and thus are important indicators of the general health of the system. Early publications describing methods of analyses of ecological energetics (Grodzinski et al. 1975) fail to mention raptors, but their importance has since become obvious.

Gessaman (1987) provided the single previous review of the terms, techniques, and equipment employed in studies of raptor energetics. His excellent survey remains the starting point for anyone attempting to begin work in this field. Much of that paper remains relevant today and anyone beginning a project involving energy analyses should consult it. Gessaman clearly pointed out the methods available at the time for measuring energy metabolism and how these measurements might be applied to studies of the activities of hawks, owls, eagles, and other raptors. Because some of these techniques have become readily available in userfriendly form or have not changed since Gessaman's review, I will not attempt to elaborate upon them, other than to present some of the basic terminology. For reviews of the literature on general avian energetics, see Gessaman (1973), Calder and King (1974), Kendeigh et al. (1977), Walsberg (1983), Blem (1990, 2000, 2004) and Dawson and Whittow (2000).

Compared with energetic studies in other avian taxa, there have been few studies of energy use by raptors. This may be due to the difficulties of maintaining sufficient numbers of relatively large, carnivorous birds in captivity, compared with smaller seed-eating birds. Likewise, caging a large bird that has been accustomed to ranging over a wide area is fraught with more difficulty than is caging a small passerine. Furthermore, because carnivorous birds sometimes egest pellets of undigested materials and drop parts of prey while preparing them for consumption, measuring energy ingestion by raptors may be a bit more difficult than in other groups of birds.

# **TERMINOLOGY AND CONCEPTS**

This chapter describes, in a generic way, the methods that have been applied to measurements of raptor metabolism, and very briefly summarizes results of the few studies that have appeared since Gessaman (1987). Those who need more detail should see Gessaman's paper, or the specific references given below.

There are numerous components of total daily energy expenditure to be considered in studies of energy balance. Historically, terms identifying each of these items have varied from study to study. The words and concepts used here are those most often applied and are in general agreement with recent, significant reviews of avian energetics (e.g., Gessaman 1973, 1987; Karasov 1990, Blem 2000, Dawson and Whittow 2000).

Fundamentally, energy use by birds may be summarized as: gross energy intake (GEI) = metabolized energy (ME) + energy in egesta (excretory energy = EXE; feces, urine, egested pellets; Fig. 1). The proportion of GEI, which becomes ME, is called the metabolizable energy coefficient (MEC; Kendeigh et al. 1977, Karasov 1990). Units of metabolism should be expressed as kJ per unit time, or watts, but in many older papers energy units are given in kcal/unit time (1 kJ = 4.184 kcal). ME is the total of the costs of: (1) basal metabolic processes ("basal metabolic rate" = BMR), (2) thermoregulation (T), (3) specific dynamic action (SDA, see below), (4) work (W), and (5) production (P) (Fig. 2). Gross energy intake, excretory energy, and production typically are measured by means of bomb calorimetry in food consumption studies (see below). Components of metabolized energy such as BMR, T, SDA, and W are measured by indirect calorimetry in which metabolism is determined from oxygen consumption or carbon dioxide production (see **Indirect colorimetry**). MEC values also can be used to characterize the relative energy values of different food items. For example, different food items have different MEC values when consumed by the same avian species. Also, the MEC of individual food items may differ among bird species consuming the item.

BMR is the rate of oxygen consumption or carbon dioxide production by a normothermic (normal body temperature) organism: (1) held at ambient temperatures that are not stressful (i.e., within the zone of thermal neutrality; see below), (2) in the inactive phase of their daily activity cycle (i.e., in the dark for some owls, during daylight for all others), and (3) in a post-absorptive condition (not recently fed and without food in the gastrointestinal tract). No major productive processes can be occurring, including molt, fattening, or reproduction. The bird cannot be in hypothermia (i.e., its body temperature [T<sub>b</sub>] cannot be below normal levels). BMR is assumed to be the minimal amount of energy expenditure by an endothermic animal under normal, nonstressful conditions. Standard metabolism (SM) is the metabolic rate of a bird measured in the same conditions as BMR measurements, except that the effects of thermal conditions are included. Thus, ambient temperature  $(T_a)$  may be so low that additional metabolic heat must be generated by the bird to maintain its body temperature, or conversely, ambient temperature is so high that the heat load begins to increase T<sub>b</sub> and metab-



Figure 1. General avian energy balance scheme (modified from Blem 2000).



