Behavioral Energetics

The Cost of Survival in Vertebrates

Edited by Wayne P. Aspey and
Sheldon I. Lustick

BEHAVIORAL ENERGETICS
The Cost of Survival in Vertebrates

Edited by Wayne P. Aspey and
Sheldon I. Lustick

Integrating research in ethology, ecology, and physiology, and synthesizing their relationship to vertebrate energetics and survival adaptations, the nine papers in this volume concentrate on three survival-strategy themes in the life energetics of vertebrates: "Making Your Way," "Reproduction and Aggression," and "Cost Benefits of Temperature Regulation and Foraging."

Included under the first of these general topics are: "Orientational Strategies in Birds," offered as a tribute to the late Professor William T. Keeton by Melvin Kreithen, of the University of Pittsburgh; "The Life Energetics of Sockeye Salmon, *Oncorhynchus nerka*," by John R. Brett, of the Pacific Biological Station in Nanaimo, British Columbia; and "Amphibians and Reptiles as Low Energy Systems," by F. Harvey Pough, of Cornell University.

Under the second: "Costs of Reproduction and Lactation among Nonhuman Primates," by Jeanne Altmann, of the University of Chicago; "Reproductive Strategies among Male Elephant Seals," by Cathleen R. Cox, of the Los Angeles County Museum of Natural History; and "Costs of Aggression in Trout and Pupfish," by C. Robert Feldmeth, of the Claremont Colleges.

And under the third: "Cost Benefit Analysis of Temperature and Food Resource Use: A Synthesis with Examples from the Fishes," by John J. Magnuson and Larry B. Crowder, of the University of Wisconsin; "Economics of Foraging Strategies in Sunbirds and Hummingbirds," by Larry L. Wolf and F. Reed Hainsworth, of Syracuse University; and "Cost Benefit of Thermoregulation in Birds: Influences on Posture, Microhabitat Selection, and Color," by Sheldon I. Lustick, of Ohio State University.

(Continued on back flap)

Damaged

p. 59 removed

OHIO STATE UNIVERSITY BIOSCIENCES COLLOQUIA

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

EDITED BY WAYNE P. ASPEY AND SHELDON I. LUSTICK

Behavioral Energetics:
The Cost of Survival in Vertebrates

OHIO STATE UNIVERSITY PRESS : COLUMBUS

Copyright © 1983 by the Ohio State University Press.
All Rights Reserved.

Library of Congress Cataloging in Publication Data

Biosciences Colloquium (7th : 1980 : Ohio State University)
Behavioral energetics.

Includes index.
1. Vertebrates—Behavior—Congresses. 2. Bioenergetics—Congresses. I. Aspey, Wayne P., 1946- . II. Lustick, Sheldon I., 1934- . III. Title.
QL750.B6 1980 591.51 82-12512
ISBN 0-8142-0332-9

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

Contents

Preface ix
SHELDON I. LUSTICK

SURVIVAL STRATEGY 1: MAKING YOUR WAY

1 Orientational Strategies in Birds: A Tribute to W. T. Keeton 3
MELVIN L. KREITHEN

2 Life Energetics of Sockeye Salmon, *Oncorhynchus nerka* 29
JOHN R. BRETT

SURVIVAL STRATEGY 2: REPRODUCTION AND AGGRESSION

3 Costs of Reproduction in Baboons (*Papio cynocephalus*) 67
JEANNE ALTMANN

4 Reproductive Behavior of Subadult Elephant Seals: The Cost of Breeding 89
CATHLEEN R. COX

5 Costs of Aggression in Trout and Pupfish 117
C. ROBERT FELDMETH

SURVIVAL STRATEGY 3: COST-BENEFITS OF TEMPERATURE REGULATION AND FORAGING

6 Amphibians and Reptiles as Low-Energy Systems 141
F. HARVEY POUGH

7 Cost-Benefit Analysis of Temperature and Food Resource Use: A Synthesis with Examples from the Fishes 189
LARRY B. CROWDER JOHN J. MAGNUSON

8 Economics of Foraging Strategies in Sunbirds and Hummingbirds 223
LARRY L. WOLF F. REED HAINSWORTH

9 Cost-Benefit of Thermoregulation in Birds: Influences of Posture, Microhabitat Selection, and Color 265
SHELDON I. LUSTICK

Index 295

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

Speakers

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

Survival Strategy 1

Making Your Way

MELVIN L. KREITHEN

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

1

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.

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260

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.

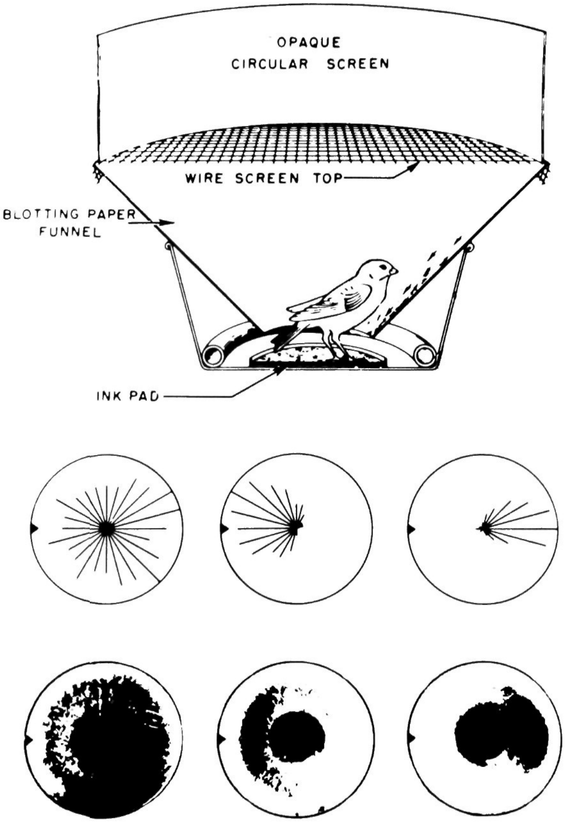

Fig. 2. Funnel cages record the migratory activity of indigo buntings under star patterns. A floor pad provides a fresh ink supply for each jump. Top views of three blotter paper funnels (*bottom*) show records of active birds; increasing degrees of directional bias are shown left to right. Densities 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 migrating in high density patterns. Armed with this knowledge, the Canadian air control system is beginning to incorporate procedures for protecting aircraft from the seasonal hazards of migrating birds.

By combining radar films from several stations, flocks of birds can be followed along their entire migratory routes. Air traffic control radars in northeast Canada, Nova Scotia, and Cape Cod detect when flocks take off; then shipboard radars track the progress of the flights over the open ocean. Two other radar stations, on the islands of Bermuda and Puerto Rico, pick up and follow the same flocks of birds as they fly past, but do not land on, these islands. As a result of the radar studies, it has been possible to track the remarkable 3,000 km nonstop transoceanic migratory flight of some songbird species. The flights last about 80 hours. The birds leave Nova Scotia and Cape Cod heading southeast on a course toward Africa; at about 25° north latitude they pick up the northeast trade winds and turn toward the Caribbean with following winds. The trade winds blow them to their final destinations in the Barbados or along the coast of Venezuela.

Blackpoll warblers, one of several species of small land birds that make this annual trip over the Atlantic Ocean, cannot land on water without drowning; they must fly nonstop for 4 days and nights (fig. 3). The warblers ordinarily weigh less than 10 grams; they arrive at their final destinations with about half of their body weight consumed as fuel. Tim and Janet Williams report that these flights represent a gasoline-equivalent fuel efficiency of 720,000 miles per gallon. (Merkel and Wiltschko, 1965; Emlen, 1967a,b, 1969, 1970, 1975a,b; Nisbet and Drury, 1967; Gauthreaux and Able, 1970; Wiltschko, 1972a,b; Wiltschko and Wiltschko, 1972, 1974, 1975, 1976; Able, 1973, 1974a,b, 1978; Wiltschko and Gwinner, 1974; Emlen et al., 1976; Emlen and Demong, 1978; Gwinner and Wiltschko, 1978; Richardson, 1978; Williams and Williams, 1978.)

STRATEGIES OF HOMING BIRDS

The biannual, long-distance migrations of birds are intriguing and offer unique opportunities for discovery; but migration is technically difficult to study, since the birds express their navigational skills for only a few days of each year. The homing pigeon is a more convenient bird to study. Homing pigeons are excellent navigators, and they will fly home almost any day of the year. Although homing and migration are different types of spatial orientation, they share enough mechanisms to permit some general observations about bird navigation. Furthermore, the monumental work of G. Kramer, W. T. Keeton, and

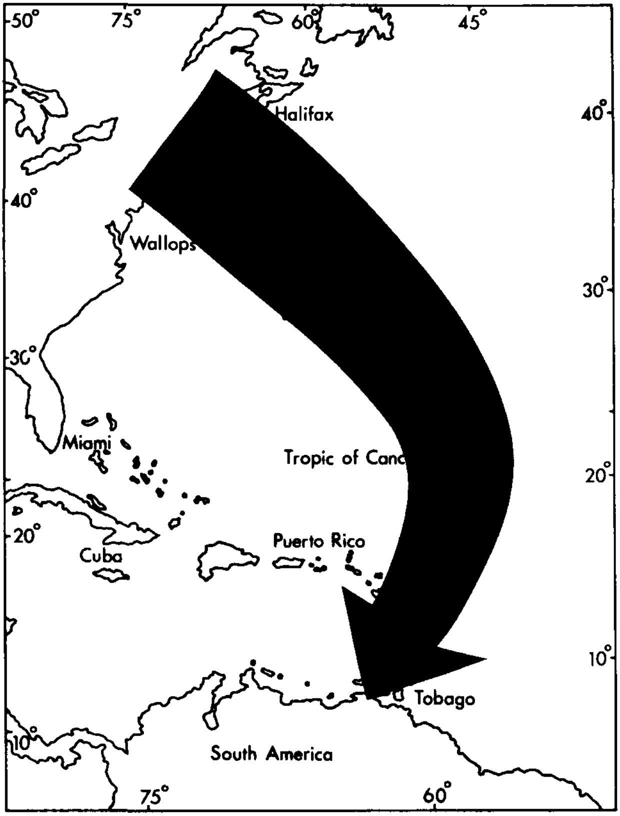

Fig. 3. Transoceanic migration route followed by small songbirds, such as the blackpoll warbler, that cannot land on water. Reconstructed from land and ship radar data. The 3,000 km flight lasts four days. At 25° north latitude the birds encounter the NE trade winds, turn, and fly to their destinations with aid from following winds.

others has created a solid foundation of data on the orientation and flight performance of pigeons under hundreds of different experimental circumstances (Griffin, 1969; Keeton, 1974c, 1979b).

The racing phenotypes of pigeons were developed by hobbyists who bet money on their birds. The hobbyist whose bird returns home fastest wins the purse. Selection for speed, endurance, and accuracy has been ruthless, and it has resulted in a number of racing breeds that are well suited for navigation research. The genetic strains of pigeons used at Cornell by Keeton, and at my new loft in Pittsburgh, are able to fly 600 miles nonstop in a single day. Unlike nocturnal migrants, homing pigeons are diurnal birds and, under most circumstances, fly only during the daylight hours. Even with the daylight restriction, the performance of some of the long-distance fliers is remarkable. At a recent awards dinner of pigeon fanciers in Texas, the principal award was given to the owner of a bird that had flown 1,540 miles from Manitoba to Texas in 2 days and 9 hours—flying only during the daylight hours. Such performances make the homing pigeon a reasonable model for the study of long-distance flight mechanisms, even though homing pigeons do not migrate.

Pigeons' strategies for finding their way range from mechanisms that require detailed observation of the sun to mechanisms that allow the birds to find home even when they cannot see at all. K. Schmidt-Koenig and H. Schlichte in Germany developed a method of covering the eyes of pigeons with frosted contact lenses. The blinded pigeons returned home. Both C. Walcott at SUNY Stony Brook and Keeton at Cornell repeated these tests and confirmed the results. Blinded by translucent lenses or goggles, the pigeons still flew; and they continued to fly for 100 miles until they landed within 1/4 mile of the home loft (fig. 4).

The pigeons' vision, when not impaired by frosted goggles or lenses, is excellent; and one visual cue important for pigeon orientation is the sun, which the birds use as part of a compass mechanism. G. V. T. Matthews proposed a complex solar navigation model for pigeons, using both sun arc and elevation; but most experimental data support Kramer's interpretation of the pigeons' use of the sun as a simple compass, combining only time and position along the arc. The birds observe the sun's position and combine this information with the time provided by their internal biological clocks.

The biological clock plays an integral role in many animal orientation strategies. To show that the sun is used as part of a clock and compass mechanism, birds are kept for about 5 days in an enclosed room with artificial lights on an automatic timer. A 6-hour phase shift of the light cycle produces a 90° shift in flight orientation in outdoor tests, or roughly the same 15° per hour produced by the apparent movement of the sun along its arc through the sky. Control birds are kept in similar rooms, but with the artificial lights synchronized with the times of sunrise and sunset. Control birds do not shift their flight orientation. These results are consistent with the notion of a simple clock and sun azimuth compass.

A compass, however, has limitations. It does not yield any information about location; it only indicates the direction of north, south, east, and west. Even a very good compass does not tell you where you are or which way leads toward home, because a compass does not provide

Fig. 4. Nonvisual homing is tested with goggles made of frosted plastic that obscures the image vision but allows light to pass. Because homing pigeons prefer to fly in daylight, goggles are preferable to blindfolds. The birds fly as far as 100 miles and land within ¼ mile of the home loft. George Silk Photo; reprinted by permission.

the equivalent of a "map" reading. The birds must determine where they are relative to home before a compass is useful. Given a map reading, however, a compass is very helpful; and the sun compass is one of the dominant mechanisms of pigeon orientation. If pigeons are given any opportunity to use the sun, they will; clock shifts will produce the appropriate deflections of orientation under partial cloud cover or through thin but uniform overcast. If the position of the sun is at all localizable, the pigeons will make use of it.

Pigeons can also find home, however, without using the sun. Under dense and total overcast, when the sun is not visible, pigeons can orient toward home and succeed in returning home. The mechanisms of direction-finding under heavily overcast skies appear to be different from those used under sunny skies. Evidence for this comes from the birds' choices of departure direction under overcast skies. The initial orientation direction of pigeons under total overcast is always toward home, even when the birds are clock-shifted. This implies that some alternate mechanism is guiding the birds home under overcast skies, a mechanism that, unlike the sun compass, does not require the internal biological clock (fig. 5).

This important discovery by Keeton was the earliest evidence of redundancy in the birds' navigation systems. There is apparently more than one way to find home. Redundancy is common in the anatomy and physiology of any living creature; it should be only a small surprise then, when one discovers that behaviors, too, are redundant. Redundancy is what makes living systems more reliable than machines, and I am certain that redundancy will become a central theme in many studies of the survival strategies of organisms in the natural world. Multiple navigation strategies allow a bird to switch to a backup system of cues when a particular behavioral or sensory system is not working up to the bird's expectation. But this redundancy presents technical difficulties to the cautious scientific investigator. Although access to

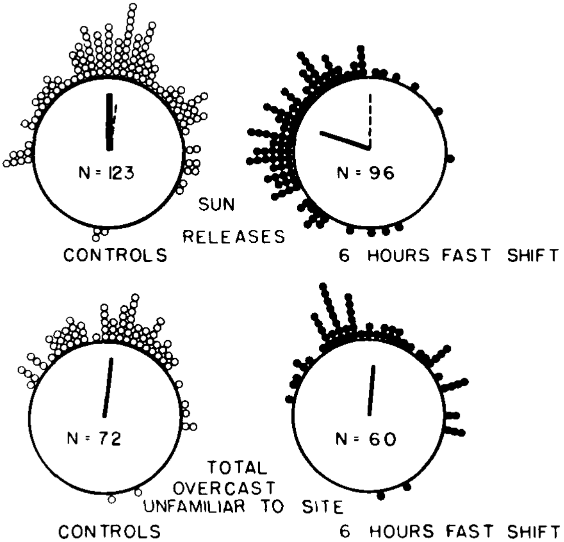

Fig. 5. Pigeon navigation under sunny skies differs from navigation under totally overcast skies. Under sun (*top*), birds with a 6 hour clock shift (*solid circles*) orient 90° to the left of the control birds (*open circles*). A similar release under overcast skies results in the homeward orientation of both groups (*bottom*), implying that different mechanisms are used under overcast skies. Each dot represents the vanishing direction of one pigeon. The solid bar from the center of the circle outward is the mean vector sum of all of the vanishing bearings. In all four circle diagrams, the data are pooled from a number of tests. Individual test diagrams are rotated so that the home direction is straight up on the circle.

multiple cues is useful to the bird, to the experimenters it means that an important element may be missed merely because the bird does not choose to rely on the cue we are testing for that day. (Kramer, 1951, 1952, 1957, 1959; Schmidt-Koenig, 1960; Matthews, 1968; Keeton and Gobert, 1970; Schmidt-Koenig and Schlichte, 1972; Schlichte, 1973; Schmidt-Koenig and Keeton, 1977, 1978; Schmidt-Koenig and Walcott, 1978.)

For years the effects of magnets attached to homing pigeons were obscured by the birds' use of multiple cues. Pigeons wearing magnets were flown only on sunny days with clear skies, as it was thought that poor weather was an unnecessary and confusing variable; however, the orientation mechanisms that are sensitive to magnets attached to the birds' backs are rarely activated unless the skies are overcast. Magnets under sunny skies affect the birds very little, whereas magnets under overcast skies can completely disorient the birds and affect their initial choices of direction. Walcott, J. Kirschvink, and others have found particles of magnetite in the heads of pigeons. It is too soon to tell whether these particles have anything to do with magnetic orientation, but they have aroused a flurry of excitement.

To compound the problem further, even the pigeons wearing magnets manage to get home; the net effect is about a one-hour delay compared to the flight times of control birds wearing brass bars. The initial effect of magnets is to produce random departure choices, but the birds still find the path home (fig. 6). Is this the first evidence for yet another cue system? (Keeton, 1971, 1972, 1977a,b; Keeton et al., 1974; Walcott and Green, 1974; Beaugrand, 1976, 1977; Larkin and Keeton, 1976, 1978; Wiltschko and Wiltschko, 1976; Bookman, 1977; Kiepenheuer, 1978a; Walcott, 1978; Visalberghi and Alleva, 1979; Walcott et al., 1979; Kirschvink and Gould, 1981.)

A recent contribution to the growing list of possible orientation cues is the idea that pigeons may "smell" their way home. Floriano Papi and his colleagues at the University of Pisa have hypothesized that as birds grow up at the home loft, they become familiar with the windborne odors from all directions around the loft. When the birds are released at an unfamiliar location, they recognize the local odors and compare them with the memory of the same odors carried by winds to the home loft. If, for example, a bird is released north of home and recognizes the local odors as similar to those carried home by the north winds, then the bird will proceed as if it is north of home and fly south. Note that this is a "map" step that actually tells the bird its location relative to home. The bird can then use whatever compass mechanisms it has to fly in the right direction.

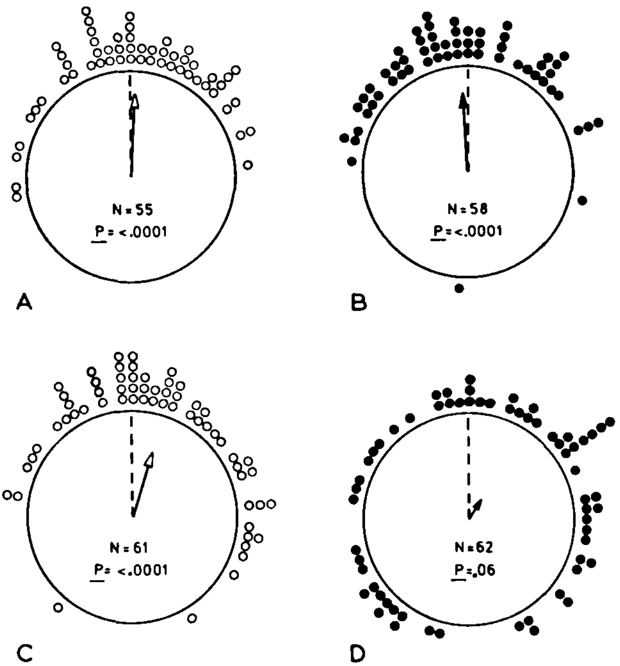

Fig. 6. Vanishing bearings of birds wearing bar magnets (*solid circles*) or brass bars (*open circles*). Under sunny skies (*top, A* and *B*) magnets have little effect. Under overcast skies (*bottom, C* and *D*) control birds orient homeward, whereas birds carrying magnets are disoriented and vanish in random directions. Data are pooled from several releases with home set to straight up. Arrow is the direction and length of the mean vector of the vanishing bearings. *P* values are derived with a uniform distribution of points as the null hypothesis.

Experimental verification of this hypothesis consists of tests in which olfactory cues are placed in conflict with other cues. One such experiment is the wind deflector cages (fig. 7). The cages are of three kinds. In all three cages the birds can see and smell their surroundings through vertical slats but cannot escape. In two of the cages the wind and, presumably, the wind-borne odors are deflected by transparent wings attached at 45° angles to the sides of the cages. One cage rotates the wind 90° clockwise with respect to the visible cues from the surrounding landscape, and the other cage rotates the wind 90° counterclockwise. The results of these experiments are consistent with the hypothesis of olfactory orientation: the birds, when flown, show appropriate directional shifts. J. Phillips and J. Waldvogel at Cornell, however, suggest that there may be other explanations for the changes

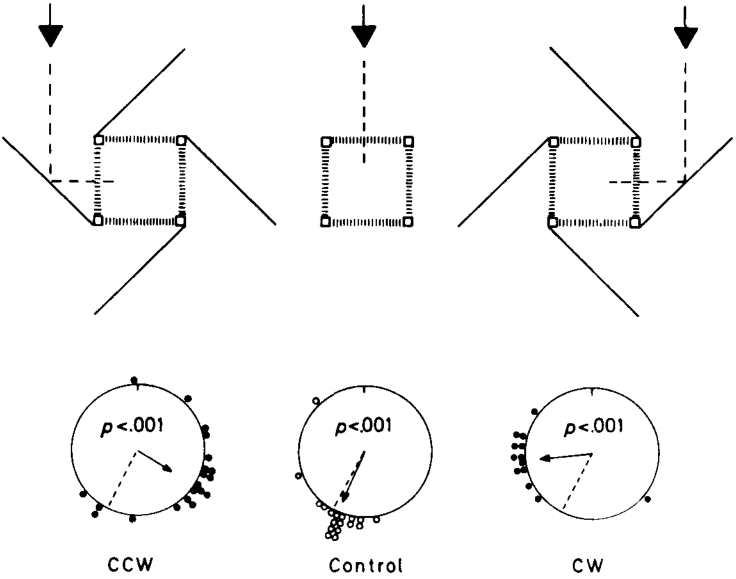

Fig. 7. Schematic drawings from above (*top*) of outdoor cages used to test the olfactory hypothesis of bird navigation. Birds kept inside the cages can look out through vertical slats and can experience winds and odors. The control cage (*center*) allows normal flow of wind. Transparent panels attached to the other two cages deflect the winds and odors by 90° either clockwise (*CW*) or counterclockwise (*CCW*); the birds look through the transparent panels at undeflected scenery. Birds from each of the cages are flown from the same release site but depart in different directions (*bottom*). The mean vanishing bearings (*solid arrows*) are rotated from the true home direction (*dashed line*) in a direction predicted by the oldfactory "map" hypothesis; however, similar cage-induced departure bearings have been obtained from birds made anosmic by surgery.

in initial orientation of the test birds. One alternative explanation they offer is that the birds may be viewing reflections in the deflector panels of the sky, sky polarization patterns, and other visible cues. (Papi et al., 1972, 1973, 1978; Keeton, 1974a; Baldaccini et al., 1975a,b, 1978; Oley et al., 1975; Tucker et al., 1975; Benvenuti et al., 1977; Hartwick et al., 1977, 1978; Keeton et al., 1977; Kiepenheuer, 1978b; Schmidt-Koenig and Phillips, 1978; Wallraff, 1980a,b; Wallraff et al., 1980; Waldvogel, 1981.)

Gustav Kramer proposed his "map and compass" interpretation of pigeon navigation in the 1950s. He could explain most of the experimental data if he assumed that the birds were performing two independent orientation steps: a map step to tell where they were, and a compass step to pick a homeward direction. There are several mechanisms that could provide compass cues: the birds could use a sun compass, a polarized skylight compass, or a magnetic compass. But there have been few suggestions as to what provides the map information. Olfaction has been suggested as a map cue. Another possibility is that geographic locations where birds display anomalous orientation may provide a key to the map sense. Two locations where birds consistently display unusual orientation are Castor Hill and Jersey Hill. There are many other exceptional geographic locations, but I will focus in this discussion on only two.

Castor Hill is located about 90 miles north of Ithaca, New York. Birds released from Castor Hill do not head straight for home. Instead, they orient far to the right of the home direction, departing with a 70° clockwise bias. It is not just Ithaca birds that are deflected; birds from other lofts to the south, the east, and the west have been tested here with the same results. The birds fly a course that is 70° to the right of the home direction for about 15 miles; then they make a left turn and fly swiftly home on course. It is as if some "map" feature of the landscape were rotated at this site. Accurate measurements of gravity, of magnetic fields, and of visible horizon tilting have produced no unusual readings. Only the birds know what is rotated at this site.

Jersey Hill is about 70 miles west of Ithaca. This location confuses the birds completely. Not only do birds wander about aimlessly and choose random departure bearings, but many of the birds become permanently lost. For a well-trained and experienced homing pigeon to get lost is a highly unusual event. At the end of an entire summer's flying season, over 90% of the birds will still be in residence, even after thousands of miles of flights. Yet on a single test at Jersey Hill, more than half of the birds may get lost and never be seen again. The navigation system becomes so seriously disrupted that the birds wander off for hundreds of miles and do not recover their home coordinates. Cornell birds released at Jersey Hill have been found alive in central Canada years later.

Usually birds tested at Jersey Hill depart with random orientations. Two curious exceptions were magnet tests performed under overcast skies in October of 1977 and 1979. In these two tests the birds all agreed to go only one way: south. This was good orientation, but in the wrong direction: east was the way home. Although the birds all agreed on a direction, they were still lost, as only a few birds actually made it home. Under normal circumstances, at other release sites, magnets produce random vanishing bearings under overcast skies but the birds get home; in these tests at Jersey Hill, the birds wearing magnets were oriented, albeit in the wrong direction, but they did not return home (fig. 8). No standard geophysical maps or measurements of gravity or magnetic fields indicate anything unusual about these locations. Only orienting animals understand the extraordinary nature of Jersey Hill, Castor Hill, and other unique sites (Keeton, 1973, 1974b).

THE SENSORY WORLD OF BIRDS

As we learn more about the abilities of birds, it is becoming clear that they are highly skilled navigators and that they are aware of many aspects of the world around them. We have discovered some of their skills: they know star patterns, they know the movements of the sun and the stars, they are aware of magnets, they know something about the structure of weather patterns. But we still cannot combine this

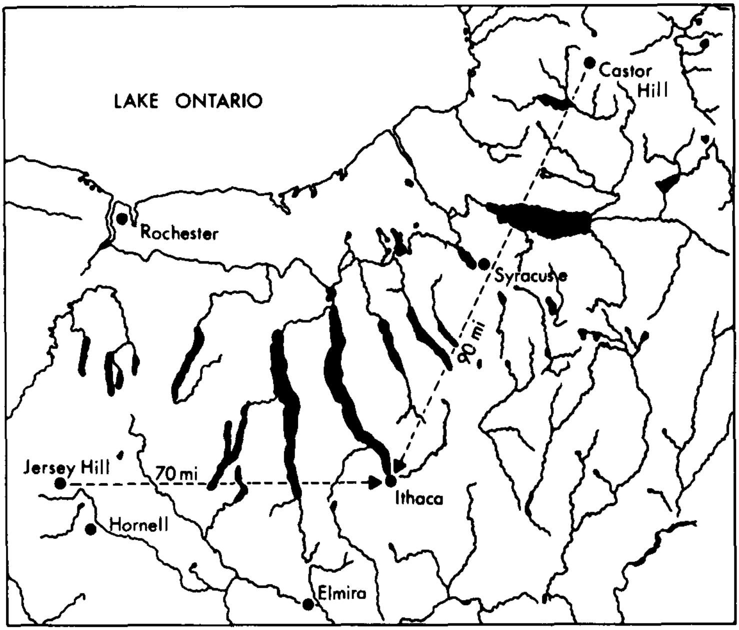

Fig. 8. Locations of two sites where birds exhibit anomalous orientation. Birds flown from Caston Hill, 90 miles north of Ithaca, New York, consistently depart 70° to the right of the home bearing. Birds flown from Jersey Hill, 70 miles west of Ithaca, are totally disoriented and exhibit random vanishing bearings. Site-related anomalous behavior suggests a way to probe the "map" component of bird navigation.

information to produce a predictive model of what birds will do when released from an unfamiliar location. It will contribute to our ability to predict orientation behavior if we can identify some of the sensory mechanisms involved in orientation and if we can measure accurately the birds' sensory acuity to each orientation cue.

For the past nine years I have been testing the sensory capabilities of homing pigeons in the laboratory, where conditions can be more precisely controlled than in outdoor tests. To test the color vision of homing pigeons, I place a bird in the path of a beam of calibrated monochromatic light. EKG electrodes monitor the bird's cardiac responses to external stimuli. When a shutter is opened and the light beam shines on the bird, the heart rate of the bird will increase if the light is detectable. This technique, though simple, is sufficient to map accurately the spectral sensitivity of the bird's color vision. Homing pigeons respond to all of the colors we can see, but they are also sensitive to ultraviolet light wavelengths (310–400 nm), which are invisible to us.

To test the pigeons' sensitivity to polarized light, I again employed the technique of monitoring cardiac accelerations (fig. 9). The rotation of the axis of the polarized light source was detected by some, though not all, of the pigeons. The pigeons' heart rates would increase only if the stimuli were placed either high overhead or at a horizontal distance of 2 m or more. The birds are not able to respond to the polarization on

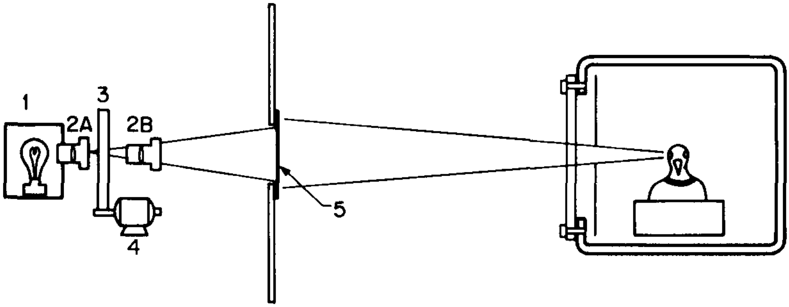

Fig. 9. Schematic diagram of the apparatus used for demonstrating the sensitivity of birds to polarized light. A light source (1) is polarized by a filter (3) on a rotating mounting (4). Lenses (2A and 2B) concentrate the polarized beam onto a rear projection screen (5). The bird views the screen at a distance of two meters or more, since polarization can only be detected if it is presented either far overhead or at a distance sufficient to approximate a patch of polarized skylight.

a screen placed a few inches in front of their eyes. In short, polarized light is detectable only if it falls on the area of the pigeon's retina that normally receives skylight. To be detected, the stimulus must be presented in a biologically relevant location.

Homing pigeons were the first birds shown to be sensitive to ultraviolet light and to polarized light (fig. 10). They were not, however, the first animals known to see and to use these cues. Foraging honey bees use two ultraviolet cue systems. First, many flowers provide conspicuous patterns of UV reflectance that guide bees to the part of the flower where they will find pollen and nectar. Second, the blue sky emits directional information in the form of scattered short-wavelength light. Sky patterns of ultraviolet intensity and of linear polarization provide the foraging honey bee with complete information about the position of the sun. The sun compass mechanism of the honey bee

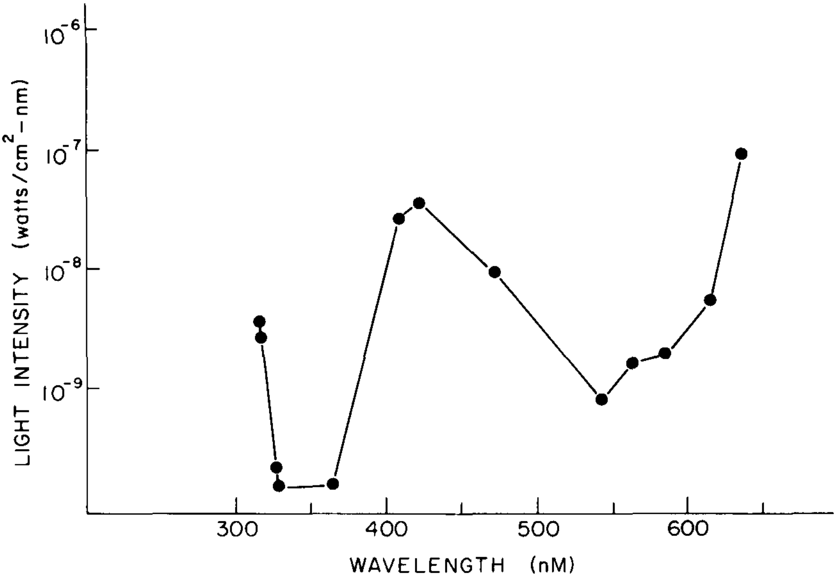

Fig. 10. Visual sensitivity of the homing pigeon shows two regions of low thresholds (high sensitivity). One region is the ultraviolet wavelengths near 350 nM; the other region is a band of visible wavelengths near 550 nM. Each filled dot is a threshold (50%) determined by cardiac conditioning techniques. From Kreithen and Eisner, 1978. Reprinted by permission from *Nature*, vol. 272, pp. 347–48. Copyright © 1978. Macmillan Journals Limited.

assigns a higher priority to UV patterns of sky polarization than to the direct view of the sun's image. (Frisch, 1967; Wright, 1972; Kreithen and Keeton, 1974c; Delius et al., 1976; Kreithen and Eisner, 1978.)

Ultraviolet light and sky polarization patterns are useful cues for spatial orientation. It was encouraging to discover that pigeons, like honey bees, are sensitive to both of these cues. But much work remains. The pigeons' receptor cells for polarized and ultraviolet light are still not located, and outdoor tests involving these cues have not yet been performed. But the preliminary laboratory work has been successful and points to the feasibility of performing tests outdoors.

Migratory birds choose carefully when and where they fly, and their selective flight behavior is linked to the movements of the weather and to wind patterns. Since the aneroid barometer, a pressure-sensing instrument, can aid humans in weather forecasting, it seemed reasonable to ask whether birds are able to sense air pressure changes and to use them to select optimal conditions for flying. I tested homing pigeons in a sealed pressure chamber where the only cues were pressure changes. The birds proved to be even more sensitive to air pressure than I would have anticipated. The apparatus had to be rebuilt several times before the limits of the birds' sensory abilities were reached. It is clear that a bird can detect easily the difference in air pressure between the ceilings and the floors of our rooms. The pressure response improves as the rate of change of pressure increases; at the equivalent of a rate of climb of 0.04 m/sec, a pigeon can detect an altitude change of as little as 4 mm! Pressure-detecting systems that are this sensitive may be useful for interpreting the pressure changes associated with weather patterns and at the same time may give birds an altitude-sensing system to help them maintain a level and efficient flight path.

Another way birds may sense remote weather patterns is by listening to the infrasounds produced by distant air movements. Infrasounds are low-frequency sounds produced by large-scale movements of air. Loud infrasounds are produced by thunderstorms, earthquakes, winds blowing over valleys, aurora borealis, and many other geophysical events of large physical dimensions. Because low-frequency sounds have long propagation distances, infrasounds can be detected by suitable microphone arrays located thousands of miles from the sources of the sounds (fig. 11). Infrasounds generated by winds passing over the Canadian Pacific Rocky Mountains and the Andes in Argentina can be detected by microphone arrays in the United States. Might these same infrasounds, or others, be used by navigating birds as a set of acoustic beacons that help them locate their position?

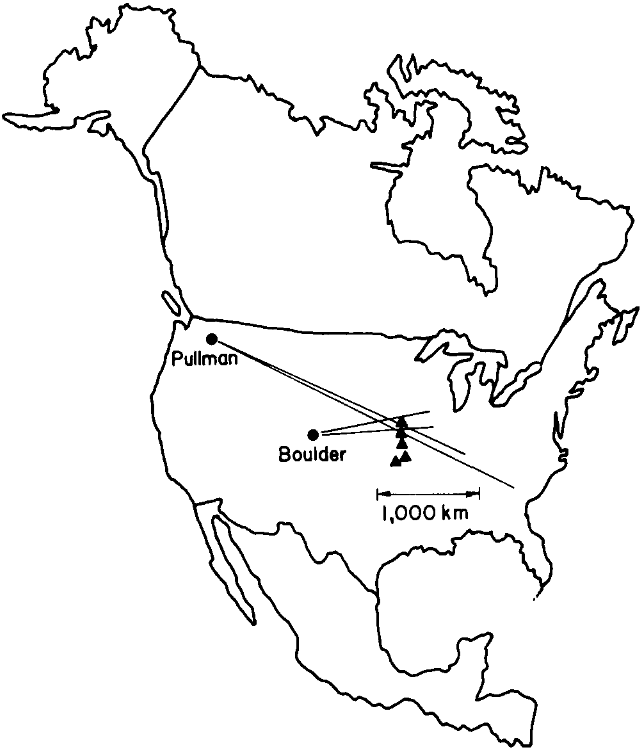

Fig. 11. Infrasound microphone arrays can track atmospheric disturbances several thousand miles from their sources. Two infrasound tracking stations (*circles*) follow the path of a severe thunderstorm (*triangles*). Two tracking stations are required, since the microphone arrays indicate direction, but not distance.

Homing pigeons can detect very low frequency sounds. In an infrasound testing chamber in my laboratory (fig. 12), pigeons exhibit conditioned cardiac responses to frequencies as low as 0.05 Hz (three cycles per *minute*). No one has ever tested animals at such low frequencies before, though there are many potential uses associated with such long wavelength sounds. In the range of 1–10 Hz, where there is some overlap of bird hearing and human hearing, the pigeons are 200 times more sensitive to low-intensity sounds than we are. We have laboratory experiments that show us that the birds are very sensitive to infrasonic frequencies, but we have too little information about their actual use of infrasounds outdoors under natural conditions, where winds and turbulence produce interfering "pseudosounds" that tend to mask the true infrasounds. More tests are required if we are to under-

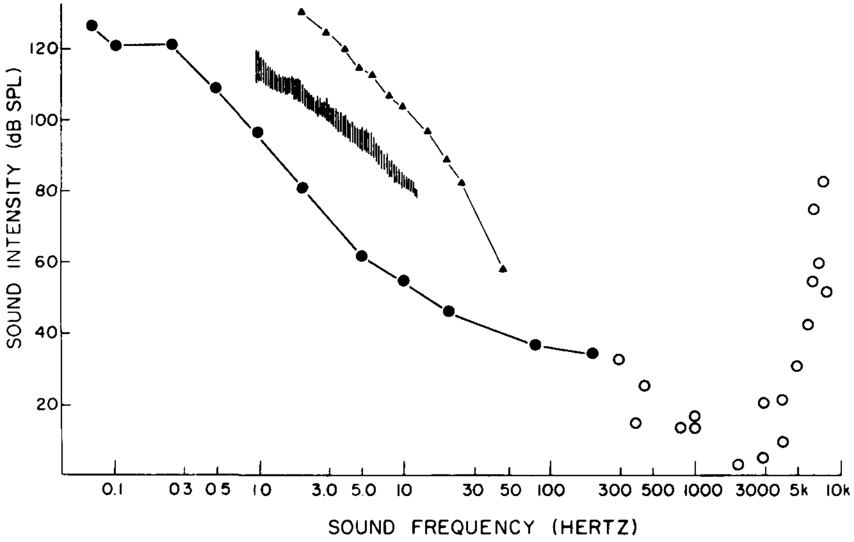

Fig. 12. Thresholds of infrasound detection by homing pigeons (*solid circles*) extend to 0.05 Hz. Environmental noise levels (*hatched region*) are above threshold levels and should be detectable by the pigeons. Auditory thresholds from the literature (*open circles*) provide the responses above 200 Hz. Human low-frequency thresholds (*triangles*) are much higher than the birds'; therefore we cannot hear many of the natural low-frequency sounds. Sound pressure reference: 0 dB = 20 microPascals.

stand how birds use their low-frequency hearing. (Kreithen and Keeton, 1974b; Yodlowski et al., 1977; Kreithen and Quine, 1979; Quine and Kreithen, 1981.)

It is apparent that the senses of birds extend beyond our own in many ways. Some of these senses may help make migration and homing more precise; other senses may enhance survival in other ways. We do know that animals are *not* engaging in a random search pattern when they navigate. They have efficient and redundant strategies that allow them to migrate and to find home with a minimum of energy consumption. But the final solution to the puzzle of animal orientation eludes us; we still cannot navigate the way animals do. Aircraft, land vehicles, and surface and submarine ships all navigate with the aid of expensive and complex radio navigation beacons. The birds may help us find a simpler, less expensive, and, perhaps, surer way to guide our travels around the earth. The study of navigating animals offers the possibility of useful discoveries in both bioenergetics and animal behavior.

I am not able to predict what other discoveries will be made in future animal navigation research, but the past has been so bright that I am confident that the future will be rewarding. I regret that we may no longer share our discoveries with William Keeton, who contributed so much to maintaining the excitement and the clarity of thinking necessary to advance the field to its current level.

ACKNOWLEDGMENTS

I thank Bertha Blaker, Kari Lavalli, Hugh McIsaac, and John Willis for assistance in the preparation of the illustrations, and I thank Marian Kreithen for her careful reading of the manuscript.

DISCUSSION FOLLOWING DR. KREITHEN'S PRESENTATION

Question: As you may know, there is a small amount of literature suggesting that there are infrasounds with frequencies measured in millihertz in caves. I am wondering if you know anything more about this? I know of only one paper; are there any possibilities that "critters" living in these places use infrasound?

Answer: I think this relates to what I will call "acoustic beacons." It is difficult to make infrasound outdoors artificially. Indoors, you can verify the area of a pressure chamber, but outdoors you need a loudspeaker that is on the order of the size of the sound's wavelength. So, if I had a loudspeaker that was 3 km across, there would be no problem in making infrasounds to test birds with. But I do not have a loudspeaker that is 3 km across. One of the things that Don Griffin suggested for experimental testing was a matched pair of caves in two different locations, where you ask the birds to choose between the various resonances of the caves. In fact, caves are resonant cavities that emit, when the wind is right, a kind of "coke bottle" sound. These sounds are on the order of hundredths of a hertz, sounds that are within the range of some animals but not humans. By the way, sound detection by pigeons is far lower than anything ever tested for whales, something like 11 or 12 octaves below middle C, several octaves lower than speculated for whale hearing. So, I think at this point they hold the record for low-frequency hearing. In that range there are lots of environmental sounds: caves, mountains, valleys, surf, volcanoes.

Question: Much of what you've talked about associated with these pigeons is that they have gone through extensive selection regimes. Do you have any evidence that these selection regimes have sharpened the pigeons to make them better navigators?

Answer: The first thing in terms of these extensive sensory abilities is that it looks like not just other pigeons but also other bird species have them. The visual capacity for polarized light and ultraviolet sensitivity is there. Many other species have been tested for pressure senses and infrasound sensitivity. I have had a golden plover, two blue jays, and one Swainson's thrush that seemed to be able to do the same kinds of things. The selection process for pigeons in the racing field is not a professional but a hobbyist's field, and seems to select for flight velocity and sustained flight. If you take ordinary pigeons from church steeples, barn roofs, city parks, and statues, they will initially provide you with exactly the same directional choices. What they won't do is fly 30 miles. After 30 miles they quit and do the more realistic thing biologically, which is to resettle. Homing pigeons of the racing strain keep flying, and they have the muscle stamina to go 600 miles or even more in a single day's flight. I think that the real selection pressure is for flight speed and endurance, and not just for navigational abilities.

Question: About a decade ago at Duke University, Vance Tucker explained to me that when a conductor moves through a magnetic field, a current is induced. Vance then calculated that when a bird wing, or the arteries of a bird wing, moves through the earth's magnetic field in certain orientations, enough current could be induced that would be detectable in certain biological systems. Therefore, possibly such fields could be detected by the bird. Could this be used in bird orientation and does anyone have any data?

