ENERGETICS OF FREE-RANGING SEABIRDS

Hugh I. Ellis

Department of Biology
University of San Diego
San Diego, CA 92110

INTRODUCTION

I have chosen to address three major areas in the energetics of free-ranging adult seabirds: basal metabolism, locomotion, and energy budgets. More information is available on basal metabolism than on the other major areas of this chapter, a reflection both of the type of information most often collected in the past and of the difficulties inherent in working with pelagic birds. Basal metabolism not only provides a baseline and starting point for a discussion on free-ranging energetics, but it also has certain interesting ecological correlates that may help elucidate the energetics of seabirds. One such correlate involves plumage color and has thermoregulatory implications (treated by Lustick in a separate chapter), especially for birds of low (warm) latitudes. Such other correlates of basal metabolism as climate and flight and foraging behaviors are also discussed; these correlates may suggest to readers possible avenues for future research.

The energetics of activity is of particular importance to a general study of free-ranging energetics. Probably the activity most amenable to measurement in adult seabirds is the cost of incubation, which is discussed by Grant elsewhere in this book. The only activity I treat here is locomotion. Although not numerous, there are sufficient experimental and analytical studies to allow comparisons of flapping and gliding flight as well as surface and underwater swimming. Walking is treated briefly, but LeMaho provides a more detailed analysis for penguins in another chapter.

Finally, energy budgets are considered. Energy budgets may be developed indirectly using time-activity information converted with

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estimated energy costs or directly using isotopically labeled water. I have cited all the published and available but unpublished literature on seabird energy budgets measured directly using isotopes of water (see also the chapter on penguin energy budgets by Davis and Kooyman); these works shall be augmented soon by several studies currently in progress by different investigators. As more information becomes available, a general analysis of seabird energy budgets will be possible. For now, I have attempted to summarize the available information for seabirds and evaluate the different methods used to develop energy budgets. Regardless of whether energy budgets are developed directly or indirectly, they have profound ecological implications. Wiens, in his chapter, develops some of these implications for the population and community ecology of seabirds.

The survey of free-ranging energetics is confined largely to four orders of seabirds: Sphenisciformes (penguins), Procellariiformes (albatrosses, shearwaters, petrels), Pelecaniformes (pelicans, boobies, frigatebirds), and Charadriiformes (terns, gulls, auks). Other orders also include seabirds: Gaviiformes (loons), Podicipediformes (grebes), and Anseriformes (sea ducks), but these are not included in this survey due to a lack of data and because these groups include no entirely pelagic birds. The scientific names of most birds treated in this chapter are provided in Table 1 if not in the text.

BASAL METABOLISM

The most common unit used for energy expenditure is basal metabolic rate (BMR). Multiples of basal metabolism have been used to describe the cost of flight (Raveling and LeFebvre, 1967; Utter and LeFebvre, 1970; Tucker, 1972; Baudinette and Schmidt-Nielsen, 1974); energy budgets of individuals (Utter and LeFebvre, 1973, Pennycuick and Bartholomew, 1973; MacMillen and Carpenter, 1977; Ettinger and King, 1980; and reviews by Calder, 1974; King, 1974; and Walsberg, 1983; and population energetics (Furness, 1978). The use of basal metabolism as a base line is not unreasonable: BMR is measured on postabsorptive, resting endotherms in thermoneutrality and so provides a repeatable measure of the low end on the normal metabolic spectrum, notwithstanding shifts with circadian (Aschoff and Pohl, 1970) or seasonal (Kendeigh et al., 1977) cycles. King (1974:83) suggests BMR as a highly reliable (i.e., precise) measure.

Energy budgets are sometimes presented in terms of "predicted" metabolic rates. Lasiewski and Dawson (1967) provided an allometric equation to predict BMR for nonpasserine birds (including seabirds) on the basis of mass:

$$BMR = 327.8\ m^{0.723} \qquad (1)$$