**Figure 2.** Components of energy use by raptors under differing environmental conditions. P = tissue production energy, W = energy expended in activities involving work, SDA = energy expended when food is being digested (specific dynamic action), T = cost of thermoregulation, and B = basal metabolism (modified from Blem 2000). The model assumes that there is a fixed maximum level of energy use which may vary seasonally and among individual birds.

olism increases along with it. SM changes with insulation, but apparently does not differ significantly among avian classes (Dawson and Whittow 2000). The cost of thermoregulation (T) is a function of the difference between T<sub>b</sub> and T<sub>a</sub> and how well the bird is insulated. Fasting metabolic rate (FMR) is BMR plus the metabolic costs of activity in the respirometry chamber. Resting metabolic rate (RMR) is usually measured over a range of ambient temperatures when the animal is relatively inactive, but may have recently eaten (i.e., is not post-absorptive; Kennedy and Gessaman 1991). Specific dynamic action (SDA) is the additional energy generated by digestion of food. This is a function of the exothermic digestive reactions and varies with composition of the food. Existence energy (Kendeigh et al. 1977) is the rate of energy use by a bird that is feeding, and subject to varying T<sub>a</sub>, but restrained in a cage so that costs of locomotion are minimal (Stalmaster and Gessaman 1982, Hamilton 1985a). Existence energy usually is measured by food-consumption studies (see below) with tests extending for one to several days. Metabolized energy in free-living birds includes existence energy plus the costs of activity plus the costs of various productive processes such as molt, fat, deposition, and reproduction.

# METHODS

The major methods for measuring avian metabolism include: (1) indirect calorimetry, (2) food-consumption studies, (3) doubly labeled water studies, (4) applications of telemetry interfaced with methods (1) or (2), and (5) time-energy budgets.

Indirect calorimetry and food consumption studies (by bomb calorimetry) remain the two most common methods for measuring the rate of energy metabolism of birds. Indirect calorimetry is a method by which oxygen consumption and carbon-dioxide production, or both, are measured by special gas analyzers. The specific techniques are complex and computation of energy use depends upon the method used (Gessaman 1987). Food consumption studies are less common but provide a means for quantification of energy metabolism and costs of production by measuring energy content of food, egested materials, and any associated productive processes (production of eggs, changes in biomass, and molt). The energy content of biological materials is commonly measured by means of bomb calorimetry. Total energy balance is a compromise between energy

intake and all of the costs of existence: (1) thermoregulation, (2) kinetic energy of locomotion, (3) expenditures in production of body tissues such as reproductive tissues, new plumage, muscle mass, and energy storage as fat, and (4) maintenance. Note that energy storage can be a source or sink of energy, depending upon changes in body-tissue mass.

#### Laboratory Measurements

Indirect calorimetry. Indirect calorimetry is a method in which oxygen consumption or carbon-dioxide production is quantified, usually by means of open-flow respirometry. In this technique, a stream of air is drawn through a chamber housing the test subject in the dark or, alternatively, air is drawn through a mask fastened on the bird's head in such a fashion that all expired air is captured by the system. The chamber or masked bird is either held within a constant-temperature cabinet, or T<sub>a</sub>, is monitored. The general configuration (Fig. 3) usually includes absorbers for carbon dioxide and water for the incoming air stream, and similar absorbers for outgoing air leaving the chamber but prior to going into the oxygen analyzer. Special oxygen analyzers, carbon dioxide detectors, or both, permit quantification of gas concentrations and, ultimately, respiration rates. Gessaman (1987) provides several photographs and diagrams, which illustrate variations in chambers and masks.