Answer: The only data on induction that is really good is from the elasmobranch fishes, which have a sensitive electric detecting system used for locating prey. When they move through the water they generate electrical fields due to the movements through the earth's magnetic field. They can also be trained to detect these fields under simple laboratory conditioning tests. I must admit to having put 2,000 hours of my own time into testing the induction hypothesis on pigeons in the laboratory, and as yet, in 2,000 hours of hard work, not a single response. So if they do it, they don't do it easily. By and large, what work is done with birds suggests that they do it some other way than by induction.

LITERATURE CITED

Able, K. P. 1973. The role of weather variables and flight direction in determining the magnitude of nocturnal bird migration. Ecology 54(5):1031–41.

Able, K. P. 1974a. Environmental influences on the orientation of free-flying nocturnal bird migrants. Anim. Behav. 22:224–38.

Able, K. P. 1974b. Wind, track, heading, and the flight orientation of migrating songbirds. *In* S. Gauthreaux (ed.), Proceedings, a conference on the biological aspects of the bird/aircraft collision problem. 5–7 February 1974, Clemson University, Clemson, S.C.

Able, K. P. 1978. Field studies of the orientation cue hierarchy of nocturnal songbird migrants. *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 228–38. Springer-Verlag, Berlin, Heidelberg, New York.

Baldaccini, N. E., S. Benvenuti, V. Fiaschi, P. Ioale, and F. Papi. 1978. Investigation of pigeon homing by means of "deflector cages." *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 78–91. Springer-Verlag, Berlin, Heidelberg, New York.

Baldaccini, N. E., S. Benvenuti, V. Fiaschi, and F. Papi. 1975a. New data on the influence of olfactory deprivation on the homing behavior of pigeons. *In* D. A. Denton and J. P. Coghlan (eds.), Olfaction and taste, V, pp. 351–53. Proc. of the Fifth Int. Symp., Melbourne, Australia. Academic Press, New York.

Baldaccini, N. E., S. Benvenuti, V. Fiaschi, and F. Papi. 1975b. Pigeon navigation: effects on wind deflection at home cage on homing behaviour. J. comp. Physiol. 99:177–86.

Beaugrand, J. P. 1976. An attempt to confirm magnetic sensitivity in the pigeon, Columba livia. J. comp. Physiol. 110:343–55.

Beaugrand, J. P. 1977. Test of magnetic sensitivity in seven species of European birds using a cardiac nociceptive conditioning procedure. Behav. Processes 2:113–27.

Benvenuti, S., V. Fiaschi, and A. Foa. 1977. Homing behaviour of pigeons disturbed by application of an olfactory stimulus. J. comp. Physiol. 120:173–79.

Bookman, M. A. 1977. Sensitivity of the homing pigeon to an earth strength magnetic field. Nature 267:340–42.

Delius, J. D., R. J. Perchard, and J. Emmerton. 1976. Polarized light discrimination by pigeons and an electroretinographic correlate. J. comp. Physiol. 90:560–71.

Emlen, S. T. 1967a. Migratory orientation in the indigo bunting, *Passerina cyanea.* Part 1: Evidence for use of celestial cues. Auk 84(3):309–42.

Emlen, S. T. 1967b. Migratory orientation in the indigo bunting, *Passerina cyanea.* Part 2: Mechanism of celestial orientation. Auk 84(4):463–89.

Emlen, S. T. 1969. Bird migration: influence of physiological state upon celestial orientation. Science 165:716–18.

Emlen, S. T. 1970. The influence of magnetic information on the orientation of the indigo bunting, *Passerina cyanea.* Anim. Behav. 18:215–24.

Emlen, S. T. 1975a. Migration: orientation and navigation. *In* D. S. Farner and J. R. King (eds.), Avian biology, 5:129–219. Academic Press, New York.

Emlen, S. T. 1975b. The stellar-orientation system of a migratory bird. Sci. Amer. 233(2):102–11.

Emlen, S. T., and N. J. Demong. 1978. Orientation strategies used by free-flying bird migrants: a radar tracking study. *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 283–93. Springer-Verlag, Berlin, Heidelberg, New York.

Emlen, S. T., W. Wiltschko, N. Demong, R. Wiltschko, and S. Bergman. 1976. Magnetic direction finding: evidence for its use in migratory indigo buntings. Science 193:505–8.

Frisch, K. von. 1967. The dance language and orientation of bees. Harvard University Press, Cambridge. 566 pp.

Gauthreaux, S. A., and K. P. Able. 1970. Wind and the direction of nocturnal songbird migration. Nature 228(5270):476–77.

Griffin, D. R. 1969. The physiology and geophysics of bird navigation. Quart. Rev. Biol. 4:255–76.

Griffin, D. R. 1973. Oriented bird migration in or between opaque cloud layers. Proc. Amer. Phil. Soc. 117(2):117–41.

Gwinner, E., and W. Wiltschko. 1978. Endogenously controlled changes in migratory direction of the garden warbler, *Sylvia borin*. J. comp. Physiol. 125:267–73.

Hartwick, R. F., A. Foa, and F. Papi. 1977. The effect of olfactory deprivation by nasal tubes upon homing behavior in pigeons. Behav. Ecol. Sociobiol. 2:81–89.

Hartwick, R. F., J. Kiepenheuer, and K. Schmidt-Koenig. 1978. Further experiments on the olfactory hypothesis of pigeon navigation. *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 107–18. Springer-Verlag, Berlin, Heidelberg, New York.

Keeton, W. T. 1971. Magnets interfere with pigeon homing. Proc. Nat. Acad. Sci. USA 68:102–6.

Keeton, W. T. 1972. Effects of magnets on pigeon homing. *In* S. R. Galler et al. (eds.), Animal orientation and navigation, pp. 579–94. NASA SP-262. U.S. Government Printing Office, Washington, D.C.

Keeton, W. T. 1973. Release-site bias as a possible guide to the "map" component in pigeon homing. J. comp. Physiol. 86:1–16.

Keeton, W. T. 1974a. Pigeon homing: no influence of outward-journey on initial orientation. Monitore Zool. Ital. (N.S.) 8:227–34.

Keeton, W. T. 1974b. The mystery of pigeon homing. Sci. Amer. 231(6):96–107.

Keeton, W. T. 1974c. The orientational and navigational basis of homing in birds. *In* Advances in the study of behavior, 5:47–132. Academic Press, New York.

Keeton, W. T. 1977a. Biological sensitivity to magnetic fields in orientational responses. *In* Brain interactions with weak electric and magnetic fields. Neurosciences Res. Prog. Bull. 15(1):22–27.

Keeton, W. T. 1977b. Responses of animals to magnetic stimuli. *In* Abnormal animal behavior prior to earthquakes, 1:157–75. Proc. of conf. 1 of the National Earthquake Hazards Reduction Program. U.S. Geological Survey, Menlo Park, Calif.

Keeton, W. T. 1979a. Avian orientation and navigation. Ann. Rev. Physiol. 41:353–66.

Keeton, W. T. 1979b. Avian orientation and navigation: a brief overview. British Birds 72(10):451–70.

Keeton, W. T., and A. I. Brown. 1976. Homing behavior of pigeons not disturbed by application of an olfactory stimulus. J. comp. Physiol. 105:259–66.

Keeton, W. T., and A. Gobert. 1970. Orientation by untrained pigeons requires the sun. Proc. Nat. Acad. Sci. USA 65:853–56.

Keeton, W. T., M. L. Kreithen, and K. L. Hermayer. 1977. Orientation by pigeons deprived of olfaction by nasal tubes. J. comp. Physiol. 114:289–99.

Keeton, W. T., T. S. Larkin, and D. M. Windsor. 1974. Normal fluctuations in the earth's magnetic field influence pigeon orientation. J. comp. Physiol. 95:95–103.

Kiepenheuer, J. 1978a. Inversion of the magnetic field during transportation: its influence on the homing behavior of pigeons. *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 135–42. Springer-Verlag, Berlin, Heidelberg, New York.

Kiepenheuer, J. 1978b. Pigeon homing: a repetition of the deflector loft experiment. Behav. Ecol. Sociobiol. 3:393–95.

Kirschvink, J. L., and J. L. Gould. 1981. Organic magnetite as a basis for magnetic field detection in animals. Bio. Systems 13:188–201.

Kramer, G. 1951. Eine neue Methode zur Erforschung der Zugorientierung und die bisher damit ersielten Ergebnisse. Proc. 10th Int. Ornith. Cong., pp. 271–80. Uppsala, Sweden.

Kramer, G. 1952. Experiments on bird orientation. Ibis 94:265–85.

Kramer, G. 1957. Experiments on bird orientation and their interpretation. Ibis 99:196–227.

Kramer, G. 1959. Recent experiments on bird orientation. Ibis 101:399–416.

Kreithen, M. L., and T. E. Eisner. 1978. Detection of ultraviolet light by the homing pigeon. Nature 272:347–48.

Kreithen, M. L., and W. T. Keeton. 1974a. Attempts to condition homing pigeons to magnetic stimuli. J. comp. Physiol. 91:355–62.

Kreithen, M. L., and W. T. Keeton. 1974b. Detection of changes in atmospheric pressure by the homing pigeon, *Columba livia*. J. comp. Physiol. 89:73–82.

Kreithen, M. L., and W. T. Keeton. 1974c. Detection of polarized light by the homing pigeon, *Columba livia*. J. comp. Physiol. 89:83–92.

Kreithen, M. L., and D. B. Quine. 1979. Infrasound detection by the homing pigeon: a behavioral audiogram. J. comp. Physiol. 129:1–4.

Larkin, T. S., and W. T. Keeton. 1976. Bar magnets mask the effect of normal magnetic disturbances on pigeon orientation. J. comp. Physiol. 110:227–32.

Larkin, T. S., and W. T. Keeton. 1978. An apparent lunar rhythm in the day-to-day variations in initial bearings on homing pigeons. *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 92–106. Springer-Verlag, Berlin, Heidelberg, New York.

Matthews, G. V. T. 1968. Bird navigation. 2d ed. Cambridge University Press, London.

Merkel, F. W., and W. Wiltschko. 1965. Magnetismus und Richtungsfinden zugunruhiger Rotkehlchen (*Erithacus rubecula*). Die Vogelwarte 23(1):71–77.

Nisbet, I. C. T., and W. H. Drury, Jr. 1967. Orientation of spring migrants studied by radar. Bird-Band. 38:173–86.

Oley, N., R. Dehan, D. Tucker, J. Smith, and P. Graziadei. 1975. Recovery of structure and function following transection of the primary olfactory nerves in pigeons. J. Comp. and Physiol. Psych. 88(2):477–95.

Papi, F., V. Fiaschi, S. Benvenuti, and N. E. Baldaccini. 1973. Pigeon homing: outward journey detours influence the initial orientation. Monitore Zool. Ital. (N.S.) 7:129–33.

Papi, F., L. Fiore, V. Fiaschi, and S. Benvenuti. 1972. Olfaction and homing in pigeons. Monitore Zool. Ital. (N.S.) 6:85–95.

Papi, F., W. T. Keeton, A. I. Brown, and S. Benvenuti. 1978. Do American and Italian pigeons rely on different homing mechanisms? J. comp. Physiol. 128:303–17.

Quine, D. B., and M. L. Kreithen. 1981. Frequency shift discrimination: can homing pigeons localize infrasounds by doppler shifts? J. Comp. Physiol. 141:153–55.

Richardson, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–72.

Sauer, E. G. F. 1957. Die Sternenorientierung nachtlich zeihender Grasmucken (*Sylvia atricapilla, borin and curruca*). Z. Tierpsychol. 14:29–70.

Schlichte, H.-J. 1973. Untersuchungen uber die Bedeutung optischer Parameter fur das Heimkehrverhalten der Brieftaube. Z. Tierpsychol. 32:257–80.

Schmidt-Koenig, K. 1960. Internal clocks and homing. Cold Spring Harbor Symp. Quant. Biol. 25:389–93.

Schmidt-Koenig, K., and W. T. Keeton. 1977. Sun compass utilization by pigeons wearing frosted contact lenses. Auk 94:143–45.

Schmidt-Koenig, K., and W. T. Keeton (eds.). 1978. Animal migration, navigation, and homing. Springer-Verlag, Berlin, Heidelberg, New York. 462 pp.

Schmidt-Koenig, K., and J. B. Phillips. 1978. Local anesthesia of the olfactory membrane and homing in pigeons. *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 119–24. Springer-Verlag, Berlin, Heidelberg, New York.

Schmidt-Koenig, K., and H.-J. Schlichte. 1972. Homing in pigeons with impaired vision. Proc. Nat. Acad. Sci. USA 69:2446–47.

Schmidt-Koenig, K., and C. Walcott. 1978. Tracks of pigeons homing with frosted lenses. Anim. Behav. 26:480–86.

Tucker, D., P. Graziadei, and J. C. Smith. 1975. Recovery of olfactory function in pigeons after bilateral transection of the olfactory nerves. *In* D. A. Denton and J. P. Coghlan (eds.), Olfaction and taste V, pp. 369–73. Proc. of the Fifth Int. Symp., Melbourne, Australia. Academic Press, New York.

Visalberghi, E., and E. Alleva. 1979. Magnetic influence on pigeon homing. Biol. Bull. 156:246–56.

Walcott, C. 1978. Anomalies in the earth's magnetic field increase the scatter of pigeons' vanishing bearings. *In* K. Schmidt-Koenig and W. T. Keeton (eds.), Animal migration, navigation, and homing, pp. 143–51. Springer-Verlag, Berlin, Heidelberg, New York.

Walcott, C., J. L. Gould, and J. L. Kirschvink. 1979. Pigeons have magnets. Science 205:1027–29.

Walcott, C., and R. P. Green. 1974. Orientation of homing pigeons is altered by a change in the direction of an applied magnetic field. Science 184:180–82.

Waldvogel, J. A. 1981. An experimental re-evaluation of the deflector-loft effect in pigeon homing. Ph.D. thesis, Cornell University.

Wallraff, H. G. 1980a. Does pigeon homing depend on stimuli perceived during displacement? I. Experiments in Germany. J. Comp. Physiol. 139:193–201.

Wallraff, H. G. 1980b. Olfaction and homing in pigeons: nerve-section experiments, critique, hypotheses. J. Comp. Physiol. 139:209–24.

Wallraff, H. G. 1980c. Olfaction as a basic component of pigeon homing. *In* Olfaction and taste, 7:327–30. IRL Press, London.

Wallraff, H. G., A. Foa, and P. Ioale. 1980. Does pigeon homing depend on stimuli perceived during displacement? II. Experiments in Italy. J. Comp. Physiol. 139:203–8.

Williams, T. C., and J. C. Williams. 1978. An oceanic mass migration of land birds. Sci. Amer. October, pp. 166–76.

Wiltschko, W. 1972a. Einige Parameter des Magnetkompasses der Rotkehlchen (some parameters of the magnet compass orientation in the European robin) (*Erithacus rubecula*). Verhandlungsbericht Der Deutschen Zoologischen Gesellschaft 65:281–85.

Wiltschko, W. 1972b. The influence of magnetic total intensity and inclination on directions preferred by migrating European robins (*Erithacus rubecula*). *In* S. R. Galler et al. (eds.), Animal orientation and navigation, pp. 569–78. NASA SP-262. U.S. Government Printing Office, Washington D.C.

Wiltschko, W., and E. Gwinner. 1974. Evidence for an innate magnetic compass in garden warblers. Die Naturwissenschaften 61(9):406.

Wiltschko, W., and R. Wiltschko. 1972. Magnetic compass of European robins. Science 176:62–64.

Wiltschko, W., and R. Wiltschko. 1974. Bird orientation under different sky sectors. Z. Tierpsychol. 35:536–42.

Wiltschko, W., and R. Wiltschko. 1975. The interaction of stars and magnetic field in the orientation system of night migrating birds. Z. Tierpsychol. 37:337–55; 39:265–82.

Wiltschko, W., and R. Wiltschko. 1976. Interrelation of magnetic compass and star orientation on night-migrating birds. J. comp. Physiol. 109:91–99.

Wright, A. 1972. The influence of ultraviolet radiation on the pigeon's color discrimination. J. Expt. Analysis Behav. 17:325–37.

Yodlowski, M. L., M. L. Kreithen, and W. T. Keeton. 1977. Detection of atmospheric infrasound by the homing pigeon. Nature 265:725–26.

JOHN R. BRETT

Life Energetics of Sockeye Salmon, *Oncorhynchus nerka*

2

INTRODUCTION

Most salmon are anadromous. Their early development is in fresh water, followed by major growth and initial maturation in the sea and a return, as fully mature adults, to their natal stream to spawn. Their complex life history involves inhabiting and migrating from stream to lake, to river, to coastal waters, and thence to distant high seas, followed by the reverse of this sequence. According to species and race they may remain for varying lengths of time in fresh water—from a few months to a number of years. Sea life is rarely less than one and one-half years and, in more northern stocks, may extend to five or even six years. In the past, mystery has surrounded their migrations, even their "disappearance" in the vast oceans in which they roam. Stories of their accurate homing migrations over thousands of miles have been doubted, only to be proven correct when adequate study was afforded.

As a fishery, salmon are ideal. They comb the ocean for its abundant food, convert this to delectable flesh, and return regularly in hordes to funnel through a limited number of river mouths exposing themselves to the simplest of capture—a gill net, trap, or seine net. Such vulnerability can be devastating if uncontrolled. In the marketplace their round, silvery appearance, red flesh, and fine texture command a high price. Nations compete for them. Federal regional offices and interna-

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia, Canada V9R 5K6

tional commissions manage them. Their economic and social importance is strikingly revealed by the fact that annually three billion young salmon are raised artificially and released in the coastal streams of the Pacific Northwest to maintain and enhance the resource (McNeil and Himsworth, 1980). As a result of the wide-ranging research that has been generated, there is a large body of literature on the ecology and physiology of Pacific salmon. Intensive and extensive studies on stream, lake, and ocean, combined with simple and advanced technology, have served to reveal much of the complex life habits.

Of the five species of North American Pacific salmon (genus *Oncorhynchus*), and of the multitude of races that are distributed in rivers from California to Alaska, I have selected one species, one race and one age-class to examine the life energetics in detail—namely, the Babine Lake sockeye salmon that mature in four years $(4_2)^1$. Babine Lake, 160 km long, lies in the Cascade range of mountains in central British Columbia, discharging its waters via the Babine River into the Skeena River, which in turn flows westward for a total of 380 km to empty into the ocean just south of the Alaska panhandle (fig. 1). Two comprehensive references in particular provide much of the broad background of knowledge of Pacific salmon from which a great deal of the life history account is drawn: Foerster's 1968 voluminous bulletin entitled "The sockeye salmon, *Oncorhynchus nerka*," and a systematic review of the "Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean" compiled by French et al. in 1976. Additional references are noted as used in the text omitting repeated reference to the above two sources for much of the life history account.

Insight on the energetics arose from the great concern for the continued survival of these migratory species when their very existence was threatened by main-stem hydroelectric dams and, as might be expected, from ever-increasing pollution of major rivers like the Columbia and Fraser. In consequence, governments were prepared to support the type of searching physiological inquiry that examined the metabolic and growth processes in relation to the major environmental factors. In the case of our laboratory, it led to the development of the tunnel respirometer and the growth-metabolism tank, both with precise environmental control (Brett, 1964; Brett et al., 1971). Specific interest in salmon energetics led in time to compiling the broader treatise "Bioenergetics and growth" (Hoar et al., 1979), which constitutes the fourth major source of reference material applied in this compilation.

By virture of these circumstances it is possible to put together a comprehensive estimate of the life energetics of an average sockeye

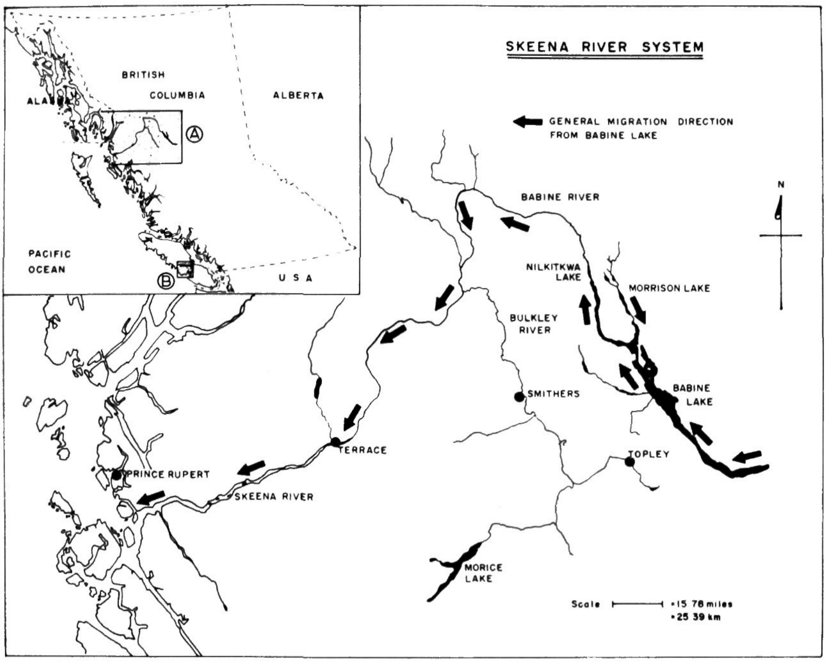

Fig. 1. Map of the Skeena River system showing the migration route of sockeye salmon smolts from Babine Lake to the coastal area of British Columbia. Inset shows location of area within the province. From Groot, (1965); reprinted by permission.

salmon that commences life as a fertilized egg weighing 0.013 g containing 372 cal (Dueñas, 1980) and terminates growth as a 2,270 g adult containing 4,200 kcal when entering fresh water on its final journey.

Each life stage will be examined for its characteristic habits and energetic components, and summarized in a life table (see below). Insofar as they can be identified, energy-saving strategies are noted and discussed.

ENERGY BUDGETS AND ENVIRONMENTAL FACTORS

The simplest expression of the energy budget is: energy ingested (I) = metabolism (M) + growth (G) + excretion (E). Among fish, excretion, with its various fecal and soluble nitrogenous wastes, is rarely measured. Growth is more readily determined, either directly or indirectly through scale or otolith readings. Total metabolism, with its components of *standard* (basal), *routine*, and *active* metabolic rates,[2] still defies field measurement but can be monitored closely and effectively in the laboratory. For ingestion the quality of the food consumed is revealed in stomach contents but the daily quantity, like metabolic rate, also defies direct field measurement.

More often than not when compiling energy budgets growth is measured, metabolism estimated, assimilation efficiency assumed, and excretion deduced. Difficulty in estimating field metabolic rates accurately undoubtedly introduces the greatest error; assimilation efficiency varies with the nature of the food and hence can compound the error if not taken into account.

The components of the balanced equation are sensitive to, and respond differently to, the chief variables of temperature, body size, and activity. It is only insofar as these functional relations between environmental stimulus and physiological response can be ascertained with a relatively high degree of accuracy that the task of computing the energy budgets becomes a meaningful exercise. Fortunately, and remarkably, the sockeye case appears to meet these requirements.

Within the limitations indicated above, three methods of determining metabolic rate have provided the greatest insight for applying to energy expenditure in nature. The determinaton of power-performance curves (equations), in which swimming cost is related to swimming speed, provides one avenue (Brett, 1964). Daily feeding metabolic rate in relation to amount fed (ration) provides a second approach (Brett, 1976). The third is direct measurement of the depletion of body reserves of migrating fish, which fortuitously do not feed on their upstream migration (Idler and Clemens, 1959). Each of these methods will be applied where appropriate, in relation to the aforementioned environmental factors.

METABOLIC RATE PARAMETERS

Salmon are rarely inactive. Competing, predating, escaping, migrating, feeding, and digesting—all these leave little time for indulging in resting metabolism. Consequently the abiotic and biotic factors bearing on metabolic rate have to apply to some pattern of routine or active metabolism.

Temperature (T)

For a fixed level of activity, such as swimming at a constant speed, the metabolic rate increases exponentially (nearly) with increasing temperature. The equation approximates: $\log (M/W) = a + bT$. Level of activity determines the intercept a. For a 50 g sockeye performing at an intermediate sustained speed of 2 L/sec (36 cm/sec),[3] the antilog of *a* has a value of 180 mg O_2/kg/h (14 kcal/kg/day) (Brett, 1964). The rate of increase *b* has a value of 0.036. This may be shown to be equivalent to a Q_{10} of about 2.3 in the central range of thermal tolerance for the species (12 ± 5° C).

Salinity (S)

Because the work of maintaining ionic balance is performed at any salinity, and osmotic freedom can only occur in the brief transition through the brackish water of the estuary, no change in rate function with salinity is required for total life metabolism (cf. Clarke and Blackburn, 1977).

Weight (W)

The effect of weight on metabolic rate has been examined more often than not in relation to standard metabolic rate. The general relation is described by the allometric equation: $\log M = a + b \log W$.[4] The rate per unit weight (M/W) diminishes with increasing size such that the standard rate of a 3 kg salmon is about one-fifth that of a 1 g fry. A mean value of 0.88 for *b* at all temperatures was determined for sockeye salmon (Brett, 1965a; Brett and Glass, 1973). Increasing activity elevated the value to approximately 0.99 for active metabolism (i.e., nearly weight-independent). An intermediate value of $b = 0.92$ has been selected for routine (or intermediate) levels of metabolism as developed for sockeye.

Feeding Metabolic Rate

The effect of various levels of ration on the daily metabolic rate of fish was early studied by Saunders (1963) on Atlantic cod (*Gadus morhua*). Subsequently, Averett (1969) extended the approach in an effort to determine energy budgets of young coho salmon (*O. kisutch*) when feeding at different levels of intensity. The interrelation of ration and temperature on the daily metabolic rate of 20 ± 10 g sockeye salmon was determined by Brett (1976), who developed a model displaying the metabolic rates as isopleths for all levels of feeding (0–7% body wt/day) over the full range of tolerable temperature (0–25° C) (fig. 2). This model, which applied to fish constantly swimming at about 1 L/sec (12 cm/sec), proved to have good predictability for estimating the daily oxygen consumption rates of similar sized hatchery coho (McLean, 1979). There remained the further refinement of determining the parameter of weight effect, to make the model sensitive to the annual cycle of growth. Both Saunders (1963) and Edwards et al.

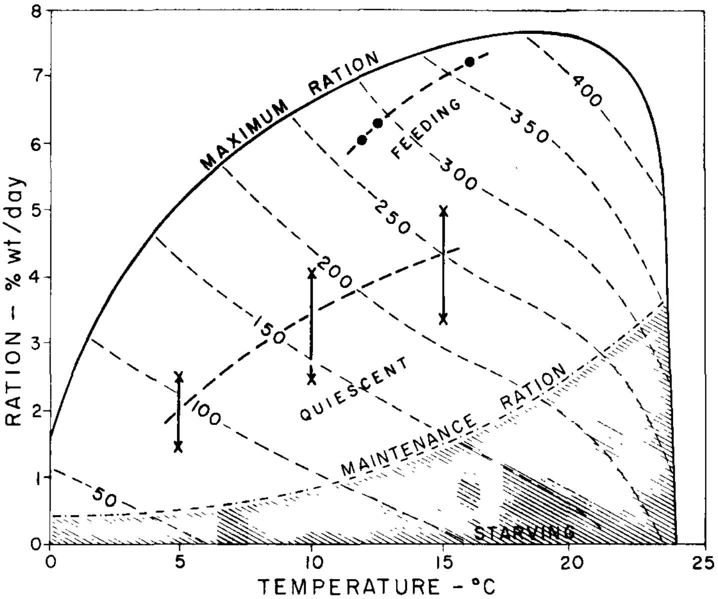

Fig. 2. Isopleths of feeding metabolic rate (mg O_2/kg/h) for fingerling sockeye salmon (20 ± 10 g) in relation to ration level and temperature. Ration is expressed in dry weight of food as a percentage of dry weight of fish. The peripheral boundary line of the response surface defines the maximum food intake for this weight; the inner, maintenance line defines the boundary for positive growth. Metabolic rates of juvenile chinook salmon in hatchery troughs are shown from Elliott (1969): *upper points* (●), 20 g chinook fed twice a day; *lower points* (*X*), fish weighing 6 and 18 g when not fed and considered quiescent under normal hatchery activity. From Brett (1976).

(1972), working with Atlantic cod, evolved weight exponents (b)[5] ranging from 0.76 to 0.83. Because the general level of daily metabolism for young sockeye when feeding heavily lies halfway between that for standard and active metabolism, the weight exponent b for this species was chosen as 0.92,[6] the value that applies to the corresponding level of activity—one-half maximum (fig. 3) (Brett, 1965a).

The metabolic rates accompanying different levels of feeding have been applied extensively in the compilation of sockeye salmon life energetics. The existence of a "salmon growth model" (McLean, 1979)[7] and experience in raising salmon in seapens have provided a means of assessing the likely feeding rate in nature. From recorded growth rates, and knowing the average weight and temperature, it is a simple matter to determine what ration level would be required to achieve such growth. For instance, if the observed natural growth rate

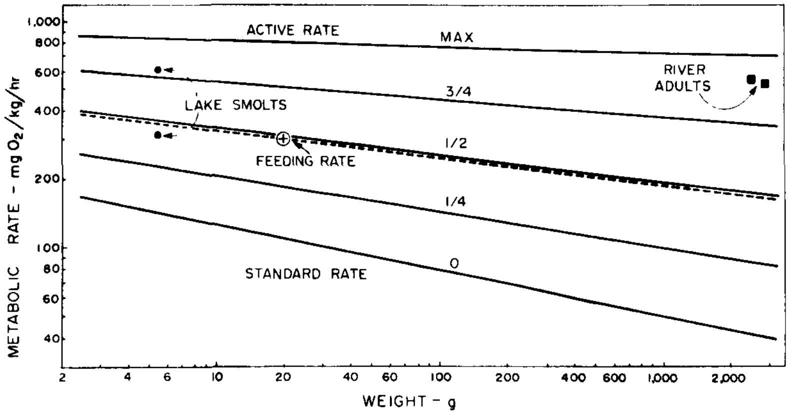

Fig. 3. Metabolic rate of sockeye salmon in relation to weight at 15° C. Upper and lower lines give the active and standard rates. Intermediate lines apply to ¼, ½, and ¾ of the maximum sustained swimming speed. Feeding metabolic rate, when on maximum ration, approximates ½ active rate for a 20 g sockeye (*broken line*); other weights are assumed to follow the same relation. The metabolic rates of lake-migrating smolts are indicated (subsurface and surface), and that for river-migrating adults—both male and female (Idler and Clemens, 1959). Basic data from Brett (1965a); figure adapted from Brett (1965b).

approaches the maximum growth rate predicted by the model, then the metabolic rate for maximum ration can be applied.

It turns out that the freshwater, lacustrine period of the fingerling is one of retarded growth and restricted ration. At a weight of 5 g the year-old smolts achieve only one-third of their potential size (Brett, 1971). Once in the sea the story is reversed. Growth is rapid and sustained throughout ocean life, curtailed only with homeward migration. Indeed, natural ocean growth rates still exceed anything that can be produced by the salmon farmer, despite highly researched diets and frequent feeding. Assigning natural feeding rates and corresponding metabolic rates therefore poses no great problem.

One major difficulty remains, however, in the overall task of assessing total daily metabolic rates in nature. The protected environment of a growth-metabolism tank or hatchery pond contrasts with the search-attack-avoid-escape patterns of real life. An attack or escape episode involving 20 sec burst speed was shown, in terms of energy expended, to be equal to that of 15 min of active metabolism (maximum sustained swimming speed) or about 3 h of basal metabolism (Brett and Groves, 1979). Since sockeye remain mainly plankton eaters throughout life, feeding chiefly on crustaceans, major episodes of attack do not feature in their life to the same extent as must be the case for other Pacific salmon that become largely piscivorous. Greatest losses from predation appear to occur in early life and at times of massive congregation when migrating schools converge on river entry or exit—the vulnerable interfaces between habitats. Increasing size brings relief from the smaller predators, but such relative giants as mackerel shark, large chinook salmon, and pelagic fur seals must take a persistent toll. The additional energy expended cannot be disregarded; nor can it be conceived as incessantly present. For this compilation an average of 10 burst speeds per day is arbitrarily assigned, totaling 3.3 min of high energy expenditure per day, over and above the daily feeding metabolic rate. This adds approximately 12% to the daily total energy expended (incorporated in composite table 1, below).

UNITS AND EQUIVALENTS

Almost all the data and determinations compiled in this study appear in table 1, in the "Life Table of Energetics" section, below. Various metabolic and other energy transformations have been made in order to set the basis for estimating the monthly energy budget throughout life. The particular units and equivalents are noted as follows.

Dry Weight

As a salmon grows from an emerging fry to a spawning adult its body composition changes considerably. Relative moisture content decreases from about 82% in the young form to close to 67% as a mature fish reentering fresh water. The dry weight calculations in table 1 reflect this change. As noted by Groves (1970), there is a greater change in lipid, which responds to different diet and developmental stages, being greatest just before the homing migration and final formation of a mature gonad.

Caloric Content

The lipid changes obviously affect the caloric value of the dry weight. Fish that are lean from a low ration have a reduced energy content equivalent to about 5.4 kcal/g, or less if starving (e.g., table 3, p. 2371, in Brett et al., 1969). Highest values occur in fast-growing, older fish. The maximum applied was 5.8 kcal/g. This might appear too low when compared with the mean caloric value of 5.97 kcal/g for muscle tissue of adult sockeye salmon (Nishiyama, 1977). However, when the head, viscera, skeleton, and skin are combined, the whole-body value drops closer to that applied in table 1.

Oxycalorific Equivalent

For years the metabolic rate of fish was transformed into units of heat by applying the equivalent used for mammals—3.40 cal/mg O_2 respired. Recognizing that the end product of nitrogen metabolism in fish is different from that of mammals, and that fish normally obtain energy from both protein and lipid catabolism, Brafield and Solomon (1972) developed the value of 3.25 cal/mg O_2. This has been applied in the calculations of table 1 to obtain energy expended from the developed metabolic rates.

Digestibility and Excretion

As noted elsewhere, the diet of sockeye salmon, particularly as a young fish, is largely crustacean zooplankton and some amphipods. Elliott (1976) examined the fecal energy loss of brown trout, *Salmo trutta*, feeding on gammarids. On a maximum ration the fecal loss decreased with increasing temperature, falling from 29% at 4° C to 20% at 19° C. At intermediate temperatures an average reduction of 23% applied. To this digestibility loss must be added the fraction excreted as ammonia, urea, and soluble amines. This nonfecal loss amounts to about 7% (Brett and Groves, 1979), bringing the total reduction to 30% when feeding on invertebrates with a hard exoskeleton. Older sockeye, particularly in certain geographic areas of the North Pacific, may feed heavily on squid (LeBrasseur, 1966, 1972). To my knowledge no tests on digestibility of this invertebrate have been performed. Consequently, a 30% fraction of ingestion has been ascribed to excretion throughout the life table.

Should new information bring modifications to any of the equivalents or parameters applied in table 1, the complete accounting has been shown to permit adjustment accordingly.

EGG-TO-FRY STAGE

Behavior and Energy Relations

The start of life, the fertilized single cell, is always so insignificant in terms of energy. In the case of sockeye salmon, although the egg is comparatively large (and shed with 3,000 others from a single female), it contains only 0.37 kcal (Dueñas, 1980), equal to 0.0016% of the caloric content of the mature adult. Eggs are deposited in cool streams in small groups of a few hundred, occupying pockets in the gravel as the female digs the redd, progressively moving forward so that the excavation of a new pocket covers the old one. The gravel is loose and porous. Water slowly streams through the interstices occupied by the eggs. Within three months, depending on temperature, the egg hatches releasing a small alevin with a large yolk sac. It can wiggle and will later move among the gravel with surprising ease, provided that sediments have not seriously reduced the intergravel spaces.

This submerged environment, tucked between the gravel particles, does not just offer protection from free-swimming predators. The alevin exhibits a strong righting reflex. Should it roll to one side or the other it immediately rights itself and presumably moves to a space offering better support. This is one small energy-saving strategy—but not of minor significance. If the alevin is not supported, as in former flat hatchery trays, the constant effort of righting can reduce the yolk by 30% of its original content (Bams et al., 1965; Bams, 1970). A smaller fry emerges in the spring. Size is important at all times, particularly at the bottom of the predator ladder. The larger the fry, the better the survival.

Under normal conditions in nature, yolk conversion efficiency, from storage to flesh, is the most efficient of all "food" conversions. On the average, given proper support, the emerging fry will contain 67 ± 3% of the original egg energy (Marr, 1966). Furthermore, it has gained in weight by absorbing water. From an egg with a moisture content of 59% it has transformed into an 82% moist, soft-skeletoned fry.

FRY-TO-SMOLT STAGE

Behavior, Feeding, and Growth

At a weight of approximately 0.2 g (McDonald, 1969) the young fry emerge from the gravel at night and migrate downstream to enter the lake, in late May or early June. Stream temperatures are in the region of 5° C, with lake temperatures a degree or so higher at 6–7° C. Although there is a downstream orientation and swimming is downstream, at least in quiet pools, the migration is rapid mainly because of stream velocity, usually involving short distances to the lake (0.1–5 km). The young fish are mostly carried passively and frequently traverse the distance during the first night. Should dawn occur before they reach their destination, they secrete themselves in the gravel interstices, emerging the following night to continue migration. This is the usual circumstance. Progeny from spawners below the lake move upstream, hugging the shallow depths and keeping to the lesser velocities and back eddies near the riverbank. This is a more energy-demanding experience but not prolonged. For the average sockeye fry, moving downstream to the lake is merely one day of routine metabolism. We will set the date as 1 June.

Feeding begins immediately upon reaching the lake. For the complete year, as stated, one or another form of zooplankton constitutes the major portion of the diet, usually a copepod or cladoceran. The fry fan out from the stream mouth, aggregating in foraging schools that soon move offshore into the open waters of the lake. As the season advances and the lake becomes thermally stratified, a remarkable pattern of daily vertical migration develops. During the bright daylight hours they seek the cold hypolimnion waters, migrating vertically downward at dawn to remain at a depth of 30–40 m, where the temperature averages 4–6° C. As twilight comes they ascend through the thermocline to feed actively in the upper, warm epilimnion (16–18° C) for about a 2 h period. With night darkness overtaking the dusk, the fry settle 10 m or so into the area of the upper thermocline, at 14–15° C. They rise at dawn for a second, somewhat less intensive feeding, followed by retreat to depth and colder water again as full daylight penetrates the epilimnion (Narver, 1970).

This pattern gradually diminishes as surface waters cool in October. The juvenile salmon have reached 3.5 g. By November, when the fall turnover brings uniformity of temperature throughout the lake, vertical migration has ceased. In winter the small fingerlings roam the lake at temperatures of 3–4° C, locked in by ice cover from late December to spring breakup in early May of the following year. By this time they have reached about 5 g and have transformed into saltwater-tolerant smolts ready to migrate to sea.

Energy Relations

The voluntary, daily oscillation in temperature (and depth) by lake fry was considered by Brett (1971) to be an energy-saving device when food was limited. McLaren (1963) had earlier formulated such a theory to account for vertical migration of plankton, suggesting that food conversion efficiency would be improved in thermally stratified waters by feeding near the surface and digesting in deeper, colder waters. By examining alternative hypotheses, and drawing on the growth × ration × temperature data for juvenile sockeye, physiological support for this energy-conserving strategy was presented (Brett, 1971). Subsequently, Biette and Geen (1980) conducted an on-site experiment duplicating the temperature and natural feeding relations of captured Babine Lake sockeye. Their findings lend undoubted support to the bioenergetic hypothesis. That food was limited could be readily demonstrated. By computing the average daily temperatures experienced throughout the year, and programming these in the growth model developed for sockeye, a year-end weight of nearly 4 times that observed was obtained when on (programmed) maximum ration. Lake residence consumes considerably more energy in metabolism—approximately 2½ times—than is stored in growth (see table 2, below).

The midsummer daily oscillation of metabolism was computed by Brett (1971) for a 2.0 g fry (fig. 4). The pattern bore marked resemblance to that for the little brown bat, *Myotis lucifugus*, which also appears to conserve energy by restricting its activity to the dawn and dusk periods (crepuscular). Brett (1971) concluded that, under the year-long food-limiting conditions of lake residence, sockeye have evolved a pattern of thermoregulation adapted to maximize growth through the selective pressure of bioenergetic efficiency.

By summing the hourly metabolic rates throughout the daily oscillation characterizing the period when thermal stratification creates a distinct epilimnion in the lake, it was shown that a 2 g fry would consume oxygen at the rate of 183 mg O_2/kg/h (14 kcal/kg/day). The average size and metabolic rate of juveniles during the first year of life are shown in table 1. By 15 May, just under a year since lake entry, the mean size is 5.0 g, with a caloric content of 6.21 kcal.

SEAWARD MIGRATION

Behavior

Soon after the ice has disappeared from the lake, schools of sockeye can be seen close to the surface, periodically dimpling the surface with small ripples. It is not long before these apparently random movements are formed into well-oriented swimming, directed toward the lake outlet. School upon school begin to converge from all points nearshore and offshore, from side arms and large bays of the lake. The orientation and movement of smolts from Babine Lake have been studied extensively by Groot and associates using transit, sonar, and orientation tests (Johnson and Groot, 1963; Groot, 1965, 1972; Groot and Wiley, 1965). Greatest movement is at dusk, with somewhat less activity at dawn. For 3–4 h, twice each day, at average speeds of 25–30 cm/sec

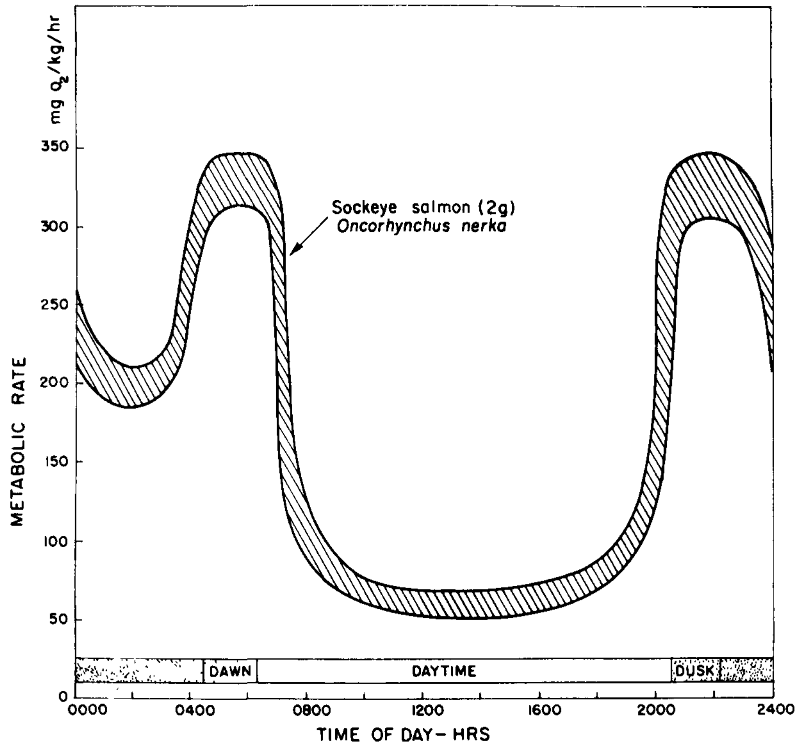

Fig. 4. Schematic representation of daily midsummer metabolic rates of young sockeye salmon in Babine Lake, British Columbia. Feeding occurs almost entirely near the surface at dawn and dusk, with descent to deep, cold water during the day. The daily mean computed to 183 mg O_2/kg/h, or 14 kcal/kg/day. From Brett, 1971; reproduced by permission of the American Society of Zoologists.

(surface) and 43–51 cm/sec (subsurface), the smolts cover 10–15 km each day. Temperatures gradually rise from 7° C at the beginning of May to 12° C at the end of May, when most fish have left the lake.

From the center of Babine Lake to the outlet is approximately 80 km. To traverse this distance only 6–7 days are required for the out-migration of millions of smolts from the central basin. The total population averages 20–30 million annually.

