

## INTRODUCTION

The imperatives that mold organismal life histories consist of self-maintenance and reproduction. Both of these processes require expenditures of two basic and pervasive resources—time and energy (King 1974). While the requirements for energy (and other nutrients) are obvious, those for time are more obscure. As a resource, time is required in the performance of such essential functions as foraging, courtship, vigilance against predators, or the completion of vital productive processes, to name but a few, and under certain circumstances may be limiting. If daylength or the seasonality of other resources is too brief to allow the completion of essential functions, or if environmental pressures (e.g., thermal stress, daylength, pressure from predators) combine to reduce the availability of time for still other essential functions (e.g., courtship and mating, care of the young, etc.), then the time required to meet these demands may be reduced below an effective minimum. Since the cumulative expenditure of energy is also a function of time, and time spent in obtaining energy (foraging) is subtracted from time allocated to other functions, it is apparent that these resources are intricately interrelated (Orians 1961). Indeed, energy acquisition (requiring time) and time spent in other vital activities cannot simultaneously be maximized (Wolf and Hainsworth 1971), a situation that poses fitness-related problems to organisms in time-limited and/or energy-limited environments.

It is a reasonable assumption that the observed diversity of life-history patterns strongly reflects the wide variety of evolutionary solutions taken in exploiting resources of time and energy. Current theory (e.g., Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977, and others) maintains that these varied life-history patterns are compromises that tend to optimize the acquisition and allocation of resources, and thus tend to maximize fitness in varied ways.

The organismal traits on which selection can act are legion, but can be segregated broadly into morphological, physiological, and behavioral characters, each of which may impose constraints on the adaptive plasticity of another. For instance, body size in homeotherms determines their minimal energy requirements, their relative thermostatic expenditure, their access to shelter, whether they are arboreal or terrestrial, volant or nonvolant, and so on. Physiological functions are, in general, much less plastic in the evolutionary sense than are behavioral characteristics, and while we can predict many physiological rates or processes principally by body size (Calder 1974), we know of no similar generalization for behavioral traits.

It follows that selection has affected primarily the activity budgets, or time budgets, of organisms, and has thus influenced energy budgets secondarily through the effects of various activities on energy budgets. Because allocations of time and energy resources are so intimately interrelated with each other and other resources, it is clearly necessary to examine energy budgets concurrently with time budgets if we are to understand how and why life-history patterns have diversified in response to various environments.

Beginning with the insights of Pearson (1954), Orians (1961), Verbeek (1964), and Verner (1965), there has been an acceleration through the 1970s in studies of time and energy budgets (for review, see King 1974, and later references summarized in the Discussion section). These have been valuable in adding to the

comparative matrix that will eventually permit the recognition of generalizations concerning the role of time and energy in forming life-history patterns, but most of them have concerned only a part of the annual cycle (usually the breeding season). Thus, it is still impossible to discern what part of the annual cycle constitutes a bottleneck of energy or time that limits an animal's distribution or abundance, or jeopardizes its survival. Furthermore, all but a few of these investigations have neglected to distinguish obligatory energy expenditure (basal and thermostatic requirements), over which an animal has only minor volitional control, from expenditures in volitional or facultative activities. This results in a serious loss of information if, as we believe, volitional (behavioral) characteristics are more sensitive to selection than are obligatory physiological processes.

As an effort to augment the fund of information about annual variation in energy and time budgets, and to provide a format that is more responsive to ecological questions, we undertook a year-long investigation of free-living Black-billed Magpies (*Pica pica hudsonia*) in southeastern Washington. To facilitate separating and estimating obligatory and facultative energy expenditure, our methods featured a detailed month by month quantification of the magpie's microclimates and its activity budgets. The activity budgets were converted to components of the energy budget by methods to be detailed later, but in general depended on known relationships between timed activities in the field and the energy consumption of such activities measured in the laboratory. We abbreviate this and similar techniques using "time-activity-laboratory" data as the "TAL" method.

The Black-billed Magpie is a medium-sized ground-foraging bird whose behavior can be readily observed. It is a permanent resident throughout most of its range, where it may be subjected to harsh weather in both summer and winter. Its general biology (e.g., Linsdale 1937, Evenden 1947, Brown 1957, Jones 1960, O'Halloran 1961, Erpino 1968, Bock and Lepthien 1975) and its thermal physiology (Stevenson 1971) are fairly well known. These characteristics make the Black-billed Magpie very well suited to investigation by TAL methods.

#### POPULATION AND STUDY AREA

The population studied occupied a 646-ha area on the west end of the Washington State University campus, an area of gently rolling hills dissected by numerous small drainages that coalesce in its eastern half and eventually empty into Paradise Creek. The difference in valley bottom elevations between the south and north end is about 61 m. The western edge of the study area extended to the main campus, while the other three sides were bordered mainly by farmland (predominantly wheat). The study area is in the *Festuca-Symphoricarpos* and *Festuca-Rosa* vegetation zones of the steppe region of Washington (Daubenmire 1970) which when undisturbed is characterized by a mosaic of habitat types. The two types important to the magpie are the *Crataegus douglassii*—*Symphoricarpos albus* and *Crataegus douglassii*—*Heracleum lanatum* types where *Crataegus* bushes afford nesting and roosting sites. The study area, however, is very disturbed and is a mixture of fields, poultry yards, pastures, farm buildings, pine plantations, fir plantations, groves of introduced exotics (honeysuckle, corrigana, lilac, apple, cherry), as well as some remnant groves of native brush (black hawthorne, *Crataegus douglassii*, predominantly, but mixed with snowberry, *Sym-*