There are many ways in which a respirometry system may be configured. In the most generic arrangement (Fig. 3), a pump pulls ambient air through or controls gas mixtures within the respirometry chamber. Pulling air may eliminate pressure problems, which



**Figure 3.** Generic arrangement of respirometry apparatus in a typical open-flow respirometry system for measuring oxygen consumption, carbon dioxide production, or both. Squares labeled  $H_2O$  and  $CO_2$  represent tubes containing materials for removal of water and carbon dioxide from the air, respectively. P is a pump and M is a flowmeter.

may affect measurements of oxygen consumption. Gessaman (1987) provides numerous diagrams illustrating potential variations on this theme, and also presents a table that illustrates how such variations may affect the methods of computation. Although the basic equipment remains available, recent computer hardware and software options eliminate many of the problems inherent in the system at the time of Gessaman's paper, thus eliminating the need for the researcher to become a plumber, electrician, and computer-software guru. Presently, complete equipment choices that can be applied without much trouble or knowledge of electronics or computer science are commercially available (e.g., Sable Systems<sup>©</sup>).

Metabolic measurements made by respirometry include BMR, **standard metabolic rate** (SMR), FMR, and RMR. The rate of energy expenditure can be calculated from the volume of oxygen consumed or carbon dioxide produced. This requires a measurement or estimate of **respiratory quotient** (RQ). RQ is the volume of carbon dioxide produced/volume of oxygen consumed. As RQ increases, the energy equivalent of oxygen consumption increases and carbon dioxide decreases (see Gessaman 1987 for a conversion table).

Open-flow respirometry studies of captive birds enclosed in chambers produce data such as those represented in Fig. 4, where basal metabolism is measured within the **zone of thermal neutrality** (aka, thermal neutral zone; TNZ), and the costs of thermoregulation



**Figure 4.** Respiratory metabolism as measured by means of openflow respirometry for the Barn Owl (*Tyto alba*), redrawn from data in Edwards (1987). TNZ = zone of thermal neutrality = thermal neutral zone. LCT = lower critical temperature. UCT = upper critical temperature.

are measured above the upper and below the lower critical temperatures. Within the TNZ, heat loss remains constant and, therefore, so does BMR. The balance is maintained by changes in insulation brought about by changes in posture, shunting of blood to and from skin and appendages, and by adjusting the thickness of plumage by fluffing or smoothing feathers. Upper critical temperature (UCT) represents the upper limit of effective thermoregulation. The T<sub>a</sub> below which metabolism increases (as a result of the onset of shivering) is the lower critical temperature (LCT). At higher T<sub>a</sub>'s above UCT, ineffective heat dissipation results in hyperthermia, which rapidly drives metabolic rates upward as a result of increases in the T<sub>b</sub>. Below the lower critical temperature, the metabolic rate increases as an inverse function of T<sub>a</sub> and the conductance of the bird's plumage. Laboratory respirometry studies typically do not consider the costs or benefits of radiation and convection, or both. These factors are important to consider in free-living birds because wind movement may cause relatively large increases in SM, whereas basking may decrease SM levels by augmenting body heat due to absorption of solar radiation.

Because SMR and BMR are functions of body mass, metabolism rates typically are expressed on a weight-specific basis. This may present some computational difficulties because metabolic ratios typically do not fit normal distributions, and division of metabolism by body mass may not eliminate the effects of mass (i.e., make measurements of birds of different sizes equal, Blem 1984). Investigators who are not aware of such problems should check methods of covariance analysis as a possible solution.

**Conductance** (C) is the reciprocal of insulation. Birds with heavy insulation have small C values. At ambient temperatures below LCT, thermal conductance (and hence the reciprocal of insulation) can be calculated as  $C = SM/(T_b-T_a)$ , but a correction must be made for heat lost from lung and skin surfaces through evaporation. Individuals in torpor (various forms of hypothermia) do not follow these rules. However, notwithstanding some New and Old World vultures (see Bahat et al. 1998, Heath 1962), there is little evidence of adaptive hypothermia in any raptor with the exception of some ephemeral periodic decline of  $T_b$  in a few species (see Gessaman 1972).