Downstream movement is difficult to observe and monitor. The clear surface waters of the lake spilling into the river are soon clouded with glacial silt poured in by cascading tributaries. Major rivers like the Skeena can become rampaging torrents as spring freshets swell to flood proportions. Where hydroelectric dams have backed a river into a series of slow-flowing reservoirs, Bell (1973) noted that the largest numbers of migrants are found close to shore and occupy the top meter of water. Rate of travel is about three times the net flow, covering 20–35 km/day. In more rapid waters like the unimpeded Skeena River, the migrants are not thought to travel much faster than the mean velocity, possibly holding up in back eddies during the day (applies to Fraser River studies; see Williams, 1969). At an average displacement (passive?) of 4 km/h, a distance of 96 km per day would be covered. For the 380 km from Babine Lake to the Skeena River estuary, approximately 4 days of travel would be involved. The river temperature in late May and early June runs between 10° and 12° C.

If 15 May is taken as the departure date from the center of Babine Lake, it can be concluded that by 25 May or so the smolts have reached the Skeena estuary and are experiencing brackish water for the first time. In all probability little if any feeding has occurred. The hazardous journey, the cloudy turbulent environment, and the sudden experience of salt water do not promote satisfying an appetite. For those that survive, the abundance of marine life and expansive, slow-moving tidal currents will provide for a surge of growth and activity as the smolts radiate out from the estuary to move along the coast.

Energy Relations

Energy expenditure of the smolt can be high during lake migration. On a calm day in late May surface temperature can rise to 10° C, whereas the subsurface may not have risen much above 5° C. Traveling at about 3 L/sec (25 cm/sec) at the surface, the smolts have a metabolic rate of approximately 300 mg O_2/kg/h (23 kcal/kg/day). However, the rate of energy expenditure is highest in the subsurface waters, where an average speed of 5 L/sec (43 cm/sec) is apparently maintained. This elevates the sustained metabolic rate to three-quarters of maximum, or about 600 mg O_2/kg/h (47 kcal/kg/day).

The metabolic rate accompanying surface migration is about the same as the highest feeding metabolic rate. Despite the increased rate below the surface, which applies to an unknown fraction of the total population, only 6–8 h/day for 4 days are involved. In the total energy accounting this can hardly be conceived as a significant energy drain. The 4-day experience would not reduce the limited energy reserves of the smolt by more than 0.4 kcal, or 5% of the total body caloric content.

COASTAL SEA LIFE

Behavior and Growth

During early June young sockeye salmon have been caught in relative abundance off the Skeena River mouth and in Chatham Sound, into which the Skeena River empties (Manzer, 1956). By mid-July the well-established young salmon have left, moving northwest along the Panhandle coast of Alaska, feeding heavily. Although sampling of young salmon on their voyage up the coast, in the sweeping arc of the Gulf of Alaska, has not been as intensive as the offshore efforts (devoted mainly to 2- and 3-yr sea life stages), nevertheless a sufficiently clear pattern of movement has been revealed (French et al., 1976; Hartt and Dell, 1978; Hartt, 1980). As each race of young sockeye enters the coast from Oregon to Alaska, the majority move in the same general direction northward and westward, occupying a band extending to at least 30 km offshore. Identification of a particular race by its lake of origin is not impossible (distinctive freshwater nucleus of the scale), but as yet this has not been systematically performed. The more southern stocks from Oregon and Washington, as well as those from British Columbia, do not appear to carry westward along the chain of the Aleutian Islands. Arriving by late summer and early fall in the general region of Kodiak Island, and at a weight of about 200 g, they commence to move further offshore westerly and southerly into the immense spiral of the Alaskan gyre. Only as a maturing adult, 2–3 yr later, will they again be in coastal waters.

From the Skeena River mouth to Kodiak Island is a distance of about 1,800 km. In the general elapsed time of 140 days the average rate of travel is 13 km/day (0.53 km/h). It is a feeding movement rather than a goal-oriented migration. Rate of growth is maximal for the temperature, size, and time. The growth model programmed for these parameters and set at maximum ration predicts something less than what is actually achieved, particularly in the first few months.

Coastal currents of the West Wind Drift, sweeping eastward in the subarctic region (lat. 40–50° N) at about 3–8 km/day, increase to 15–25 km/day[8] along the coast on a path similar to the sockeye migration. The general similarity of ocean currents and salmon velocities suggests a largely passive movement but with continued orientation in a N.W. direction until leaving the general proximity of the coast. Intensive feeding and active migration are not considered to be concurrent behaviors (Groot, 1965).

OFFSHORE, HIGH-SEAS LIFE

Behavior, Feeding, and Growth

Most of the salmon from British Columbia, including the Skeena River stocks, have been shown to spend their high-seas life in a zone bounded by 50–58° N latitude and 135–155° W longitude. This is an area of approximately 800 × 1,100 km, equal to about 900,000 km^2 (Neave, 1962). It is characterized by a slow-moving, counterclockwise spiral of water, the Alaskan gyre (fig. 5). Generated by the earth's rotation and an off-sweep of the stronger coastal currents, it moves at about 3–5 km/day as a giant oceanic "cyclone" in the Gulf of Alaska. The temperatures gradually stratify with a marked thermocline formed

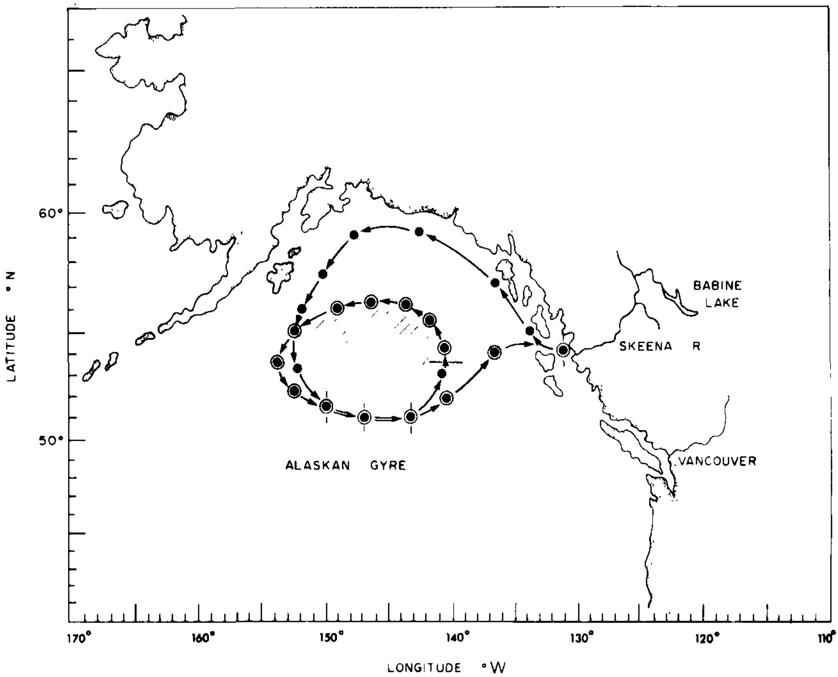

Fig. 5. Coastal and offshore movement of Skeena River sockeye during 2 yr of ocean life. Each point represents an approximate midmonth position, starting in June off the river estuary and moving up the Alaskan coast and out into the Gulf of Alaska. Circled points show second ocean year, and vertical lines indicate where these overlap the general area of the first year. Sockeye occupy the whole shaded area annually, being further north in summer and south in winter. They usually return to their river of origin either in their fourth year (as shown) or fifth year.

by early summer; this lies above the density interface of the halocline, covering a depth to 80 m. The immature salmon continue to feed heavily and grow rapidly, rising close to the surface toward evening followed by a vertical migration downward when daylight begins to penetrate the upper waters (Manzer, 1964). The diet is mostly euphausiids, the highly abundant pelagic shrimp that make up the krill of the baleen whales. Some small fish are found in the stomachs as well as some squid, but the red flesh of the sockeye attests to the heavy feeding on the carotenoid-carrying body composition of the crustaceans. The vertical migrations in the ocean do not involve the great temperature changes experienced in the lake. As shown in fig. 6, a maximum vertical difference of 4° C occurs in the summer coastal and offshore waters; this compares with 10–12° C in the lake. No food-limiting conditions characterize the naturally rapid ocean growth; and vertical mi-

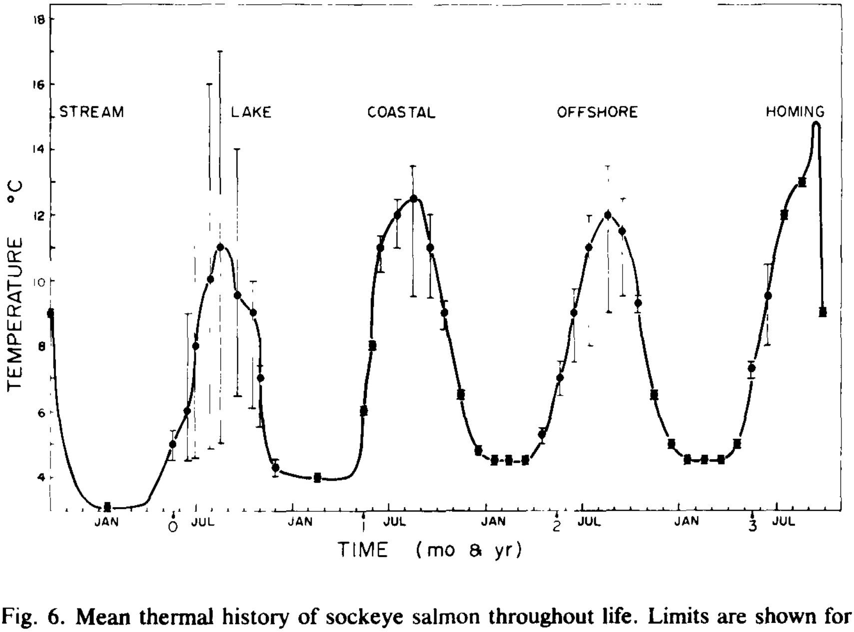

Fig. 6. Mean thermal history of sockeye salmon throughout life. Limits are shown for daily variation in experienced temperature, mainly from vertical migration in stratified waters. In the lake, juvenile sockeye feed near the surface and retreat to deep hypolimnion water during the day. In the ocean, limits are shown for temperatures at the surface and 100 ft deep. Seawater temperatures are mostly isothermal during the winter months. The homing salmon usually experience some weeks of warm river or lake water before entering a cooler spawning stream. Time is shown in months starting from the fertilized egg on 1 October. Emergence from the gravel occurs in mid-May, from which years of life are shown for a sockeye spawning in its fourth year.

gration does not generally penetrate below the thermocline. Consequently it appears likely that feeding opportunity (euphausiid and squid vertical migrations) rather than metabolic efficiency governs the behavioral pattern at sea.

Carried by the slow currents of the Alaskan gyre, the stocks of sockeye approach the northern boundary in summer and move south in winter, as surface temperatures decline and become fairly uniform throughout at about 4–5° C. In the area of the Alaskan gyre away from the coast, the isotherms tend to parallel the lines of latitude so that determining the exact east-west distribution is not of particular consequence. Only the summer north-south distribution requires identification to provide accuracy for environmental temperature, i.e., average body temperature.

The whole Gulf of Alaska has been experimentally fished, on a grid basis, using large, seagoing research vessels like our *G. B. Reed*, a 50 m trawler with 10,000 km cruising range. Either gill nets, stretching many miles in total length, or thousands of baited hooks from long surface-floating lines have been used to track the sockeye abundance—by location and season. Whenever lively, undamaged salmon were caught, they were tagged and released to provide subsequent identification when some of them were caught by inshore commercial fisheries or spotted by cannery workers or fisheries officers on their spawning-stream patrols.

A systematic figure has been developed to illustrate how the sea life can be pictured (fig. 5). For convenience it shows a sequence of monthly positions corresponding to the determined sizes and temperatures that characterize this major segment of the life history (coordinates noted in table 1). The position of the boundaries, the temperatures, the sizes, and the general seasonal shifts are amply supported (see Neave, 1964; Hartt, 1966; French and McAlister, 1970; French et al., 1976; Hartt and Dell, 1978). Salmon are the major epipelagic fish of the northern part of the North Pacific. They have established their indisputable dominance of the surface waters of this immense region. When late spring and early summer bring an evacuation of the area, particularly by cyclically dominant year-classes, a definite sparsity of epipelagic fishlife is revealed by barren catches in the offshore areas. As maturation brings enlargement of the gonads, the annual major inshore migration has commenced.

Since leaving the Skeena River outlet as smolts, the sockeye have traveled a minimum distance of 5,600 km in their first ocean year, a further 5,000 km in their second year, and now a 1,100 km journey inshore, apparently independent of the direction of ocean currents

(Neave, 1964; Royce et al., 1968). This brings them once again to the estuary of the Skeena River. Such return migrations appear to involve almost continuous well-oriented swimming in the general direction of the home river (Stasko, 1971). Speeds average 30–55 km/day (Neave, 1964; Hartt, 1966) and include active feeding, to judge from the continued excellent growth and frequency of full stomachs of the salmon when they are caught in inside waters. The deduced swimming speeds of sockeye salmon entering the waters of northern British Columbia range from 1.5 to 3.0 km/h. The homing is not always direct and precise, yet they can travel at the same general rates and maintain direction at night, frequently at an average daily speed of 2 km/h (Stasko, 1971).

Ocean growth from smolt to adult has been examined by Ricker (1976) for certain stocks of sockeye salmon (e.g., Karluk Lake, Cultus Lake). Ricker notes that each stock of sockeye has its own average growth rate and pattern of ages at maturity. From absolute values and deductions from annuli on scales, a seasonal growth curve was developed (Ricker, 1976, fig. 3A, p. 1516) that has been used to assign mid-monthly weights appropriate for a returning 5 lb (2,270 g) sockeye at the termination of feeding, i.e., just entering the Skeena River mouth.

Floating gill nets have been used to determine the vertical distribution of ocean-caught sockeye which show both diurnal and seasonal differences in how they relate to depth (Manzer, 1964). In the summer, when stratification produces a distinct thermocline, downward movement appears restricted to 30–40 m. A study of frequency of distribution with depth (and temperature) revealed that the daily mean temperature was about 1° C less than that at the surface. For the months of November to April the upper waters are largely isothermal. From an atlas of North Pacific ocean monthly mean temperatures at the surface and at 30 m (Robinson, 1976) the complete thermal history of sockeye during ocean life was derived (fig. 6).

Energy Relations in the Ocean

By applying the conversions noted in table 1 to the ocean growth of sockeye, the pattern of accrued body energy is depicted in fig. 7. With the exception of the first 3–4 mo of marine growth (which is almost explosive), the predicted weight, according to mean monthly size and temperature, was within ±15% of observed weights, and in 12 cases was even within ±3%. This simply serves to illustrate that on the basis of present understanding, growth rate in the ocean approximates

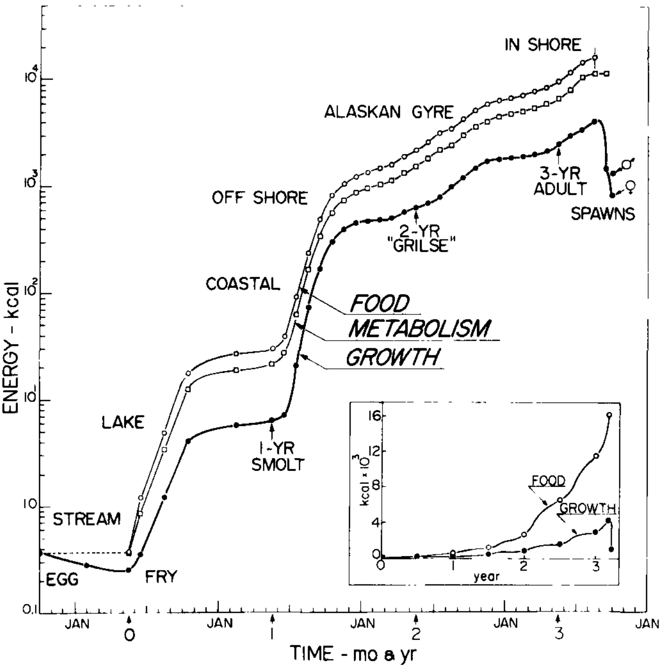

Fig. 7. The cumulative energy of growth, metabolism, and food during the life of the Babine Lake sockeye salmon spawning in its fourth year. Egg deposition is dated from 1 October. Age is shown from the time of subsequent emergence from stream gravel (15 May). Feeding ceases with river entry of the maturing adult on 1 August. Stored body energy is utilized for metabolism, and sperm and ova energy are released on spawning (1 October). The last point of the growth curve is for the spawned-out female; the final body energy of the male is shown just above it. Energy axis is in logarithmic scale; inset shows this in arithmetic scale.

maximum capacity and consequently feeding rate also approximates maximum daily intake. It must be noted, however, that the sampling of mature fish from the fishery, and the use of scales from those fish to determine growth rate, carries with it the inevitable bias of the survival of the larger fish and the greater likelihood of these being caught. This is particularly so of a gill net, but not so likely for a seine net, which surrounds whole schools. For our purposes the significance lies in the support provided for applying the metabolic rate for maximum ration, starting from the moment the fish enter the coastal zone. Hence a fairly accurate metabolic rate can be ascribed to the indicated mean monthly weights and temperatures assembled in table 1. With the exception of onshore migration, which is given separate consideration, the compilation is relatively straightforward. At 2,270 g, without distinguishing between sexes, the salmon has a body energy of approximately 4,211 kcal, having expended 7,032 kcal to achieve this energy store—only 67% more than that deposited in growth.

HOMING RIVER MIGRATION AND SPAWNING

Behavior and Energetics

On 1 August, in its fourth year, the average sockeye enters the Skeena River on a final journey to the spawning grounds. The Skeena is a large, turbid river discharging 300–600 m^3/sec, with tidal water penetrating 50 km upstream at high tide. Almost continuous swimming effort characterizes the next 21 ± 4 days, the usual time to traverse the 380 km from river mouth to lake entry.[9] At the upstream point, where Babine Lake flows into the Babine River, a fish-counting fence and trap have operated since 1946. Salmon tagged at the Skeena estuary, and waves of salmon moving upstream, have provided a means of estimating the average elapsed time.

No study has been performed on the energy expenditure of Skeena River sockeye, but a classical piece of research performed by Idler and Clemens (1959) allows direct application of a Fraser River study to the Skeena situation. River velocities and temperatures are not too different, but some sockeye stocks of the Fraser River must traverse two and three times the Babine Lake distance. One such stock, the Stuart Lake run, was tracked as its identifiable wave of salmon moved steadily upstream. By catching samples every hundred miles or so, the change in body composition was determined for a "standard" fish. Lipids were the main source of fuel at first, followed by (and in addition to) proteins. Body weight remained much the same, as water replaced the weight of consumed energy stores. Including the energy diverted into the gonads, the male sockeye expended 44.2 kcal/kg/day and the female 51.6 kcal/kg/day. Adjusting for the gonad diversion of energy, a common 43 kcal/kg/day was expended, on the average, throughout the river migration. Applying this daily rate to the Babine sockeye, a total of 2,050 kcal would be expended by fish with an average weight of 2,270 g (5 lb). By analogy with the Fraser sockeye, this rate of energy expenditure would also be close to 80% of active metabolism, the maximum sustained rate.

Cruising with relative ease in the quiet waters of Babine Lake, the female locates and enters the homestream some three weeks later and commences digging a redd; the male defends the area of the spawning bed. The expenditure of energy to this point, without income, has reduced the body content to 1,923 kcal, or 46% of that at river entry (table 1). The mature ovary averages 13.7% of the full body weight, the testis only 3.3%. At an estimated 2.98 kcal/gram wet weight, the gonads account for 927 kcal and 224 kcal, respectively. The energy expended in migration and the release of 3,000 ova have finally reduced the female to 996 kcal, not quite one-quarter of the maximum body energy achieved at the end of ocean growth. The male has not fared quite so badly at 1,699 kcal (fig. 7).

Lacking the majority of body lipids, drained of nearly half their protein, and heavy with water, the salmon die following the 2-wk spawning effort. The thousands, sometimes millions of carcasses, still carrying phosphates and nitrates from ocean feeding, remain to contribute a significant portion of the nutrients to the nursery lakes, where the fry of the next generation will grow (Krokhin, 1967). Although this cannot be conceived as an energy contribution, it is obvious that if such numbers of adult fish survived to become ravenous predators for even a brief period in the limited sockeye-producing lakes of the Pacific Northwest, the normal balance of life would be radically altered—possibly irreversibly.

ONSHORE AND RIVER MIGRATION—ENERGY-SAVING STRATEGIES

As a general energetic strategy, the ability to home accurately from distant feeding grounds is obviously important in the expedient use of body fuels. That this is the case appears to be supported by every bit of evidence. Gill nets strung out across the migration path will be entered from one side only. Seining also supports and benefits from the maintained direction and general speed of homing adults. In the case of Bristol Bay sockeye in northwestern Alaska, those homing from south of the Aleutian chain can be seen moving through the interisland passes in a uniform direction. The remarkable distances covered by tagged salmon, with recoveries 20–30 days later and 1,000–1,500 km distant, lend major support to the persistent orientation (if not navigation) of the salmon.[10] Indeed, at a younger stage, if the schools of smolts can be observed on calm evenings magically swimming just at the surface far from shore in the direction of an outlet 80 miles away, the adult can be expected to be equally well endowed. Experimental evidence supports some form of celestial or solar orientation, but not exclusively—completely overcast nights reduce but do not eliminate the phenomenon. If there is any area of confusion for the salmon (as interpreted by man), it occurs in the immediate approaches to a river like the Skeena, where inshore islands offer false courses and tides daily reverse the brackish water flow at the outlet (Madison et al., 1972; Groot et al., 1975). Small, bullet-sized sonic tags have been affixed to the dorsal musculature or slipped into the stomach. Continuous tracking, sometimes lasting 24–36 h, has confirmed the ability of salmon to maintain a single direction for mile after mile. Nevertheless, there is also evidence of backtracking and crossing of paths. Not all is perfection in the dynamic complexity of the inshore, coastal environment. It seems clear that initial celestial orientation in the open ocean must be supported or supplanted by current and odor cues, together with random search patterns in the vicinity of the coast. Delay in river entry, particularly in small rivers, is associated with abnormally low discharge and high water temperature. If maturation is incomplete the salmon can afford to wait.

One of the most searching studies on the energetics of ocean migration has been conducted on Bristol Bay sockeye salmon as they move inshore from the Bering Sea in their final month of marine life (Nishiyama, 1972, 1977). This particular stock, which in some years is exceptionally large (up to 50 million mature sockeye), travels at one of the highest daily rates recorded. Moving in the surface waters from 10 to 20 m deep, they average 55 ± 15 km/day (Hartt, 1966). In common with the high growth rate of Skeena sockeye at this terminal stage, the Bristol Bay salmon feed heavily on squid, shifting to euphausiids as they move over the shelf area.

By estimating metabolic rate from swimming speed, and using measures of observed growth rate and gonad development, Nishiyama (1972) concluded that from 34 to 114 kcal/fish/day would be required as food intake for 4-yr-old Bristol Bay sockeye salmon. At a mean weight of 2.2 kg, this equals 15–55 kcal/average-sized salmon (midpoint = 102 kcal/fish/day or 46 kcal/kg/day).[11] The large variation is based on the differences in possible speed, growth rate, and gonad maturity.

Turning to the Skeena sockeye, the rate of onshore migration during the last 30–60 days of travel appears to be about 40–50 km/day, or an average speed of 1.6–2.1 km/h (Hartt, 1966). This general velocity is supported in the review of Stasko (1971), who concluded that a range of 1.4–2.9 km/h characterized the rate of travel. French et al. (1976) noted that there was some increase in the migration speed as the maturing fish approached the coast, accounting for some of the above-noted range in speeds. Some diurnal variation is also present, the daytime swimming speeds averaging 10–20% greater than nighttime speeds.

Within their capacity for sustained performance, migrating fish have any number of choices, from slow to rapid swimming or any combination of these. To analyse the limited range of speeds actually selected by the sockeye (or salmon generally), Brett (1965b) drew up an efficiency curve in terms of energy cost per km in relation to swimming speed for a 2.3 kg sockeye, 61 cm total length (fig. 8). This curve showed that very low speeds, less than 1 km/h, would be costly simply because too large a fraction of the energy expended would be lost in maintenance metabolism spread out over too many days.[12] Intermediate speeds between 1.0 and 2.6 km/h were least costly, with an optimum efficiency at 1.8 km/h. It is surely no coincidence that these are the very swimming speeds determined for ocean migration. Higher rates, as figure 8 depicts, become excessively costly as the power requirements rise exponentially.

Unfortunately for the salmon, these efficient swimming speeds do not suffice for upstream progress when the mean river velocity of major rivers (e.g., the Fraser and Columbia Rivers) can be in excess of the maximum sustained swimming speed (see Osborne, 1961). The

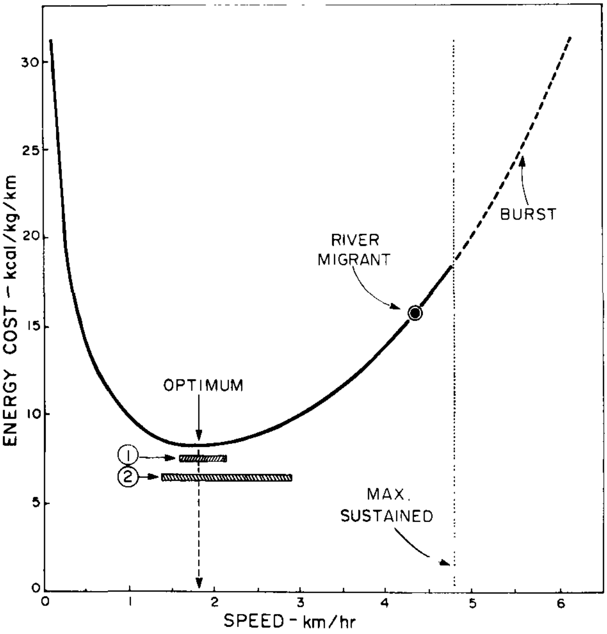

Fig. 8. Efficiency curve calculated for the swimming performance of a 2.27 kg, 61 cm sockeye salmon in terms of energy expended per km. Least cost occurs at 1.8 km/h. Range of migratory swimming speeds when homing from offshore ocean feeding grounds is shown from two sources: (1) Hartt, 1966, and (2) Stasko, 1971. Position of Fraser River migrating adult sockeye (Stuart Lake race) was applied to the Babine Lake–Skeena River energy determinations. Adapted from Brett (1965b).

track-made-good by the Babine sockeye moving up the Skeena River averages about 16–19 km/day. Assuming the same mean river velocity as applied to the Fraser River (7 km/h), the salmon would have to swim at a continuous speed of approximately 7.8 km/h. Since their maximum sustained speed is 5 km/h, it is apparent that major energy-saving devices must be in play to achieve such upstream progress. By analogy with the only documented case, that of the Fraser River sockeye (Stuart Lake race), the measured rate of energy expenditure was equal to swimming at an average speed of 4.3 km/h (Brett, 1965). When applied to the Skeena River sockeye this means an effective reduction by 46% of the apparent required swimming speed. That there could be some unrealistic assumptions in using mean river velocities is undoubtedly true. However, the calculations serve to illustrate how effective the salmon must be in selecting the paths of lesser velocity and in using their hydrodynamic properties to greatest advantage.

LIFE TABLE OF ENERGETICS

The Table

The compilation of the life energetics is presented in table 1, as noted throughout the text. The detail may seem excessive, but to my knowledge such a step-by-step accounting has not been attempted before. Not all phases carry the same validity. It is hoped that new insights will come and that these may be fitted in to the table to improve its accuracy and hence its usefulness. The weakest link still remains the estimation of total metabolism (*M*). How much activity occurs in nature that pushes the feeding metabolic rate above that observed experimentally? What is the appropriate weight exponent to apply for calculating the metabolic rate of large fish feeding on euphausiids or squid? How efficient is assimilation when on such diets, and how is this affected by meal size? Is the majority of the migration essentially passive, except for lake egress and final homing?

Although such questions remain unanswered, others become clear from the table. In the last 4 mo of ocean life the fish consumes as much food as the sum of all previous months. It takes 16,000 kcal of food to produce a 4,000 kcal salmon. Ocean growth rate, in terms of laboratory experience, is maximal (or greater!) right from early July, shortly after the smolt has become established in the coastal zone. The store of energy from ocean feeding is largely utilized in the case of the female for upriver migration and egg production. Meeting environmental change, frequently manmade, provides all too slim a safe margin of

TABLE 1

CHRONOLOGICAL ENERGETICS OF GROWTH AND METABOLISM OF SOCKEYE SALMON

Stage	Location (lat. & long.)	Date (mo/day)	Age (yr-mo)	Wt (wet) (g)	Wt (dry) (g)	Energy (dry) (kcal/g)
Fry	Lake—(Spring)	June 15	0-0	0.25	0.05	5.5
	(Summer)	Aug. 15	0-2	1.0	0.22	5.4
	(Fall)	Oct. 15	0-5	3.2	0.74	5.4
	(Winter)	Feb. 15	0-8	4.5	1.04	5.4
Smolt Yearling	(Spring)	May 15	0-11	5.0	1.15	5.4
	Coastal	June 15	1-0	5.4	1.30	5.4
	55°N; 133°W	July 15	1-1	15*	3.75	5.5
	57°N; 137°W	Aug. 15	1-2	50*	13.0	5.6
	59°N; 143°W	Sept. 15	1-3	110*	29.7	5.7
	57.5°N; 148°W	Oct. 15	1-4	200*	54.0	5.7
	56°N; 152°W	Nov. 15	1-5	250*	70.0	5.7
	54.5°N; 153°W	Dec. 15	1-6	290*	81.2	5.7
	53°N; 152°W	Jan. 15	1-7	300	84.0	5.7
	51.5°N; 150°W	Feb. 15	1-8	310	86.8	5.7
	51°; 147°W	Mar. 15	1-9	320	89.6	5.7
	51°N; 143°W	Apr. 15	1-10	350*	102	5.7
	53°N; 142°W	May 15	1-11	380*	110	5.8
2 yr immature	54°N; 141°W	June 15	2-0	420	122	5.8
	55.5°N; 142°W	July 15	2-1	480*	139	5.8
	56°N; 143°W	Aug. 15	2-2	590*	171	5.8
	56°N; 145°W	Sept. 15	2-3	720*	209	5.8
	56°N; 148°W	Oct. 15	2-4	890*	258	5.8
	55.5°N; 152°W	Nov. 15	2-5	1,000*	300	5.8
	54.5°N; 153°W	Dec. 15	2-6	1,060	318	5.7
	53°N; 154°W	Jan. 15	2-7	1,100	330	5.7
	51.5°N; 150°W	Feb. 15	2-8	1,130	339	5.7
	51°N; 147°W	Mar. 15	2-9	1,180*	354	5.8
	51°N; 143°W	Apr. 15	2-10	1,250*	375	5.8
	52.5°N; 139°W	May 15	2-11	1,400*	434	5.8
3 yr maturing	Coastal	June 15	3-0	1,670*	518	5.8
	Near shore	July 15	3-1	2,100*	672	5.8
Adult—mature	River entry	Aug. 1	3-2	2,270	726	5.8
	Spawning stream	Sept. 15	3-3	2,200	454	4.2

Energetics of sockeye salmon indicated from the stage of lake entry, on June 1 as a 0.2 g fry, to river reentry as a maturing, 5 lb (2.27 kg) adult in its fourth year (1171 days, or 3.21 yr). Coastal and high-seas locations given as latitude and longitude for likely position in each month. Last entry is for nonfeeding, homestream migrant that has maintained its wet weight through increased body water replacing utilized lipid and protein.

*Ocean weight greater than that predicted by using McLean (1979) growth model.

Body energy (growth) (kcal)	Temp mo. mean (°C)	Growth Rate (wet) (%/day)	Predicted wt (max) (g)	Feeding Metab. Rate		Total metab. rate (kcal/kg/day)	Energy† expend. (kcal)	Cumul. energy expended (kcal)
				(mg O_2/ kg/h)	(kcal/ kg/day)			
0.35	6.0	5.8	0.25	200	15.8	17.7	0.5	0.5
1.19	11.0	2.31	1.6	183	14.3	16.0	1.7	2.2
4.00	9.0	1.94	4.3	172	13.4	15.0	6.1	8.3
5.62	4.0	0.28	11.5	130	10.1	11.3	4.6	12.9
6.21	5.0	0.12	8.8	120	9.4	10.5	2.0	14.9
7.02	11.0	0.26	9.1	160	12.5	14.0	5.3	20.2
20.6	12.0	3.41	9.5	316	24.6	27.6	22.6	42.8
72.8	12.5	4.01	12	294	22.9	25.6	52.9	95.7
169	11.0	2.63	63	235	18.3	20.5	79.5	175.2
308	9.0	1.99	133	179	14.0	15.7	91.7	266.9
399	6.5	0.74	226	127	9.9	11.1	76.7	343.6
463	4.8	0.49	270	94	7.3	8.2	72.2	415.8
479	4.5	0.11	313	88	6.7	7.5	70.9	486.7
495	4.5	0.11	318	88	6.7	7.5	66.2	552.9
511	4.5	0.11	329	88	6.7	7.5	84.1	637.0
592	5.3	0.30	345	101	7.9	8.8	111.7	748.7
638	7.3	0.27	379	136	10.6	11.9	162.4	911.1
708	9.0	0.33	420	166	12.9	14.5	215.5	1,126.6
806	11.0	0.45	473	203	15.8	17.7	303.5	1,430.1
999	12.0	0.69	549	219	17.1	19.2	373.3	1,467.4
1,212	11.5	0.66	656	205	16.0	17.9	379.7	1,847.1
1,496	9.3	0.71	800	160	12.5	14.0	339.1	2,186.2
1,740	6.5	0.39	957	110	8.6	9.6	278.1	2,464.3
1,813	5.0	0.19	1,066	86	7.5	8.4	254.4	2,718.7
1,881	4.5	0.12	1,115	78	6.1	6.8	231.6	2,950.3
1,932	4.5	0.09	1,144	77	6.0	6.7	216.7	3,167.0
2,053	4.5	0.14	1,174	77	6.0	6.7	267.4	3,434.4
2,175	5.0	0.19	1,228	84	6.6	7.4	341.3	3,775.7
2,517	7.0	0.38	1,313	114	8.9	10.0	545.1	4,320.6
3,004	9.5	0.59	1,495	153	11.9	13.3	859.7	5,180.5
3,898	12.5	0.76	1,817	202	15.8	17.7	1,224.9	6,405.4
4,211	13.0	0.26	2,299	210	16.4	18.4	626.5	7,031.9
1,923	12.0	....	......	...	....	43.0‡	2,288.0	9,319.9

---

†Energy expended was determined by using the geometric mean weight (between dates shown) × geometric mean metabolic rate × interval in days.

‡Applies to rate during upstream migration only (21 days); balance of 21 days at 5 kcal/kg/day.

TABLE 1—*Continued*

Stage	Location (lat. & long.)	Cumul. food energy consumed (kcal)	Comment
Fry	Lake—(Spring)	1.2	Fry emerge, May 20–30
	(Summer)	4.8	Enter lake, June 1
	(Fall)	17.6	Min. wt = 0.1 g
	(Winter)	26.5	Seasonal data
Smolt Yearling	(Spring)	30.2	River passage, June 1
	Coastal	38.9	In Chatham Sound
	55°N; 133°W	90.6	Off Prince of Wales Is.
	57°N; 137°W	240.7	Off Chichagof Is.
	59°N; 143°W	491.7	Off Yakutat
	57.5°N; 148°W	821.3	Off Kodiak Is.
	56°N; 152°W	1,060.8	Further offshore
	54.5°N; 153°W	1,255.4	Gulf of Alaska
	53°N; 152°W	1,379.6	Alaskan gyre
	51.5°N; 150°W	1,497.0	Alaskan gyre
	51°N; 147°W	1,640.0	Alaskan gyre
	51°N; 143°W	1,915.3	Alaskan gyre
	53°N; 142°W	2,213.0	Alaskan gyre
2 yr immature	54°N; 141°W	2,620.9	Predicted wt same
	55.5°N; 142°W	3,194.4	Alaskan gyre
	56°N; 143°W	3,523.4	Alaskan gyre
	56°N; 145°W	4,370.1	Alaskan gyre
	56°N; 148°W	5,260.3	Alaskan gyre
	55.5°N; 1522⅓W	6,006.1	Alaskan gyre
	54.5°N; 153°W	6,473.9	Alaskan gyre
	53°N; 154°W	6,901.9	Min. winter temp.
	51.5°N; 150°W	7,284.2	Alaskan gyre
	51°N; 147°W	7,839.1	Alaskan gyre
	51°N; 143°W	8,501.0	Maturing
	52.5°N; 139°W	9,768.3	Inshore migration
3 yr maturing	Coastal	11,692.1	In Dixon Entrance
	Near shore	14,719.1	Off Skeena River
Adult—mature	River entry	16,061.3	15 days later
	Spawning stream	....	21 days river + 21 days to spawn

1. This notation applies to anadromous fish that spend one year in fresh water, migrate to sea in their second year, spend two full years at sea, and return in their fourth year of life to spawn. In most years it is the dominant year-class.

2. See definition of terms in Fry (1971) and Brett (1972).

3. L = total body length. A 50 g sockeye averages 18 cm in length.

4. M = mg O_2/h. When expressed as M/W, i.e., mg O_2/kg/h, b has a negative value (−0.12 in the case cited).

5. For the equation: $\log M = a + b \log W$.

6. Where $\log M/W$ is used, as in figure 3, b becomes −0.08.

7. The model, and its computer program, approximates the table of sockeye growth rates in relation to temperature and weight compiled by Brett (1974). The basic equations relating dependent and independent variables were modeled after Stauffer (1973).

8. Earlier accounts of coastal currents placed the average rate at 6–8 km/day (Dodimead and Hollister, 1962; Dodimead et al., 1962). Recent oceanographic studies, however, indicate the rate to be double the former determinations (A. J. Dodimead, personal communication).

9. Takagi and Smith (1973) record an average of 23 days for tagged 4-yr-old sockeye migrating in the months of July and August. However, no reduction in elapsed time is applied from the effects of tagging, nor from the problem of negotiating the Babine River counting fence. Each of these could easily account for a delay of one day in relation to normal migration time.

10. True navigation implies knowledge of geographic position, which, together with correct orientation, sets the appropriate course.

11. The ratio between the energy of food intake and daily metabolic rate for ocean migrating Babine sockeye (see data for maturing [coastal] salmon, table 2) is 2.25 times the metabolic energy. Applying this to the present determinations results in an estimated 41.4 kcal/kg/day intake.

12. The term *maintenance metabolism* has been adopted to signify standard metabolic rate plus unspecified maintenance costs accompanying low activity.

LITERATURE CITED

Averett, R. C. 1969. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. thesis, Oregon State University, Corvallis. 74 pp.

Bams, R. A. 1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish. Res. Bd. Can. 27:1429–52.

Bams, R. A., A. S. Coburn, and G. E. Johnston. 1965. Experimental hatchery investigation. Ann. Rep. Biol. Sta., Nanaimo, B.C. (1964–65):F1–F5.

Bell, M. C. 1973. Fisheries handbook of engineering requirements and biological criteria. Fish.-Eng. Res. Prog., Corps of Engineers, N. Pac. Div., Portland, Oregon.

Biette, R. M., and G. H. Geen. 1980. Growth of underyearling sockeye salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquat. Sci. 37:203–10.

Brafield, A. E., and D. J. Solomon. 1972. Oxy-calorific coefficients for animals respiring nitrogenous substrates. Comp. Biochem. Physiol. 43A:837–41.

Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Can. 21(5):1183–226.

Brett, J. R. 1965a. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Can. 22(6):1491–501.

Brett, J. R. 1965b. The swimming energetics of salmon. Sci. Amer. 213(2):80–85.

Brett, J. R. 1971. Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Amer. Zool. 11:99–113.

Brett, J. R. 1972. The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. Respir. Physiol. 14:151–70.

Brett, J. R. 1974. Tank experiments on the culture of pan-size sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) using environmental control. Aquaculture 4:341–52.

Brett, J. R. 1976. Feeding metabolic rates of sockeye salmon, *Oncorhynchus nerka*, in relation to ration level and temperature. Fish. Mar. Serv. Res. Dev. Tech. Rep. 675. 18 pp.

Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon, *Oncorhynchus nerka*, in relation to size and temperature. J. Fish. Res. Bd. Can. 30(3):379–87.

Brett, J. R., and T. D. D. Groves, 1979. Physiological energetics. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), Fish physiology. Bioenergetics and growth, 8:279. Academic Press, New York. 786 pp.

Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 1969. Growth rate and body composition of fingerling sockeye, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Bd. Can. 26:2363–94.

Brett, J. R., D. B. Sutherland, and G. D. Heritage. 1971. An environmental control tank for the synchronous study of growth and metabolism of young salmon. Fish. Res. Bd. Can. Tech. Rep. 283. 11 pp.

Clarke, W. C., and J. Blackburn. 1977. A seawater challenge test to measure smolting of juvenile salmon. Fish. Mar. Serv. Tech. Rep. 705:1–11.

Dodimead, A. J., F. Favorite, and T. Hirano. 1962. Salmon of the North Pacific Ocean. II. Review of oceanography of the subarctic Pacific region. Int. N. Pac. Fish. Comm., Bull. No. 13. 195 pp.

Dodimead, A. J., and H. J. Hollister. 1962. Canadian drift bottle releases and recoveries in the North Pacific Ocean. Fish. Res. Bd. Can., MS Rep. Ser. No. 141. 64 pp.

Dueñas, C. E. 1980. A study on the use of the Phillipson microbomb colorimeter with reference to calorific tests of Pacific herring larval (*Clupea harengus pallasi*), unfertilized sockeye salmon eggs (*Oncorhynchus nerka*), and prawn spawn (*Pandalus platyceros*). Spec. Adv. Course Rep., Dept. Zool., University of British Columbia. 47 pp.

Edwards, R. R. C., D. M. Finlayson, and J. H. Steele. 1972. An experimental study of the oxygen consumption, growth, and metabolism of the cod (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. 8(3):299–309.

Elliott, J. M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. 45:561–80.

Elliott, J. W. 1969. The oxygen requirements of chinook salmon. Prog. Fish-Cult. 31:67–73.

Foerster, R. E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Fish. Res. Bd. Can. Bull. 162. 422 pp.

French, R., H. Bilton, M. Osako, and A. Hartt. 1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. N. Pac. Fish. Comm., Bull. No. 34:1–109.

French, R. R., and W. B. McAlister. 1970. Winter distribution of salmon in relation to currents and water masses in the northeastern Pacific Ocean and migration of sockeye salmon. Trans. Amer. Fish. Soc. 99(4):649–63.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, 6:1–98. Academic Press, New York. 559 pp.

Groot, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behaviour. Suppl. 14. 198 pp.

Groot, C. 1972. Migration of yearling sockeye salmon (*Oncorhynchus nerka*) as determined by time-lapse photography of sonar observations. J. Fish. Res. Bd. Can. 29:1431–44.

Groot, C., K. Simpson, I. Todd, P. D. Murray, and G. A. Buxton. 1975. Movements of sockeye salmon (*Oncorhynchus nerka*) in the Skeena River estuary as revealed by ultrasonic tracking. J. Fish. Res. Bd. Can. 32:233–42.

Groot, C., and W. L. Wiley. 1965. Time-lapse photography of an ASDIC echo-sounder PPI-scope as a technique for recording fish movements during migration. J. Fish. Res. Bd. Can. 22(4):1025–34.

Groves, T. D. D. 1970. Body compositon changes during growth in young sockeye (*Oncorhynchus nerka*) in fresh water. J. Fish. Res. Bd. Can. 27:929–42.

Hartt, A. C. 1966. Migrations of salmon in the North Pacific Ocean and Bering Sea as determined by survey and tagging, 1959–1960. Int. N. Pac. Fish. Comm. 19:1–141.

Hartt, A. C. 1980. Juvenile salmonids in the oceanic ecosystem—the critical first summer. *In* W. J. McNeil and D. R. Himsworth (eds.), Salmonid ecosystems of the North Pacific, pp. 25–27. Oregon State University Press, Corvallis. 331 pp.

Hartt, A. C., and M. B. Dell. 1978. Migrations and growth of juvenile Pacific salmon and steelhead trout during their first summer in the ocean. College of Fisheries, University of Washington, Seattle. 126 pp.

Hoar, W. S., D. J. Randall, and J. R. Brett (eds.). 1979. Fish physiology. Bioenergetics and growth, vol. 8. Academic Press, New York. 786 pp.

Idler, D. R., and W. A. Clemens. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. Int. Pac. Salmon Fish. Comm., Prog. Rep. 80 pp.

Johnson, W. E., and C. Groot. 1963. Observations on the migration of young sockeye salmon (*Oncorhynchus nerka*) through a large, complex lake system. J. Fish. Res. Bd. Can. 20(4):919–38.

