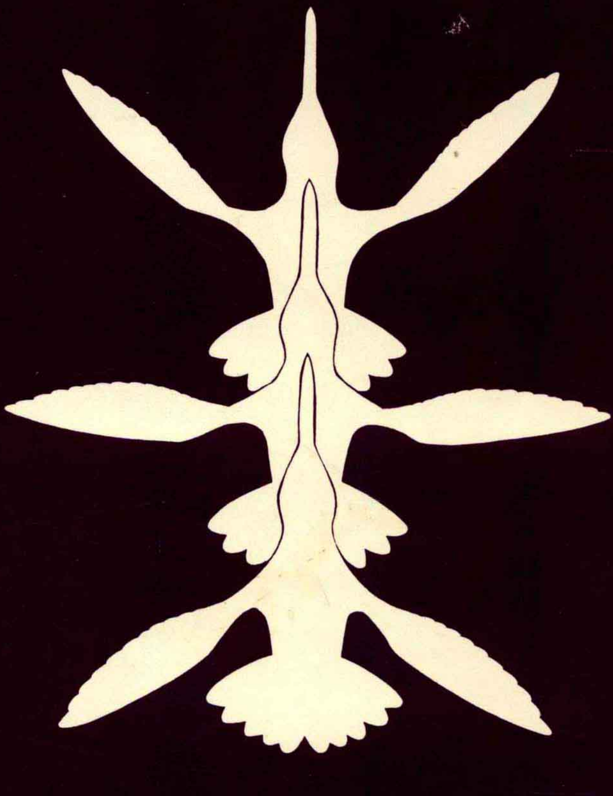
Behavioral Energetics

The Cost of Survival in Vertebrates



Edited by Wayne P. Aspey and Sheldon I. Lustick

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Behavioral Energetics: The Cost of Survival in Vertebrates

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Behavioral Energetics

THEMES, DATES, AND ORGANIZERS

Genetics and Biogenesis of
Mitochondria and Chloroplasts
5–7 September 1974
C. W. Birky, Jr., P. S. Perlman, and T. J. Byers

Regulatory Biology
4–6 September 1975
J. C. Copeland and G. A. Marzluf

Analysis of Ecological Systems
29 April–1 May 1976
D. J. Horn, G. R. Stairs, and R. D. Mitchell

Plant Cell and Tissue Culture:
Principles and Applications
6–9 September 1977
W. R. Sharp, P. O. Larsen, E. F. Paddock,
and V. Raghavan

Cellular Interactions in Symbiosis and Parasitism
7–9 September 1978
C. B. Cook, P. W. Pappas, and E. D. Rudolph

Gene Structure and Expression
6–8 September 1979
D. H. Dean, L. F. Johnson, P. C. Kimball,
and P. S. Perlman

Behavioral Energetics:
Vertebrate Costs of Survival
30 October–1 November 1980
W. P. Aspey and S. I. Lustick

Dedicated to the memory of
WILLIAM T. KEETON (1933–1980),
teacher, researcher, friend, and
internationally known authority
on bird orientation and navigation

Preface

The first speaker to accept our invitation to participate in the Seventh Annual Biosciences Colloquium was William T. Keeton, Liberty Hyde Baily Professor of Biology at Cornell University, internationally known authority on bird orientation and navigation, and author of the classic text *Biological Science* (Norton), one of the most successful textbooks ever published. We looked forward eagerly to his visit: one could sense from his book that he was a gifted, dedicated, and inspiring teacher, and those who knew him personally stood in awe of his dramatic, quality, and productive research. As plans for Dr. Keeton's visit were nearly complete, we learned of his untimely death on 17 August 1980 and were deeply saddened. It is to the memory of William T. Keeton that we dedicate this volume.

An animal, to be successful in an evolutionary sense, must be able to get food, avoid becoming someone else's food, and reproduce. Generally speaking, those animals that can carry out the above tasks at the least possible cost can be considered the most fit. Although there have been numerous investigators working on problems dealing with how animals adjust to their environment, it has only been in the past ten years that biologists have become aware of the importance of determining the cost of survival. Economic models concerning optimal foraging, reproductive strategies, territoriality, altruism, social caste systems, and thermal energy balance have led to new insights into complex problems.