Measurements of respiration provide insight into a great variety of physiological and ecological factors important in the life of raptors. For example, measurements of BMR and SMR can be used to compare thermoregulatory capacity of different raptors (Graber 1962). This is particularly useful in comparisons of differences in insulation among species, during different times of the year, and at different geographic locations (Wasser 1986, Blem 2000). SM changes with differences in insulation, magnitude, and duration of previous exposure to temperature extreme, and biochemical shifts within the bird. Changes in conductance are generally caused by increases or decreases in plumage thickness, but deposition of subcutaneous fat also may cause small changes in insulation (Blem 1990).

In addition, there may be ephemeral physiological adjustments in response to temperature. Acclimation involves compensatory physiological changes in response to maintained deviations in ambient temperature, generally under laboratory conditions. Acclimatization is a similar change under natural conditions, which may include multiple environmental changes such as seasonal adaptations.

Measurements of SM often have been applied to studies of body-temperature regulation (e.g., Chaplin et al. 1984), but respirometry also has been applied to studies of metabolism of eggs (Hamilton 1985b), roosting (Keister et al. 1985), the costs of flight (Gessaman 1980, Masman and Klaassen 1987), and development of thermoregulation in nestlings (Kirkley and Gessaman 1990).

Measurements of the energetic costs of specific activities occasionally have been combined with amount of time expended in each activity. The resulting time-energy budgets (Goldstein 1990) can be used to address ecological questions about reproduction (Meijer et al. 1989), migration (Smith et al. 1986), foraging (Tarboton 1978, Stalmaster and Gessaman 1984), nesting (Wakely 1978, Brodin and Jonsson 2003), general energy balance (Koplin et al. 1980, Wijnandts 1984, Riedstra et al. 1998), or other life-history phenomena.

*Food-consumption studies.* In food-consumption studies, the energy content of food ingested and of egesta produced during a defined period is used to compute metabolic rates. These sometimes are referred to as **bioenergetic studies** (see Duke et al. 1973, Gessaman 1978, Kirkwood 1979, Collopy 1986). In such studies, the energy content of items such as feces, pellets, food, and body components is measured by bomb calorimetry. There are several versions of bomb calorimeters, but the most commonly encountered apparatus is the Parr adiabatic calorimeter. Basically, the technique involves the combustion of a known quantity of material in a vessel containing an atmosphere of pure oxygen.

The result is the caloric equivalent (heat of combustion) of the material in kcal/g or J/g. The total energy content of biological substances can be computed by multiplying the total dry mass by its caloric equivalent. The results can be converted from kcal to kJ and vice versa by use of appropriate conversion terms. The most important step in bomb calorimetry is the method used to dry the study materials. If the substance to be analyzed is not fully dry, energy measurements will be low. If the material is exposed to excessive heat during drying, then volatile materials other than water will be driven off or the chemical composition of the material may be changed. Several studies have addressed this problem with slightly different results (e.g., Blem 1968). It appears that freeze-drying (lyophilization) is the best choice for drying substances containing fat. If there is a risk of losing energy from oven-drying materials because a freeze-drier is not available, one can perform determinations in bomb calorimeters with the addition of combustion stimulants (Blem 1968). Such determinations must be corrected for water content of the material and the addition of the combustion stimulant.

Bomb calorimeters usually can analyze only small aliquots (1 g or less) of material, so an unbiased means of sampling large samples of food or tissue is necessary. For example, one could calculate the gross energy intake of a raptor that fully consumes small rodents by converting live mass of the mammal to calories (e.g., Collopy 1986). This is done by drying the whole mammal carcass, thoroughly homogenizing it using a Wiley mill or powerful blender, and testing aliquots of the powdered specimen in the bomb calorimeter. The total energy content of the prey item then can be computed as total dry mass (g)  $\times$  heat of combustion (per g). The fresh weight of food must be corrected for moisture content; water contributes to mass but not to caloric content. A similar process can be used to measure energy content of excrement and pellets and the difference between these and gross energy intake (GEI - EXE) produces a measurement of metabolized energy (Fig. 1). Energy-use efficiency (metabolizable energy coefficient = MEC) is defined as the percent of GEI actually extracted through assimilation after energy losses due to EXE. Measuring MEC in birds is complicated by the fact that avian feces is mixed in the cloaca with urine. Thus, excretory energy represents the energy remaining in feces and pellets (unassimilated) combined with energy lost as urine (assimilated). The difference between energy intake and excretory energy loss is properly termed apparent assimilated or metabolized