Krokhin, E. M. 1967. Influence of the intensity of passage of the sockeye salmon *Oncorhynchus nerka* (Wald.) on the phosphate content of spawning lakes. Izd. "Nauka," Leningrad 15(18):36–31. (Fish. Res. Bd. Can. Trans. Ser. 1273.)

LeBrasseur, R. J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Bd. Can. 23(1):85–100.

LeBrasseur, R. J. 1972. Utilization of herbivore zooplankton by maturing salmon. *In* A. Y. Takenouti (ed.), Biological oceanography of the northern North Pacific Ocean, pp. 581–88. Idemitsu Shoten Toyko, Japan. 626 pp.

McDonald, J. C. 1969. Distribution, growth, and survival of sockeye fry (*Oncorhynchus nerka*) produced in natural and artificial stream environments. J. Fish. Res. Bd. Can. 26:229–67.

McLaren, I. A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J. Fish. Res. Bd. Can. 20:685–727.

McLean, W. E. 1979. A rearing model for salmonids. Master's thesis, University of British Columbia, Vancouver. 134 pp.

McNeil, W. J., and D. C. Himsworth (eds.). 1980. Salmonid ecosystems of the North Pacific Ocean. Oregon State University Press, Corvallis. 348 pp.

Madison, D. M., R. M. Horall, A. B. Stasko, and A. D. Hasler. 1972. Migratory movements of adult sockeye salmon (*Oncorhynchus nerka*) in coastal British Columbia as revealed by ultrasonic tracking. J. Fish. Res. Bd. Can. 29(7):1025–33.

Manzer, J. I. 1956. Distribution and movement of young Pacific salmon during early ocean residence. Fish. Res. Bd. Can., Prog. Rep. Pac. Coast Sta., 106:24–28.

Manzer, J. I. 1964. Preliminary observations on the vertical distribution of Pacific salmon (genus *Oncorhynchus*) in the Gulf of Alaska. J. Fish. Res. Bd. Can. 21:891–903.

Marr, D. H. A. 1966. Influence of temperature on the efficiency of growth of salmonid embryos. Nature 212 (5065):957–59.

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Bd. Can. 27:281–316.

Neave, F. 1964. Ocean migrations of Pacific salmon. J. Fish. Res. Bd. Can. 21(5):1227–44.

Nishiyama, T. 1972. Energy requirement of Bristol Bay sockeye salmon in the central Bering Sea and Bristol Bay. Publ. Fac. Fish., No. 15, pp. 231–343. Hokkaido University, Hakodate, Japan.

Nishiyama, T. 1977. Food-energy requirements of Bristol Bay sockeye salmon *Oncorhynchus nerka* (Walbaum) during the last marine stage. Contrib. No. 89, Res. Inst. N. Pac. Fish., Fac. Fish., Spec. Vol., pp. 289–320. Hokkaido University, Hakodate, Japan.

Ricker, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Bd. Can. 33:1483–524.

Robinson, M. K. 1976. Atlas of North Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. Naval Oceanographic Office, Ref. Publ. 2, Department of the Navy, Washington, D.C.

Royce, W. F., L. S. Smith, and A. C. Hartt. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. Fish. Bull. U.S. 66:441–62.

Saunders, R. L. 1963. Respiration of the Atlantic cod. J. Fish. Res. Bd. Can. 20:373–86.

Stasko, A. B. 1971. Review of field studies on fish orientation. Ann. N. Y. Acad. Sci. 188:12–29.

Stauffer, G. D. 1973. A growth model for salmonids reared in hatchery environments. Ph.D. thesis, University of Washington. 213 pp.

Takagi, K., and H. D. Smith. 1973. Timing and rate of migration of Babine sockeye stocks through the Skeena and Babine Rivers. Fish. Res. Bd. Can. Tech. Rep. 419. 61 pp.

Williams, I. V. 1969. Implication of water quality and salinity in the survival of Fraser River sockeye smolts. Int. Pac. Salmon Fish. Comm., Prog. Rep. 22:1–46.

Survival Strategy 2

Reproduction and Aggression

JEANNE ALTMANN

Costs of Reproduction in Baboons (*Papio cynocephalus*)

3

INTRODUCTION

Most models and analyses for allocation of effort to reproduction versus survival arise from studies of plants and animals for which these activities appear as separate seasonal or life stages. Even some very large mammals such as elephant seals (see chap. 4, below) follow the common pattern of alternating a short discrete season of intense reproductive effort with a long nonreproductive period. For such plants and animals there is a brief burst of flowering and seed production, or a few months of the year in which energies are devoted almost exclusively to mate acquisition and reproduction, perhaps followed by a brief intense period of parental care; but most of the year consists of activities that one can label nonreproductive.

It is not by accident that the most elegant work with energetics of behavior, including the more refined of the studies in the present volume, has avoided using large mammals, such as primates, that live in permanent social groups. For most primates life is quite different from that just described. There is considerable overlap in time, location, and life stage between reproductive effort and all the rest of the female's activities. In particular, the single offspring that results from each gestation remains dependent for survival on its mother for a year or more. For most days during adulthood, time and energetic effort must be apportioned simultaneously, or temporally within a single day,

Allee Laboratory of Animal Behavior and Department of Biology, University of Chicago, Chicago, Illinois 60637

between reproductive and nonreproductive effort. Almost no period is devoid of allotment to reproduction. This complex allotment demand poses a problem not only for the primate female but for the scientist as well. The energetics of various activities in all large, social mammals is difficult to measure. The temporal pattern of reproduction in primates makes it even more difficult to assign activities to reproductive or nonreproductive effort. Moreover, it becomes important under these conditions to consider time budgets and fine temporal patterning of behavior, as well as energetic expenditure over periods of varying lengths, in order to understand the costs of reproduction.

Because of the complexities in primate life history stages and in the measurement of energetics, it has not even been clear what form an investigation of primate reproductive costs would take. In this chapter I shall outline what seem to be the major parameters and problems, and the state of our knowledge of the costs of reproduction in nonhuman primates. I shall deal primarily with savannah baboons, *Papio cynocephalus*, on which my field research has been conducted in Amboseli National Park, Kenya, in collaboration with Stuart Altmann and Glenn Hausfater. In the sections that follow I shall first consider the critical features of life history and reproductive parameters and then turn to the immediate stresses of pregnancy and infant care.

BABOONS' DAILY LIFE AND LIFE HISTORY STAGES

Baboons (*Papio* spp.) are large (25 kg for adult males, 11–12 kg for adult females), relatively terrestrial old-world monkeys, most of which live in multimale, multifemale groups of about 40 animals (DeVore and Hall, 1965; Altmann and Altmann, 1970) that forage together across the savannah, spending approximately 75% of the daytime hours in feeding or walking. Baboons are omnivores that eat a wide range of mostly plant material (Hamilton et al., 1978; Post 1978, 1981, and references in both), dependent on local and seasonal availability. With a few relatively rare exceptions, each animal procures all of its own food. (For these exceptions see Hausfater, 1976, for meat distribution in baboons; Altmann, 1980, for baboon young obtaining small food scraps from adults; and Post, 1981, for data on supplantations at partially prepared food sources.) Baboons, some macaques, gorillas, and chimpanzees, unlike many other primates, exhibit no discrete birth season (Lancaster and Lee, 1965). However, for Amboseli baboons seasonal food availability seems to result in some tendency toward birth seasonality (Keiding, 1977; Altmann, 1980) in the form of a birth peak through effects on conception rates and infant mortality. Birth peaks of this sort are more difficult to detect but have been suggested by the recent long-term studies on several species (e.g., Abegglen, 1976, for hamadryas baboons; Fossey, 1979 for gorillas).

The time that animals spend in various life history and reproductive stages is a function of environmental conditions. In particular, captivity with the provision of abundant food, medical attention, and absence of predators results in an appreciable increase in the length of the adult life stage and in reduction of immature stages, including the period of infant dependence (and, consequently, interbirth intervals) and the age of first reproduction. Conversely, unprovisioned wild primates spend a larger proportion of their lives as dependent infants and as juveniles and adolescents and a smaller proportion as adults (Eisenberg, 1975; Altmann et al., 1977, 1978, 1981; Mori, 1979; Packer, 1979; Altmann, 1980; Pusey, 1980; Harcourt et al., 1981). From the standpoint of an adult female, considerably more care is provided to each offspring and for a longer period, and fewer total offspring are produced during adulthood (with the qualification that many primate females experience shorter interbirth intervals, and consequently more births, if the previous offspring dies in its first year of life).

With the few exceptions of several small monogamous new-world primates that have biparental care, monkeys and apes normally produce a single offspring at a time, after a relatively long gestation of 4–6 mo in most monkeys, 7–9 in apes. There follows an extended period of infant dependency on the mother as almost exclusive caregiver.

As with most mammals (see, e.g., Caughley, 1966), the period of infancy is one of high mortality—for Amboseli baboons first-year mortality is approximately 0.3, and second-year is only slightly lower. Moreover, no baboon under a year of age has survived its mother's death in Amboseli, and our data suggest that adult females are at a greater risk during the period of infant care than during other reproductive phases (0.15 versus 0.08). Survival differences may well depend on the extent to which environmental and social constraints combine with reproductive ones to place more or less burden on a female. Likewise, the degree of an individual's ability to affect these variables herself may well make a crucial difference to her survival and that of her offspring.

After 12–18 mo of dependence on its mother for survival, a young baboon spends several years as a growing, relatively independent juvenile. Under field conditions a female baboon first becomes pregnant when she is 5½–6 years of age, almost a year after she experiences her first menstrual cycle (menarche) and about a year before her own growth is complete; the remaining two-thirds of her life, approximately 10–12 yr, will be spent as a fully reproductive adult. It is probably quite rare for a female to live into her twenties, an age at which some captive primates experience a degree of reproductive senescence (see Wolfe and Noyes, 1981).

How is reproductive effort distributed during these 10 or 12 years of adulthood? An average of 4 menstrual cycles, each of approximately 34 days duration, occur before a parous baboon female conceives. The subsequent period of pregnancy lasts 177 days, or just under 6 mo. The single offspring produced at each birth is cared for almost exclusively by its mother, clinging to her fur and being carried about during all her normal activities and travels. Postpartum amenorrhea lasts for an average of 12 mo in Amboseli (see also and Ransom and Rowell, 1972, Nicolson, 1982, for similar results in related species in other habitats). By the end of the first year the infant is sufficiently independent of its mother that probably for the first time it has a chance of surviving if its mother were to die. Postpartum amenorrhea is again followed by about 4 menstrual cycles and another pregnancy. Thus, if the previous infant survives, interbirth intervals are a little under 2 yr (21 mo) in duration, with over three-quarters of that period spent either pregnant or caring to some degree for a single dependent offspring. The death of the previous infant curtails the period of amenorrhea within a few weeks and reduces the number of cycles before conception to 1 or 2, resulting in an appreciably shorter interbirth interval (Altmann et al., 1978).

Clearly there are only short periods of adulthood, on the order of 4–6 mo per 2 yr, during which females are not providing either uterine or postnatal care for an offspring. Our first task, then, has been to delineate the nature of requirements for care and the ways these demands can be satisfied.

PREGNANCY

In contrast to those of the postnatal period, the stresses and potential costs of pregnancy are almost entirely due to the nutritional needs of the developing fetus rather than to social or other behavioral stress. The mother must increase caloric intake to maintain the fetus at each stage and to provide for new tissue growth. The new growth, in addition, often requires large amounts of specific nutrients such as calcium. By the end of gestation the fetus is about 7% of its mother's body weight. Two-thirds of the newborn's weight is put on in the last trimester, almost half during just the last month (Hendrickx, 1971). Although it is possible that metabolism is somewhat more efficient in pregnant than in nonpregnant females (see discussion in Riopelle et al., 1975)—and this is an important area for investigation—the increase in nutritional demands is still considerable.

POSTNATAL CARE

With the infant's birth the situation changes considerably from the fairly quiet life of pregnancy. Some of the change is due to the need to provide nutrition through lactation rather than the more efficient placental system and to provide assistance at a time when the young infant has trouble clinging. As the infant begins to explore during the third or fourth week, the mother and infant must also coordinate their activities, arranging for contact and protection as needed. But one of the major changes with the infant's birth is the soaring social involvement created by the interest of other group members in the infant. We are not yet able to evaluate quantitatively the energetic or other costs and benefits of an animal's social world but here outline the main features of that experience, which are detailed by Altmann (1980).

Pregnant females have close neighbors (within 2 m; see Altmann, 1980) about 30% of the time; for new mothers the value is double that. Moreover, there is approximately a fivefold increase in most kinds of social behavior including various passive and interactive approaches and time spent in social grooming interactions. We do not yet know the net benefits or costs of this increased social life—more grooming probably results in more ectoparasite removal; more neighbors may provide some predator protection but may also subject the mother to greater feeding competition and greater chance of disease transmission. Even exclusive of grooming, the other social interactions add at least 4% to an already tight time budget.

Perhaps most important is that the social pressures are unevenly distributed among the mothers. Mothers of high dominance rank are more likely to experience the benefits and less likely to be subjected to the costs of increased social involvement than are low-ranking females. The interactions of low-ranking females include high rates of fear behavior, avoidance, and protection of the infant against aggressive group members. It remains for future research to provide cost and benefit estimates of these social behaviors.

A Model of Maternal Feeding Time

I would like to turn now to an examination of the consequences for a female of just one area of infant care, that of providing her growing infant's nutrition. In doing so, I have considered a simple algebraic model of the feeding time that a mother would require if she maintained her own body weight and provided all the energy requirements of her growing infant. That is, the basic starting point is an examination of the limits of one aspect of maternal care, provision of the infant's total caloric needs, without immediate detriment to the mother through weight loss.

Mathematical simplifications such as this one are inevitably somewhat unrealistic (see Cohen, 1972). Some likely ways of making the present model more realistic are given in italics and enclosed in brackets, but further refinement of the model itself is not warranted for the present purposes or by the available data. Moreover, the present model considers only energetic requirements and not additional requirements for specific nutrients (see Altmann and Wagner, 1978).

In the discussion I shall assume that within a season differences in feeding time among members of a single age-sex class result from differences in energetic demands. Although differences in feeding efficiency probably exist as a result of differences in dominance rank, it seems reasonable to assume that these are slight (Post, 1978; Post et al., 1980) compared with differences caused by pregnancy and lactation.

I shall make the following specific simplifying assumptions:

1. Within any given locale, age-sex class, and season, the percentage of daytime that an animal spends feeding, $f = a_0 k$ where a is a constant and k is the energetic requirement of the animal in kcal. That is, I assume that feeding efficiency is constant. [*Violations of this assumption probably occur due to the dominance rank of the mother, to the attraction and interaction of other group members with mothers of young infants (see above), and to the physical presence and movements of a semi-independent infant near and on its mother, which would reduce her efficiency. A refined model could incorporate this variability.*]

2. $k = a_1 w^{0.75}$ where w is the weight of the animal and a_1 is a constant determined by activity level but not a function of weight (Kleiber, 1961). That is, I am using an ontogenetic scaling factor of 0.75 for energetic expenditure. [*Finer analysis might suggest a variable factor ranging from about 0.66 to 1.00 (see Gould, 1975; Schmidt-Nielsen, 1977), with the relative expenditure greatest (exponent of 1.00) in the first days of life.*] Then

$$f = a_0 a_1 w^{0.75} \tag{1}$$

3. A female in late pregnancy (near term) has the same energetic requirements as a nonpregnant, nonlactating female of the same total weight (basal metabolic rate may be slightly higher but activity level is probably slightly lower), so at term or immediately at birth of her infant, the percentage of time spent feeding, f_p,

$$f_p = A(m + i_0)^{0.75} \tag{2}$$

where i_0 is the weight of the infant at birth, m is the weight of maternal tissue, and A is merely $a_0 a_1$. (I am ignoring placental tissue and fluids.) I further assume that maternal weight is constant from full-term pregnancy throughout the lactational period.

4. A mother's energetic needs while lactating are a result of energy required to maintain her own weight plus energy required to maintain her infant. The infant's weight, i, is a function of t, its age. I shall assume that the infant's basal metabolism and activity level remain constant throughout the first year of life and are the same as its mother's, that is, A is the same for both. [*I am ignoring differences in basal metabolism due to size differences. Moreover, in the first 2 mo of life, infants' activity levels are probably lower than those of their mothers; for older infants activity levels are probably higher. Incorporating this change, a more realistic model would predict a lower percentage of time spent feeding for these early months but higher percentages after month 2, compared to the percentage in the present model.*] I also assume that at each age the infant requires energy only to maintain its current weight [*i.e., for the time being I am ignoring the energy required to produce new tissue*]. Then, f_t, the percentage of time that a mother needs to spend feeding when her infant is age t, will be given by

$$f_t = Am^{0.75} + \frac{A(i_0 + t\Delta i)^{0.75}}{E} \tag{3}$$

where E = net efficiency of maternal lactation (ratio of milk calories to lactation increment in maintenance calories) and of assimilation by the infant and Δi = increment in infant weight per unit time, t, here kg per day. We can now evaluate this function utilizing currently available estimates of the relevant parameters: from laboratory data and trapping records I estimate $i_0 = 0.775$ kg (Snow, 1967) and $m = 11.00$ kg (using Snow, 1967, and Bramblett, 1969; see Altmann, 1980, for details).

From my field data I estimate that $f_p = 45$. From equation (2) we then have

$$A = \frac{f_p}{(m + i_0)^{0.75}} = \frac{45}{(11.775)^{0.75}} = 7.08$$

Then from equation (1) the percentage of the daytime required for feeding just to enable a mother to maintain her own body weight, 11 kg, is given by

$$f_m = Am^{0.75} = 7.08\ (11.00)^{0.75} = 42.76$$

I assume Δi constant over the first year of life (Snow, 1967) and estimate $E = 0.80$ (Blackburn and Calloway, 1976). Finally, we can estimate the range of values as $0.005 < \Delta i < 0.010$ (Snow, 1967; Buss and Reed, 1970).

$$f_t = 42.76 + \frac{A(0.775 + t\Delta i)^{0.75}}{E} = 42.76 + \frac{7.08}{0.80}(0.775 + t\Delta i)^{0.75}$$

This function is graphed, producing the two sloping boundary "lines" (literally curves, since age appears in the equation to the 0.75 power, not 1) in figure 1 for $\Delta i = 0.005$ and for 0.010 g/day. With respect to the estimate of maximum Δi, Buss and Reed (1970) indicate that $\Delta i =$

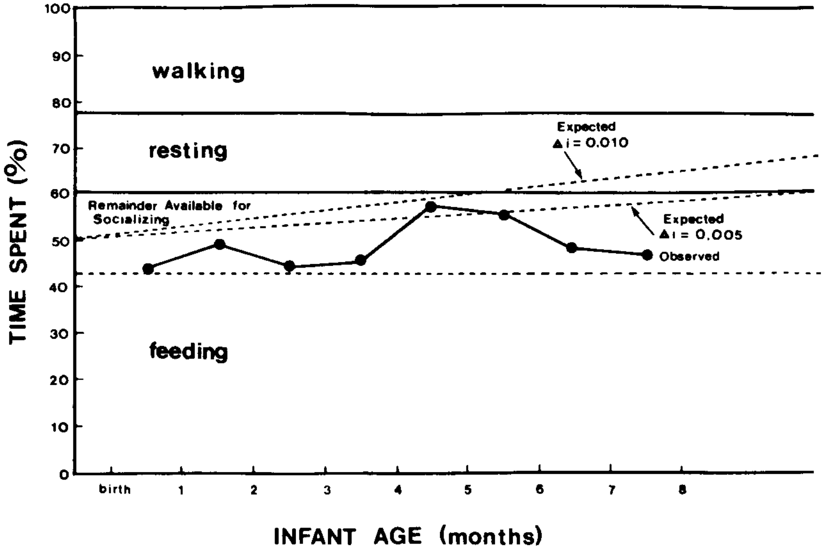

Fig. 1. Predicted and observed amount of time baboon mothers spent feeding, based on a model of necessary feeding time for mothers who provide all their infants' energetic requirements (see text for details).

0.0098 for males and $\Delta i = 0.0085$ for females are the normal growth rates in their laboratory. Snow (1967) obtained a value of 0.0082 for Δi for both males and females in a laboratory study of growth and development of approximately eight baboon infants. Here I have used the following lines of evidence for establishing the minimum value of Δi. First, the values $\Delta i = 0.0052$ for the female and $\Delta i = 0.0067$ for the male are the two values obtained by Buss and Reed (1970) for two infants whose mothers were fed the lowest-protein diet at which they could maintain their weight. Buss and Reed (1970) discontinued their study of mothers on low-protein diets after 4 mo because the infants dropped below the range of normal values obtained in their laboratory. Second, tabulating various landmarks of physical development through ages of reproductive maturation as reported by Snow (1967) and as obtained in the field in Amboseli, and by Packer (1979) for anubis baboons in Gombe Park, Tanzania, I found that the field growth rates compare with the laboratory rates as about 3 : 4.5. Applying this to obtain an estimate of Δi in Amboseli gives a value for Δi of 5–6 g per day, $0.005 < \Delta i < 0.006$, corresponding closely to the values obtained by Buss and Reed for infants whose mothers were on low-protein diets. (See also Nicolson, 1982, for recent data on weights of known-age wild anubis baboon infants.)

The value of 43% of the daytime spent feeding needed for a mother to maintain her own body weight is calculated from time budgets in which females spent approximately 17% of their time resting and 23% of the time walking, i.e., a total of approximately 83% of the time spent in these three activities, as indicated by the three horizontal lines blocking off sections of the time budget graph in figure 1: one line for feeding at 43%, blocking off a section from zero to 43%; one at 77% marking off an area from 77% to 100% indicating the time spent walking; and another at 60% blocking off a section from 60% to 77% for the 17% of the day spent resting. The remaining time might be considered uncommitted, time that could be devoted to socializing, or to more resting, feeding, or walking.

According to the model, at parturition a female would have to spend another 7% of her time (over her own 43% maintenance level) feeding just to provide energy for her newborn infant, resulting in the intercept of the two sloping lines in figure 1. Then the other values on these two lines indicate the additional time that a mother would have to devote to feeding at the two extreme rates of infant growth if all the additional energy she obtained went to the infant and not to the mother herself (except for energy she used for the infant).

It is clear from figure 1 that a female would have to increase her feeding time from the 43% of her time spent feeding to maintain only her own body weight to 58–66% during month 9 of infant life if she were providing all of her infant's energetic needs and were doing so only through lactation (these percentage incremental values are consistent with those found for humans; see Whichelow, 1976). She would still need to spend approximately 23% of her time walking, for a total of 81–89% of her day occupied just by feeding and walking. However, at these levels she would no longer be able to rest for 17% of the day, even if she could totally eliminate time spent socializing. The result is that her overall activity level would in fact be greater, creating even greater energetic requirements for her own maintenance, and she would therefore need to spend even more time foraging.

The conclusion we must reach is that even with fairly conservative estimates of energetic demands, a mother could not provide all caloric requirements for herself and her infant beyond 6–8 mo of infant age, and probably could do so up to that age only with difficulty and major restructuring of other aspects of her life. If the model were modified to incorporate the refinements I have indicated, would the apparent required feeding time be reduced? Most assumptions were conservative with respect to energetic demands, and refinements would lead to more intense time budget constraints, especially after the infant's first few months. Perhaps, then, mothers and infants have had to accommodate to these constraints as a reality. Perhaps mothers cannot always maintain their own weight and infants must provide some of their own nutrition. If so, infants' maturation and learning and other factors that facilitate the transition to nutritional independence have probably been under considerable selective pressure.

It is useful to turn to the observed feeding time for a study of Amboseli mothers. This is also plotted in figure 1. If we examine the observed values obtained during this study, it is clear that a female's time budget is affected by the fact that she has a dependent infant and by the age of that infant, but that the effect of infant age is less than that which was predicted above. Some confounding is probably produced by the moderate birth peak, the effects of which we cannot yet parcel out (see Altmann, 1980). Of greater importance, mothers are probably not maintaining their body weight (see Hytten and Leitch, 1964, and Naismith and Ritchie, 1975, for humans). It is known that women who lactate successfully and whose caloric intake during lactation is 23% over their normal maintenance intake do not maintain their body weight, whereas at 32% over normal intake, lactating women maintain steady body weight (Whichelow, 1976). If such weight losses occur in baboons, insufficient nutrition and weight loss may be a major source of maternal susceptibility to death and may place severe limits on the length and intensity of the lactational period unless females are able to store an appreciable supply of excess fat during pregnancy. Because reduced maternal health would directly affect the chances of survival of the mother's current infant, there will be immediate and evolutionary pressure for factors that enable infants to provide some of their own energetic requirements.

In sum, the time course of energetic demands seems to be as follows. During the first 2 mo of infant life the additional amount of food that a mother requires to support a dependent infant over the amount required during pregnancy is due primarily to the lower efficiency of lactation but also to some infant growth and to the energetic requirements of retrieving and attending to the infant when it is out of contact (as yet unmeasured; see below). In the next 3 mo the infant's continued growth and increased activity level place considerable strain on the mother's ability to maintain her own weight because the infant cannot contribute appreciably to its own nutrition until the end of this stage; but also I suspect that mothers lose weight during this period. If milk supplies are reduced owing to maternal nutritional strain and weight loss, infants may have additional "motivation" to eat the many plant foods that they explore. By the time their infants are 5 or 6 mo old, mothers are feeding all the time they can (60%) without sacrificing a considerable portion of social time or rest time. If they sacrifice rest time or time spent being groomed in favor of other activities, they will need to feed even more because any other activity would require more energy than these do. Thus it appears that mothers may have reached a maximum of feeding time by the time their infants are 5–6 mo old, perhaps even with weight loss. It is surely necessary for their infants to provide considerably for some of their own nutritional needs. The infants can more readily do this at 5–6 mo of age if the right foods are available (see Altmann [1980] for a discussion of weaning foods and birth seasonality in baboons and Lee [1980] and Klein [1978] for a similar discussion of the importance of weaning foods in human hunter-gatherers and vervet monkeys, respectively).

Decreased Feeding Efficiency

In the previous treatment it was assumed that feeding efficiency is not a function of reproductive status. However, additional nutritional stress may occur if a mother's foraging efficiency is reduced under some circumstances, as when she must repeatedly keep track of a playing infant in the distance or if her infant is so close as she forages that the infant blocks the mother's feeding movements (Altmann, 1980). These potential losses of efficiency require further investigation.

CONSEQUENCES OF NUTRITIONAL AND OTHER IMMEDIATE STRESSES

There are two major ways in which a primate infant might reduce its mother's future reproductive success: either through increasing the probability of her death or through delaying the conception of her subsequent offspring.

Mortality Rates

Available observations suggest that greater mortality risk might arise from several sources. If a female increases the attention she devotes to locating food and to keeping track of her infant, she may have less attention available (see Kahneman, 1973) for predator detection and be more dependent on the alarms of the other group members. Increased infant care might further render a mother more susceptible to predation if she were less able to keep up with the group and therefore stayed at the rear, as we have commonly observed (Hamilton, 1971). Additional risk would occur if she could not flee from a predator as fast because she had to retrieve the infant (if it were out of contact) and if she ran more slowly due either to the greater weight or just to poor physical condition. These factors all warrant further study.

The data from our baboon work further suggest that greater mother-infant contact leads to greater contact between the mother and other group members, which, in turn, particularly for low-ranking females, leads to increased stress and greater energy demands (Altmann, 1980), all of which would render a female more susceptible to diseases caused by bacteria and viruses. It is also possible that mothers are in a negative energy balance (see above) and may accumulate particular nutritional deficiencies as well, perhaps resulting directly in starvation or, more likely, nutritional diseases.

Interbirth Intervals

Infants affect not only their mothers' survival chances but also their reproductive success, in particular through the direct effect they have on future reproduction (see Altmann et al., 1978, and references therein; Nicolson, 1982). Mothers of surviving Amboseli infants experience approximately 12 mo of postpartum amenorrhea and then take an average of 4 cycles to conceive, whereas infant death results in resumption of cycles within 1 mo of the death and conception after only 1 or 2 cycles on the average ($P < 0.02$; see Altmann et al., 1978, for details).

Delay of future reproduction may be accomplished through the direct hormonal effects of sucking (Konner and Worthman, 1980) or through nutritional and other stress, perhaps including weight loss (Frisch and Revelle, 1971). This is the one area in which evidence is most available for at least the broad outlines of apparent reproductive costs (see Jain et al., 1970; Saxena, 1977; Altmann et al., 1978; Lee, 1980). Yet this information is still inadequate for determining the effects of differences in amounts of maternal care of infants at various developmental stages on the timing of subsequent reproduction in wild primates. In Amboseli there is no correlation between the amount of time an infant spent on the nipple and the length of its mother's interbirth interval (unpublished data). We are currently investigating the effects of interbout suckling intervals on amenorrhea and subsequent conception.

Investment Options

The question then arises, Could baboon mothers increase their reproductive effort either through greater investment in the current infant or through initiating a new pregnancy at an earlier time? The form of maternal investment most often considered is nutritional, through lactation, and the most obvious form of parent-offspring conflict is thought to be nutritional weaning. Initially a mother provides all of her infant's energetic needs, primarily through lactation. Is she being selfish not to continue to do so for an infant that is older than 5 or 6 mo of age? Consider a baboon mother who ordinarily spends over 55% of her time feeding, approximately 23% walking, and 20% resting or engaged in grooming interactions when her infant is about 5 mo old. At this stage her infant spends 30% of its time in contact with her. This is the age at which pronounced dramatic tantrums occur. It is 6 mo before most mothers resume cycling and 9–12 mo before most become pregnant again. It is most unlikely that the mother of even a 6–9-mo-old could provide enough care for survival of the infant and also support the strains of a new pregnancy. Therefore, let us assume that a mother "decides" to provide additional care to her current infant by nursing it more. In order to do so she will have to spend more time feeding. Yet the sum of the mother's resting, grooming, and walking time will be decreased if the time spent in the one remaining activity, feeding, is increased. Furthermore, walking time is primarily determined by the movements of the whole social group during its day route rather than being subject to appreciable individual variability. Moreover, additional food acquisition requires, if anything, more, not less, walking. Thus it is the mother's resting and grooming that will suffer. To the extent that these activities usually are beneficial, there will probably be a loss to both mother and infant.

Deleterious changes in allocations of time, energy, or attention, if they affect life history at all, are likely to have immediate consequences in terms of reduced chances of survival for the mother or her current infant. That is, in the absence of evidence to the contrary, it seems more reasonable to assume that the greatest effects on biological fitness of an act appear shortly afterward and that in general they are usually a nonincreasing function of the time since the act occurred. Costs to the mother are therefore likely to involve either immediate reduction in the chance of surviving or diminished ability to provide care for the current infant—for example, reduced feeding efficiency, reduced attentiveness to predators, or inability to keep up with the group. In this context it is important to remember that the current infant's survival is entirely contingent on its mother's survival: in all cases of maternal death in baboons, her infant under a year of age has also disappeared.

Alternatively, if a mother cannot increase reproductive effort, would it be advantageous for her to redistribute it? It has been suggested that mothers could improve their reproductive success if they reduced care of the current infant, for example by weaning their infants earlier (e.g., Trivers, 1974), thereby reducing the length of postpartum amenorrhea and investing their energy in a subsequent pregnancy. Although this has certainly been the case among humans in developing countries in recent years (see Hauser and Duncan, 1959; Lee, 1980), such a result is dependent on (1) infant mortality rates not being appreciably increased by early weaning, and (2) the mortality risk of childbirth and early stages of infant care being low. Weaning foods and even a semblance of modern medicine are probably sufficient to satisfy these conditions in developing countries. It is unlikely, however, that these conditions prevailed until recently for humans, or that they are satisfied in most animal habitats, including that of the Amboseli baboons. However, Nicolson (1982) provides data suggesting that such a situation exists for the anubis baboons living on the Cole ranch in Gilgil, Kenya, where maternal mortality is low, as is infant mortality from sources other than from falling in the ranch water tanks.

Finally, any weighing of the advantages of investment in a current infant versus diverting effort toward future reproduction would be expected to involve evaluation of the reproductive value of the two. Because mortality rates are high throughout the first year of life, an infant who has already survived the first 6 mo has a higher reproductive value than does one who has not, thus further favoring investment in the current offspring.

In sum, it is quite possible that in the absence of ecological factors favoring early weaning, females obtain higher reproductive success by engaging in fairly long periods of infant care than they would by reducing the period spent caring for a current infant in order to reduce the interbirth interval.

The demographic problems that face most human and nonhuman primate mothers are in many ways similar, in that high rates of infant mortality and appreciable maternal risk have probably been characteristic of most human and other primate populations. Ecological and social factors that affect mortality will be important aspects of motherhood and infancy and major determinants of reproductive strategies. The task of delineating and quantifying these relationships has just begun.

ACKNOWLEDGMENTS

I am greatly appreciative of the foresight and hospitality of the people and government of Kenya and the cooperation of the past and present wardens of Amboseli National Park, D. Sindyo, J. Kioko, and B. Oguya, who have helped make the long-term Amboseli research project possible. Financial support has been provided by the American people through grant MH 19617 from the U.S. Public Health Service. I have been greatly assisted in data analysis and manuscript preparation by Rebecca McCauley and Joan Luft. My colleagues Stuart Altmann and Glenn Hausfater have shared with me the maintenance of the long-term study and the many years of spirited and critical exchanges that have contributed immeasurably to the projects each of us has done.

Figure 1 and parts of the text on the model of maternal feeding time are reprinted from *Baboon Mothers and Infants*, by Jeanne Altmann, Cambridge, Mass.: Harvard University Press, Copyright © 1980 by the President and Fellows of Harvard College. Courtesy of Harvard University Press.

DISCUSSION FOLLOWING DR. ALTMANN'S PRESENTATION

Question: With regard to infanticide, several years ago you and Stuart Altmann brought this topic up at one of the Midwestern Animal Behavior Society meetings. When you were talking about the probability of mortality for the mother and the infant being so related, does it appear that the infant is stressing the mother to the point that she is declining in some way? If so, are there data to suggest that she will kill or abandon her young?

Answer: Certainly, mothers are sometimes incompetent, but what is more surprising is how often mothers with infants that are sure to die keep investing in them. This seems to be one of the real puzzles. Mothers who reject their infants earlier give less maternal care, but they don't seem to be the ones in poorer condition or of lower rank. I think these parents push their infants to be independent earlier.

Question: Have you looked at the distribution of infant mortality? Is it evenly distributed or does it peak within the first days?

Answer: It is much more even than I expected. Certainly, we do have a fairly high stillbirth rate, and it is possible that some of the ones called stillbirths are extremely early mortality and that we are missing those in the first few hours or half day. There is virtually no miscarriage, or natural abortion, which is odd. During the first few days, and even the first month, there doesn't seem to be a higher mortality period. If anything, Stuart thinks that one of the really high mortality times is the weaning stage, which is common in some other mammals. So, it is not the first six or eight months but what happens just afterward. It may be balancing mortality from some early causes, but mortality from others is only felt a little later. The danger of mortality from direct social causes is probably in the first month or so, and I think that is why you see a whole complex of behaviors that mothers have to prevent other females from inflicting mortality.

Question: Does the initiation of lactation within the first few days after birth seem to be a weak point?

Answer: It doesn't seem to be. The infants are on the nipple right away. The only time I thought that happened was with a mother who had carried her infant upside down and backward for the first day, and the infant just didn't get on the nipple. As far as I could tell, the female was probably lactating, but the infant died several weeks later. It probably has helped a lot that most primates carry their infants in a position to be on the nipple so that the amount of nipple stimulation initiates lactation. Suckling is very asymmetric, and whether that has anything to do with one breast producing more milk than the other or not, we don't know. But the infants do have a favorite side, so maybe this indicates some problem of milk failure, but there is also a safety factor in having two breasts.

Question: My question also relates to infant mortality. There is some laboratory evidence in rodents that if you take a pregnant rat and fast it for a couple of days prior to parturition, the rate of fetal lung maturity increases. Do you have any evidence to indicate that female baboons, in the days just prior to parturition, voluntarily limit their food intake or alter the nature of their intake? If they do, does this in some way tie in to the death of neonates, which would be due to some of them not having adequately developed lungs?

Answer: First of all, we haven't had any data on lung immaturity or on mothers' actual food intake. Actually there is one set of behavioral data that we could look at that hasn't been looked at in that way. In my observations of mothers and infants, I only had, or have, time budget data, and there is certainly nothing striking there. Mothers seem to be resting more and more just before parturition. But there is nothing sufficiently clear-cut by way of a sharp change in time budget that ever allows me to tell when parturition is going to occur. In fact, I can tell better when a female is going to give birth by when she got pregnant than by watching her bottom day in and day out before she gives birth. There is no dramatic change in the feeding.

Question: It is apparently related to maternal hypoglycemia, or so this researcher thinks. I question whether it has any relevance in nature.

Answer: I don't know; they seem to just keep stuffing their mouths, except that you get the sense that they are dragging more, as any primate in late pregnancy seems to do.

Question: In your slides of the histories of the females, I noticed that there is a fair degree of asynchrony of when females become pregnant and when they gave birth. I have two questions about that. At Amboseli there is also a fair degree of seasonality. Do the kinds of subtle costs that you are talking about seem to vary as a function of when the females actually give birth? The second part is, in birds, at least, there seems to be a fair amount of evidence that females will go through an energy storage cycle during the period of breeding activities. For example, during egg production and just after egg production, they lose a lot of weight and then gradually build it back up. Do you see any pattern like that, or can you interpret any of the behaviors that you saw that were in any way related to the seasonal cycles in Amboseli?

Answer: First of all, yes, there is considerable asynchrony but also moderate seasonality of births, and there may be a seasonality of mortality. Not only are somewhat more infants born at the time that I think best, and that is in terms of later food availability, but also more of those infants survive than infants born at other times. The time that females most readily get pregnant is in a rainy season when food seems more abundant.

Question: In terms of looking between seasons, when do the animals spend less time just feeding?

Answer: They spend less time feeding in December, January, and February than at other times. An interesting aspect is that females who get pregnant in December, January, or February have their babies at a poor time. But around six months of age, when it was looking like the stress on mothers would be greatest, also corresponds to the time when infants finally have the dexterity for both climbing trees and getting foods. That's back to the good time of the year—not only a good time in terms of overall food availability, but also a good time for what I call "weaning food," the really easy foods to eat. I think that the reason there isn't more seasonality in baboons is that you get a type of time gamble. Consider when an infant dies: a lot of the lack of seasonality in the birth comes from mothers whose previous infant dies, or from females who were about to experience their first pregnancy. What it seems is that maybe those females are in better condition than are mothers with surviving infants who will still be providing some care for those infants part way through the subsequent pregnancy. That's one possibility in terms of your saying that females differ in condition at different times.

Another thing is this trade-off that probably has reduced the pressure for seasonality by the fact that some "off-season" infants survive. I think that probably by a lot of behavioral maneuvers the best coordinated mother-infant pairs can reduce stress and get through a bad season. Also, there is enough year-to-year variability in the rains to confound synchronization, but we do have this moderate seasonality imposed on what in many ways looks like an asynchronization.

I have a wild thought with respect to mothers building up their own weight and so on. It occurred to me that mothers could manipulate their own older infants. If a mother, because of the season or because it was a bad year, would be better off in a fairly low weight condition with an opportunity to build up weight for her next pregnancy, she could delay the onset of the next pregnancy. Then a mother could impose on her infant a patterning of suckling, which many people would interpret as the infant delaying the mother's reproduction to its own advantage. If weight gain and fat storage are crucial to whether a mother survives a pregnancy or not, she may be more concerned with surviving that pregnancy than getting pregnant a little sooner. It's the males who may be pushing her to get pregnant a little sooner; it may be for this former infant and her own best interest to delay slightly. She could manipulate that older infant by a temporal pattern of the sucking—not providing it with any more nutrition, and therefore allowing more fat buildup for the next pregnancy.

Question: I have a question concerning first infants. You mentioned that the infants of young mothers were more likely to die but that the mothers would survive. Can you turn that around and talk about the infants of less experienced mothers? There is a hypothesis that floats around that first infants are for "practice," and are more or less expendable in terms of both the population and the mother's own reproduction. These are the ones that are born at the wrong time of the year and so forth. Can you look at first infants compared to all others?

Answer: Yes, and certainly laboratory and field studies from lots of mammals do show higher mortality for the first infant. In baboons, where so much is invested in each infant, I think that the argument that the first infant is expendable, or that the first pregnancy really doesn't hold as much weight, is wrong, and from an evolutionary perspective, infants produced early in life are more, not *less*, important. I think that probably one of the key features is that the mothers usually haven't completed their own growth, and that may be as important as any "practice." They have lots of opportunity to practice lots of mothering, and that is always argued as why the juveniles are interested in infants and so on. And even the evidence for that is really weak. Certainly, the total "clunky" behavior is only seen in the first couple days with first mothers who seem to vary about as much as the other mothers. It's taken a long time to demonstrate that there is any higher mortality. With the first-infant mortality, one year it would be one way and another year it would be another way; it seems that some females have bad reproductive chances, as we know from humans. They had troubles with their first infant, but then they also had trouble with a sequence of others. There is probably something there. But like sex differences, it is being damped by more important factors, I think.

Question: Does the male contribute any energetics in the form of bringing anything to the female or taking charge of the young for a short time?

Answer: In some of the small New World primates, particularly those such as the marmosets and the tamarins that produce twins, you have an extensive system of sharing. What happens is that the male and the previous siblings asssume virtually all of the carrying and the other energetic costs, transferring the infants to the mother just for feeding. In most other primates there is little of that. Males provide some protection against conspecifics. The evidence that they provide any direct protection for mothers from predators is still anecdotal and qualitative for most species. But against conspecifics I found, for example, that baboon mothers that were restrictive, low ranking, and fearful would let their infants explore more when the male was nearby. This is primarily a passive association, but sometimes the males threaten conspecifics who are being hard on the infant. An older infant will stay near the male and get scraps of food—not that the scraps are handed over by the male, but that the male tolerates the infant much closer than he does other group members. But these instances are specific to infants; males will tolerate the infant nearby, and there are always some scraps from an adult feeding. It is these scraps of food that the infants cannot obtain by themselves. An infant also gets such scraps from its mother by this type of feeding as it gets older. Again, this food is not handed to them, but the scraps are around and the infants are tolerated. In general, if males can command a better food source and an infant has a close association with that male, the infant then has priority of access to a food source it would not otherwise have. A good bit of it is passive, but the outcome is helpful, and in the youngest orphan I have observed, the male's aid seemed to have a critical effect. So in the second year of life, if an infant is orphaned, you will see the infant start sleeping with the male to obtain warmth and protection at night.

LITERATURE CITED

Abegglen, J.-J. 1976. On socialization in hamadryas baboons. Ph.D. thesis, University of Zurich.

Altmann, J. 1980. Baboon mothers and infants. Harvard University Press, Cambridge.

Altmann, J., S. A. Altmann, and G. Hausfater. 1978. Primate infant's effects on mother's future reproduction. Science 201:1028–30.

Altmann, J., S. A. Altmann, and G. Hausfater. 1981. Physical maturation and age estimates of yellow babooms, *Papio cynocephalus*, in Amboseli National Park, Kenya. Amer. J. Primatol. 1:389–99.

Altmann, J., S. A. Altmann, G. Hausfater, and S. A. McCuskey. 1977. Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. Primates 18:315–30.

Altmann, S. A., and J. Altmann. 1970. Baboon ecology: African field research. University of Chicago Press, Chicago.

Altmann, S. A., and S. S. Wagner. 1978. A general model of optimal diet. Rec. Adv. Primatol. 4:407–14.

Blackburn, M. W., and D. H. Calloway. 1976. Energy expenditure and consumption of mature, pregnant, and lactating women. J. Amer. Diet. Assoc. 69:29–37.

Bramblett, C. A. 1969. Non-metric skeletal age changes in the Darajani baboon. Amer. J. Phys. Anthrop. 30:161–72.

Buss, D. H., and O. M. Reed. 1970. Lactation of baboons fed a low protein maintenance diet. Lab. Anim. Care 26:709–12.

Caughley, G. 1966. Mortality patterns in animals. Ecology 47:906–18.

Cohen, J. 1972. Aping monkeys with mathematics.*In* R. H. Tuttle (ed.), Functional and evolutionary biology of primates. Aldine-Atherton, Chicago.

DeVore, I., and K. R. Hall. 1965. Baboon ecology. *In* I. DeVore (ed.), Primate behavior: field studies of monkeys and apes. Holt, Rinehart & Winston, New York.