The complexity of contemporary biology has led to extreme specialization among biologists, which has resulted in a breakdown of communications between disciplines. Although each level of biology has its particular questions and provides us with answers to these specific questions, explanations of mechanism are usually found at the cellular and molecular level, and the significance of these mechanisms is found at the higher levels of integration (ecology, behavior). The organism and the environment form an inseparable pair; one can be defined only in terms of the other. Thus if we, as biologists, are to determine how organisms maximize their fitness under natural conditions, we must deal with biology as a continuum.

One often hears the field ecologist say that studies conducted in the laboratory are not realistic because the animal has been taken out of its environment—since the environment and the animal are inseparable, one no longer has the same animal. At the same time, the laboratory scientist claims that there are too many uncontrolled variables in the field to obtain relevant data. Both are correct if one thinks as a specialist and looks at a small part of the big picture. One cannot separate behavior, physiology, morphology, and ecology; scientists from the various disciplines must work together. Although it is more difficult to study problems with more than one variable, we must in order to obtain ecologically relevant answers to questions dealing with the cost of aggression, reproduction, migration, foraging, and thermal energy balance.

The concept that total energy flow (production and respiration) in ectotherm populations may be similar to that of some endotherm populations is a product of the combined effort of ecologists, physiologists, and behaviorists. Previously, ectotherms were thought to be low-energy systems; on a per gram basis the energy required by ectotherms is low compared to endotherms. Yet on the population level, ectotherms, which may have much higher biomass per unit area than endotherms, require similar quantities of energy. This is due to the fact that endotherms use all but 1 to 3% of the assimilated energy for maintenance, whereas ectotherms allocate 20% or more of the assimilated energy for production. Therefore, ectotherm populations may not be low-energy systems as previously thought, but rather energy-efficient systems producing more biomass per unit energy consumed. By combining physiology, behavior, and ecology we are beginning to see that endotherms can reduce the energy required for maintenance by proper use of the microhabitats and by use of solar radiation.

Due to the integration of the disciplines of ecology, behavior, morphology, and physiology in the past decade, major advances have occurred in understanding the cost of survival in animals at all levels of integration. The papers that compose this volume not only deal with important theories on aggression, optimal foraging, migration, reproduction, and thermal balance, but also demonstrate the importance of an integrated approach to answering complicated questions.

Sheldon I. Lustick

Seventh Annual Biosciences Colloquium
College of Biological Sciences
Ohio State University
30 October–1 November 1980

BEHAVIORAL ENERGETICS:
VERTEBRATE COSTS OF SURVIVAL

Organizers

Wayne P. Aspey, Department of Zoology, Ohio State University
Sheldon I. Lustick, Department of Zoology, Ohio State University

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John R. Brett
Cathleen R. Cox
C. Robert Feldmeth
Melvin L. Kreithen
Sheldon I. Lustick
John J. Magnuson
F. Harvey Pough
Larry L. Wolf

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Survival Strategy 1

Making Your Way

MELVIN L. KREITHEN

Orientational Strategies in Birds: A Tribute to W. T. Keeton

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This paper was scheduled to be given by William T. Keeton, but his death in August 1980, which deprived the field of biology of one of its best scientists and finest teachers, prevented his making another of his stimulating presentations. He left no manuscript or notes of his intended speech, so I have taken the liberty of including those topics that, in my view, Dr. Keeton might have selected. Ultimately, the choices and the words are my own, but our ten years of close association at Cornell University leave me confident that this survey will not fall too far from the mark he intended to strike.

The past decade has produced an unprecedented level of research into the question of how birds and other migratory animals travel thousands of miles each year between winter and summer territories and between roosting and feeding sites. Long-distance flight is a costly activity, and many of the unique biological adaptations of birds are related to the energy costs of migratory flights, homing flights, and other travels. Some examples of the conservation mechanisms of birds are light feathers, hollow bones, seasonal recrudescence of gonads, and efficient and redundant navigational and spatial orientation mechanisms. In this review of recent studies in avian orientation, I will include navigational strategies that relate to bioenergetics.