**fraction**. Division of the metabolized fraction by GEI produces the apparent metabolized coefficient (Kendeigh et al. 1977; also see Karasov 1990). This technique can be used to evaluate digestive efficiency under a variety of environmental conditions (Tollan 1988) or to quantify the bird's ability to extract energy from different foods (Blem 1976a). Conversely, it also can be used to evaluate **use efficiencies** (UC) of different foods (Karasov 1990). UC values are highest in nectarivores (~ 98%) and seed-eaters (80%), but raptors eating arthropods (77%) or vertebrates (75%) also are very efficient (Karasov 1990). Herbivores feeding on grass or conifer needles have low efficiencies, often 40% or less.

Using calorimetric techniques, variation in body composition can be interfaced with energetics to quantify the energetics of lipid deposition (Blem 1976b, 1990), predation (Barrett and Mackey 1975, Wallick and Barrett 1976, Tabaka et al. 1996), development of young (Kirkley and Gessaman 1990, Lee 1998), molt, egg formation, and other life-history phenomena (e.g., Pietiainen and Kolunen 1993, Weathers et al. 2001). Knowledge about energy content of prey can be used to assess hypotheses about prey selection (e.g., Wallick and Barrett 1976, Postler and Barrett 1982, Kirkley and Gessaman 1990, Blem et al. 1993).

Energy storage, particularly lipid reserves, has been quantified in many bird species, but there are few studies involving raptors (but see Smith et al. 1986, Massemin et al. 1997). The lipid depots are composed of triglycerides (triacylglycerols) consisting of three fatty acid molecules attached to a glycerol "backbone." The fatty acids may be of various sizes and caloric contents, and the efficiency of use of them may vary with length of their carbon chain (see Blem 1976b, 1990, for reviews). There has been little, if any, work on the composition of triglycerides in raptors (Blem 1990). Lack of knowledge about triglyceride dynamics in raptors is unfortunate because the pattern of lipid storage and usage in a large carnivorous bird may present unusual clues to important adaptations to stress (Massemin and Handrich 1997). The ability to accumulate fat reserves, which promote survival over extended periods of prey scarcity or during migration, could well be a most significant adaptation in raptors. Lipid provides a rich energy store without great wing loading because of its high heat of combustion (9.0-9.5 kcal/g = 37.7-39.7kJ/g), and because lipid storage is not accompanied by deposition of much water. Carbohydrate energy stores, such as glycogen, have about one half of the energy content of lipid stores and are accompanied by accumulation of about 3 g of water for every g of glycogen reserve (Blem 2000, 2004).

Energy expenditure has been measured in adult raptors (e.g., Gessaman 1972, Koplin et al. 1980, Hamilton 1985a), young raptors (e.g., Hamilton and Neill 1981, Collopy 1986, Kirkley and Gessaman 1990), and in eggs (e.g., Hamilton 1985b, Meijer et al. 1989). Many studies have focused on basic variations of metabolism (Hayes and Gessaman 1980, 1982; Daan et al. 1989, Pakpahan et al. 1989), effects of body size on metabolic rate (Mosher and Matroy 1974), and comparison of the metabolism of different species (Graber 1962, Ligon 1969, Gatehouse and Markham 1970, Ganey et al. 1993). The energetic costs of flight (Masman and Klaassen 1987), growth (Lee 1998), thermoregulation (Arad and Bernstein 1988, Weathers et al. 2001), reproduction (Meijer et al. 1989, Brodin and Jonsson 2003), incubation (Gessaman and Findell 1979), savings during roosting (Keister et al. 1985, McCafferty et al. 2001) and foraging (Wallick and Barrett 1976, Tarboton 1978, Postler and Barrett 1982, Beissinger 1983) also have been measured. I can find no studies of the energetic costs of molt or lipid deposition in raptors. In a few instances, several of the above techniques have been combined to construct energy budgets (e.g., Wakely 1978, Kirkwood 1979, Stalmaster and Gessaman 1982, Wijnandts 1984, Higuchi and Abe 2001), to compare components of energy use (e.g., Graber 1962), or to evaluate ability to survive starvation, harsh winter conditions, or both (Koplin et al. 1980, Handrich et al. 1993a,b, Hohtola et al. 1994, Thouzeau et al. 1999).