Eisenberg, J. 1975. Phylogeny, behavior, and ecology in the mammalia. *In* P. Luckett and F. Szalay (eds.), Phylogeny of the primates. Plenum Press, New York.

Fossey, D. 1979. Development of the mountain gorilla (*Gorilla gorilla beringei*): the first thirty-six months. *In* D. A. Hamburg and E. R. McCown (eds.), The great apes. Benjamin/Cummings, Menlo Park, Calif.

Frisch, R. E., and Revelle, R. 1971. Height and weight at menarche and a hypothesis of menarche. Arch. Dis. Childh. 46:695.

Gould, S. J. 1975. Allometry in primates, with emphasis on scaling and evolution of the brain. *In* G. Szalay (ed.), Approaches to primate paleobiology. Karger, Basel.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theoret. Biol. 31:295–311.

Hamilton, W. J., R. E. Buskirk, and W. H. Buskirk. 1978. Omnivory and utilization of food resources by chacma baboons, *Papio ursinus*. Amer. Natur. 112:911–24.

Harcourt, A. H., D. Fossey, K. J. Stewart, and D. P. Watts. 1980. Reproduction in wild gorillas and some comparisons with chimpanzees. *In* R. V. Short and B. J. Weir (eds.), The great apes of Africa, pp. 59–70. Journals of Reproduction and Fertility, Ltd., Cambridge, England.

Hauser, P. M., and O. D. Duncan. 1959. The study of population. University of Chicago Press, Chicago.

Hausfater, G. 1976. Predatory behavior of yellow baboons. Behaviour 56:44–68.

Hendrickx, A. G. 1971. Embryology of the baboon. University of Chicago Press, Chicago.

Hytten, F. E., and R. I. Leitch. 1964. The physiology of human pregnancy. Blackwell, Oxford.

Jain, A. K., T. C. Hsu, R. Freedman, and M. C. Chang. 1970. Demographic aspects of lactation and postpartum amenorrhea. Demography 7:255–71.

Kahneman, D. 1973. Attention and effort. Prentice-Hall, Englewood Cliffs, N.J.

Keiding, N. 1977. Statistical comments on Cohen's application of a simple stochastic population model to natural primate troops. Amer. Natur. 111:1211–19.

Kleiber, M. 1961. The fire of life. John Wiley & Sons, New York.

Klein, D. 1978. The diet and reproductive cycle of a population of vervet monkeys (*Ceropithecus aethiops*). Ph.D. thesis, New York University.

Konner, M., and C. Worthman. 1980. Nursing frequency, gonadal function, and birth spacing among !Kung hunter-gatherers. Science 207:788–91.

Lancaster, J. B., and R. B. Lee. 1965. The annual reproductive cycle in monkeys and apes. *In* I. DeVore (ed.), Primate behavior: field studies of monkeys and apes. Holt, Rinehart & Winston, New York.

Lee, R. B. 1980. Lactation, ovulation, infanticide, and women's work: a study of hunter-gatherer population regulation. *In* M. N. Cohen, R. S. Malpass, and H. G. Klein (eds.), Biosocial mechanisms of population regulation. Yale University Press, New Haven.

Mori, A. 1979. Analysis of population changes by measurement of body weight in the Koshima troop of Japanese monkeys. Primates 20:371–98.

Naismith, D. J., and C. D. Ritchie. 1975. The effect of breast-feeding and artificial feeding on body weights, skinfold measurements, and food intakes of 42 primiparous women. Proc. Nutr. Soc. 34:116A–117A.

Nicolson, N. 1982. Weaning and the development of independence in olive baboons. Ph.D. thesis, Harvard University.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Anim. Behav. 27:1–36.

Post, D. 1978. Feeding and ranging behavior of the yellow baboon (*Papio cynocephalus*). Ph.D. thesis, Yale University.

Post, D. G. 1981. Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. Anim. Behav. 29:357–74.

Post, D. G., G. Hausfater, and S. A. McCuskey. 1980. Feeding behavior in yellow baboons (*Papio cynocephalus*): relationship to age, gender, and dominance rank. Folia Primatol. 34:170–95.

Pusey, A. 1980. Inbreeding avoidance in chimpanzees. Anim. Behav. 28:543–52.

Ransom, T. W., and T. E. Rowell. 1972. Early social development of feral baboons. *In* F. E. Poirier (ed.), Primate socialization. Random House, New York.

Riopelle, H. J., C. W. Hill, S.-C. Li, R. H. Wolf, H. R. Seibold, and J. L. Smith. 1975. Protein deprivation in primates. IV. Pregnant rhesus monkeys. Amer. J. Clin. Nutr. 28:20–28.

Saxena, P. C. 1977. Breast-feeding: its effects on post-partum amenorrhea. Social Biol. 24:45–51.

Schmidt-Nielsen, K. 1977. Problems of scaling: locomotion and physiological correlates. *In* T. J. Pedley (ed.), Scale effects in animal locomotion. Academic Press, London.

Snow, C. C. 1967. The physical growth and development of the open-land baboon, *Papio doguera*. Ph.D. thesis, University of Arizona.

Trivers. R. L. 1974. Parent-offspring conflict. Amer. Zool. 14:249–64.

Whichelow, M. J. 1976. Success and failure of breast-feeding in relation to energy intake. Proc. Metr. Soc. 35:62A.

Wolfe L. D., and M. J. S. Noyes. 1981. Reproductive senescence among female Japanese macaques (*Macaca fuscata fuscata*). J. Mammal. 62(4):698–705.

CATHLEEN R. COX

Reproductive Behavior of Subadult Elephant Seals: The Cost of Breeding

4

Most studies of intrasexual competition among males tend to focus on the characteristics and behavior of the males who appear to be most successful in gaining access to females. Generally these are the most dominant males in a hierarchically organized species, or those best able to secure and defend resources in a territorially organized species. In both cases success is likely to be strongly and positively correlated with age (Scott, 1942; Robel, 1967; Geist, 1971; Kruijt et al., 1972; Le Boeuf, 1972, 1974; Wiley, 1973; Campanella and Wolf, 1974; Lill, 1976; Trivers, 1976; Gibson and Guinness, 1980) or with size (Evans, 1936; Kitchen, 1974; Potter et al., 1976; Dittus, 1977; Howard, 1978, 1980; Clutton-Brock et al., 1979; Davies and Halliday, 1979; Packer, 1979; Borgia, 1980, 1982; Thornhill, 1980), and possibly with experience (Kruijt et al., 1972; Trivers, 1972; Payne and Payne, 1977; Howard, 1978). When just a few males are doing the majority of the breeding, the obvious corollary is that the majority of males are breeding infrequently, or not at all. These males tend to be young, small, and inexperienced.

It has been argued that in species where dominance or the ability to accrue resources is age-related, each male may be expected to sire approximately the same number of offspring over the course of his lifetime (Rowell, 1974; Hausfater, 1975). That is, although a male may

Department of Biology, University of California at Los Angeles, Los Angeles, California 90024, and Section of Ornithology, Los Angeles County Museum of Natural History, Los Angeles, California 90007

be unsuccessful when he is young and low ranking, his social dominance and consequently his reproductive success will increase as he ages. However, the fact is that in many species annual mortality is substantial, and it may be inferred that very few young males survive long enough to achieve high social status and correspondingly high reproductive success. For example, consider the following estimates of annual male mortality in some polygynous species: prairie chickens, 39–77% (Hamerstrom and Hamerstrom, 1973); sage grouse, 52% (Wiley, 1973); red-winged blackbirds, 38% (Laux, 1970); indigo birds, 45–52% (Payne and Payne, 1977); Uinta ground squirrels, 58% (Slade and Balph, 1974); marmots, 47% (Johns and Armitage, 1979); reindeer, 35% (Leader-Williams, 1980); caribou, 27% (Miller, 1974); Alaskan fur seals, 38% (Johnson, 1968); northern elephant seals, 45% (Le Boeuf, 1974); Weddell seals, 50% (Siniff et al., 1977). In such species the majority of males must either breed as social subordinates or risk not breeding at all. To the extent that males who do attempt to breed might be expected to leave more offspring than males who do not, we might expect to observe subordinate males attempting to breed, regardless of the obstacles they may face. Indeed, descriptions of alternate reproductive strategies employed by small or subordinate males are beginning to appear in the literature with increasing frequency (see references cited in text discussion, below).

The northern elephant seal, *Mirounga angustirostris*, is typical of a polygynous species in which male-male competition is intense and breeding is monopolized by just a few large and dominant males. Le Boeuf's (1974) long-term studies on Año Nuevo Island (ANI) have shown that 86–97% of males born may die prior to reaching the age of 6 or 7 (puberty occurs at age 5–6), and thereafter annual mortality averages 45%. These high mortality rates might be expected to favor early breeding activity in males, as outlined above. Still, it is clear that young males account for a small proportion of the copulations observed each year (Le Boeuf, 1974). In this paper I report on the reproductive activities of young male elephant seals and the factors that act to limit the success of these activities.

It is well known that dominant elephant seal bulls attempt to prevent lower ranking males from breeding by interrupting their mounts by threats or direct attack (Bartholomew, 1952; Le Boeuf and Peterson, 1969; Le Boeuf, 1974). However, this is likely to be only one of several variables that exert a negative influence upon the reproductive success of subordinate males. The questions to be explored in this paper include the following: What proportion of subordinate males attempt to mate? How frequent and how persistent are their attempts to mate?

How adept are they in their attempts to mate? What proportion of their mounts fail to lead to intromission as a result of mounting nonestrous females, lack of persistence, or interruption by more dominant males? In addition, I describe the ways in which the behavior of successful young males differs from that of unsuccessful young males; and I present data concerning the cost of attempting to breed for young males as compared to fully developed, mature males.

ELEPHANT SEAL BIOLOGY

Elephant seals show marked sexual dimorphism in appearance and behavior. Females reach sexual maturity at 2–3 years of age, males at 5–6 years. Both males and females continue to develop past puberty. Females simply get larger; males increase even more dramatically in size and, in addition, the tissue surrounding the ventral and lateral portion of the neck becomes rugose and cornified and the proboscis becomes progressively enlarged. Males between the ages of 5 and 8 are referred to as subadults. By age 9 all males are fully grown and are considered to be adults. Maximum life span for both sexes is 14 years; however, few animals survive to that age.

Each year between December and March northern elephant seals congregate on offshore islands along the coast of California and Mexico where breeding and parturition take place. Females are highly gregarious and gather on the beaches in pods or "harems." Each female remains continuously on land for approximately 34 days, and during the last 3–5 days of this period she copulates several times with one or more males.

Direct competition among males for access to females is intense. The form and function of male-male agonistic encounters have been detailed elsewhere (Bartholomew, 1952; Le Boeuf and Peterson, 1969; Le Boeuf, 1972, 1974; Sandegren, 1976; Cox, 1981), so only the points most salient to the present paper will be summarized here.

The outcome of agonistic interactions among pairs of males is the establishment of a linear dominance hierarchy. The highest ranking males reside within the female pod and attempt to keep other males from approaching females. Reproductive success of males, as indicated by frequency of copulation, is highly correlated with social rank. Only one-third or fewer of the males present during the breeding season copulate; the single highest ranking bull accounts for 12–100% of all the copulations observed in any given year, depending on beach topography and harem size (Le Boeuf, 1972, 1974). The highest ranking males are always adults, and most breeding is accomplished by fully adult males. The majority of nonbreeding males are subadults—young, sexually mature males who are not yet fully grown.

The number and percentage of subadult males who mate are variable but generally low relative to the number and percentage of adults who mate. On ANI the percentage of subadults mating has ranged from 0 (1968) to 36% (1972). In 1973, the base year in which the data reported in this paper were calculated, subadult males represented 71% of the male population but obtained only 11% of the copulations recorded. Older subadults were more successful than younger subadults. Males between 8 and 9 years of age obtained 7% of the copulations, males between the ages of 6 and 7 obtained 4% of the copulations, and 5-year-old males obtained less than 0.5% of all copulations. In short, the reproductive success of young males tends to be quite low.

METHODS

Observations were made during the 1973, 1974, and 1975 breeding seasons on Año Nuevo Island, San Mateo County, California. The bulk of the quantitative data reported below was gathered during the 1973 season, when females formed dense aggregations on two beaches; one was a large, sandy point (Point Beach) where 426 females congregated, the other was a small cove (Cove Beach) where 34 females resided. In addition, two females gave birth and bred in the middle of the island in an area referred to as the Saddle. On Cove Beach breeding was completely monopolized by a single male, and the Saddle was similarly dominated by one male. Thus, the only opportunity for the majority of males to breed was on Point Beach.

One hundred eighty males visited the island during the 1973 season. All males who were present for at least one week (n = 161) were permanently tagged and individually bleach marked (see Le Boeuf and Peterson, 1969). At the time of marking each male was assigned to one of four age categories based on comparison of overall size and development of secondary sexual characteristics with that of tagged known-age animals. These four categories were as follows:

Subadult male 2 (SA2): 5 years of age, about 11 feet long, nose just beginning to develop; a pubertal male.

Subadult male 3 (SA3): 6–7 years of age, about 12 feet long, neck shield beginning to develop and nose just beginning to dangle; a male who underwent puberty in the previous year.

Subadult male 4 (SA4): 7–8 years of age, about 13 feet long, incompletely developed neck shield and nose; well past puberty, but not quite fully grown.

Adult male (AD): 8–14+ years of age, 14–16 feet long with fully developed neck shield and a dangling proboscis approximately one foot long; a fully grown male.

Insofar as the ability to dominate others was size-related, a male's age category also indicated his relative status in the dominance hierarchy: all adults were dominant to SA4s, SA3s, and SA2s; all SA4s were dominant to SA3s and SA2s; all SA3s were dominant to SA2s.

During the 1973 breeding season observation commenced 14 December 1972 and continued through 3 March 1973. All observations of sexual and aggressive behavior were made during daylight hours from a blind overlooking Point Beach. The beach was scanned from left to right until a sexual interaction was described, and then the scan was continued from the point at which it had been interrupted. At least eight hours of behavioral data were recorded daily.

Each time a male was observed to mount a female the individuals involved and the outcome of the attempted copulation were noted. When feasible, durations of mounts and copulations were recorded. *Mount* was operationally defined as the pattern of behavior in which the male approached a female, placed his foreflipper over her back, and brought his genital region to bear against that of the female. A mount could end in only one of three ways: self-termination, interruption, or copulation. *Self-termination* refers to cases in which the male dismounted of his own accord, prior to obtaining intromission. *Interruption* refers to cases in which the mounting male was displaced prior to achieving intromission by threat or attack by a more dominant male. *Copulation* refers to cases in which the mounting male achieved intromission, an outcome readily identified by the male's lumbar flexure (Le Boeuf, 1972).

Three times daily on each of thirty days the entire eight-acre island was surveyed and the location of each male and his proximity to females were recorded. If a male was located on Point Beach, his position was categorized as being either inside or outside of the harem. Specifically, males intersected by or within the boundaries of an imaginary line drawn around the females on the periphery of the harem were considered to be inside the harem, and all other males were considered to be outside.

During the 1974 and 1975 breeding seasons the tags of all males landing on ANI were read. Le Boeuf's observations have shown that males always return to breed on the islands on which they first bred. Therefore, if a male present in 1973 was not subsequently seen on ANI, he was considered to have died. For a detailed statement of the rationale for this inference see Le Boeuf (1974).

RESULTS

Attempts to Mate

Sexually active males. Table 1 shows the number of males present and the percentage of males in each age category that were observed to mount at least once during the breeding season. These males will subsequently be referred to as sexually active males. Only 57% of SA2s were observed to mount during the course of the breeding season as compared with 87% of the adult males. In short, the likelihood of a male initiating sexual activity increased considerably with age.

Even considering only the sexually active males, adult males still accounted for a disproportionate share of the copulations observed. Sexually active adults represented only 36% of the total number of sexually active males, but they obtained 89% of all copulations.

Frequency and success of mounts. Table 1 also shows mean number of mounts, mean number of copulations, and mean ratio of copulations to mounts for sexually active males within each age category. On the average, adult males mounted more than twice as frequently as SA4s, six times as frequently as SA3s, and twenty-four times as frequently as SA2s. Having mounted, adults were more than three times as likely to

TABLE 1

SEXUAL ACTIVITY OF MALES VARYING IN AGE

Age Category	No. Active Males / No. Males Present	No. Mounts	No. Copulations	Copulations / Mounts
Adult	40/46 = 87%	55.47 ± 60.53	27.67 ± 39.84	0.36 ± 0.24
		1–233	0–123	0.0–0.66
SA4	21/28 = 75%	18.10 ± 24.76	3.71 ± 6.94	0.10 ± 0.14
		1–98	0–28	0.0–0.39
SA3	38/64 = 59%	8.82 ± 13.80	1.34 ± 4.20	0.06 ± 0.18
		1–66	0–20	0.0–0.30
SA2	13/23 = 57%	2.27 ± 1.58	0.07 ± 0.27	0.07 ± 0.27
		1–6	0–1	0.0–1.00
Statistics				
F		11.26	10.14	16.96
d.f.		3,108	3,108	3,108
P		< 0.01	< 0.01	< 0.01

NOTE: Only observations on sexually active males (those observed to mount at least once) are included in computation of means, standard deviations, and ranges.

obtain intromission as males in any of the younger age categories. Thus, both the number of mounts attempted and the likelihood that a mount would culminate in copulation increased with age.

Reproductive efforts and deterrence from breeding. It is possible that the low frequency of mounting by subadults resulted simply from lack of effort to gain proximity to females, or from deterrence as a result of actual or implied threats of older males who were situated in the harem and whose presence prevented subordinate males from entering. It is difficult to distinguish lack of effort from deterrence; however, the spatial distribution of males on ANI may be analyzed in order to explore this point. At any instant in time individual males in the vicinity of ANI could be found in one of three types of localities: on nonbreeding beaches, on the periphery of breeding beaches, or in female harems. Obviously, gaining entrance to a harem was a prerequisite for mounting.

I interpret time spent on nonbreeding beaches as "time-out," or time during which a male was not making any attempt to breed, and time spent on the breeding beaches (either on the periphery or in the harem) as time during which the male's efforts were directed toward gaining access to females. Table 2 shows the frequency with which sexually

TABLE 2

PROXIMITY TO FEMALES AND FREQUENCY OF MOUNTING BY SEXUALLY ACTIVE MALES

Age Category	No. Observations on Point Beach	No. Obs. in Harem / No. Obs. on Point	No. of Mounts / No. Obs. in Harem
Adult	34.30 ± 26.93 (n = 40)	0.74 ± 0.35 (n = 40)	1.76 ± 0.97 (n = 36)
SA4	14.76 ± 14.69 (n = 21)	0.56 ± 0.37 (n = 19)	1.70 ± 0.73 (n = 17)
SA3	9.95 ± 11.21 (n = 38)	0.44 ± 0.38 (n = 36)	1.86 ± 2.01 (n = 31)
SA2	4.07 ± 4.28 (n = 13)	0.18 ± 0.31 (n = 10)	2.56 ± 2.32 (n = 5)
Statistics			
F	15.82	8.48	0.48
d.f.	3,108	3,108	3,85
P	< 0.01	< 0.01	ns

NOTE: The maximum number of times a male could be observed on Point Beach was 90.

active males were sighted on the main breeding beach as a function of age (each male's location was noted 3 times daily on each of 30 days, yielding a total of 90 possible sightings for each individual). Time spent on breeding beaches increased with age, and adults were seen on the breeding beaches with considerably greater frequency than were subadults. Assuming that time spent on breeding beaches is proportional to breeding effort, the data show that breeding effort increased markedly with age, and adult males exerted more than twice the effort of males in any of the subadult age categories.

I believe that once a male landed on a breeding beach, only deterrence (subtle or direct threats) by more dominant males prevented the male from actually entering the harem. The younger, and correspondingly the lower in social rank, a male, the greater the number of potentially more dominant males present, and the greater the likelihood of being threatened or attacked when attempting to enter the harem. Table 2 shows for each age category the ratio of time spent in the harem to total time on the breeding beach. Clearly subadult males on the breeding beach spent a relatively small proportion of their time actually among the females, and I infer that this was a result of deterrence by the actual or implied threats of more dominant males residing in the harem.[1] Thus, it appears that both lack of effort and greater deterrence acted to minimize the amount of time spent by young males in close proximity to females.

Frequency of mounting given proximity to females. Means of ratios obtained by dividing the total number of mounts a male attempted by the number of times he was observed in the harem are shown for each age category in the last column of table 2. Given proximity to females there were no significant differences among males in the four age categories with respect to likelihood of mounting. Indeed, visual inspection suggests that the younger males were more likely rather than less likely to mount under these conditions.

In summary, the lower reproductive success of subadult males resulted directly from fewer attempts to mate as judged by the low frequency with which subadult males were observed to mount females, and also from less success in those attempts. Low frequency of mounting was associated with fewer attempts to gain access to females—that is, less time spent on the breeding beaches—and also with greater deterrence by the relatively large number of more dominant males who were positioned in close proximity to females. However, given success in gaining entrance to the harem, males of all ages were equally likely to attempt mating.

Factors Limiting the Success of Mating Attempts

Mate selection. The vast majority of mounts observed during the three breeding seasons were directed to females; however, many of these females were clearly not in estrus—that is, they were pregnant, in the process of giving birth, or accompanied by very young pups. Lack of external signs of estrus make it difficult for the human observer to be certain of a female's reproductive condition. However, it was clear that from the time of the arrival of the first female on ANI until the time of the first copulation, none of the females present were estrous. In 1973 the first copulation occurred on 20 January, and it may be inferred that all attempts to copulate prior to that date were directed to nonestrous females.

The percentages of mounts that occurred prior to 20 January are shown in table 3. Assuming that at least some mounts occurring subsequent to this date were also directed to nonestrous females, these figures are conservative estimates of the frequency with which nonestrous females were mounted.[2] Only 5% of the mounts by adults occurred prior to the availability of estrous females, whereas more than 40% of the mounts by SA2s took place at this time.

Mounting females who cannot be impregnated is certainly a significant factor in limiting the success of efforts to mate by subadult males. We can only speculate as to why young males direct so much of their energy to this apparently futile activity. Perhaps the subadult male is unable to distinguish between estrous and nonestrous females. Indeed, it may be through the process of random mounting that young males learn to make this discrimination. Or, such mounts may be a form of practice that enables young males to improve their sexual skills and

TABLE 3

MOUNTS PRIOR TO THE DAY ON WHICH THE FIRST FEMALE CAME INTO ESTRUS

Age Category	Total No. Mounts	No. Mounts before 1/20/73	Percentage of All Mounts before 1/20/73
Adult	2219	96	4
SA4	378	29	8*
SA3	335	63	19*†
SA2	34	14	41*†‡

*Percentage significantly greater ($P < 0.01$) than that observed for adult males.
†Percentage significantly greater ($P < 0.01$) than that observed for SA4 males.
‡Percentage significantly greater ($P < 0.01$) than that observed for SA3 males.

thus increase the probability of gaining intromission at some later age. In addition, dominant males may direct more of their efforts toward preventing subordinates from mounting estrous rather than nonestrous females. In this case, subadult males would have a greater opportunity to approach and mount females in the latter category. Data that support the latter idea can be found in a previous study (Cox, 1981). Protested mounts to estrous females were more likely to be interrupted by direct threat than protested mounts to nonestrous females.

Persistence, skill, and speed. Table 4 shows that during the period when estrous females were present, young males were more likely than adults to terminate their mounts voluntarily prior to obtaining intromission. These self-terminated mounts were *not* preceded by any obvious threats from neighboring males. Furthermore, table 4 also shows that subadult males did not persevere in their attempts to copulate as long as adult males did. The average duration of self-terminated mounts by subadults was half the duration of self-terminated mounts by adult males. Put more descriptively, the young males appeared to be timid in their attempts to copulate.

Younger males also appeared less skillful in their attempts to copulate than adult males. Even when females responded receptively, young males were occasionally observed to have extreme difficulty in

TABLE 4

PERCENTAGE AND DURATION OF SELF-TERMINATED MOUNTS AND DURATION OF MOUNTS THAT LED TO COPULATION

Age Category	Percentage of Self-Terminated Mounts	Duration of Self-Terminated Mounts (seconds)	Duration of Mounts Leading to Copulation (seconds)
Adult	36 (n = 2123)	50.01 ± 69.39 (n = 183)	116.21 ± 85.88 (n = 185)
SA4	38 (n = 349)	17.03 ± 21.00 (n = 32)	143.20 ± 105.97 (n = 15)
SA3	45* (n = 272)	18.00 ± 24.68 (n = 13)	233.60 ± 340.50 (n = 5)
SA2	47 (n = 20)	....	....
Statistics			
F		4.84	3.79
d.f.		2,225	2,195
P		< 0.01	< 0.01

*Percentage significantly greater ($P < 0.01$) than that observed for adult and SA4 males.

gaining intromission. In this situation the subadult would repeatedly bite the passive female or slam his forequarters against her neck. This would in turn lead the female to struggle, which would attract the attention of a neighboring male who would then threaten and displace the subadult.

When subadult males did succeed in gaining intromission, it took them longer than adult males to do so. Table 4 shows the mean durations of successful mounts, that is, those that were followed by copulations. It took SA2s more than twice as long as adults to gain intromission.

Interrupted mounts. The single most obvious factor that interfered with the reproductive efforts of young males was direct interruption of mounts by the threats or attacks of more dominant males. Table 5 shows the number of mounts that occurred during the period in which estrous females were present and indicates the percentage that were interrupted. Nearly one-half of the mounts attempted by subadults were interrupted, as compared to less than one-fourth of those attempted by adult males.

TABLE 5

INTERRUPTED MOUNTS DURING
PERIOD WHEN ESTROUS FEMALES WERE PRESENT

Age Category	Number of Mounts	Percentage Interrupted
Adult	2123	23
SA4	349	43*
SA3	272	46*
SA2	20	50*

*Percentage significantly greater ($P < 0.01$) than that observed for adult males.

Distribution of Outcomes of Mounts

In table 6 the number of mounts by males in each age category and their outcomes are shown. Mounts that did not lead to copulation were unsuccessful either because they took place prior to the availability of estrous females, they were interrupted by more dominant males, or the mounting males voluntarily terminated their mounts prior to obtaining intromission. For SA2s poor timing of reproductive efforts—that is, attempting to mate prior to the availability of estrous females—was the

TABLE 6

OUTCOMES OF ALL MOUNTS OBSERVED

Age Category	Total No. of Mounts	% Successful Copulations	% Unsuccessful Mounts		
			Before 1/20/73	Interrupted	Self-Terminated
Adult	2219	43	4	22	31
SA4	378	21	8	40	31
SA3	335	10	19	37	34
SA2	34	3	41	29	27

most significant factor limiting the success of copulatory attempts. For SA3s and SA4s interruption by more dominant males had the greatest negative influence on the success of copulatory attempts. In contrast, lack of persistence—that is, terminating mounts prior to obtaining intromission—was the single most important factor limiting the success of copulatory attempts by adult males. Self-termination by adult males often occurred when the adult moved off to threaten a subordinate male who was attempting to mate.

To summarize, the generally low reproductive success of subadult males resulted in part from lack of reproductive effort (less time spent on the breeding beaches); in part from inept and misdirected efforts (mounts to nonestrous females and aggression toward apparently receptive females); and in part from obstruction of reproductive efforts by more dominant males (implied or actual threats and attacks). Generally, as males increasd in age, their reproductive efforts increased and the timing of their reproductive efforts improved. However, interruption by still more dominant males came to play an increasingly important role in limiting the success of their attempts to breed. Only the most dominant males were able to breed without interruption.

Successful Strategies of Subadult Males

Despite the generally low reproductive success of most subadult males, a few subadults were at least moderately successful in breeding. Although their copulatory success was considerably less than that of the most successful adult males, it was considerably greater than that of many middle to low ranking adult males to whom the subadults were subordinate.

For example, consider the 1973 breeding season in which the population of marked males on ANI consisted of 46 adults, 28 SA4s, 64 SA3s, and 23 SA2s. The most successful adult copulated 123 times. The most successful SA4 copulated 28 times, a score lower than that of 11 adults, but higher than that of the remaining 35 adults. The most successful SA3 copulated 20 times, a score less than that of 14 adults and 1 SA3, but greater than that of 32 adults and 27 SA4s. The only successful SA2 copulated once, faring better than 10 adults, 17 SA4s, and 59 SA3s.

In order to copulate repeatedly each of these successful subadults had to be persistent, at least moderately skillful, *and* able to avoid interruption by more dominant males. Threat vocalizations by females play a very important role in attracting the attention of neighboring males, making interruption of a mount by a more dominant male likely (Cox and Le Boeuf, 1977). Thus, in theory, a subordinate male could reduce the chances of interruption if he behaved so as to minimize the likelihood of female protest, or if he was the most dominant male within range of the female's vocalization. The behavior of the most successful subadult males with respect to these possibilities is described below.

SA2s. Only one SA2, "Boss," bred during 1973. This male simply appears to have been lucky. He was sighted on the breeding beach on just one occasion. On this day he approached the harem in a location where the nearest male was occupied in copulation and was facing away from the periphery. The subadult moved directly toward, and mounted, a female on the periphery who did not protest, and he intromitted quietly and quickly. He was not detected by any other males and successfully completed the copulation. He was not observed to attempt any other mounts. No SA2s bred during the 1974 or 1975 seasons.

SA3s. In 1973 the most successful SA3, "IM6," was a very persistent male who spent considerable time in the harem. IM6 was sighted in the harem on 60 occasions during a season in which 5.8 was the average number of times individual SA3s were observed in the harem. IM6 frequently mounted females but immediately deferred whenever threatened by another male. He was able to maintain his location in the midst of the harem by behaving in a very subordinate fashion, literally keeping a low profile, and never himself threatening other males. IM6's atypical but highly adaptive behavior was to move deeper into the harem rather than away from it when avoiding the threats of a more dominant male. As soon as the threatening male tired of the chase, IM6 attempted another mating. A similar pattern of behavior was shown by "Thor," the most successful SA3 during the 1974 season.

During the 1975 season the most successful SA3 was "BMW," also a very persistent subadult who spent considerable time in the harem and was able to remain there as a result of his immediate deference to more dominant males. BMW's unique pattern of behavior was to mount females in rapid succession, immediately moving on as soon as a female began to protest, persisting in his mount (and usually copulating) only when the female did not protest.

SA4s. The most successful SA4 during the 1973 season was "XO," a male who behaved in a fashion similar to that of higher ranking adult males. That is, he both mounted frequently and continued in his mounting activities despite the protests of females. Unlike the young males just described, XO was aggressive in his attempts to prevent other males from breeding, frequently challenging lower ranking males who attempted to enter the harem. Because he was lower ranking than most of the other males in the harem and at the same time highly conspicuous due to his size and the protests of females, he was frequently detected and chased out of the harem. His copulatory success resulted from his repeated entries into the harem and persistence in mounting. XO was the only SA4 to manifest such persistence, and he obtained nearly twice the number of copulations as the next most successful SA4.

Another relatively successful SA4 in 1973 was "Honk," with 15 copulations. Honk rarely entered the harem but spent a great deal of time along the periphery of the breeding beach. There he encountered females leaving the harem and heading toward sea on their last day of estrus. Because he was of higher rank than most of the other males residing nearby, Honk was able to copulate without interruption in several such instances.

A third successful pattern of behavior shown by SA4s was to colonize new breeding grounds where few females were present and competition from more dominant males was absent (Le Boeuf et al., 1974; Le Boeuf and Panken, 1977).

Cost of Reproductive Efforts

During the course of a breeding season males do not feed for upwards of two months, and they expend considerable energy threatening subordinate males and avoiding the threats of more dominant males. At the close of the season many of the males appear to be in poor condition and considerable weight loss is evident. Information on elephant seal mortality further suggests that the costs of male reproductive efforts are high: (1) male mortality is greater than female mortality, (2) rate of mortality increases once males reach sexual maturity, and (3) male mortality is greater during the five-month period immediately following the breeding season than during the subsequent five-month period preceding the next breeding season (Le Boeuf, personal communication).

In order to test specifically the hypothesis that reproductive efforts were costly to the males observed in the study reported here, males in each age category were divided into two equal-sized groups, which will be referred to as "most effort" and "least effort" on the basis of the number of days they were sighted on Point Beach during the peak of the 1973 breeding season (20 January through 24 February). The number of days spent on Point Beach may be taken as an index of the relative effort expended in reproductive activities. Table 7 shows the mean number of days spent on the breeding beach by the males in each group and age category. The proportion and percentage of males in each group who survived to the following breeding season are also shown. Interestingly, efforts expended in reproductive activities appear to be particularly costly only for young subadult males, SA2s and SA3s. For males in these two categories, the probability of males in the "least effort" group surviving for another year was twice that of males in the "most effort" group. Unfortunately, in an observational study such as this one, it is not possible to assign individuals randomly to "effort treatments," so the analysis is of an ex post facto nature. However, the data do suggest that the cost of reproductive activity is greater for young males than for older ones. This point takes on even greater meaning when the number of days on Point Beach is compared across age categories. Even though young males invested considerably less effort in reproductive activity, as inferred from the amount of time

TABLE 7

Cost of Attempting to Breed

Age Category	Most Days on Point Beach		Least Days on Point Beach		z	P*
	$\bar{x}$ Days	Survival Rate to 1974	$\bar{x}$ Days	Survival Rate to 1974		
Adult	30.0 ± 2.4	10/23 = 43.5%	11.5 ± 7.8	8/23 = 34.8%	0.61	0.77
SA4	22.7 ± 5.7	7/14 = 50.0%	4.4 ± 3.4	8/14 = 57.1%	0.37	0.36
SA3	13.5 ± 5.0	7/32 = 21.9%	2.7 ± 2.3	13/32 = 40.6%	1.62	0.05
SA2	5.6 ± 2.5	2/12 = 16.7%	0.3 ± 0.5	4/11 = 36.4%	1.07	0.14

Number of days spent on Point Beach in 1973 and proportion and percentage of males that survived to 1974. Males in each age category assigned to groups on the basis of the number of days they were observed on Point Beach during the peak of the breeding season (20 January through 28 February).

*One-tailed test.

spent on Point Beach, they were more likely to suffer mortality than adult males.

DISCUSSION

In the introduction to this paper it was generally argued that when annual mortality is high, males who attempt to breed just as soon as they reach sexual maturity would be expected to leave more offspring than those who forego breeding and risk mortality prior to the subsequent breeding season. That is, certainty of some small amount of reproductive success may outweigh the greater reproductive success that would be possible at a later age when the low probability of surviving to such an age is considered.

However, the observations on ANI show that one of the primary causes of low reproductive success among subadult male elephant seals is lack of reproductive effort. At first consideration the data appear paradoxical. The apparent resolution to this paradox may be found in the data on actual mortality for males who spent the most time on the breeding beach. Reproductive effort appears to be more costly for subadult than for adult males. Whatever the mechanism that precipitates the death of young males, it is clear that subadult males who expend more reproductive effort than other members of their age cohort are less likely to survive to breed as adults. This suggests that the males who do survive long enough to become alpha males probably did not attempt to breed as subadults, and Le Boeuf's observations (1974) are consistent with this inference. Thus the behavioral strategy of most young males appears to be one of delaying investment in reproductive efforts until a time when the costs may be less and the payoffs may be greater, a pattern consistent with the theoretical formulations of life history parameters proposed by Williams (1966) and Gadgil and Bossert (1970).

Insofar as most males invest little effort in reproductive activities during their subadult years, it is not clear why they even haul out on the rookeries during the breeding season. Perhaps these peripheral males are gaining important experience, through observational learning, or through their limited contact with females, which may facilitate their reproductive success in subsequent years.

Despite the relatively high costs of reproductive efforts, a few young males in each age category do spend a moderate amount of time on the main breeding beach and experience a small degree of reproductive success. This observation suggests the possibility of a behavioral polymorphism in timing of reproductive effort, that is, an alternate reproductive strategy.[3]

Alternate reproductive strategies have now been described for a wide range of invertebrate and vertebrate species. Small or subordinate males may avoid direct combat with more dominant males but can sometimes gain access to females through nonaggressive means. In some species these males may lack secondary sexual characteristics that are present in the more aggressive males (Gadgil, 1972; Hamilton, 1979; Otte and Stayman, 1979; Eberhard, 1980). Alternate strategies that have been reported include: "pseudofemale" appearance and behavior, which may permit a small male to gain easy entrance to the territory of a more dominant male and access to females in the territory (Morris, 1952; Barlow, 1967; van den Assem, 1967; Rowland, 1979; Dominey, 1980); sneaking up to, or streaking past, a female attracted by a more dominant male (Constantz, 1975; Warner et al., 1975; Kodric-Brown, 1977; Eberhard, 1980); adopting submissive postures and sitting quietly within the territory of an advertising male, occasionally intercepting females advancing toward the territory holder (Hogan-Warburg, 1966; van Rhijn, 1973; Alcock, Eickwort, and Eickwort, 1977; Cade, 1979); or opportunistically assuming control of the territory as soon as it is vacated by the original owner (Emlen, 1976; Wells, 1977; Howard, 1978; Fellers, 1979). Other strategies may include variation in where males search for females (Barrows, 1976; Alcock, Jones, and Buchmann, 1977; Hamilton, 1979) or in the timing of dispersal and subsequent mating attempts (Bekoff, 1977; Eberhard, 1980). In all of these cases the seasonal reproductive success associated with the alternate strategy appears to be less than that associated with that of more dominant or territorial males. Indeed, in initial reports of such behavior, particularly pseudofemale behavior, the small male was perceived as acting in an aberrant and maladaptive fashion (Morris, 1952). However, more recent analyses have suggested that the alternate patterns of behavior are less costly than those of territorial or dominant males. Thus, males adopting the alternate strategy might be expected to live longer and thus breed in a greater number of years. Over the course of a lifetime such a male may produce a number of offspring equivalent to that of the territorial or dominant type males. In this case alternate strategies may be seen as balanced behavioral polymorphisms resulting from opposing selective forces (Gadgil, 1972).

In order to determine if alternate strategies are equally adaptive, it is necessary to have population data on the number of males showing various patterns of behavior, annual reproductive success associated with each pattern, and annual mortality associated with each pattern. Though descriptions of alternate strategies have become commonplace, quantitative data of the type just described have proved difficult to obtain. The data in this paper represent one such preliminary attempt.

In northern elephant seals, attempting to breed at an early age, which entails gaining access to females by behaving unaggressively and avoiding detection and threats by more dominant males, could be viewed as an alternate strategy. However, early breeding attempts appear to be more costly than delayed reproductive activity, and few young males adopt this pattern of behavior. Attempting to breed at an early age may be relatively costly for males of other species as well (Wooler and Coulson, 1977; Ainley and DeMaster, 1980). Thus, on the surface it does not appear that such early breeding attempts are necessarily adaptive. However, it is possible that such a strategy could be maintained in a population if the individuals employing it produced several offspring who also bred at an early age and if annual mortality for the population was substantial. In such a case the individual alternate strategists would be producing fewer offspring per season and per lifetime, but a greater number of these individuals would survive long enough to reproduce. If such were the case, the payoff of the alternate strategy would rise with any increase in annual mortality of males who delayed reproduction, even though annual mortality of such males remained lower than that of the early breeders.

At present there is no empirical data to support the idea that age of first reproduction is transmitted from parent to offspring in elephant seals, and the long lifespan of the elephant seal makes it unlikely that such data will be forthcoming in the near future. Commercial harvesting of several different pinniped populations has been followed by a decrease in the age at which males first attempt to reproduce (Carrick et al., 1962; Chapman, 1964; Sergeant, 1966, 1973). In at least one of these populations (Sergeant, 1966), only pups were culled, suggesting that age of first reproduction may be variable within individuals. Thus age at which a seal first attempts breeding may be conditional, depending on availability of resources and degree of competition. There is little evidence to support the notion that variability in age at which individual seals first attempt to breed is the result of opposing selective forces acting on distinct genotypes.

At this time, determining the adaptiveness of alternative strategies appears to be a complex task. It is necessary to measure costs and benefits for various patterns of behavior in extant populations. However, such costs and benefits may be expected to vary for individuals of different ages, with population structure (see Davies and Halliday, 1979; Borgia, 1980; Warner and Hoffman, 1980) and number of individuals adopting each strategy (Parker, 1978), and with variation in factors affecting annual mortality such as food supply, parasite transmission, and predator population. In order to determine if variations in patterns of reproductive behavior represent balanced polymorphisms or are simply ways in which some males attempt to "make the best of a bad job" (Dawkins, 1980), it will be necessary to work out expected costs and benefits for each of these parameters. Herein lies a promising avenue for future research.

SUMMARY

The generally low reproductive success of subadult males is the product of several factors. For SA2s and SA3s one of the primary causes underlying lack of reproductive success is lack of reproductive effort. A great many males in this age range simply failed to compete for access to females. Forty percent of these males never approached or attempted to mount a female, and the 60% who did attempt to do so mounted infrequently—fewer than nine times over a period of three months. Moreover, these males did not persist in their attempts as long as older males did. In short, males between the ages of 5 and 7 tended to invest minimal energy in reproductive activities. The energy that SA2s and SA3s did invest was not allocated as efficiently as that of older males. These young males sometimes behaved aggressively toward passive or receptive females, they took longer to achieve intromission, and they were generally less skillful. They were also more likely to mount nonestrous females.

SA4s mounted more frequently, persistently, and skillfully than the younger subadults. However, a subadult of any age who persisted in mounting an estrous female was still more likely to be interrupted by a higher ranking male than to succeed in copulation. Indeed, the most likely outcome of mounts by SA4s was interruption.

Despite these numerous barriers to reproductive success, some males in each age category succeeded in copulating. Those who were most successful displayed strategies that were quite distinct from those of high ranking males (except in the case of XO). Successful subadult males tended to avoid physical confrontations with more dominant males, either by breeding in peripheral or newly colonized areas where older males did not compete for females or by residing unobtrusively in large harems where they seldom behaved aggressively toward other males and always responded submissively when threatened. However, the costs of early breeding attempts were substantial. When members of each age category were divided into two groups on the basis of reproductive effort, it was found that the more active SA2 and SA3 males were more than twice as likely to suffer mortality in the following year as the less active males in these age categories.

ACKNOWLEDGMENTS

I thank Burney J. Le Boeuf for stimulating and facilitating this research, and Robert A. Pugsley for his comments on the manuscript. The field work was supported in part by a Stanford University Fellowship to the author and by NSF Grant BMS 74-01363AO2 to B. J. Le Boeuf. Subsequent analysis of the data was funded by NIMH Grant T32 MH14280 to the Animal Behavior/Biopsychology Training Program of the American Museum of Natural History and the City University of New York.

DISCUSSION FOLLOWING DR. COX'S PRESENTATION

Question: In the brook trout observed at the University of California research station, the sneakers have always been a curiosity to me and I think of your subadult seal [IM6]. Apparently you didn't have the opportunity of witnessing his comeback and maintaining his sneak strategy or his low profile.

Answer: He changed when he came back, but he was more aggressive, and he died the second year.

Question: I was curious because in the brook trout the sneakers sometimes obtained a population. Is there any information in the literature regarding their success in subsequent years? The other question or the second relative point: you never mentioned any kind of nocturnal activity, and I assume that there is none. Are they sleeping?

Answer: Last question first. Yes, there is nocturnal activity. We have gone out with starlight scopes and looked, and it appears that what is going on is the same. Now granted, no one stays up all night every night and watches, but it appears that the same kind of behavior is going on. Yes, they are almost as active at night as they are in the day. In terms of the fish, I have a reference to bluegill sunfish in which sneaker males that looked like females would enter into a territory. By aging them, we found it to be a dimorphic strategy; sneakers were not young males.

Question: I assume, more or less, that all copulations create equally. Is that in fact true? Are females copulated more than once, and if so, is there any bias associated with age or dominance characteristics? And is the best time to copulate predictable to the male?

Answer: These are data that are difficult to determine because we can't go cutting up elephant seals. Yes, elephant seals do copulate more than three to five times. We don't know which one of the males has paternity. The best guess is that the first one does, because in the southern species they've done dissections following the first copulation and have found that the eggs already appear to be fertilized. My guess is that the first one is the most likely, and, in fact, that the more dominant males are more likely to meet the female first. They don't seem to show much interest in passive females who resist their attempts.

Question: I'm puzzled by the very high mortalities that you seem to be getting, which don't seem to be congruent with the remarkable research in elephant seals. It occurred to me that as much as you're working on one island, you can distinguish between mortality and an animal who goes somewhere else in subsequent years. Is it possible to interpret your data saying that an animal who is successful is more likely to return in subsequent years than one who didn't copulate, who is more likely to go off and establish one of these new breeding areas?