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STRATEGIES OF MIGRATORY BIRDS

Among the long-distance fliers are many small songbirds (Passeriformes) that migrate at night. They use the star patterns of the night sky as a compass to keep a straight course, thereby avoiding fuel-wasting directional searches. The beginning of the migratory cycle of these birds is marked by a change in behavior, as the birds switch from their normal daytime activity to a period of intense nocturnal activity. Seasonal changes in photoperiod trigger a change in the birds' hormone levels, which in turn control the nocturnal migratory activity. It is possible to record and quantify the directional biases of the migratory activity by placing the birds in testing cages. If the night sky is visible through the top of the cage, the bird's activity becomes oriented in the migratory direction appropriate for the season. In a planetarium, under projected star patterns of the night sky, properly motivated birds show an oriented directional bias that clearly demonstrates that they recognize the projected star patterns; they orient as they would if they were viewing the natural sky.

E. F. Sauer (1957) first observed young European warblers orienting correctly to sky patterns in a planetarium. Since the young birds he had chosen were in their first summer and therefore had never experienced a migratory flight, he concluded from his evidence that the naive birds must have an "inborn star map" complete with star patterns and seasonal directional preferences. But S. T. Emlen showed later that the birds do not have an inborn star map; instead, they have a far more sophisticated ability. When extremely young, even before they are fledged, birds view the night sky and memorize the star patterns and motions. In a planetarium, young birds shown a projected pattern of stars will treat the axis of rotation as north even when a different star, say Betelgeuse, is used as the pole star (fig. 1). When they are shown the projected sky later, during the migratory season, the birds' orientation, even under a stationary sky, is directed appropriately for migration (fig. 2). This implies that the young birds detect the slow rotation of the sky and transfer the rotational axis onto their memorized map of the star patterns. Birds translate the axis of rotation into a migratory direction whether they are shown projected star patterns of the true night sky or arbitrary star patterns made by changing the holes in the planetarium projection sphere. The ability of migratory birds to memorize and to orient to arbitrary star patterns and false rotational axes demonstrates that they have a flexible strategy for star orientation, one that provides for the slow changes in the tilt of the earth, and even changes in the positions of the stars.

Fig. 1. The planetarium at Cornell University arranged for experiments with migratory birds in funnel cages. Birds can view the sky but not the projector. The projector has several star masks and can display realistic or unrealistic sky patterns. Young birds will imprint on and memorize any star pattern they are shown. Cornell University Photo; reprinted by permission.

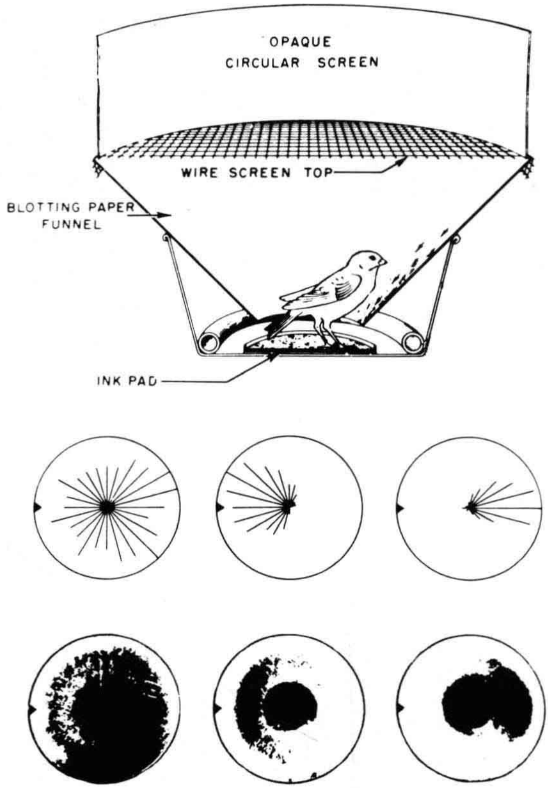

Fig. 2. Funnel cages record the migratory activity of indigo buntings under star patterns. A floor pad provides a fresh ink supply for each jump. Top views of three blotter paper funnels (*bottom*) show records of active birds; increasing degrees of directional bias are shown left to right. Densities are analyzed for each sector of a funnel and shown in a diagram (*center*).

Another important way that migrating birds conserve energy is by using the winds to their advantage. Data from radars, ceilometer beams, and moon watching have quantified the direction and the amount of migration on any given night and have established that many nocturnal migrants wait on the ground for several nights and will fly only if they can be assured of the assistance of tail winds for the night's flight. By selecting wind and weather patterns carefully, the birds avoid being blown off course, or even backward, by winds that often exceed the birds' air speed. It is now possible, using a synoptic weather map, to forecast the locations where birds are likely to be