### **Field Measurements**

Most of the studies mentioned above employed captive birds. Field studies are more difficult and require special techniques such as those described below.

**Doubly-labeled water studies.** A less common, more expensive technique for measuring total energy expended during a specific period of time under unrestrained conditions (i.e., the costs of free existence) involves the use of so-called doubly labeled water. This method measures the disappearance rates of isotopes of H\* and O\* (typically <sup>18</sup>O and <sup>3</sup>H), which are injected into the test subject. The hydrogen isotope is lost through breathing, urination, and evaporation across the skin. The oxygen isotope is lost in water and in carbon dioxide produced during respiratory metabolism. The loss rate for labeled oxygen is greater than that for labeled hydrogen. As a result, there is a greater difference between slopes of labeled hydrogen and oxygen when greater amounts of carbon dioxide are produced (see Ricklefs et al. 1986, Goldstein 1990).

The method typically used under field conditions is to inject a known amount of doubly labeled water into the bird. The labeled water is then allowed to equilibrate throughout the bird's body fluids. Subsequently, a blood sample is drawn to establish a baseline. At a later time, a second sample of blood is taken and new isotope levels are measured. The difference between the rates of loss of different isotopes between the two sample times can be used to estimate the rate of carbon dioxide creation. The metabolic rate then can be calculated from the rate of CO2 production. This technique is expensive, but provides a means of measuring energy use by birds involved in natural behavior, such as flight or reproduction. In some instances, the method has been used to measure daily energy expenditure (Masman et al. 1983) and to compare energetics of different sexes (Riedstra et al. 1998).

Telemetric methods. Use of radiotransmitters which can monitor heart rates, electrocardiograms, or breathing rates have been available for guite some time (e.g., Owen 1969, Johnson and Gessaman 1973). Under well-defined circumstances these devices can provide reliable indexes to rates of avian oxygen consumption (Goldstein 1990). Early studies involved relatively large transmitters attached externally that probably contributed to energy demands of flight because of increased friction and wing loading (see Gessaman et al. 1991). Modern devices can be implanted within the body cavity along with small data loggers that can store extensive amounts of information. Under carefully controlled conditions, heart rate can be used reliably to estimate oxygen uptake, although one must be certain to consider a variety of confounding problems (Gessaman 1980, Gessaman et al. 1991).

*Time-energy budgets.* Time-energy budgets are constructed from extended observations of avian activity interfaced with measurements or estimates of the energetic costs of specific activities. Daily behavior is divided into categories for which energy measurements have been established or estimated, and total energy use is then calculated by adding the products of activity time and energy use for each activity (e.g., Soltz 1984, Craig et al. 1988). In addition to less complex models, comprehensive energy models have been assembled for some birds by combining data from several sources including estimates of energy intake, thermoregulation, and the like. These usually take the form of time-ener-

gy budgets to which measurements of productive energy (P) and physiological costs of thermoregulation (T) have been added.

# CONCLUSIONS

Methods for measuring metabolism in raptors have changed relatively little since Gessaman's (1987) review. Exceptions include the fact that instrumentation is more reliable now and that computer software is greatly improved. Techniques are now user-friendly, and a novice investigator does not have to deal with many of the problems encountered earlier. Other than the refinement of stable-isotope techniques, little has been added to the researcher's arsenal. The literature in this area has developed slowly and numerous aspects of raptor life history, physiology, and energetics remain uninvestigated.

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