Answer: I would be worried about that, too, if all the animals on all the islands weren't color tagged. In fact, the seven or eight different breeding islands have animals tagged with particular colors, so you don't have to know the numbers to know where they are from. Le Boeuf periodically visits the different islands during the breeding season to see if there are any green-tagged males who are from Año Nuevo there. It is a very rare thing to see that; it seems that if they don't return they are never seen again.

Question: I am curious to know about the role of female choice in these matings. Could you elaborate on that? It seems that the female has the opportunity to get rid of a male.

Answer: That is in fact what females most frequently do. I have a whole paper on this. To summarize briefly, people used to see elephant seals as not having any choice because animals who where passive seemed to be receptive, and the ones who were resistant were seen to be uninterested. When I marked and followed females over the course of an entire breeding season it turned out that this wasn't the whole story: 100% of all mounts to females who had not copulated (I'm referring to those that were not yet estrous) were totally protested by females for the entire duration of the mount, but after the first copulation, the most frequent responses of females to subsequent males is still total protest, and that happens about 79% of the time. The effect of female protest is to attract the attention of neighboring males. If there is a more dominant male, he will chase off the mounting male. Although he doesn't necessarily mount the female at that time, his action does prevent the subordinate male from doing so. On the other hand, a dominant male just mates in spite of female protesting. This seems to be sort of a "nonthinking" way of treating all the males the same and letting them fight among themselves. Although this is a gross generalization, there are also some interesting data on one female who did not protest. On the very last day of estrus, after three to five days of breeding, chances are that the females are already inseminated. It may just be the easiest way to get from the center of the beach to the periphery—instead of attracting other males who are going to keep you there, just quietly leave and give in to anything that may happen along the way. Another thing that happens is that females always protest subadult males, unless it is the very last day of estrus. Typically, they protest dismount by subadults as well. Twenty percent of all mounts that aren't protested are mounts that are made by adult males. I was interested in the question of whether they are discriminating males on the basis of their size or something behavioral. I looked at the activity of the males through the three-minute period prior to mounting, and at the female's response. It turns out that if a male has just threatened and dominated another male, the female is less likely to protest than if the male has just been lying there or if he has been dominated by another male, and this works for either subadult or adult males.

Question: A question about adult males mounting nonestrous females: you said that at least 40% of all mounts by adult males were directed to nonestrous females. From the point of view of ultimate causation of behavior, it seems rather incompetent for males to be wasting their efforts. Are you sure these were all nonestrous females? And if they were, can you see any selective pressure for giving one's attention so selectively?

Answer: I am sure that they hadn't copulated before. We don't have any physiological way of determining estrus. I know that they had been there for 28 days, had been mounted many times but had never been copulated with, and then, suddenly, after the first copulation, I'm calling them in estrus. They copulate one-quarter of the times that they are mounted after that.

Question: Why would adult males want to mount nonestrous females?

Answer: One of the frustrating things about elephant seals is that there are so many things that you can't answer. That's why I'm studying birds now! Maybe the first copulation is the most important one, the one most likely to inseminate the female. Perhaps what these high ranking males are doing is ensuring that they are going to be first. They keep trying and eventually the female will come into estrus and the male will then be in the right place at the right time!

1. The effect of rank on access to females is well illustrated by incidental observations made during the 1975 breeding season. During the peak of the 1975 season the alpha position was held for a brief period by each of four males in succession. Each of these males remained in the harem after losing the alpha position, and their mounting behavior after falling in rank can be compared to that observed when holding the alpha position. The frequency with which these males mounted females decreased significantly with the fall in social rank ($\bar{x}$ for alpha position = 6.43 mounts per day, $\bar{x}$ for lower rank = 2.83 mounts per day; $t = 12.11$; d.f. = 3; $P < 0.01$). It is unlikely that the motivation of these males to mount varied during this brief time period, and the decrease in frequency of mounting with the fall in rank may be attributed to deterrence by more dominant males.

2. Precise quantitative data on mounts to estrous versus nonestrous females are available for a ten-day period during the peak of the 1975 breeding season when 25 females in a discrete harem on the west side of Point Beach were marked and observed continuously. Even during this period, when many estrous females were present, males of all ages were observed to mount nonestrous females. Subadult males directed a greater proportion of their mounts to nonestrous females than did adult males. The percentages of mounts directed to nonestrous females by SA3s, SA4s, and adults were 57, 63, and 44 respectively.

These data were also analyzed to test the hypothesis that males did not discriminate between estrous and nonestrous females. Using the binomial test for differences between expected and observed proportions, the differences between the proportions of mounts to estrous females that would be expected to occur by chance and the proportions that were observed were converted to z scores. For each age category the scores were summed over a ten-day period and means and standard deviations were computed. Using t tests, each of the three means was then tested for differences from the means expected by chance, and the three means were tested for difference from each other. Only the scores of adult males were significantly different from zero ($P < 0.01$), and adult males scored significantly higher than SA3s and SA4s ($P < 0.01$ in both cases). There were no significant differences between SA3s and SA4s. It may be concluded that only adult males mounted estrous females more frequently than would be expected by chance.

3. *Strategy* is used here to refer to a pattern of behavior that is the product of an underlying biological substrate and is subject to natural selection. Cognition on the part of the animal displaying the particular pattern need not be invoked.

LITERATURE CITED

Ainley, D. G., and D. P. DeMaster. 1980. Survival and mortality in a population of Adélie penguins. Ecology 61:522–30.

Alcock, J., G. C. Eickwort, and K. R. Eickwort. 1977. The reproductive behavior of *Anthidium maculosum* (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. Behav. Ecol. Sociobiol. 2:385–96.

Alcock, J., C. E. Jones, and S. L. Buchmann. 1977. Male mating strategies in the bee *Centris pallida* Fox (Anthophoridae: Hymenoptera). Amer. Natur. 111:145–55.

Barlow, G. W. 1967. Social behavior of a South American leaf fish, *Polycentrus schomburgkii*, with an account of recurring pseudo-female behavior. Amer. Midl. Natur. 78:215–34.

Barrows, E. M. 1976. Mating behavior in halictine bees (Hymenoptera: Halictidae): II. Microterritorial and patrolling behavior of males of *Lasioglossum rohweri*. Z. Tierpsychol. 40:377–89.

Bartholomew, G. A. 1952. Reproductive and social behavior of the northern elephant seal. Univ. Calif. Pub. Zool. 47:369–742.

Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. Amer. Natur. 111:715–32.

Borgia, G. 1980. Sexual competition in *Scatophaga stercoraria*: size- and density-related changes in male ability to capture females. Behaviour 75:185–205.

Borgia, G. 1982. Experimental changes in resource structure and male density: size-related differences in mating success among male *Scatophaga stercoraria*. Evolution 36:307–15.

Cade, W. 1979. The evolution of alternative male reproductive strategies in field crickets. *In* M. S. Blum and N. A. Blum (eds.), Reproductive competition and sexual selection, pp. 343–79. Academic Press, New York.

Campanella, P. J., and L. L. Wolf. 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera) I: *Plathemis lydia* (Drury). Behaviour 51:49–87.

Carrick, R., S. E. Csordas, and S. E. Ingham. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.) IV. Breeding and development. C.S.I.R.O. Wildl. Res. 7:161–97.

Chapman, D. G. 1964. A critical study of fur seal population estimates. Fish. Bull. Fis. Wildl. Serv. U.S. 63:657–69.

Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guinness. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). Anim. Behav. 27:211–25.

Constantz, G. D. 1975. Behavioral ecology of mating in the male gila topminnow, *Poeciliopsis occidentalis* (Cyprinodontiformes: Poeciliidae). Ecology 56:966–73.

Cox, C. R. 1981. Agonistic encounters among male elephant seals: frequency, context, and the role of female preference. Amer. Zool. 21:197–209.

Cox, C. R., and B. J. Le Boeuf. 1977. Female incitation of male competition: a mechanism in sexual selection. Amer. Natur. 111:317–35.

Davies, N. B., and T. R. Halliday. 1979. Competitive mate searching in male common toads, *Bufo bufo*. Anim. Behav. 27:1253–67.

Dawkins, R. 1980. Good strategy or evolutionarily stable strategy? *In* G. W. Barlow and J. Silverberg (eds.), Sociobiology: beyond nature/nurture?, pp. 331–67. Westview Press, Boulder.

Dittus, W. 1977. The social regulation of population density and age sex distribution in the toque monkey. Behaviour 63:281–322.

Dominey, W. J. 1980. Female mimicry in male bluegill sunfish—a genetic polymorphism? Nature 284:546–48.

Eberhard, W. G. 1980. Horned beetles. Sci. Amer. 242:166–82.

Emlen, S. T. 1976. Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1:283–313.

Evans, L. T. 1936. A study of a social hierarchy in the lizard, *Anolis carolinensis*. J. Genet. Psychol. 48:88–110.

Fellers, G. M. 1979. Aggression, territoriality, and mating behaviour in North American treefrogs. Anim. Behav. 27:107–19.

Gadgil, M. 1972. Male dimorphism as a consequence of sexual selection. Amer. Natur. 106:574–80.

Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. Amer. Natur. 104:1–24.

Geist, V. 1971. Mountain sheep. University of Chicago Press, Chicago.

Gibson, R. M., and F. E. Guinness. 1980. Differential reproduction among red deer (*Cervus elaphus*) stags on Rhum. J. Anim. Ecol. 49:199–208.

Hamerstrom, F., and F. Hamerstrom. 1973. The prairie chicken in Wisconsin. Techn. Bull. 64. Dept. of Nat. Res. Madison, Wis.

Hamilton, W. D. 1979. Wingless and fighting males in fig wasps and other insects. *In* M. S. Blum and N. A. Blum (eds.), Reproductive competition and sexual selection, pp. 167–219. Academic Press, New York.

Hausfater, G. 1975. Dominance and reproduction in baboons (*Papio cynocephalus*). Contrib. Primatol. 7:1–150.

Hogan-Warburg, J. A. 1966. Social behavior of the ruff, *Philomachus pugnax* (1.) Ardea 54:109–229.

Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850–71.

Howard, R. D. 1980. Mating behavior and mating success in woodfrogs, *Rana sylvatica*. Anim. Behav. 28:705–16.

Johns, D. W., and K. B. Armitage. 1979. Behavioral ecology of alpine yellow-bellied marmots. Behav. Ecol. Sociobiol. 5:133–57.

Johnson, A. M. 1968. Annual mortality of territorial male fur seals and its management significance. J. Wildl. Manag. 32:94–99.

Kitchen, D. W. 1974. Social behavior and ecology of the pronghorn. Wildl. Monogr. 38:1–96.

Kodric-Brown, A. 1977. Reproductive success and the evolution of breeding territories in pupfish (*Cyprinodon*). Evolution 31:750–66.

Kruijt, J. P., G. J. de Vos, and I. Bossema. 1972. The arena system of black grouse. Proc. XVth Int. Orn. Congr. The Hague 1970. pp. 399–423.

Laux, L. J. 1970. Non-breeding surplus and population structure of the red-winged blackbird (*Agelaius phoeniceus*). Ph.D. diss., University of Michigan.

Leader-Williams, N. 1980. Population dynamics and mortality of reindeer introduced to South Georgia. J. Wildl. Manag. 44:640–57.

Le Boeuf, B. J. 1972. Sexual behavior in the northern elephant seal, *Mirounga angustirostris*. Behaviour 41:1–26.

Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. Amer. Zool. 14:163–76.

Le Boeuf, B. J., D. G. Ainley, and T. J. Lewis. 1974. Elephant seals on the Farallones: population structure of an incipient breeding colony. J. Mammal. 55:370–85.

Le Boeuf, B. J., and K. J. Panken. 1977. Elephant seals breeding on the mainland in California. Proc. Calif. Acad. Sci. 41:267–80.

Le Boeuf, B. J., and R. S. Peterson. 1969. Social status and mating activity in elephant seals. Science 163:91–93.

Lill, A. 1976. Lek behavior in the golden-headed manakin, *Pipra erythrocephala* in Trinidad (West Indies). Advances in Ethology 18:1–84.

Miller, F. L. 1974. Biology of the Kaminuriak population of barren ground caribou. Part 2: Dentition as an indicator of age and sex; composition and socialisation of the population. Can. Wildl. Serv. Rep. Ser. 31:1–88.

Morris, D. 1952. Homosexuality in the ten-spined stickleback. Behaviour 4:233–61.

Otte, D., and K. Stayman. 1979. Beetle horns: some patterns in functional morphology. *In* M. S. Blum and N. A. Blum (eds.), Reproductive competition and sexual selection, pp. 259–92. Academic Press, New York.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Anim. Behav. 27:1–36.

Parker, G. A. 1978. Searching for mates. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural ecology: an evolutionary approach, pp. 214–44. Blackwell Scientific Publications, Oxford.

Payne, R. B., and K. Payne. 1977. Social organization and mating success in local song populations of village indigobirds, *Vidua chalybeata*. Z. Tierpsychol. 45:113–73.

Potter, D. A., D. L. Wrensch, and D. E. Johnston. 1976. Aggression and mating success in male spider mites. Science 193:160–61.

Robel, R. J. 1967. Significance of booming grounds of greater prairie chickens. Proc. Amer. Phil. Soc. 111:109–14.

Rowell, T. E. 1974. The concept of social dominance. Behav. Biol. 11:131–54.

Rowland, W. J. 1979. Stealing fertilizations in the fourspine stickleback, *Apeltes Quadracus*. Amer. Natur. 113:602–4.

Sandegren, F. E. 1976. Agonistic behavior in the male northern elephant seal. Behaviour 70:136–58.

Scott, J. W. 1942. Mating behavior of the sage grouse. Auk 59:477–98.

Sergeant, D. E. 1966. Reproductive rates of harp seals, *Pagophilus groenlandicus* (Erxleben). J. Fish. Res. Bd. Can. 23:757–66.

Sergeant, D. E. 1973. Environment and reproduction in seals. J. Reprod. Fert., Suppl. 19:555–61.

Siniff, D. B., D. P. DeMaster, and R. J. Hofman. 1977. An analysis of the dynamics of a Weddell seal population. Ecol. Monogr. 47:319–35.

Slade, N. A., and D. F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology 55:989–1003.

Thornhill, R. 1980. Sexual selection within mating swarms of the lovebug, *Plecia nearctica* (Diptera: Bibionidae). Anim. Behav. 28:405–12.

Trivers, R. L. 1972. Parental investment and sexual selection. *In* B. G. Campbell (ed.), Sexual selection and the descent of man. Aldine, Chicago.

Trivers, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:253–69.

van den Assem, J. 1967. Territory in the three-spined stickleback *Gasterosteus aculeatus* L. Behaviour, Suppl. 16:1–164.

van Rhijn, J. G. 1973. Behavioural dimorphism in male ruffs, *Philomachus pugnax* (L.). Behaviour 47:153–227.

Warner, R. R., and S. G. Hoffman. 1980. Population density and the economics of territorial defense in a coral reef fish. Ecology 61:772–80.

Warner, R. R., D. R. Robertson, and E. G. Leigh. 1975. Sex change and sexual selection. Science 190:633–38.

Wells, K. D. 1977. Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology 58:750–62.

Wiley, R. H. 1973. Territoriality and non-random mating in sage grouse, *Centrocerus urophasianus*. Anim. Behav. Monogr. 6:87–169.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Amer. Natur. 100:687–92.

Wooler, R. D., and J. C. Coulson. 1977. Factors affecting the age of first breeding of the kittiwake *Rissa tridactyla*. Ibis 119:339–49.

C. ROBERT FELDMETH

Costs of Aggression in Trout and Pupfish

5

The fact that dominant male fishes often aggressively defend discrete breeding territories is well established (Greenberg, 1947; Barlow, 1961; Clarke, 1970; Kodric-Brown, 1978). It would appear that considerable time and energy is expended threatening, biting, and chasing fish and other aquatic animals from reproductive territories. Also, nonreproductive territories are vigorously defended by many fish species (Gerking, 1953; Jenkins, 1969). In protecting a territory, be it a holding position in a stream, a spawning area, eggs, or even young, considerable energy must certainly be expended. The purpose of this paper is to examine the territorial behaviors of two very different fishes and attempt to estimate the metabolic costs involved in their aggressive activities.

The two fish chosen for these behavioral energetic studies were pupfish (*Cyprinodon*) and trout (*Salmo*). The former live in certain clear pools and shallow streams in western North America, in relatively warm-water habitats, and the latter occur in the cold streams and lakes normally found in mountainous areas.

Trout in a stream situation establish a dominance hierarchy that tends to space out fish to allow sufficient area for both feeding and cover. Few aggressive interactions are observed, and these are usually resolved in a few seconds. Trout thus do not appear to be strongly territorial.

To provide a contrast for energetic comparison, the pupfish was chosen. The small, brightly colored reproductive males of this genus

Joint Science Department, The Claremont Colleges, Claremont, California 91711

often continually defend the same territory for many days (Soltz, 1974; Kodric-Brown, 1978).

EXPERIMENTAL APPROACH

To determine the energetic or metabolic costs of the aggressive behaviors involved in territory defense for these two fishes, metabolic rates were measured in the laboratory using circulating water tunnel respirometers (Eriksen and Feldmeth, 1967; Feldmeth and Jenkins, 1973). Metabolic measurements were made for fish of various sizes, swimming in water of various water temperatures over a wide range of current velocities.

Next, swimming speed and the amount of time spent in swimming behavior as opposed to holding were measured in the field by observation or filming of activity. Knowing swimming speed, amount of time spent in swimming, water temperature, and fish size allowed estimates of caloric consumption to be made from the laboratory metabolic rate data.

TROUT

The experiments on trout energetics were carried out at the Sierra Nevada Aquatic Research Laboratory located in eastern California near the community of Mammoth Lakes. Rainbow trout (*Salmo gairdneri*) approximately 100 g in weight were placed in a 27 l Blazka-type water tunnel respirometer. By varying the current velocity in the tunnel, measurements of tail beat frequencies and oxygen consumption rates could be made for the fish swimming at different speeds.

Field observations were made in a small, controlled-flow stream diverted from Convict Creek. The stream was divided into sections by horizontal plastic pipe barriers, and observation towers allowed behavior monitoring continually during daylight hours.

In the stream a group of newly introduced trout soon established positions with a dominance hierarchy normally determined by size. The alpha fish usually selected a holding position that required slow but continual swimming movements. Often this preferred holding position was adjacent to cover provided by undercut stream banks.

Subordinate fish also assumed holding positions that required swimming. When a dominant or alpha fish left its position to feed on a drifting insect, it could be replaced by a subordinate fish. When the alpha fish returned to its preferred position, an aggressive encounter normally occurred. Another more common type of aggressive bout took place when subordinate fish slowly moved downstream toward the holding position of the alpha fish. Once the intruder entered its territory, the dominant fish would leave its holding position and chase the subordinate fish upstream again.

The cost of this type of territorial behavior must thus involve both the holding of a position and the aggressive activities required to maintain that preferred position. Holding a position appears to require continual activity on the part of the dominant fish. Subordinate fish, by contrast, can at times rest under a stream bank or in a dead current space.

Methods

The basic problem involved in calculating the energetic cost of defense of this type of territory is to estimate or by some means measure how fast fish are swimming both in holding and during aggressive bouts with subordinate fish. An attempt was made to determine current velocities in portions of the stream by dividing stream sections into a system of grids and then measuring flow rates for each area of the grid with a current meter. If the holding position of the fish could be located, ideally its swimming speed could then be estimated. We found, however, that a small lateral movement of a few centimeters could result in a current velocity change of up to 25%. Hence this method of estimating swimming speed had to be abandoned.

In observing swimming fish in the water tunnel respirometer, it became clear that caudal or tail beat frequency changed with current velocity. Fish of various sizes were thus placed in the water tunnel respirometer and tail beat frequencies were determined for a range of current velocities (fig. 1). By counting the tail beat frequency for alpha fish while holding or in aggressive encounters with subordinates for a specific period of time, it was possible to estimate swimming speed for these activities using the relationship shown in figure 1.

The relationship of oxygen consumption in various current velocities for rainbow trout is presented in figure 2. By knowing water temperature, fish weight, fish length, and tail beat frequency (therefore swimming speed) it is possible to calculate metabolic rate. For example, using figure 1 we can see that a 200 mm fish holding in a current velocity requiring 120 tail beats per minute would be swimming at a speed of 20 cm/sec. If the fish weighed 100 g and the water temperature was 15° C, using figure 2 we see that the rate of oxygen consumption is 100 ml/kg/h.

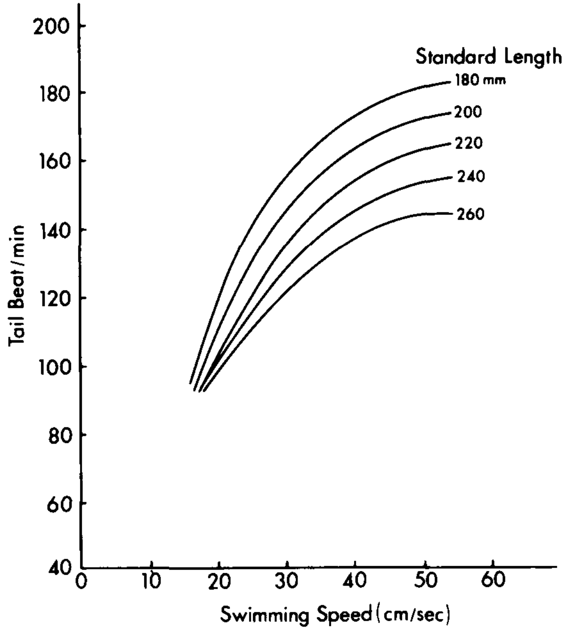

Fig. 1. Relationship between swimming speed and tail beat frequency determined in a Blazka-type water tunnel respirometer. Lines are drawn through mean values of 10 observations at swimming speeds of 15.5, 24.5, and 51.7 cm/sec.

Results

In an analysis of swimming speeds in the stream using the methods described above, rainbow trout were found to hold both day and night in a current velocity of about 16 cm/sec (table 1). This rate of swimming results in a mean energy expenditure of 388.5 cal/kg/h, or about 932 cal/day for a 100 g fish. A resting fish in the same stream would consume about 290 cal/kg/h, or about 697 cal/day. Thus maintenance of the holding position costs the alpha fish about 235 cal/day, which is about 25% of the energy it expends in a day's time.

The next step is to ask what additional cost there is for the aggressive behavior that allows the preferred holding position to be maintained. To answer this question, behavioral interaction data obtained by my colleague Thomas Jenkins, Jr., was analyzed. In Jenkins's experiment five brown trout (*Salmo trutta*) were introduced into a stream section. The fish were given several days to establish a dominance hierarchy and then positions were observed for a period of 15 h (the daylight portion of a long, early summer day). The time spent in aggressive

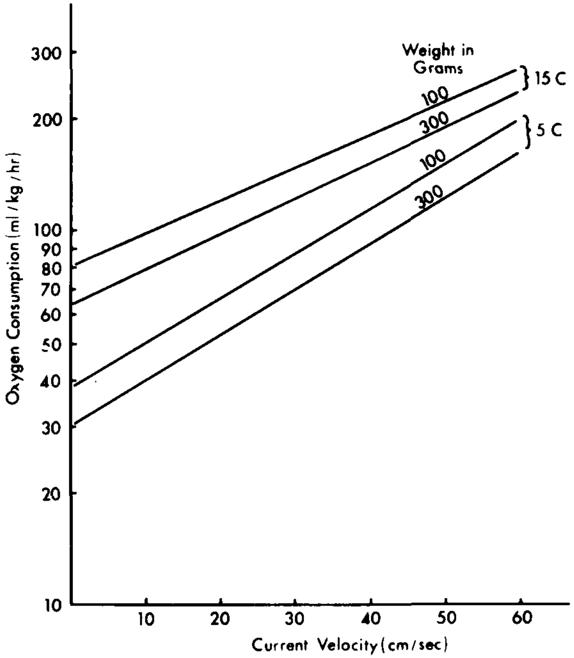

Fig. 2. Relationship between swimming speed and metabolic rate expressed as milliliters of oxygen consumed per kilogram per hour. Values of oxygen consumption for 100 g and 300 g rainbow trout (*Salmo gairdneri*) at 5° and 15° C were plotted from regression equations determined by Rao (1968).

behavior by both the alpha and subordinate fish was recorded. From tail beat frequency data, swimming speed velocities for both holding and aggressively swimming fish were estimated. The energy expended in each behavior was also calculated. An example of the method of estimating energy expended on aggressive activities follows: The alpha fish (18.2 cm, 83 g) had 125 aggressive bouts and spent 663 sec in aggressive behavior (mean swimming speed 37.5 cm/sec). A total of 50,038 sec were spent holding at 15.0 cm/sec. Total observation time was 15.75 h. Therefore 1.2% of the time was spent on aggressive activity.

Table 2 shows the time and energy expended on aggressive behavior (holding and agonistic bouts) for the three groups of fish (five fish per group), on three different days for three separate stream sections. The alpha trout in each experiment spent between 0.18 and 0.33 h in aggressive bouts, which amounts to only 1.2–2.2% of the total observa-

TABLE 1

COMPARISON OF DATA FOR RAINBOW TROUT (SALMO GAIRDNERI)

Date	Time Period (PST)	Water Temperature (°C)	Standard Length (cm)	Weight (g)	Mean Swimming Speed (cm/sec)	O_2 Consumption (ml/kg/h)	Energy Expenditure (cal/kg/h)
Sept. 21	0700–1300	13.5	24.5	279.8	15.8	88.0	440.6
Sept. 30	1300–1900	11.0	22.5	226.7	15.6	70.0	350.5
Oct. 1	1900–0100	11.5	19.4	119.3	15.4	80.0	400.6
Oct. 9	0100–0700	12.0	19.3	123.7	16.0	74.0	370.5
Oct. 12	1200–1800	12.0	19.9	136.3	18.1	82.0	410.6
Oct. 18	1200–1800	11.5	20.5	143.8	15.9	71.5	358.0
Means		11.9	21.0	171.6	16.1	77.6	388.5

SOURCE: Modified from Feldmeth and Jenkins (1973). Reproduced by permission of the *Journal of the Fisheries Research Board of Canada.*

Mean swimming speed and mean energy expenditure were not significantly different for the five time periods. A caloric equivalent for oxygen of 5.007 kcal/l was used to convert oxygen consumption data to energy expenditure in calories.

NOTE: A 100 g fish in 12° C water resting in no current would have an O_2 consumption rate of 58 ml/kg/h, which equals an energy expenditure of 290.4 cal/kg/h.

tion time. The energy spent to support this behavior amounted to 12.0–21.7 cal, which is 1.9–3.6% of the total energy expended during the lighted part of a long summer day.

To estimate energy expended in holding behavior the following calculation was made: A total of 56,038 sec were spent holding at 15 cm/sec. Therefore respiration was 100 ml/kg/h and energy consumed was 500.7 cal/kg/h (caloric equivalent for oxygen assumed to be 5.007 cal/l). Fish weight was 83 g, which means 41.6 cal were consumed per hour. Since 56,038 sec (15.57 h) were spent at this swimming speed, a total of 648 cal were consumed while holding.

Discussion

From the data in table 1 it is apparent that little energy is spent by these trout in the aggressive activities required to establish a dominance hierarchy. Holding stream fish, whether dominant or subordinate in rank, must expend considerable energy to maintain a feeding position in the stream. Resting under a bank involves an energy savings of about 25% but undoubtedly greatly lowers the chance of encountering drifting food items.

In an examination of the relationship of feeding rates to the density of drifting invertebrates (Jenkins et al., 1970), an attempt was made to measure differences in feeding success for trout of different sizes by

TABLE 2

Time and Energy Expended on Aggressive Behavior (Holding and Agonistic Bouts)

Fish	Number of Aggressive Bouts	Time Spent Holding	Time Spent in Aggression	Percentage of Time Spent in Aggression	Cal Spent Holding	Cal Spent in Aggression	Percentage of Total Energy Spent in Aggression
Group 1 Fish length = 18.2 cm Fish weight = 83 g Total time = 15.75 h	125	56,038 sec (15.6 h)	633 sec (0.18 h)	1.2	648	12.0	1.9
Group 2 Fish length = 18.2 cm Fish weight = 85 g Total time = 14.97 h	131	53,189 sec (14.8 h)	694 sec (0.19 h)	1.3	630	12.9	2.0
Group 3 Fish length = 19.0 cm Fish weight = 82 g Total time = 15.17 h	225	53,419 sec (14.8 h)	1,193 sec (0.33 h)	2.2	608	21.7	3.6

In this experiment 3 groups of fish were tested (5 fish per group) on 3 different days for 3 separate stream sections.

introducing pairs of trout into each stream section. Presumably the dominant fish would hold a preferred position and hence feed more successfully. The preliminary results suggested that there were not significant differences in stomach contents, and hence the feeding experiments were continued using only one fish per stream section.

In light of the small cost in maintenance of territory by alpha trout in the experimental stream, it seems reasonable that the benefits of feeding would be small. It may be that the subordinate fish feed almost as well but must expend more energy swimming in less desirable holding positions or in areas of irregular currents. They must therefore also move around more to find drifting food items and avoid alpha fish in the preferred holding positions of the stream.

It appears that territorial behavior serves to space out individual trout in a stream, probably because food resources are limited. For example, in the experimental stream only fish smaller than 100 g were able to realize a maintenance ration during the feeding studies. Wild trout in the stream also tend to be quite small. Aquatic invertebrates available as food items are in too low a density to support large fish or more than a few fish per 10 m section of stream.

In summary, the costs of maintaining a preferred holding position are about 25% higher than resting metabolic rates, and presumably such a position allows easier access to food items and cover. The amount of time and energy the alpha trout expended in aggressive bouts with subordinate fish was so small (1.9–3.6% of the total) that the benefits in terms of feeding or energy gained must also be very small.

PUPFISH

To provide a contrasting example, the cost of territorial maintenance in pupfish was examined. Pupfish were chosen because as part of their courtship, dominant males vigorously defend small territories (Barlow, 1961). Population studies by Soltz (1974) and Kodric-Brown (1978) indicate that aggressive behavior occurs almost continuously throughout the daylight hours, with all fish apparently settling to the substrate and remaining inactive at night.

Male fish thus defend a small area and only allow gravid females to approach and spawn in the territory. Dominant males in densely populated habitats defend small territories that number up to 20 per m^2. In pools and streams with lower population densities, territories are larger, and as few as 4 may be present per m^2 (Kodric-Brown, 1978).

The males must vigorously defend their specific territories to keep all egg-eating animals out and to prevent satellite or sneak males from spawning females in their territory. The various threats and displays and other agonistic behaviors exhibited by territorial males have been classified into categories by describing the various motor patterns involved (Barlow, 1961). Kodric-Brown (1978) has described the evolution of breeding territories as well as reproductive success and has also described how territories are established and defended.

The most obvious aspect one notices while observing reproductive behavior is the almost frantic activity level maintained by the brightly colored adult males. They are almost continually darting back and forth from one side of the territory to the other, threatening with various aggressive displays, biting and charging other fish that swim into their territory.

Certainly all this activity must be expensive from an energetic perspective. What does it cost the dominant male pupfish to maintain their territories?

Methods

To approach this question I first established a pupfish habitat in the laboratory. Three large males, 5 mature females, and approximately 20 smaller male and female fish were placed in a circular pool 2 m in diameter. A sand and gravel substrate was provided as well as several small cobbles. A reproductively optimum, long day period of 16 h of light and 8 h of dark was established, and the water was maintained constant at 26° C.

In a few days several territories were established and breeding behavior was observed. Aggressive behavior exhibited by the dominant males was filmed using a super 8 movie camera. The swimming path of each fish was then traced using a stop-action projector. A grid of 20 cm squares placed over the pool allowed swimming distance to be measured. A stopwatch was filmed so that an exact film speed, and hence swimming speed, could be determined. Analyzing the film allowed the amount of time spent actively swimming by dominant males, and their swimming speed, to be calculated.

To determine the metabolic cost of swimming, large male pupfish were placed in a small recirculating respirometer (Eriksen and Feldmeth, 1967) and rates of oxygen consumption were measured at different current velocities. The respiratory rates of holding fish were determined using closed flasks. By allowing large males to adjust for a period of 24 h to a 250 ml glass container, minimum metabolic levels were approached. A small amount of coarse sand was present in each chamber, and water was circulated to keep the dissolved oxygen level near saturation. The jars, each containing one pupfish, were then sealed and placed in an aquarium with other free-swimming fish. The enclosed dominant fish were thus visually excited but could not swim after other fish. Their activity in these chambers appeared to approach closely the behavior observed for fish holding while defending territories.

To determine how much energy would be expended by the same fish without the stimulus of territorial behavior, the day length was shortened from 16 to 8 h. The fish were allowed 15 days to adjust to the new light regime and behavior was again filmed.

Field measurements of territorial behavior were made by analyzing films taken of two different pupfish species. Amargosa pupfish (*C. nevadensis amargosae*) from Tecopa, California, were filmed (pool temperature, 26° C) using the same techniques as described above. The swimming speed of dominant male fish was then analyzed from the films. The amount of time spent in active defense of territory (swimming) was also calculated.

In addition, films used in a territory study on the pupfish *C. pecosensis* were obtained from Astrid Kodric-Brown. The fish were filmed at Bottomless Lakes State Park, New Mexico, in a water temperature of 26.0° to 26.8° C. Swimming speed and the amount of time spent in active defense of territory were calculated for alpha males, satellite males, and juveniles using a large-screen stop-action film editor.

Results and Discussion

Using the stop-action techniques it was possible to trace the activity of an alpha male pupfish in territorial defense (fig. 3). An analysis of such a tracing provides the total distance a fish swam, and since the amount of swimming time was also recorded, the time spent in activity and the mean swimming speed could also be calculated. For the dominant male fish in the laboratory pool, the swimming speed ranged from 5.8 to 35.5 cm/sec, with a mean of 14.5 cm/sec (table 3). The swimming speed for alpha males of this same species (*C. n. amargosae*) in the field ranged from 6.9 to 31.0 cm/sec, with a mean swimming speed of 17.7 cm/sec (table 3).

The time the alpha male fish spent actively swimming in defense of their territories in the laboratory pool ranged from 56.9 to 82.7%, with a mean of 73.1% (fig. 4). In the field the alpha males spent between 77.2 and 100% (mean 93.3%) of their time swimming in defense of territory. By contrast, when the light period (day length) was shortened from 16 to 8 h, the amount of time alpha male fish spent actively swimming fell to 21.9% (fig. 4).

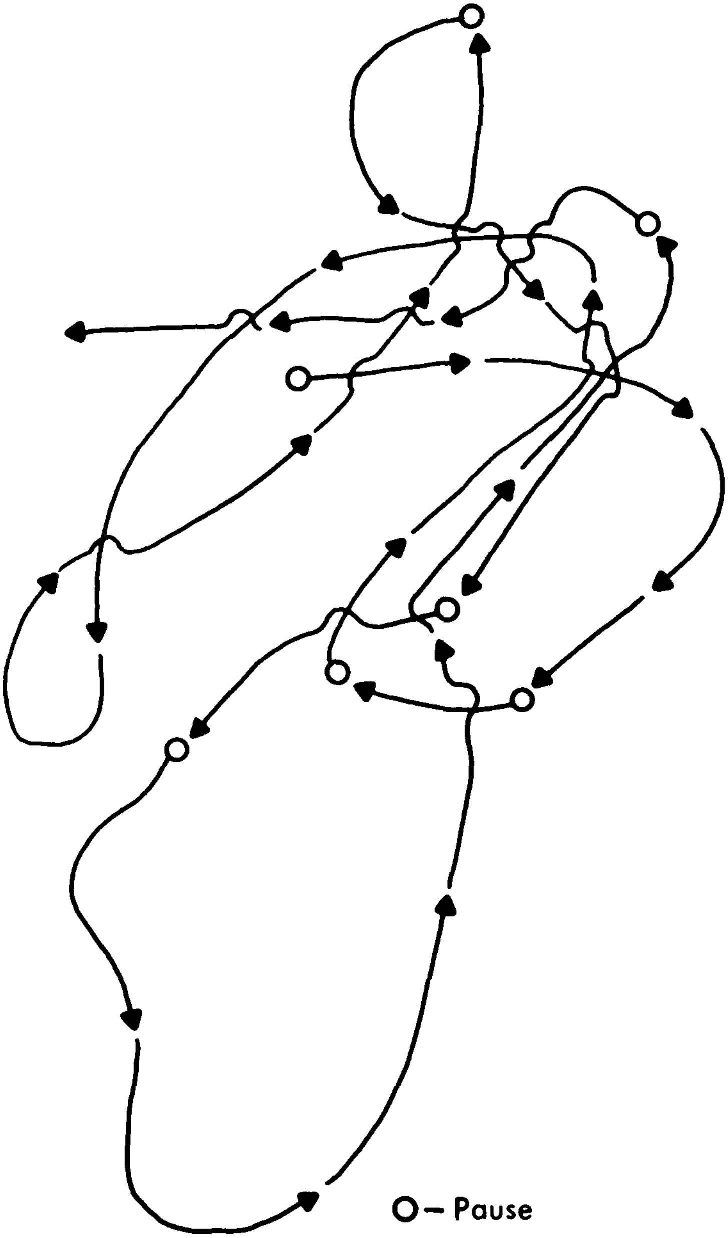

Fig. 3. Tracing of movements of an alpha male Amargosa pupfish (*C. nevadensis amargosae*) for one analyzed film sequence (approximately one-third actual size). Starting point and holding positions (pauses) indicated by *circles*. *Arrows* show swimming direction.

TABLE 3

SWIMMING SPEEDS OF TERRITORIAL MALE PUPFISH (C. NEVADENSIS AMARGOSAE)

Location	Mean Swimming Speed (cm/sec)	95% Confidence Interval
Laboratory Pool (7 films; 49 sequences analyzed)	14.5	0.68
Miller's Pond (6 films; 25 sequences analyzed)	17.7	1.76

A calculation of the metabolic cost of the activity required by alpha male Amargosa pupfish to defend their territories can now be made. Using the water tunnel respirometer–metabolic rate data for fish swimming in current velocities of 5–25 cm/sec (fig. 5) and the above data on swimming speed in the laboratory pool and field habitat (table 3), a metabolic cost of holding behavior in a territory would be 33.6 cal per 16 h day.

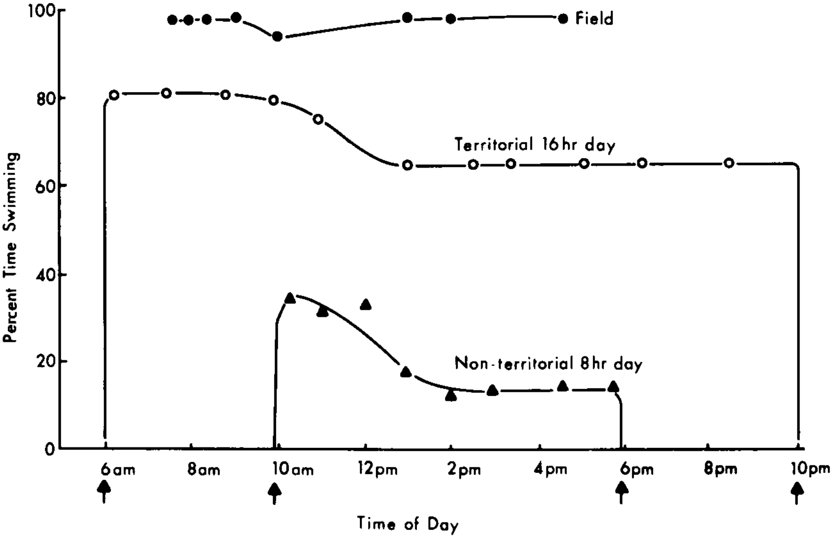

Fig. 4. Percentage of time spent in swimming behavior by territorial (alpha) male Amargosa pupfish (*C. nevadensis amargosae*): *solid circles*, fish observed in the field; *open circles*, fish in the laboratory on a 16 h day; *arrows*, nonterritorial fish in the laboratory on an 8 h day.

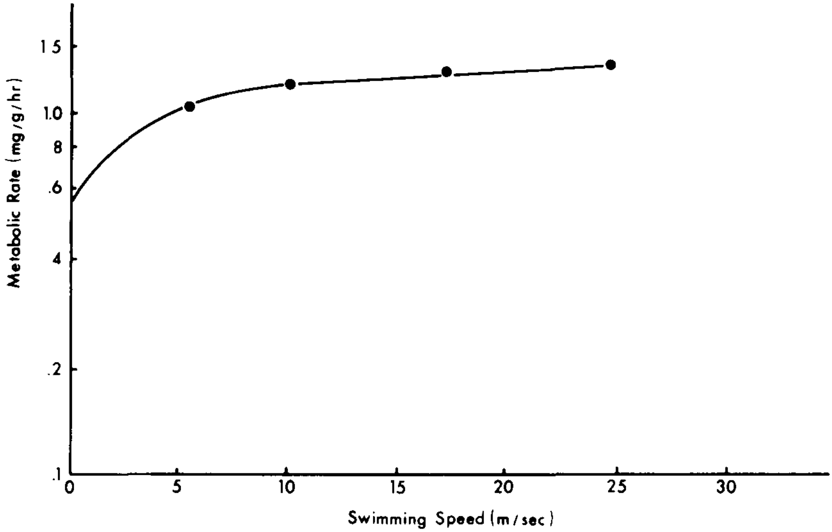

Fig. 5. Metabolic rates of large male Amargosa pupfish (*C. nevadensis amargosae*) swimming in various current velocities in a small recirculating respirometer. *Erratum*: swimming speed is measured in cm/sec.

Since the metabolic cost of swimming approximately doubles at speeds greater than 5 cm/sec, swimming displays, darting, or other active behavior responses will require the expenditure of considerably greater amounts of energy. If an alpha male in the laboratory spends approximately 75% of a 16 h day actively defending its territory (mean swimming speed, 14.5 cm/sec), it expends approximately 42.1 cal. The remaining 4 h spent holding cost an additional 9.6 cal, for a total of 51.7 cal for the entire day. Since alpha males of this species were active approximately 15.2 h, or 98% of the 16 h day in the field, 76.1 cal would be expended in activity and an additional 1.2 cal would be spent holding over the territory, for a total cost of 77.3 cal. By contrast, a holding fish would expend 38.4 cal per 16 h day, approximately half as much energy. Swimming is thus expensive energetically, but it is essential for both feeding and predator avoidance, as well as reproduction, especially with respect to territorial defense.

In making observations of various pupfish populations in the field, it became apparent that there is a high level of activity on the part of all individuals. We have examined the activity level and energetic cost for the alpha male of Amargosa pupfish in both the laboratory and the field. However, it is important to determine how much energy satellite males and juveniles expend in their various behaviors.

To approach this question it would be best to examine behavior in habitats of various population densities, since territory size and perhaps activity levels in territorial pupfish may be related. The *C. pecosensis* population in Mirror Lake (Bottomless Lakes State Park, New Mexico) provides a well-studied situation where population density and territory size vary considerably for different areas along the lake's shore (Kodric-Brown, 1977, 1978).

Again the stop-action film analysis method allowed the calculation of the time spent swimming and the time spent holding for these pupfish (table 4). The amount of time spent actively moving about ranged from 55.5 to 74.4% for 32 different film sequences or activity traces analyzed. Satellite or nonterritorial males were actively swimming for 78.9 to 88.2% of the time (64 film sequences analyzed). Territorial males actively defended their territories 68.8 to 87.7% of the time in the 125 film sequences analyzed.

TABLE 4

TIME SPENT IN SWIMMING AND HOLDING BEHAVIORS BY MALE PUPFISH (C. PECOSENSIS)

Fish	Percentage of Time Spent Swimming	Percentage of Time Spent Holding	Number of Samples
Juveniles			
Roll 6	55.5	44.5	14
Roll 4	74.4	25.6	18
Satellite (nonterritorial) males			
Roll 6	88.2	11.8	9
Roll 4	89.1	10.9	23
Roll 1	78.9	21.1	32
Territorial males			
Roll 1	68.8	31.3	34
Roll 4	87.7	12.3	32
Roll 5	85.6	14.4	29
Roll 2	77.6	24.4	13
Roll 6	75.1	24.9	17

The energetic cost of the activity levels maintained by these various social class groups is presented in table 5. Holding or resting metabolism would require 31.5 cal per 15 h day. Juvenile fish, which are active for about 60% of the time, expend 44.3 cal per 9 h of swimming and 15.1 cal per 6 h of holding, for a total of 59.4 cal per 15 h day. Both

TABLE 5

TOTAL ENERGY COST FOR A 15 H DAY FOR CYPRINODON PECOSENSIS

Fish	Swimming Speed (cm/sec)	Energy Expended (Resting Metabolism = 31.5 cal/15 h)	
Juveniles	12.6	Holding	15.1 cal/6h
		Swimming	44.3 cal/9 h
		Total	59.4 cal/15 h
Satellite males	16.4	Holding	5.7 cal/2.25 h
		Swimming	62.8 cal/12.25 h
		Total	68.5 cal/15 h
Dominant males	18.3	Holding	7.6 cal/3.0 h
		Swimming	59.1 cal/12 h
		Total	66.7 cal/15 h

the satellite males and the alpha males have higher levels of activity and have total energy expenditures per 15 h day of 68.5 and 66.7 cal, respectively.

The surprising result that other social classes of pupfish in the population expend as much or more energy than do the territorial males leads to a reanalysis of the Amargosa pupfish films and data. The amount of time spent in activity was higher for the satellite males for each sequence examined (table 6). Note that swimming speeds were higher for the satellite males as well.

It thus appears that territoriality in pupfish is energetically expensive, but satellite males expend as much or more energy in their activities. Since observations by Soltz (1974) and Kodric-Brown (1977, 1978) indicate that individual alpha male pupfish occupy the same territory for many days, this high level of activity must be sustained almost continually. Satellite males do not have to maintain a constant vigil in the effort to spawn females, and hence the levels of activity observed for them in the analysis of the films may not give an accurate assessment of their total metabolic costs. However, after observations in the field and the careful analysis of hundreds of feet of film, it would appear that almost all fish in the area of the breeding territories, even juveniles, are quite active.

The only exception are the mature females, which tend to form slow-moving schools or loose aggregations in areas away from the

TABLE 6

TIME SPENT IN SWIMMING AND HOLDING, PLUS SWIMMING SPEEDS, FOR CYPRINODON NEVADENSIS AMARGOSAE (AT MILLER'S POND)

Sequence Analyzed	Fish	Percentage of Time Spent Swimming	Percentage of Time Spent Holding	Swimming Speed (cm/sec)
Film 6	α male	91.1	8.9	12.24
	Satellite 1	93.2	6.8	22.68
	Satellite 2	93.5	6.5	18.00
Film 13	α male	90.5	9.5	6.97
	Satellite 1	92.3	7.7	26.2
	Satellite 2	93.1	6.9	30.3
Film 17	α male	92.3	7.7	12.35
	Satellite 1	92.5	7.5	21.32
	Satellite 2	93.2	6.8	20.45

breeding territories (Soltz, 1974). Since the metabolic cost of egg production in cyprinodontids is considerable (Hirshfield, 1980), it would be an advantage to maintain low levels of activity and concentrate upon feeding.

If a school of females approaches an area where males are defending territories, the school is repelled by the alpha males. To enter a breeding territory, single females normally approach from above. The male begins spawning behavior by nipping the female's anal region. The female approaches the substrate with the male close beside, and spawning occurs (Liu, 1969). The eggs adhere to the substrate and hatch within a few days (Soltz, 1974).

Again it appears that the cost of territorial maintenance is not very great as compared with the normal activities of other social groups within a population of fishes. Perhaps the fact that the size of territories is small when population numbers are high helps to minimize the amount of swimming required. Often the alpha male can hold over the territory and perhaps by threat display alone repel other alpha males, satellite males, and other intruders. Holding is much less expensive than the darting behavior observed for the satellite males that often continually circle the territory.

A major question that still must be answered involves how alpha males, which continually defend a small territory, find enough food to maintain their high metabolic rates. Many feeding acts were observed in the analysis of the films, but it is clear that these feeding movements are secondary in importance to territorial maintenance. Perhaps male fish feed and reach a size and state of vigor that allows them to defend a territory for several days with only the minimal food present in this small area. After this active reproductive period, they surrender the territory and resume nonsexual activities such as feeding.

To approach this problem of how much feeding is taking place while males are holding the territories, a series of lab and field experiments have been designed to observe the caloric gain in feeding of territorial and nonterritorial pupfish. With this information we should begin to have a clearer idea of what the cost and benefits of aggressive territorial behavior are for this highly territorial fish.

CONCLUSIONS

Although both socially dominant trout and territorial male pupfish expend considerably greater amounts of energy in aggressive activities than resting or nonswimming (holding) fish, it appears that other social classes within the population are also quite active and pay as high or higher a metabolic price than do the dominant fishes. It is important, however, to consider the benefits of territorial behavior as well. Whether we are dealing with the maintenance of a dominance hierarchy of trout in a cold mountain stream or the small reproductive territory of pupfish in a warm desert pool, there must be benefits as well as metabolic costs of such behavior.

In the case of the trout, the energetic cost paid by dominant fish holding a preferred stream position probably allows access to more drifting invertebrates with a minimal amount of extra swimming necessary to capture prey. In the alpha male pupfish there are considerable genetic benefits in maintaining a territory. By contrast, subordinate trout must swim back and forth in search of food, encountering a wider range of stream current velocities and presumably using more energy to obtain the same amount of food. Satellite male pupfish must also continually move about in their attempt to spawn female pupfish in the territory of an alpha male. This activity is clearly costly, and the chance of successful spawning must be far below that of the dominant males.

It would thus appear that although trout and pupfish are very different in terms of the amount of aggressive behavior observed during their normal activities, both dominant fishes probably do not expend as much energy as do their nonterritorial counterparts in the social or reproductive hierarchy. Aggressive territorial behavior is definitely a benefit to both fish and is perhaps not as costly from an energetic perspective as would appear from casual observation. By a quantitative analysis of the energetic costs of aggressive behavior, it becomes evident that aggressive activities probably require less energy expenditure for the dominant fish than do the various other activities of subordinate fishes.

DISCUSSION FOLLOWING DR. FELDMETH'S PRESENTATION

Question: You have picked up these fish and handled them, taking into consideration the general adaptation syndrome. I would be interested in your comments regarding the extent to which you would expect a difference in the bioenergetics of these fish if you were to conduct your experiments under natural conditions and not in a constrained environment.

Answer: I know handling is important because when I was a student at Toronto we did a lot of fish respiration work and we found that respiration was raised for a period of about 12 or 15 h after handling. So I'm very aware of the sensitivity of fish and other organisms to their environments. To begin with we were trying to determine the feeding rate. We attempted to starve fish for a period of time to allow evacuation of their stomachs. We then introduced them into the stream and found they wouldn't feed, because they had been handled. We then tried a number of other methods including taking little bits of salmon eggs and cheese balls and shooting them out with peashooters, hoping to put a plug in the stomach so that we could see what they were feeding on after that. We found that in these situations the stomach contents were turned around. We then came up with the idea that if we grabbed the fish and we didn't use electric shock, but used two bag nets to pull them out and placed them right in the anesthetic, we could pump their stomachs and place them back in the stream. With this treatment the fish began feeding immediately from the time they were introduced into the stream. The feeding studies lasted for 6 h and the fish fed throughout the entire time. At the end of the 6 h feeding block we would electrofish them out of the stream and analyze the contents. We found that they were feeding quite well and that the gut contents were similar to that of the wild fish that we could catch in the stream section without any barriers. With respect to the pupfish, most of these data were obtained in the field under natural conditions, especially since we were observing them from afar with a telephoto camera. I believe we were getting a pretty good idea of what goes on in the field.

Question: I'd like to ask a question about the way you described energy to aggression. Essentially the activity away from the holding position is what you described as aggression in both cases. I'm wondering what your feelings are and how you would answer the question of what proportion of activity is ascribed as aggression versus feeding versus the other things that were going on simultaneously in both cases.

Answer: I'm glad you asked that. They do feed when they are out on an aggressive foray. If they shoot out of that holding position they will often pick up a piece of food on the way. And when they come back they will often have a combative bout. Jenkins would say that these were overestimates of aggressiveness behavior. And it is much less than this. What we did was, every time a fish shot out of a holding position, we assumed that it was swimming at a much faster speed. We looked at the time that it took to get from one place to another and we calculated the swimming speed by measuring fin beat frequency. I would say that for the trout we have overestimated the time spent on aggression, and holding is the main cost.

Question: In terms of the trout, holding in a good position to get an abundance of food, is there any evidence to indicate that they are in fact defending a portion of the stream that has a higher dissolved oxygen content rather than just a higher food content.

Answer: No. It appears that in these streams the oxygen is pretty uniform. I would imagine that in a slow-moving river or a lake situation that would be possible, but these streams are pretty uniform. The thing that they are defending also is a nearby source of cover. There is usually an undercut bank or a piece of brush or something that they can get to. Some recent work by some Canadian biologists would indicate that cover might be more important in the holding position selection than the feeding or the amount of food that comes. However, in the stream that we looked at we see selection again and again in the same sort of area. The bottom is a coarse sand, which indicates the same current velocity in each instance. It seems to be a pool below a ripple where insects are generated, and we know from drift studies throughout the stream that drifting occurs basically off the riffles. And if you have drift below the pool you are going to catch the most food. It seems that food and feeding are important; the cover is probably secondary.

Question: This relates to both species of fish. Every time the pupfish would go out on an aggressive foray it will be moving at a speed that is commensurate with its maximum VO_2, whereas the trout is operating at less than maximum VO_2. At what percentage of the maximum VO_2 do the trout operate?

Answer: Dr. Brett has that data. His students have generated a lot of data for that. And we know that it is considerably higher than the numbers that I am working with. For example, I was working with swimming speeds of about 30 cm/sec, whereas that curve went up to 60 cm/sec, twice that speed; and I would imagine that, depending on the size of the fish, it could go even higher than that.

Question: I'm really impressed with what you've done. So much of it is necessary when you can see the fish and make the types of measurements that you are making. One of the things that we have always wondered about, and I wonder if it really isn't a follow-up of another question that was put to you, is, What would you ascribe to excitement behavior? When we studied fish for 24 h in the respirometer, we could find no relation between swimming speed and energy expended. It was simply because the fish were excited. It seems to me so vital to determine whether a fish is in an excited state. We see salmon in an excited state when they are in the presence of an alarming odor. And they aren't swimming, they aren't doing anything, but their whole fin movements and their respiratory movements simply increase. I wonder how much of this is caused just by the presence of other aggressive fish.

Answer: The data that I presented for the trout I feel pretty confident about because it's very similar to the work that has been done by other people. For the pupfish I think that you are right; there is a great deal of excitement. I didn't present any of the variance at all, but everyone who has done this work knows that there is a tremendous amount of variability. The amount of variability around that pupfish curve is extreme. There is a lot of excitement going on. I was trying to make an estimate so I drew a line through the middle of these data, as I know you have done before.

We tried to make an estimate, and as a result, I think that the excitement thing cannot be played down too much with respect to fish because of their particular psychology. One worker in Europe found that if the top of the respirometer did not have water over it, the fish would have a higher metabolic rate. If there was a plexiglass chamber that was just exposed to the air there was a problem. So I always fill my tunnel up and have water on top of it so that it does not have an air-water interface. People coming into the room while you are doing experiments probably do a lot to excite them as well. All I can say is that it looks to me that the pupfish in the field are excited also. It looks to me that they are really putting out a lot of energy. There is a tremendous amount of excitement going on there that I would say is probably near maximal. That's why I feel sort of justified presenting that curve even though my respiration data for the pupfish may not be valid. They are really putting out at maximum VO_2 in warm water (26°–27° C), and in some cases we have observed some fish at 42° C.

Question: Does that VO_2 Max of the pupfish at those elevated speeds represent the VO_2 Max not just of swimming but of the pupfish itself?

Answer: It probably would. I didn't measure that. I didn't take one and shake it up and put it in a bottle and measure it, but it probably is as much as they can do. As I said, there was a range and so it could go up higher, but this is about the mean at those speeds. And I would imagine it would be about the same for an excited fish, although I didn't measure that.

Question: Does the pupfish swim at speeds faster than that?

Answer: Probably slightly faster, especially in elevated temperatures; they seem to really be able to shoot.

One thing I am going to do next is look at sprint velocity of these fish at different temperatures. And this is an evolutionary question. I'm studying two populations that are in different environments. One is in cool water in the winter and warm water in the summer, while the other population is in constant temperature. And we're looking at the width of the thermal niche and we're going to study sprint velocity. There seem to be a lot of relationships between speed and temperature, which makes sense from the point of view of what we know about muscle work and temperature.

Question: If I understood what you were saying—that the pupfish was defending a nesting site and the trout were primarily defending a feeding site—are you suggesting that the cost of aggression is well compensated for?

Answer: On the trout I would say the cost of aggression is very low, because it is also feeding while out there on these aggressive bouts. Except that I consider the holding position part of territorial maintenance, and so that cost has to be included.

Questioner interrupts: In territorial maintenance we're trying to defend some kind of limited resources, right? There must be a reason for expending this energy. In the trout you're suggesting that they're getting more food in this spot than in another.

Answer: That experiment is a little bit difficult to do because you can't always get fish to feed when you want them to feed, and so forth. But it appears that the dominant fish, the alpha fish, in the stream section has more in his stomach in a given period of time than the subordinate fish. That seems to suggest that it's true, but we can't get the data to look good enough to get it published. That seems to be the case.

Question: What about the possibility that there could be a difference in energy expenditure in one place or another, rather than a difference of food intake?

Answer: I definitely think there is—you mean between the subordinate fish?—yes, or from one site to another; there is one spot the fish has to expend more energy. That may be, but these are for three stream sections; each was a different portion of the stream. We have done this for about six different stream sections, for many, many fish, and the holding is always the same. If you have a fish about the same size they are almost always holding at 15 cm/sec.

LITERATURE CITED

Barlow, G. W. 1961. Social behavior of the desert pupfish, *Cyprinodon macularius*, in the field and the aquarium. Amer. Midl. Natur. 65:339–59.

Clarke, T. A. 1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda*. Ecol. Monogr. 40:189–212.

Eriksen, C. H., and C. R. Feldmeth. 1967. A water-current respirometer. Hydrobiol. 29:495–504.

Feldmeth, C. R., and T. M. Jenkins, 1973. Measurement of energy expenditure of rainbow trout in a small mountain stream. J. Fish. Res. Bd. Can. 30:1755–59.

Gerking, S. D. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology 34:247–365.

Greenberg, B. 1947. Some relations between territory, social hierarchy, and leadership in the green sunfish (*Lepomis cyanellus*). Physiol. Zool. 20:267–98.

Hirshfield, M. F. 1980. An experimental analysis of reproductive effort and cost in the Japanese medaka, *Oryzias latipes*. Ecology 61(2):282–92.

Jenkins, T. M., Jr. 1969. Night feeding of brown and rainbow trout in an experimental stream channel. J. Fish. Res. Bd. Can. 26:3275–78.

Jenkins, T. M., C. R. Feldmeth, and G. V. Elliott. 1970. Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. J. Fish. Res. Bd. Can. 27:2356–61.

Kodric-Brown, A. 1977. Reproductive success and the evolution of breeding territories in pupfish (*Cyprinodon*). Evolution 31:750–66.

Kodric-Brown, A. 1978. Establishment and defense of breeding territories in pupfish (Cyprinodontidae: *Cyprinodon*). Anim. Behav. 26(3):818–34.

Liu, R. K. 1969. The comparative behavior of allopatric species (Teleostei-Cyprinodontidae: *Cyprinodon*). Ph.D. thesis, University of California, Los Angeles.

Soltz, D. 1974. Variation in the life history and social organizations of some populations of Nevada pupfish, *Cyprinodon nevadensis*. Ph.D. thesis, University of California, Los Angeles.

Survival Strategy 3

Cost-Benefits of Temperature Regulation and Foraging

F. HARVEY POUGH

Amphibians and Reptiles as Low-Energy Systems

6

INTRODUCTION

One of the surprising aspects of the biology of amphibians and reptiles is the number of features that are common to the two classes. Evolutionary history does not account for these similarities. The Recent taxa of amphibians and reptiles are the products of several hundred million years of separate evolution. The anthracosaur and temnospondyl lineages of labyrinthodont amphibians had separated from other amphibians by the Mississippian, and the gephyrostegid anthracosaurs, which gave rise to reptiles, are known from the early Pennsylvanian. Living amphibians may have had a common phylogenetic origin or may be derived from as many as three distinct Paleozoic lineages (Parsons and Williams, 1963; Romer, 1966; Wake, 1970; Carroll, 1977a; Carroll and Holmes, 1980). If a common phylogenetic origin of the Lissamphibia is accepted, the oldest fossil evidence of separate evolutionary lineages suggests that frogs and salamanders were distinct by the Permian; if a polyphyletic origin is postulated, the separation of Recent lineages must have been at least as early as middle Carboniferous. Thus frogs, salamanders, and apodans have been evolving independently of each other for at least 250 million years and possibly for as long as 350 million years.

The fossil record is more detailed for reptiles than it is for amphibians and indicates an initial separation of the phylogenetic lineages leading to the living orders of reptiles in the upper Carboniferous,

This contribution is dedicated to Robert H. Whittaker.

Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853

about 300 million years ago (Carroll, 1969, 1977b). Most of the Recent suborders had appeared by the middle Mesozoic, some 150 million years ago (Romer, 1966).

Despite the uncertainties of the timetable, it is apparent that living orders of reptiles have more recent genetic continuity with mammals than they do with amphibians, and among the reptiles the crocodilian lineage separated from that of birds some 50 million years more recently than its separation from other reptilian stocks. Clearly there has been enough evolutionary time for amphibians and reptiles to have evolved differences among living taxa as great as those that separate amphibians and reptiles on one hand from birds and mammals on the other. The failure of such diversification to occur is striking and suggests that an underlying reason, some general adaptation of the two classes of vertebrates, should be sought to explain their persistent similarities.

THE GENERAL ADAPTATION OF AMPHIBIANS AND REPTILES

Two basic physiological characteristics distinguish amphibians and reptiles from birds and mammals—ectothermy and reliance upon anaerobic metabolism to generate energy for high levels of activity. That contrast explains the different roles the two sorts of animals play in ecosystems and provides a context in which the physiology, morphology, and behavior of amphibians and reptiles are seen as specialized rather than primitive (Pough, 1980a). Amphibians and reptiles represent an entirely different approach to terrestrial vertebrate life from that which characterizes birds and mammals. Amphibians and reptiles have low rates of energy flow and high efficiencies of biomass conversion, whereas birds and mammals have high energy flow and low conversion efficiency. Sixteen species of small birds and mammals converted an average of only 1.4% of the energy they assimilated into new biomass (range 0.5–3.0%), whereas eight species of amphibians and reptiles had an average conversion efficiency of 43.6%, with a range of 19.5–87.0% (calculated from table 3 in Pough, 1980a).

The high conversion efficiencies of amphibians and reptiles give them a unique importance in terrestrial ecosystems despite their low rates of energy flow and the small proportion of net primary production they consume. For example, in the Hubbard Brook Ecosystem in New Hampshire, the population of red-backed salamanders (*Plethodon cinereus*) produces 4922 kcal/ha·yr. This biomass production is approximately five times that of the entire avian community of the forest and about the same as that of the small rodents (Burton and Likens, 1975). The annual biomass production of a population of the small lizard *Uta stansburiana* in a desert habitat varied from 336 to 536 kcal/ha·yr (average of 3 years = 469 kcal/ha), and a second species of lizard in that habitat (*Cnemidophorus tigris*) had an estimated annual production of 200 kcal/ha. In a somewhat more mesic desert habitat the annual production of four species of small rodents ranged from 39.5 to 541 kcal/ha·yr (average = 184 kcal/ha·yr) (Turner et al., 1976). Still higher values of energy consumption and production have been estimated for small tropical species of lizards (Bennett and Gorman, 1979).

Thus, in three quite different habitats amphibians and reptiles produce as much new biomass annually as do birds and mammals, despite the fact that they consume a very much smaller fraction of the net primary production of the ecosystem they inhabit. From the viewpoint of a predator, amphibians and reptiles may be an even more important potential source of food than birds and mammals for two additional reasons. First, because they lack an indigestible covering of hair or feathers, amphibians and reptiles may offer a predator more assimilable protein than a bird or mammal of the same body size (Burton and Likens, 1975). In addition, characteristics of the exercise physiology of most amphibians and reptiles result in their rapid exhaustion when they are forced to sustain high levels of activity (Bennett, 1978). Because amphibians and reptiles tire quickly when they are pursued, they may be relatively easy for some predators to capture.

As a result of their physiological characteristics and of the ecological and behavioral consequences of those characteristics, amphibians and reptiles have an entirely different significance in an ecosystem from that which ecologists assign to birds and mammals. The importance of the latter is traditionally considered in relation to the proportion of the net primary production of the ecosystem that they consume. In contrast, amphibians and reptiles are most appropriately considered in relation to the energy they make available to other organisms. In that context their quantitative role in ecosystems is as great as, or even greater than, that of birds and mammals.

Interlocking Physiological and Ecological Features

The high efficiency of secondary production by amphibians and reptiles is a direct consequence of their ectothermy. Because they rely upon external sources of energy to raise their body temperatures to levels suitable for activity instead of generating heat metabolically as do birds and mammals, amphibians and reptiles do not require the high resting metabolic rates that are characteristic of the endotherms. The source of energy used to raise the body temperature is the important distinction between endothermy and ectothermy: there is a broad overlap in the actual body temperatures maintained during activity by the two kinds of tetrapods (Cowles, 1962).

In essence, amphibians and reptiles pay the costs of thermoregulation primarily in behavioral currency, whereas birds and mammals pay those costs largely in units of energy. The constraints that limit thermoregulation by terrestrial ectotherms are expressed in terms of the times of day or seasons of the year during which thermoregulation is feasible and hence activity is possible, or in the habitats or microhabitats in which an animal can thermoregulate (Huey and Slatkin, 1976). The difference between summer and winter or even between day and night is of obvious importance to an ectotherm, but much more subtle differences shape a species' niche.

For example, three sympatric species of *Ameiva* lizards in Costa Rica feed on very similar kinds of prey in approximately the same proportions and maintain the same body temperatures during activity. These three species divide the habitat in a manner directly related to their body size and appear superficially to be responding to potential or actual interspecific competition. In fact, the differences in habitat utilization by the three species can be explained by two aspects of the interaction between the lizards and their physical environment: the rate at which a lizard of a given body size cools in the shade and the equilibrium temperature it reaches in the sun (Hillman, 1969, and personal communication). The smallest species, *Ameiva quadrilineata*, forages primarily in areas of low open vegetation, where 74% of the substrate receives direct solar radiation. The middle-size species, *A. festiva*, forages at the edge of the forest, where only 60% of the substrate is sunlit; and the largest species, *A. leptophrys*, forages under the forest canopy, where 38% of the substrate receives insolation.

All three species have similar thermoregulatory behavior: a lizard basks in the sun until its body temperature reaches about 38° C and then forages through sunlight and shade until its body temperature has fallen to about 36.5° C, when it must bask again. When tethered in the shade an *Ameiva quadrilineata* cooled from 38° to 36.5° C in 1.5 min, whereas an *A. festiva* required 2 min and an *A. leptophrys* 4 min for the same change in body temperature. As a consequence of this difference in their rates of cooling, the larger species of lizards are able to exploit shady habitats more effectively than *A. quadrilineata* because they have more time to forage between periods of basking. In the open habitat, however, it is the smallest species that is at an advantage.

Computer simulations indicate that in full sun *A. quadrilineata* would reach an equilibrium temperature of 39° C, about 3° C below its lethal maximum temperature, whereas the two larger species would continue to heat above their lethal temperatures. Thus, the smallest species of *Ameiva* is excluded from the forest habitat because it cools too rapidly to forage effectively and the larger species risk overheating if they forage in the open habitat. The paramount importance of biophysical considerations in this case of habitat partitioning is emphasized by the behavior of juveniles of *A. leptophrys*, the largest of the three species. These juveniles are close to the body size of adult *A. quadrilineata* and have the same biophysical relationship to their environment as adults of the smallest species. The juvenile lizards forage in open habitats rather than in the forest habitat of the adult *A. leptophrys*.

The subtlety of this interaction between thermoregulation and habitat utilization by the lizards contrasts with the ability of birds and mammals to extend activity into periods of inclement weather or stressful habitats. It seems unlikely that such small differences in the physical parameters of microhabitats limit the habitats utilized by birds and mammals. Examples of habitat partitioning among syntopic species of endothermal vertebrates appear to reflect primarily biological factors such as competition or predation instead of biophysical effects (Orians and Willson, 1964; Grant, 1972; Brown et al., 1979; Nevo, 1979; Landres and MacMahon, 1980).

Functional Properties of Ectothermy

Thermoregulatory behavior is a feature of the biology of many species of ectothermal tetrapods. The most extensive documentation of this phenomenon is based on lizards, but other reptiles and many amphibians also thermoregulate (Brattstrom, 1970; Avery, 1982). Reptilian thermoregulation was recognized independently in the late 1930s by R. B. Cowles and C. M. Bogert (1944), who worked in the deserts of California, and by A. Sergeyev (1939) in Asia. More than three decades after the initial discovery of reptilian thermoregulation, new subtleties and complexities are still being recognized. These include the existence of temperature gradients within an animal's body that are maintained by physiological or behavioral adjustments, changes in the body temperatures an animal maintains in response to nutritional or reproductive state, and the flexibility of thermoregulation in habitats of varying availability of radiant energy (Ruibal and Philibosian, 1970; White, 1973; Huey and Webster, 1976; Regal, 1978; Lang, 1979; Avery, 1982; Bartholomew, 1982; Huey, 1982).

Despite the complexities of thermoregulation, generalizations apply to most species of amphibians and reptiles. In particular, their thermoregulatory behavior permits these animals to achieve a considerable degree of stenothermy. The range of body temperatures they experience during activity on a daily or seasonal basis is limited to 10° C in a variety of species and to 4–5° C in many lizards. The body temperatures at which a species carries on its normal daily functions is the activity temperature range (Cowles and Bogert, 1944). The activity temperature range integrates the biochemical and physiological properties of a species with its ecological setting.

From a physiological perspective limiting the range of body temperatures experienced during activity simplifies the problem of integrating diverse biochemical processes that have different temperature sensitivities and that proceed in a milieu that is itself altered by changing temperature. Adaptations that adjust an animal's functional properties to its species-specific activity temperature range have been demonstrated at all levels of biological organization from the molecular to the organismal (Dawson, 1975; Bennett and Dawson, 1976; Pough, 1980b).

The specializations of reptiles and amphibians for ectothermy include morphological features as well as biochemical and physiological characteristics. Reptilian heart morphology permits systemic blood flow to be augmented as a thermoregulatory mechanism, and the absence of an insulative covering of hair or feathers permits effective use of cutaneous circulation to enhance heat exchange and thereby to stabilize body temperature (Cowles, 1958; White, 1976). Some amphibians achieve the same end by absorbing water through the ventral surface of the body and evaporating it from the dorsal surface (Lillywhite, 1970).

Energetic Consequences of Ectothermy

The diversity and interlocking nature of the adaptations that allow amphibians and reptiles to function effectively as ectotherms indicate that this form of thermoregulation should be regarded as a specialization of those classes. The principal consequence of the specialization of amphibians and reptiles as ectotherms is a reduction in their energy requirements. Because they do not have to generate heat by metabolic processes, the resting metabolic rates of amphibians and reptiles at body temperatures in their activity temperature ranges are nearly an order of magnitude lower than those of birds or mammals of the same body masses (fig. 1). These low resting metabolic rates are only part of the energy saving achieved by an ectotherm in comparison with an

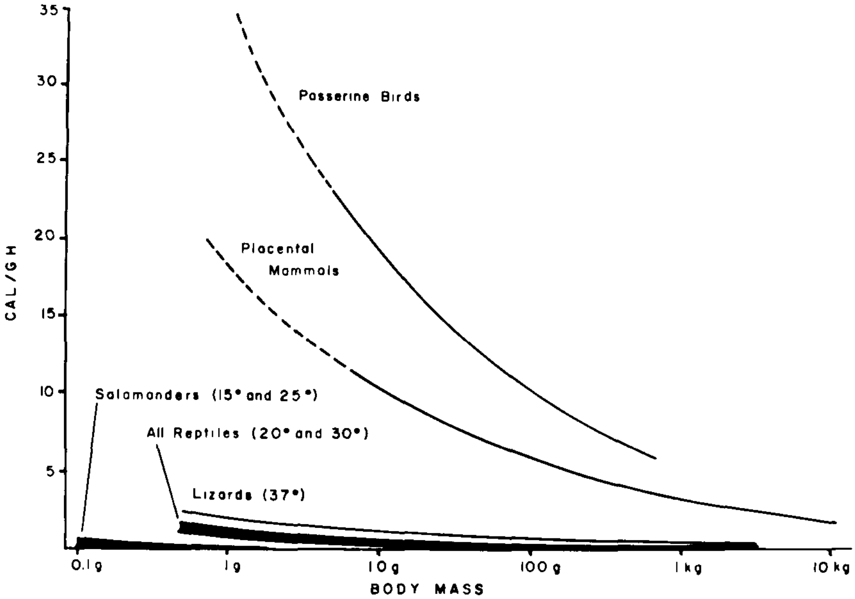

Fig. 1. Resting metabolic rate as a function of body size in terrestrial vertebrates. Metabolic rates for salamanders are shown for 15° and 25° C (as the lower and upper limits of the darkened area), and data for all reptiles combined are shown at 20° and 30° C. The metabolism-mass relationship for anurans falls within the "all reptiles" area, and the relationship for nonpasserine birds is similar to that for placental mammals. Dotted portions of the lines show hypothetical extensions into body sizes below the minimum adult sizes of most birds and mammals. From Pough (1980a). Reprinted from *The American Naturalist* by permission of The University of Chicago Press. © 1980 by The University of Chicago.

endotherm. An important additional component is the reduction in metabolic rate that accompanies daily periods of low body temperature. Activity temperatures are maintained for only a portion of the day; inactive animals normally move to shelters where their body temperatures fall to ambient levels. (Some nocturnally active species have higher body temperatures when they are inactive during the day than when they are foraging at night.) Under laboratory conditions many reptiles select low temperatures for a portion of the day even when high temperatures are continuously available to them (Regal, 1980).

The Q_{10} for resting metabolic rate in amphibians and reptiles is usually between 2 and 3 at temperatures below the activity temperature range, and a daily period of low body temperature reduces the energy requirement of an ectotherm substantially. For example, within its activity temperature range the western fence lizard (*Sceloporus occidentalis*) has a resting metabolic rate 13% of that of a bird or mammal of the same body mass. A free-ranging fence lizard, however, consumes only 3–4% as much energy per day as a bird or mammal because its body temperature falls when it is inactive (Bennett and Nagy, 1977). The energetic savings of torpor that are enjoyed by a relatively few species of birds and mammals are an integral part of the low energy flow of amphibians and reptiles.

Daily energy requirements are only one facet of the difference between endotherms and ectotherms. The ecological consequences of ectothermy permeate virtually all aspects of the biology of amphibians and reptiles, and these animals have a variety of behavioral and ecological features that differ markedly from those of birds and mammals. For example, activity can readily be suspended for days or longer. The herbivorous lizard *Sauromalus obesus* stops feeding and retreats to a rock crevice when the water content of the plants it eats falls below the level it requires to maintain a positive water balance. Some of the lizards fast for 8 months until succulent vegetation becomes available the following spring (Nagy, 1972). Male water snakes (*Nerodia sipedon*) forage actively during the spring but then become secretive and subsist upon adventitiously encountered prey (Feaver, 1977). A balance between the advantages of obtaining additional food and the risks of predation during foraging may explain this behavior. The Neotropical forest lizard *Corytophanes cristatus* appears to spend virtually all its time perched on tree trunks, motionless but alert. Its cryptic color pattern and body form make it hard to detect until it moves. This species of lizard feeds on large insects and ignores small prey. Because large insects are relatively rare in the forest habitat, individual *Corytophanes* may feed less often than once a day. The sedentary behavior of this lizard species may be a response to intense predatory pressure (Andrews, 1979). Extremely secretive or sedentary habits as a way of avoiding predators may be more widely developed among amphibians and reptiles than among birds and mammals because of the low energy requirements of the ectotherms.

Many species of amphibians and reptiles exploit transient food supplies and rely upon energy stores, rather than an alternative food source, to endure periods when food is not available. Egg-eating snakes (*Dasypeltis*) feed during the two annual breeding periods of birds and fast during the intervening months (Gans, 1952). Terrestrial salamanders may frequently have their access to food limited during warm, dry days (Jaeger, 1980). On most sampling days a majority of red-backed salamanders (*Plethodon cinereus*) had negative energy budgets but a few individuals contained more than a day's metabolic requirement. A feast-or-famine existence of this sort is more feasible for an ectotherm than for an endotherm. The ability to exploit an abundant resource for a brief period and then to await its renewal in an alert but energetically inexpensive condition offers ectotherms an opportunity to divide resources in ways that are probably not available to endotherms.

Metabolic Responses to Exercise

When mammals are stimulated to the maximum levels of activity, they can sustain rates of oxygen consumption 5–10 times the resting rates. (There are exceptions to this generalization; see Ruben and Battalia, 1979, for an example.) Reptiles and amphibians are capable of the same relative increase in their resting rates during activity (Bennett, 1978), but because their resting rates are nearly an order of magnitude lower than those of birds and mammals, the maximum rates of oxygen consumption by the ectotherms barely reach the resting rates of the endotherms. The energetic cost of locomotion is the same for ectotherms and endotherms with similar locomotor modes (Bennett, 1978; Gleeson, 1979), and many amphibians and reptiles rely upon anaerobic metabolism for more than half the total energy input associated with high levels of activity (Bennett and Dawson, 1976; Bennett, 1982). Because this anaerobic metabolism depletes metabolic substrates and high-energy phosphate stores, the animals tire quickly. Many amphibians and reptiles become completely exhausted by 3–5 min of activity and require several hours of inactivity to return lactate levels to resting concentrations (Gratz and Hutchison, 1977; Hutchison et al., 1977). Mammals obtain a far smaller proportion of their total energy input from anaerobiosis (Ruben and Battalia, 1979).

A physiological response to exercise that involves rapid exhaustion and requires several hours for recovery is not, at first glance, an obviously advantageous specialization for an animal, but it does have important benefits in an energetic context. The high maximum rates of oxygen consumption achieved by birds and mammals are a consequence of their high resting metabolic rates. Thus the endurance of birds and mammals is purchased at the price of continuously high energy requirements. In contrast, reliance upon anaerobic metabolism for energy generation gives amphibians and reptiles the ability to mobilize energy when it is required without the continuing cost of maintaining a high resting metabolic rate or an elaborate enzymatic control system.

VARIATIONS ON A THEME

In general terms ectothermy and a dichotomous system of energy generation are intimately related physiological features of amphibians and reptiles that form the basis of their low-energy approach to terrestrial vertebrate life. Ectothermy permits low resting metabolic rates, and the daily energy requirements of amphibians and reptiles are at least an order of magnitude lower than those of birds or mammals of similar body size. Reliance upon anaerobic metabolism allows rapid energy input when it is needed without the high maintenance costs that are the concomitant of an exercise physiology based upon aerobic energy generation. These two features characterize amphibians and reptiles and account for the ecological and behavioral features that distinguish them from birds and mammals (Pough, 1980a).

All amphibians and reptiles are clearly not identical, however. They differ morphologically, ecologically, and behaviorally—do they also differ physiologically? If there are physiological differences among amphibians and reptiles, can patterns of adaptation be detected within those classes that express the same sorts of differences among amphibians and reptiles as those that distinguish the ectotherms from birds and mammals? If amphibians and reptiles, in general terms, are low-energy specialists compared to birds and mammals, are there taxa or ecological groupings within the ectotherms that carry such specializations to an extreme and others that have evolved away from those features, possibly toward higher energy flows?

Energy Requirements and Body Forms

One of the striking consequences of the low energy requirements of amphibians and reptiles is the release it permits from many of the constraints that limit the body size and proportions of endotherms. A large animal requires a larger total quantity of food in a day than a small one, but because energy requirements for an animal at rest increase approximately as the 0.75 power of body mass, a small animal requires more food per unit mass of body tissue than a large animal. Because of that allometric relationship the mass-specific energy requirements of endotherms increase almost asymptotically at small body sizes (fig. 1). The narrowness of the thermoneutral zones of many small endotherms (Tracy, 1977) raises the energy requirements of these animals still further. The result of these forces is a nearly infinite energy requirement for a very small endotherm, and it is not feasible to satisfy an infinite energy requirement in a finite world. Instead, most of the endotherms we normally think of as being very small, such as mice and sparrows, have body masses in the range of 10–20 g. Of 82 species of rodents (pocket mice, mice, voles, rats, squirrels, and gophers) tabulated by Millar (1977), none have adult body masses below 5 g and only one is smaller than 10 g. Most of the species have body masses greater than 20 g.

The relatively large size of these small mammals contrasts with the extremely small body size of many amphibians and reptiles (Pough, 1980a). A substantial number of species of amphibians and reptiles have adult body masses less than 1 g, an extreme not approached by birds or mammals. Amphibians are especially small tetrapods: 20% of the species of salamander and 17% of the anurans are smaller than 1 g as adults, and 65% of salamanders and 50% of anurans are smaller than 5 g (fig. 2). These animals occupy an adaptive zone that is bare of mammals or birds and may have their primary predatory and competitive interactions with arthropods (R. G. Jaeger, personal communication).

Reptiles as a group are larger animals than amphibians, but nonetheless 8% of the species of lizards and 2–4% of the snakes and amphisbaenians are smaller than 1 g as adults. Nearly 80% of the species of lizards weigh less than 20 g and thus are substantially smaller than most species of birds and mammals.

There are striking heterogeneities in the distributions of body sizes among amphibians and reptiles. All of them are ectotherms, but by no means all of them are small. Do the patterns of body size follow energetic lines? That is, are the orders with many small species also characterized by exceptionally low metabolic rates, or do other factors outweigh energetic considerations?

The variation in metabolic rates among amphibians and reptiles is very much less on an absolute scale than the difference between ectotherms and endotherms. A priori it appears that there would be relatively less scope for selection of especially low energy approaches to life from the small variation among ectotherms than there is in the large difference between ectotherms and endotherms.

Among the amphibians, salamanders have lower metabolic rates than anurans (which fall within the "all reptiles" area in fig. 1) and they also have relatively more small species and fewer large ones than anurans. These two orders of amphibians do follow the pattern suggested by the hypothesis that energy requirements limit the feasibility of small body masses. Lizards and snakes, however, contradict that prediction. Lizards have many more small species and fewer large ones than snakes, but the metabolic rates of lizards and snakes do not differ when they are measured at the same temperatures (Bennett and Daw-

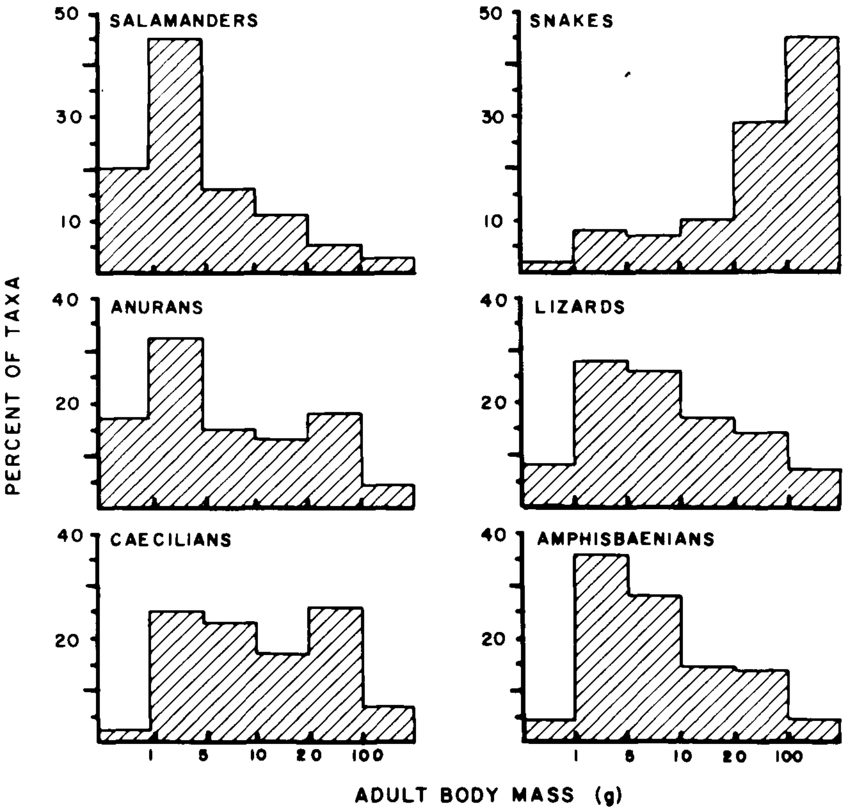

Fig. 2. Adult body masses of amphibians and reptiles. The percentages of the total number of taxa surveyed with body masses in the ranges < 1, 1–5, 5–10, 10–20, 20–100, and > 100 g are shown. Sample sizes: salamanders, n = 198; anurans, n = 1,330; caecilians, n = 160; snakes, n = 1,592; lizards, n = 1,780; amphisbaenians, n = 110. Based on table 2 in Pough (1980a).

son, 1976). Lizards in general maintain higher body temperatures than snakes (Brattstrom, 1965; Avery, 1982) and would have correspondingly higher metabolic rates than snakes during their periods of activity. Thus, if there is a difference in energy costs between lizards and snakes it is in a direction opposite that predicted by the hypothesis that the association between small body size and low metabolic rate seen in a comparison of endotherms with ectotherms can be extended to comparisons among ectotherms.

Caecilians and amphisbaenians are burrowing animals that are subject to constraints on body size and shape that are different from those of surface-dwelling animals. The generally small body masses of these fossorial animals probably are a response to the requirements of tunneling (Gans, 1960). It is likely that these mechanical considerations are the primary factors responsible for the body size and shapes of fossorial reptiles and amphibians rather than any aspect of the resting energy requirements of the animals.

It is probable, however, that such attenuate burrowing animals can only be ectotherms because of the great heat loss that would be associated with large surface-to-mass ratios that result from the elongate shapes. Even the degree of elongation of the trunk that characterizes mammals such as weasels is purchased at an energetic cost; weasels lose twice as much heat at low ambient temperatures as mammals of the same body size but more conventional shapes (Brown and Lasiewski, 1972). An endothermal snake is probably a physiologically impossible package, despite the advantages of a serpentiform body. Serpentiform tetrapods have evolved in diverse lineages of amphibians and reptiles since the first appearances of the two classes. Elongate species occur among salamanders, caecilians, amphisbaenians, and lizards in addition to snakes. The adaptive radiation of snakes is especially striking because of the ecological diversity that has been achieved within a very specialized body form. Snakes have radiated so widely since their appearance in the Cretaceous that the Neogene could reasonably be called the "Age of Snakes" (Stanley, 1979). Part of the success of snakes may derive from their relative freedom from competition with endotherms of similar body form. That freedom may explain why so many more species of snakes than lizards have body masses in the size range of birds and mammals (Pough, 1983).

Snakes use hunting methods that are not accessible to predatory mammals, but lizards and salamanders do not have that advantage. Species of lizards and salamanders in size ranges that overlap those of small mammals probably exploit the same sorts of prey in the same manner as do the endotherms. The very small body size of many ectotherms is a morphological specialization that opens to them a feeding niche that is largely free of competition from mammals and birds. Their small body sizes add a qualitative difference to the roles of ectotherms and endotherms in an ecosystem. Not only are small amphibians and reptiles producing biomass efficiently, but in addition they are exploiting prey species too small to be directly available to birds and mammals.

Dietary Habits and Energy Requirements

There is a considerable amount of variation in the basal metabolic rates of species of mammals, and some of this variation cuts across taxonomic divisions and appears to be related to specific environmental or biological features (McNab, 1974, 1980). Species that have a food supply that varies in abundance seasonally, that collect food in an indiscriminate manner, or that use food with a low energy content or with high processing costs appear to have low basal metabolic rates. In contrast, species that utilize stable food resources or food with a high energy content have high metabolic rates. Species from temperate and arctic regions have higher metabolic rates than species from the tropics. Desert-dwelling species may have lower metabolic rates than species from mesic habitats. Distinguishing climatic and dietary influences in these generalizations is complicated by the geographic limitation of some foodstuffs and the relationship between metabolism and water requirements. The following phenomena could be expected to have counterparts among amphibians and reptiles:

1. Insectivorous (and sanguinivorous) species of bats have lower metabolic rates than species with frugivorous, nectarivorous, or carnivorous food habits (McNab, 1969).
2. Mammals that feed on ants or termites have low basal rates of metabolism (McNab, 1974, 1980).
3. Arboreal folivores have low basal metabolic rates, and those rates vary inversely with the proportion of the diet composed of leaves (McNab, 1978).
4. Carnivores appear to have high metabolic rates (Iverson, 1972).

Amphibians and reptiles provide relatively little scope to test the generality of these phenomena. There appears to be less diversity in the dietary habits of most groups of amphibians and reptiles than there is among mammals. All adult amphibians are carnivorous. Differences in the sorts of prey they consume appear to result from differences in foraging sites, foraging methods, and modes of locomotion (Emerson, 1976; Toft, 1980), and the sorts of metabolic specializations that accompany those dietary specializations are probably more subtle than differences in resting metabolic rates. All snakes are carnivorous or insectivorous, as are all crocodilians, all amphisbaenians, and the tuatara. Only among turtles and lizards is there variation in diet on the scale seen among mammals.

An analysis of the dietary habits of turtles is complicated by taxonomic and ecological divisions that parallel food types. The most fully terrestrial turtles, the tortoises (Testudinidae), are also the largest group of herbivores. The most carnivorous turtles (Chelydridae, Trionychidae, Chelidae) are also among the most aquatic. Many species of turtles with ecological requirements between these extremes are relatively omnivorous. Careful selection of species would allow comparisons between at least some categories of food habits, but there are too few metabolic measurements of turtles to warrant an analysis at present.

Lizards offer more opportunity than other reptiles for analyzing metabolic correlates of dietary habits, but their ectothermy introduces complications that are not present in the case of mammals. A lizard's metabolic rate varies with the temperature at which the measurement is made, and this variation is neither linear nor even smoothly curvilinear. Ectotherms, unlike endotherms, do not have a thermoneutral zone in which the metabolic rate reaches a minimum; instead, the metabolic rate of an ectotherm declines with decreasing temperature until the animal dies. The ecological analogue of the thermoneutral zone of an endotherm is the activity temperature range of an ectotherm. It would be logical to make comparisons of species when each was measured at the midpoint of its own activity temperature range. Unfortunately, the activity temperature ranges are known for comparatively few species of reptiles. In the absence of that information it is necessary to make comparisons among species using measurements at a common arbitrary temperature. This compromise may introduce distortion because the midpoints of the activity temperature ranges of species of lizards vary by nearly 20° C (Brattstrom, 1965; Avery, 1982) and Q_{10} values for whole-animal oxygen consumption range from 1.5 to 3.1 (Dawson, 1967).

In figure 3 the metabolic rates of lizards at body temperatures of 30° and 37° C are compared to the regression derived for all lizards at those temperatures (Bennett and Dawson, 1976). The food habits of the species reflect a pattern of differential resource use by lizards of different body sizes: small species are usually insectivorous whereas larger species are carnivorous (preying on animals larger than insects), omnivorous, or herbivorous (Pough, 1973). Energetic relationships appear to underlie this pattern. Small lizards can make an energy profit by ingesting insect-size packages of energy. At larger body masses the cost of capturing prey is greater, and at some body size it becomes energetically unfeasible to rely solely upon insects as food. At that body size a lizard can incorporate larger prey species into its diet or adopt a herbivorous diet. Either response requires behavioral, morphological, and probably physiological specializations. The importance of the energetic constraints is emphasized by the similarity of body sizes at which the dietary transitions occur in several families of lizards. Among skinks, agamids, iguanids, gerrhosaurids (Pough, 1973), and gekkonids the change in diet occurs among species with adult body masses be-

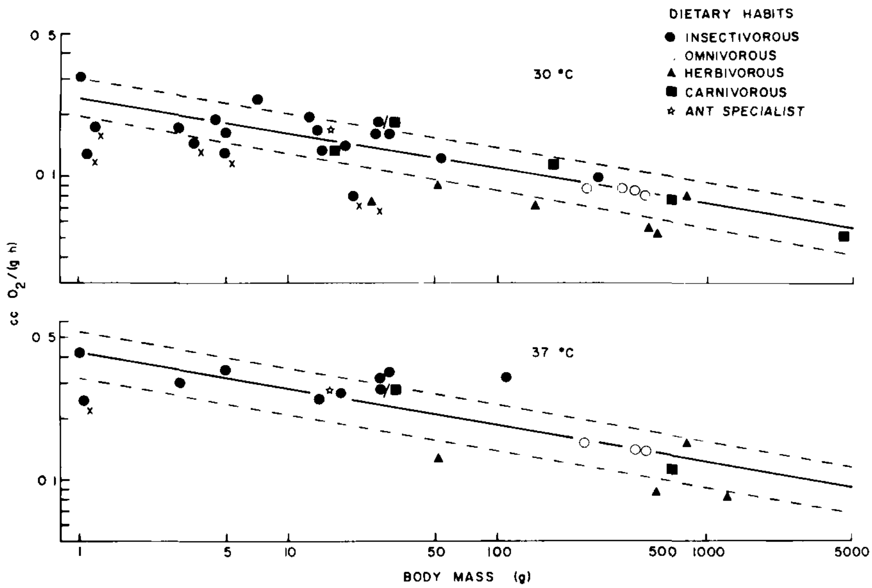

Fig. 3. Metabolic rates of lizards in relation to diet. Points marked with an *X* are xantusiids. Metabolic rates and regressions for oxygen consumption versus body mass at 30° and 37° C (*solid lines*) are from Bennett and Dawson (1976); data for xantusiids are from Mautz (1979). *Dashed lines* show metabolic rates 75% and 125% of the expected values.

tween 100 and 300 g. Lizards smaller than 100 g as adults are virtually all insectivorous, whereas lizards larger than 300 g are carnivores (for example, *Varanus* and *Tupinambis*), herbivores (*Iguana, Uromastyx*), or omnivores (*Tiliqua, Trachydosaurus*).

Juveniles of large species of lizards face an interesting quandary that is particularly striking in the case of herbivores. The normal adult diet of their species may be inappropriate for them or even entirely unavailable. The cost of prey capture for a juvenile of a large species should be the same as that for an adult of a smaller species, and to the extent that these energetic constraints determine dietary habits, it would be reasonable to expect juvenile lizards to have diets appropriate to their body size rather than to their species. A considerable literature of field observations (summarized by Pough, 1973) indicates that there is an ontogenetic change in the diet of many large species of lizards from insectivorism as juveniles to herbivority as adults. Insofar as it is possible to identify the body sizes at which adult diets are adopted, they appear to fall in the 100–300 g range that characterizes the shift of dietary habits in interspecific comparisons. Such a dietary shift would seem potentially advantageous for a small lizard because there is about twice as much assimilable energy in a unit mass of animal tissue as there is in vegetation (Pough, 1973). That difference may be especially important for small lizards that have guts too small to process large volumes of food. When a juvenile *Sauromalus obesus*, a specialized herbivore as an adult, adopted a diet of insects in the laboratory, it grew faster than two cagemates that ate only plants (Mayhew, 1963), and juveniles of the herbivorous lizard *Dipsosaurus dorsalis* grow more slowly than do juveniles of five sympatric species of insectivorous lizards (Parker, 1972).

Structural modifications of the colon of several genera of "truly herbivorous" iguanine lizards may be associated with extreme specialization for herbivority (Iverson, 1980). Similar structures were found in a genus of agamid herbivores (*Uromastyx*) and one herbivorous species of skink (*Corucia zebrata*). These specialized herbivores may show less ontogenetic change in diet than less specialized genera like *Basiliscus* and *Physignathus* that lack colic modifications but nevertheless include a large quantity of plant material in their diets as adults (Iverson, 1982). Ontogenetic changes in the diets of lizards may be quite variable and depend upon the relative availability of different sorts of food. Some of the changes may be subtle: W. J. Mautz (personal communication) has observed juvenile *Dipsosaurus* feeding predominantly on very small (10 mg) flowers. He suggests that this situation represents the utilization by juvenile lizards of an energy-rich food source that is not readily harvested by adults.

Three groups of species can be distinguished with varying degrees of conviction in figure 3, and some of the dietary relationships that have been detected among mammals do not appear to apply to lizards.

1. Xantusiid lizards, regardless of diet, have low metabolic rates.
2. Herbivorous lizards have metabolic rates that are generally lower than expected for their body masses. The relationship between herbivority and low metabolic rates in lizards is greater at 37° C than at 30° C.
3. At 30° C carnivorous lizards have metabolic rates that equal or slightly exceed those expected for their body masses, but the elevation is small. There are too few data at 37° C to extend the comparison to that temperature.

The eleven nonxantusiid species of insectivorous lizards represent six families and three infraorders. These insectivorous lizards generally conform to the metabolic rates expected on the basis of body mass. A combination of two factors probably explains why low metabolic rates are observed for insectivorous bats and not for insectivorous lizards.

First, insectivorism is the predominant dietary mode among lizards, and insectivorous species contributed more of the data on which the general relationship was based than did any other dietary category. Species of lizards with adult body masses less than 100 g are mostly insectivorous, and 93% of the species of lizards have body masses in that range (Pough, 1973, 1980a). Morphological specializations for eating insects have apparently distinguished lizards since their evolutionary origin in the Triassic (Carroll, 1977b). Certainly an adaptive zone of that antiquity and one that includes more than 90% of the species of a suborder of animals can reasonably be considered typical of that taxon, but the restricted range of body sizes of insectivorous lizards introduces problems of interpretation when comparisons are made to species that differ in both diet and body size. Some of these problems may be avoided if omnivorous lizards, which also conform to the general metabolic relationship, can be considered the extension of a generalized lizard pattern to large body sizes.

Second, there are biological reasons to expect that the low metabolic rates of insectivorous bats would not be duplicated by lizards. Seasonal shortages of flying insects appear to be the basis for the low metabolic rates of insectivorous bats. Birds that feed on flying insects also have low metabolic rates, whereas birds that forage for insect larvae normally have high rates (McNab, 1974). The sorts of insects preyed upon by lizards may not have the fluctuations in abundance that characterize flying insects. Furthermore, low temperatures and dry periods may simultaneously curtail the activity of lizards and of their insect prey, thereby insulating the lizards from some effects of a shortage of food.

Only one ant-eating specialist, the horned toad *Phrynosoma m'calli*, is represented by a metabolic measurement in figure 3. Its metabolic rate is no lower than those of other insectivorous lizards. The low metabolic rates of ant-eating mammals may represent a combination of responses to the quantity of nonnutritive material engulfed during feeding and to the metabolic costs of detoxifying the defensive chemical secretions of the ants (McNab, 1980). The feeding behavior of ant-eating lizards appears to be as selective as that of other insectivorous lizards, and lizards have become specialized for eating ants without the extensive morphological modifications of the jaws and tongue that characterize ant-eating mammals. Probably the small body sizes and low energy requirements of insectivorous lizards make the transition to eating very small insects like ants relatively simple. Far more extensive adaptation has clearly been necessary to permit mammals to satisfy their energy requirements with ant-size prey.

Carnivorous lizard species at 30° C have metabolic rates that range from just below those expected from body mass to about 20% above expected rates, whereas most herbivorous lizards have rates that are 25% below expectation at 30° C and 35% below at 37° C. These relative deviations from expected metabolic rates are similar to the median values observed among rodents from xeric versus mesic environments, bats, ungulates, and mustelids (McNab, 1969, 1973, 1978; Iverson, 1972).

Several problems of scaling complicate interpretation of the divergent metabolic rates of carnivorous and herbivorous lizards. The extrapolation from measurements based primarily on small lizards has already been discussed. That difficulty is not encountered among mammals because food habits are not so closely tied to body size.

A second scaling problem derives from the absolute magnitudes of the differences in metabolic rates among groups of lizards with different diets. Because the resting metabolic rates of lizards are very much smaller than those of mammals, the absolute difference in the quantity of energy expended by a carnivore and a herbivore is also small. For 500 g individuals, the approximate difference in the basal metabolic rates of low-rate versus high-rate rodents is 0.53 cc O_2/g·h (derived from fig. 2 in McNab, 1973). The difference between the estimated resting metabolic rates of a carnivorous and herbivorous lizard at 30° C is only 0.022 cc O_2/g·h.

Which measure of variation in energy use is meaningful—the absolute quantity of energy or the relative requirement—depends upon whether the energy expenditure being considered scales with metabolic rate or with body mass. In a situation in which an animal's requirement for energy is proportional to its metabolic rate, a given relative reduction in metabolism has the same importance at any absolute level. The length of time an animal can fast is an example of that situation. If the energy requirement is related to body mass—the cost of locomotion, for example—it is the absolute quantity of energy involved that is critical.

That line of reasoning suggests that variations in the basal metabolic rates of endotherms are more likely to have adaptive significance than similar variations among ectotherms. Because the energy flow of an endotherm is so much greater than that of an ectotherm, modifications of that flow are more likely to have both relative and absolute significance to endotherms than to ectotherms. Alternatively, the relative change in metabolic rate of an ectotherm that is necessary to produce a significant absolute change may be so great that it must be accompanied by a broad range of changes in ecology and behavior. Both lines of reasoning lead to the hypothesis that adaptive alterations of energy requirements, per se, are likely to be more widespread among endothermal tetrapods than ectotherms.

An example of the sorts of interlocking adaptations that may be the rule among amphibians and reptiles is provided by lizards of the family Xantusiidae (Mautz, 1979). The xantusiids are a distinctive family containing fewer than a dozen species of lizards with body masses ranging from 1 to 30 g. The species occupy a variety of habitats including deserts, montane forests, and tropical lowlands. The unifying characteristic of these ecologically diverse lizards is secretive behavior. They appear to restrict their activity to the confines of their retreats, rarely venturing from shelter. This reclusive behavior presumably limits the food resources available to the lizards. Thus the low metabolic rate that characterizes these lizards regardless of habitat or diet (fig. 3) is probably an adaptive response to the energy restrictions produced by their secretive behavior. Other facets of the biology of xantusiids appear also to reflect specialization for extremely low energy flow: xantusiids regulate their body temperatures at low levels and have slow growth rates, late maturity, and the lowest reproductive potentials known among small lizards (Mautz, 1979).

The metabolic rates of salamanders are very similar to those of xantusiids, and many species of salamanders are secretive, sedentary animals (Feder, 1976). These observations suggest that the view of ectothermal tetrapods as specializing in a low-energy-flow approach to life can be extended to particular groups of ectotherms that have carried those characteristics beyond the level of most species. Achieving that degree of specialization appears to require a broad spectrum of modifications of morphology, ecology, and behavior as well as of physiology.

The existence of especially low energy flow specialists among ectothermal tetrapods complements the view presented by McNab (1980) that high metabolic rates among endotherms are advantageous because they are related to high reproductive potential. That contrast emphasizes the dichotomous approaches of ectotherms and endotherms to terrestrial vertebrate life. Investigations of species in each group that appear to be specializing in the direction of the other group—that is, low-energy-flow endotherms and high-energy-flow ectotherms—

should be especially instructive in defining the differences between the ectothermal and endothermal modes of life.

ARE THERE MORE SUBTLE PATTERNS?

Predatory Behavior and Energetic Efficiency

Function, in its broadest context, is the basis for comparisons in physiological ecology, and detailed, quantitative information about the behavior and activities of organisms under natural conditions is essential. Activities that can be observed and quantified under field conditions and that seem to be important in shaping physiological systems include foraging, intraspecific interactions, and possibly defensive behavior.

Defensive behavior has received the most attention of these three topics, but it is the least likely to lead to insights and has not yet produced any useful generalizations. It is not clear that defensive behavior, as such, often has a directing role in shaping large elements of the biology of most species of animals. Among amphibians and reptiles it seems more likely that the defensive behaviors available to a species are limited by the species' other adaptations. Among anurans, for example, it is probable that the morphological specializations associated with walking and burrowing evolved in response to the selective advantage of exploiting concentrated sources of food (Emerson, 1976). Those modifications precluded long, rapid leaps and presumably required the concomitant evolution of chemical defenses and the associated colors and behaviors that characterize many anurans with static modes of escape from predation. Similarly, among snakes the muscle morphology that allows constriction and that which permits rapid locomotion appear to be at opposite ends of a continuum (Ruben, 1977). It would be perverse to interpret the divergent physiological characteristics of a constrictor and a racer primarily as adaptations for static and active defense.

In contrast to the derived nature of defensive behaviors, foraging mode lies at the core of the "adaptive syndrome" of features that characterizes a species (Eckhardt, 1979). The foraging modes of amphibians and reptiles extend through a spectrum from passive (or "sit-and-wait") foragers through various levels of "cruising foragers" to "intensive foragers" (terminology of Regal, 1978). The focus upon a spectrum of behaviors instead of the usual emphasis on only two extremes seems essential if accurate characterizations are to be attempted.

Field and laboratory observations of foraging modes of lizards have identified species in each category. In a laboratory apparatus the rate of spontaneous activity of the teiid lizard *Ameiva chrysolaema* was the same as that of a small mammal, whereas the iguanid lizard *Leiocephalus schreibersi* moved less than 5% as much. These differences resembled the behaviors of the animals in the field. *Ameiva* were moving during 70% of their daily activity period, whereas *Leiocephalus* moved less than 1% of the day (Regal, 1978). In the laboratory apparatus the xantusiid lizard *Klauberina riversiana* was active at a rate intermediate between that of the intensive and passive foragers. The behavior of *Klauberina* under field conditions is unknown, but related lizards appear to fit the description "cruising foragers" (Mautz and Case, 1974; Mautz and Lopez-Forment, 1978). In the thorn scrub habitat of the island of Bonaire the iguanid lizard *Anolis bonairensis* appears to be another cruising forager; the individuals observed spent 32% of their time in locomotion. In the same habitat a teiid lizard, *Cnemidophorus murinus*, spent 77% of its time in locomotion (Bennett and Gorman, 1979).

The generalized predatory mode of lizards may lie within the cruising forager part of the spectrum, with passive foragers and intensive foragers representing specializations in opposite directions (Regal, 1978). Because foraging activities occupy a large portion of an animal's day, expose it to the risk of predation, and may represent an important energy cost, it is likely that the energetic requirements and consequences of different foraging modes will be reflected in a variety of features of the biology of an animal species. Can any general patterns be traced among amphibians and reptiles?

Intensive foraging is an energetically expensive behavior. While walking at foraging speed (0.14 km/h) at a body temperature of 40° C, a *Cnemidophorus murinus* consumes 0.89 ml O_2/g·h. This rate is approximately four times the resting metabolic rate at that body temperature (Bennett and Gleeson, 1979). The estimated metabolic rate of the sympatric cruising predator, *Anolis bonairensis*, is 0.45 ml O_2/g·h during activity at 33° C, three times its resting rate (Bennett and Gorman, 1979).

Assuming that the hourly metabolic cost of an intensive forager is twice that of a cruising forager, what is the energy return on that investment? A study of the iguanid lizard *Sceloporus jarrovi* and the teiid *Cnemidophorus exsanguis* addressed that question (Andrews, 1982). The two species occur together in pine-oak woodlands in southeastern Arizona, and females of the two species are approximately the same size and have similar diets. *Sceloporus jarrovi* appear to conform to the pattern of passive or cruising foragers; individuals remain exposed for long periods on rocks or trees. *Cnemidophorus exsanguis*, like the other teiid lizards studied, was active for only a portion of the day and moved over the ground surface in its search for prey. The estimated daily metabolic cost for *C. exsanguis* was 1.4 times that of *S. jarrovi* and its calculated daily food intake exceeded that of the iguanid lizard by the same factor. The relative allocation of net energy to production by females of the two species was similar—32% of assimilated energy for *C. exsanguis* and 28% for *S. jarrovi*. As a consequence of its higher energy intake, the absolute quantity of energy allocated to production by the teiid was 1.7 times that of the iguanid. Thus the cost of the intensive foraging utilized by *C. exsanguis* was balanced by the additional energy obtained and was translated into a higher mass-specific production than was characteristic of the less active predator.

Two features common to these three interspecific comparisons suggest a general relationship among foraging mode, temperature regulation, and production efficiency among lizards. In each case the intensive forager is active at a high body temperature for a restricted period, whereas the passive or cruising forager has a lower body temperature and a longer period of activity (table 1).

Intensive foraging could be efficient for a species of lizard that maintains a high activity temperature if the cost of locomotion increases less rapidly with increasing body temperature than the resting metabolic rate. Under those circumstances, intensive foraging would require a smaller factorial increase in resting metabolic rates at high body temperatures than at low temperatures.

The cost of locomotion is independent of body temperature over a broad range of speeds and temperatures in two large species of lizards, *Iguana iguana* and *Uromastyx aegyptius*, but not in a small species, *Dipsosaurus dorsalis* (Moberly, 1968; Dmi'el and Rappeport, 1976; John-Alder and Bennett, 1981). If locomotion for most lizards requires a smaller factorial increase in resting metabolism at high body temperatures than at low temperatures, one can predict that intensive foragers will be primarily species that have high activity temperature ranges, whereas cruising and passive foragers should be found among species with lower body temperatures. Intensive foragers may also have higher capacities for aerobic metabolism than cruising or passive foragers (see Pough, 1980a).

High activity temperatures are achieved at a high energy cost, however, and that cost should be incompatible with a low-energy-flow, high-efficiency approach to life. The metabolic cost of intensive forag-

TABLE 1

BODY TEMPERATURES AND DURATION OF ACTIVITY PERIODS OF SYNTOPIC PAIRS OF LIZARDS WITH DIFFERENT FORAGING MODES

PASSIVE OR CRUISING FORAGERS			INTENSIVE FORAGERS			SOURCE
Species	Average Body Temperature	Duration of Activity	Species	Average Body Temperature	Duration of Activity	
Leiocephalus schreibersi	....	Sunrise to sunset	*Ameiva chrysolaema*	....	4–5 h	Regal, 1978
Anolis bonairensis	33.4° C	Sunrise to sunset	*Cnemidophorus murinus*	40.4° C	6 h	Bennett and Gorman, 1979
Sceloporus jarrovi	34.2° C	8–12 h	*Cnemidophorus exsanguis*	40.0° C	3–4 h	Andrews, 1981

ing is apparently limited by short activity periods. While they are not foraging, both species of *Cnemidophorus* that have been studied allow their body temperatures to fall more than 10° C, to levels below those maintained by the still-active passive or cruising foragers. It is the long daily period of low body temperature that is responsible for the high production efficiency of *C. exsanguis* (Andrews, 1982).

These generalizations, although plausible, are based on comparisons of lizards from only two families, Iguanidae and Teiidae, drawn from the two great divisions of the lizards, the Ascalobata and Autarchoglossa. These two groups of lizards differ in many aspects of their behavior, ecology, and sensory modalities (Regal, 1978). They clearly represent very different patterns of adaptation in many features of their biology besides their predatory modes. A more rigorous test of the hypothesis that high activity temperatures and brief periods of activity are part of the intensive forager mode requires a comparison of closely related lizards. Species of *Anolis* that include thermoregulating and nonthermoregulating populations in different habitats (Ruibal and Philibosian, 1970; Huey and Webster, 1976) seem an ideal system for these comparisons.

A second generalization about the energetics of different modes of foraging is suggested by the allometric relationships of resting metabolism and the cost of transport: intensive foraging may be energetically more efficient for large lizards than for small ones. That prediction is derived from the difference in the mass-specific exponent of resting metabolism (which is -0.18 for lizards at 37° C) and the exponent of the mass-specific net cost of transport, -0.25 (Gleeson, 1979). Because the cost of transport decreases faster with increasing body mass than the resting metabolic rate, a smaller multiple of resting metabolism is required for activity by a large animal than a small one. Qualifications attached to this hypothesis include the errors that may have been engendered by extrapolating data based predominantly upon small lizards as well as the potential effects of exposure to predators during foraging periods.

Partitioning Energy Input During Activity

The costs and benefits of reliance upon anaerobic metabolism probably balance to different sums in different contexts. At the molecular level anaerobic metabolism appears costly: the resynthesis of glycogen from lactate requires more energy than was released by the conversion of one glucosyl unit to two lactate molecules. At the tissue level, however, the balance is somewhat different because lactic acid produced at one site may be the substrate for aerobic metabolism elsewhere in the body. In an organismal context the ability to generate high-energy phosphate compounds rapidly when they are needed without the ongoing expense of maintaining a high resting metabolic rate makes reliance upon anaerobic metabolism an energetically parsimonious way to fuel infrequent bursts of activity. The total energy production (aerobic plus anaerobic) of the lizard *Dipsosaurus dorsalis* during 5 min of maximum activity at a body temperature 37° C is slightly greater than that of two rodents of similar body size (Ruben and Battalia, 1979). Furthermore, the relative temperature insensitivity of anaerobic metabolism may allow a cold ectotherm to generate energy to escape from a predator that has located its retreat site. The ability to function at low body temperatures is an important consideration for animals that rely upon periods of low temperature to reduce metabolic costs.

Although the role of anaerobic metabolism in sustaining high levels of activity is more pronounced in amphibians and reptiles than among birds and mammals, the ectotherms are far from uniform in their patterns of reliance upon anaerobiosis. The absolute and relative amounts of energy derived from aerobic and anaerobic pathways differ among species (Bennett, 1978). Furthermore, there is an interspecifically variable component of temporal variation in the routes of energy input during a bout of activity (fig. 4). The significance in an animal's overall energy budget of the energy expended in resynthesizing glycogen from lactate generated during activity will depend in part upon the frequency of occurrence of episodes of activity that must be supported by anaerobic metabolism. The rates of energy input that can be sustained solely by aerobic metabolism differ among species (fig. 5) and may be related to differences in behavior and patterns of activity.

These sources of variation offer material from which a rich fabric of adaptive response could be woven. Differences in physiological characteristics can be expected to be as subtly blended and as continuous as the gradations of behavior and ecology with which they are associated. Formulating and testing hypotheses about these sorts of adaptations require an open-minded approach to the complexity of biological variation; the dichotomous "either-or" approach is probably too crude to detect the sorts of variations that are likely to be most interesting.

The exercise physiology of anuran amphibians has been interpreted in the context of modes of defense against predators—"active" for animals that escape with rapid leaps and "static" for species that rely upon chemical defenses. Species with active defensive behavior have been characterized as having a high dependence upon anaerobic me-

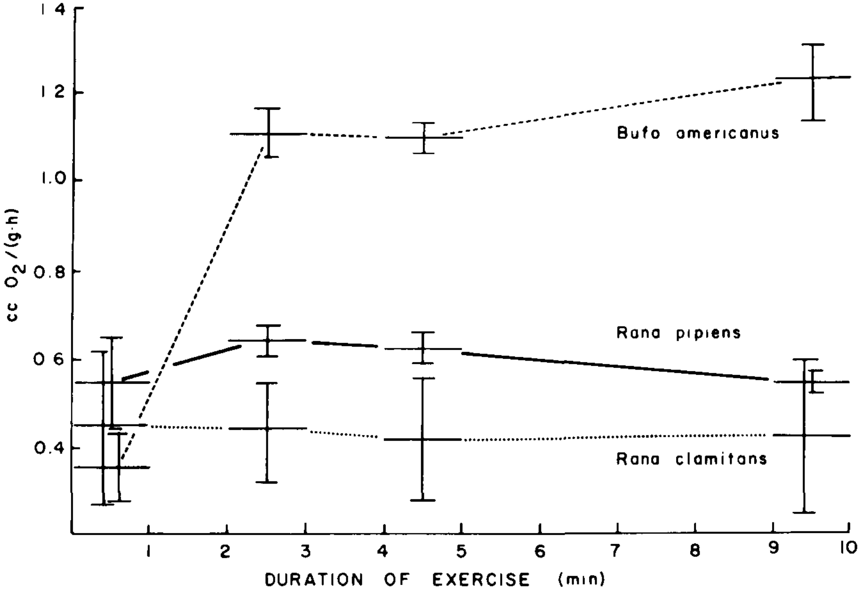

Fig. 4. Interspecific variation in patterns of temporal change in oxygen consumption during activity in anurans. The horizontal lines mark mean rates of oxygen consumption during the 1 min periods indicated by the positions of the lines. Vertical line is ± 1 standard error of the mean. The animals were exercised at 20° C in a revolving chamber at the maximum speeds they could sustain. Gas volumes are corrected to STPD. Data from T. L. Taigen (personal communication).

tabolism and a low aerobic capacity, whereas species with static defense are said to have the opposite balance (Bennett and Licht, 1974; Hutchison and Miller, 1979).

In view of the large number of species of anurans that exist and their great morphological, ecological, and behavioral diversity, a simple dichotomy of partitioning energy input seemed likely to be an artifact of a small and taxonomically restricted sample size. Consequently we examined 17 species of anurans chosen to represent a range of morphological and ecological specializations in 8 families (Taigen et al., 1982). In our sample both aerobic and anaerobic energy input were distributed through a spectrum of values (fig. 6). All possible combinations of high and low aerobic and anaerobic inputs were observed, as well as a variety of intermediate conditions. There was statistically significant interspecific variation in both measures.

Is there an underlying pattern to this variation? For illustration values of oxygen consumption and lactic acid concentration were split

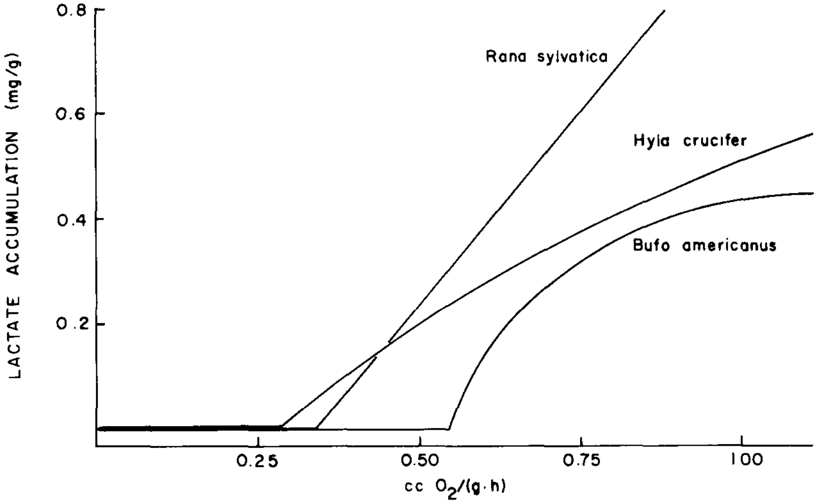

Fig. 5. Interspecific variation in partitioning of energy input among anurans. Lactic acid begins to accumulate at submaximal rates of oxygen consumption, and the relative energy input derived from aerobic and anaerobic pathways varies among species and changes with the level of activity. The animals were exercised at 20° C in a revolving chamber for 4 min at speeds of rotation adjusted to produce different levels of activity and oxygen consumption. At the end of the exercise period whole-body lactic acid concentration was measured enzymatically. Gas volumes are corrected to STPD. Data from Taigen and Beuchat (1982).

into three ranges and combined to form a 3 × 3 grid (fig. 7). The species we tested occupied eight of the nine squares of the grid (fig. 7a).

The simplest hypothesis postulates phylogenetic conservatism in the balance of aerobic and anaerobic energy input. That hypothesis predicts that species from a given family should occur in the same or adjacent squares of the grid, but such is clearly not the case (fig. 7a). No family of anurans shows a homogeneous combination of levels of maximum oxygen consumption and lactic acid concentration.

The absence of a phylogenetic basis at the family level for differences in patterns of energy input suggests that the distribution of sources of energy used for activity may have been subject to selection. Because the allometric relationships of body mass to maximum oxygen consumption and to lactate concentration do not differ from 1, body size does not account for the interspecific differences in metabolic patterns.

What alternative hypotheses can be formulated? In addition to the suggestion that patterns of energy generation are related to escape

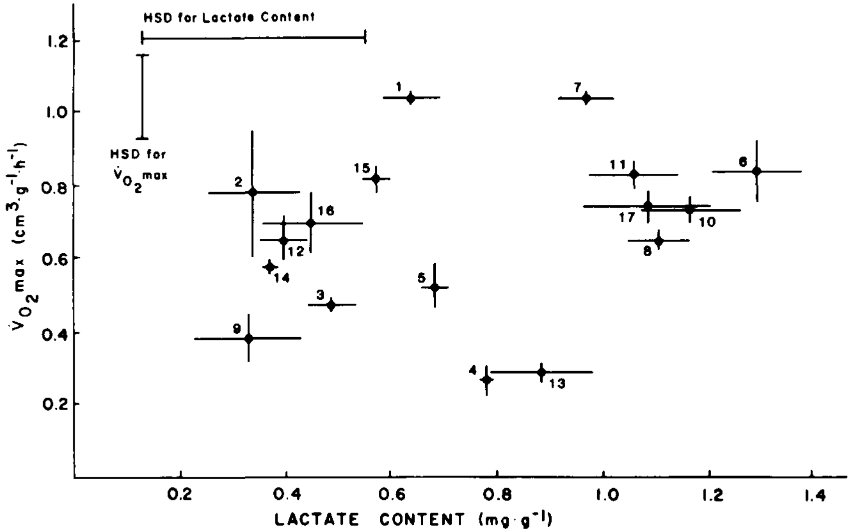

Fig. 6. Relative power input from aerobic and anaerobic metabolism during maximum activity of anurans. Code: Bufonidae: 1. *Bufo americanus*, 2. *B. calamita*. Discoglossidae: 3. *Bombina orientalis*, 4. *Discoglossus pictus*. Hylidae: 5. *Agalychnis callidryas*, 6. *Hyla arenicolor*, 7. *H. crucifer*, 8. *Osteopilus septentrionalis*, 9. *Pternohyla fodiens*. Hyperoliidae: 10. *Hyperolius viridiflavus*, 11. *Kassina senegalensis*, 12. *K. weali*. Leptodactylidae: 13. *Eleutherodactylus coqui*, 14. *Odontophrynus americanus*. Microhylidae: 15. *Gastrophryne carolinensis*, 16. *Kaloula pulchra*. Ranidae: 17. *Rana sylvatica*. The Honestly Significant Differences (*HSD*) are shown for lactate content and for maximum rate of oxygen consumption ($\dot{V}_{O_2}$max). There is significant interspecific variation in the magnitude of power input from both sources. The animals were exercised at 20° C for 4 min in a revolving chamber at the maximum speeds they could sustain. Whole-body lactate content was analyzed enzymatically at the end of the exercise period. Gas volumes are corrected to STPD. Modified from Taigen et al. (1982).

behavior, the modes of locomotion and foraging of the 17 species and their forms of intraspecific combat seem to be features of ecology and behavior that might be reflected by physiological adaptations.

Only two modes of escape from predators can be distinguished from information available in the literature: *active* escape behavior as we defined it consists of an extended series of bursts of activity such as a prolonged series of leaps, whereas *static* behaviors include a single leap followed by crypsis as well as aposematic displays. Our effort was to separate behaviors that required a capacity for sustaining high levels of energy input from those that involved either very short (< 30 sec) bursts of energy or low continuous inputs. This definition accommodates much of the diversity of predator avoidance behaviors, but it

A

ANAEROBIC METABOLISM (mg lactate/g) \ AEROBIC METABOLISM (ml oxygen/g·h)	LOW (0.3-0.6)	INTERMEDIATE (0.6-0.9)	HIGH (0.9-1.2)
HIGH (0.9-1.2)	E coqui	H arenicolor H viridiflavus O septentrionalis R sylvatica K senegalensis	H crucifer
INTERMEDIATE (0.6-0.9)	D pictus A callidryas	G carolinensis	B americanus
LOW (0.3-0.6)	B orientalis P fodiens	K pulchra K wealii O americanus B calamita	

B

ANAEROBIC METABOLISM (mg lactate/g) \ AEROBIC METABOLISM (ml oxygen/g·h)	LOW (0.3-0.6)	INTERMEDIATE (0.6-0.9)	HIGH (0.9-1.2)
HIGH (0.9-1.2)	STATIC	ACTIVE ACTIVE UNKNOWN ACTIVE ACTIVE?	STATIC
INTERMEDIATE (0.6-0.9)	ACTIVE STATIC	ACTIVE	STATIC
LOW (0.3-0.6)	STATIC STATIC	STATIC STATIC STATIC STATIC	

C

ANAEROBIC METABOLISM (mg lactate/g) \ AEROBIC METABOLISM (ml oxygen/g·h)	LOW (0.3-0.6)	INTERMEDIATE (0.6-0.9)	HIGH (0.9-1.2)
HIGH (0.9-1.2)	J-W	J J J J W	J
INTERMEDIATE (0.6-0.9)	J J-W	W-H	H-B
LOW (0.3-0.6)	H H-B	W-H-B W H-B W-B	

D

ANAEROBIC METABOLISM (mg lactate/g) \ AEROBIC METABOLISM (ml oxygen/g·h)	LOW (0.3-0.6)	INTERMEDIATE (0.6-0.9)	HIGH (0.9-1.2)
HIGH (0.9-1.2)	PASSIVE	UNKNOWN UNKNOWN PASSIVE PASSIVE PASSIVE	PASSIVE
INTERMEDIATE (0.6-0.9)	UNKNOWN PASSIVE	ACTIVE	ACTIVE
LOW (0.3-0.6)	UNKNOWN ACTIVE	ACTIVE UNKNOWN UNKNOWN ACTIVE	

Fig. 7. Classification of biological features of anurans in relation to the sources of power input during maximum exercise. *A*. The distribution of the species shown in figure 6. The full names of the species and the families to which they belong are shown in the legend of that figure. *B*. Predator avoidance behaviors. There is no consistent relationship between sources of power input and reliance upon active escape or static defense. *C*. Modes of locomotion. Most species of anurans that jump (*J*) have intermediate or high levels of anaerobic power input and low or intermediate levels of aerobic power input. In contrast to that pattern, most species that walk (*W*), hop (*H*), or burrow (*B*) have low or intermediate anaerobic power input and intermediate or high aerobic power input. *D*. Modes of foraging behavior. Anurans that rely upon passive foraging have intermediate or high levels of anaerobic power input during exercise whereas active foragers have intermediate or low anaerobic power input.

Comparison of *B*, *C*, and *D* indicates that there are suites of interrelated physiological, morphological, behavioral, and ecological characteristics among anurans. Modified from Taigen et al. (1982).

unquestionably oversimplifies a complex situation. Active and static defensive modes are not mutually exclusive, and an anuran may switch from one to the other in the middle of an encounter with a predator, use different behaviors for different predators, or show geographic variation in defensive behavior (Marchisin and Anderson, 1978; Bajger, 1980).

The hypothesis that anurans that rely upon active escape have low levels of maximum oxygen consumption and high levels of lactate production whereas those that utilize static defenses have the reciprocal balance was not supported by our data (fig. 7b). Static defensive mechanisms are found among species in six of the eight occupied squares in the grid. *Eleutherodactylus coqui* has exactly the combination of metabolic characteristics expected from an anuran that relies upon active escape but its defensive behavior is based on crypsis.

In contrast to the absence of a relationship between the partitioning of energy input and escape behavior, there does appear to be a pattern when the analysis is repeated classifying the species by their foraging modes (fig. 7d). Those species classified as active foragers have relatively high levels of maximum oxygen consumption and low lactate concentrations, whereas passive foragers occupy the low oxygen–high lactate portion of the grid. Uncertainty in this case attaches to the allocation of species even to the proper ends of the crude continuum of foraging modes we utilized. Literature records for most species were entirely inadequate for firm decisions so we used a combination of our own field experience and that of our colleagues, plus indirect evidence derived from stomach contents. The analysis in figure 7 is presented as a hypothesis to be tested with a combination of field observations and laboratory experiments rather than as a relationship of which we are confident. The apparent correlation between foraging mode and the pattern of energy input does suggest, however, that subtle relationships between physiological characteristics and ecology and behavior exist and are accessible to experimental analysis.

A third situation in which the ability to generate energy in a manner compatible with an ecological requirement may be significant is intraspecific combat. Agonistic behavior is a prominent feature of the reproductive biology of some species of anurans but is unknown in other species (Wells, 1977a). Intraspecific combat normally takes the form of wrestling matches, usually between males. The duration and intensity of combat vary interspecifically. Males of the Neotropical toad *Bufo typhonius* may struggle for 30 min, whereas in the North American green frog, *Rana clamitans*, 40% of the combats lasted less than 30 sec and 75% were over in 2 min (Wells, 1978, 1979). Fights between green frogs that lasted several minutes were composed of multiple bouts; the combatants separated and rested between rounds. After these prolonged fights the frogs appeared exhausted and rested in shallow water, breathing rapidly, for 30 or 40 min. Some were so tired that they were unable to maintain an upright posture and listed to one side (Wells, 1976).

Clearly these intraspecific combats can force an anuran to the maximum exertion of which it is capable, and success in combat is directly reflected in reproductive success (Wells, 1977b, 1979). Consequently, intraspecific combat provides a situation in which the ability of an anuran to generate energy can be related to its fitness. It seems likely that only species of anurans with high aerobic capacities would be able to generate the sustained high levels of energy input required for prolonged and intense combat.

The information available about intraspecific combat among anurans is rarely sufficiently detailed to address the question of the intensity and length of bouts of fighting (Wells, 1977a). Of the species we have examined, intense and prolonged fighting is known to occur only in *Bufo americanus*. Brief or low-intensity combat is known in three species: *Agalychnis callidryas, Hyla crucifer,* and *Eleutherodactylus coqui* (Wells, 1977a, personal communication; M. M. Stewart, personal communication; personal observation). Male *Rana sylvatica* clasp females for prolonged periods and hold their hind legs in position to kick other males that try to clasp the same female, but the situation is largely static with only brief periods of activity (Banta, 1914). Only *Hyperolius viridiflavus* appears a possible exception to the generalization that species of anurans with high reliance upon anaerobic energy input do not engage in prolonged, intense combat. Published descriptions of male-male combat in this species give the impression of considerable intensity but do not provide information about the length of bouts (Rose, 1962; Wager, 1965; Stewart, 1967). Thus most of the information available suggests that intraspecific combat imposes a great metabolic demand on an anuran and that the level of intensity and the duration of combat can be predicted from knowledge of a species' metabolic capacity.

These analyses indicate that there are suites of anuran characteristics that cut across taxonomic divisions and include features of morphology, physiology, ecology, and behavior. For example, it is apparent from figure 7 that among the species we sampled there is a group of terrestrial, burrowing anurans belonging to four families that have low to intermediate anaerobic and intermediate to high aerobic power input, active modes of foraging, and static predator avoidance behaviors. These characteristics cannot be considered independently: burrowing requires a continuous moderate power input (Seymour, 1973) that is best sustained by aerobic metabolism, a feature that is also associated with active foraging. The morphological specializations of burrowing anurans preclude long, rapid leaps to escape from predators and are associated with static defense mechanisms such as reliance upon toxins. Species of anurans that are relatively immune from predators because they are toxic are likely to have intraspecific combat (Shine, 1979), a feature that is also associated with high levels of aerobic power input. Cause-and-effect relationships must be considered in a holistic context; single factor correlations are easy to find but of limited significance. Furthermore, the choice of experimental species to test hypotheses about the evolutionary or functional significance of physiological characteristics must be based on detailed consideration of the biology of the organisms being studied.

An area of potential investigation is the relationship between the capacity of an individual anuran to generate energy and its success in intraspecific encounters. There is a large component of individual variation in the aerobic metabolic performance of American toads (*Bufo americanus*). Experiments conducted by T. L. Taigen (personal communication) revealed that 74.4% of the variation in measurements of maximum oxygen consumption of toads replicated after 24 h could be ascribed to repeatable differences among individuals (table 2). In a second experiment in which male and female toads were matched for body mass, 34.6% of the variation among individuals was accounted for by sex. The repeatability of the individual variation makes it feasible to observe combats and the mating success of individual toads in breeding choruses and then return them to the laboratory for measurement of metabolic capacities. In this way it may be possible to establish a relationship between a specific physiological character and the reproductive fitness of an animal in its normal environment and possibly even the heritability of that character.

Intraspecific Comparisons

An important functional difference between ectothermal tetrapods and endotherms is the range of body sizes over which a basically unchanged morphological system must support an individual as an independent and self-sufficient entity. Among both amphibians and reptiles adult body masses regularly exceed those of newborn or newly metamorphosed juveniles by three orders of magnitude. Furthermore

TABLE 2

SOURCES OF VARIATION IN MAXIMUM RATES OF OXYGEN CONSUMPTION OF TOADS (BUFO AMERICANUS)

Source of Variation	df	Sum of Squares	Mean Square	F-Ratio	Expected Mean Squares	Estimate of Variance Component	Percentage of Total Variation
11 individuals, body masses from 0.65 to 27.96 g ($\bar{x}$ oxygen consumption ± 1 s.e.: 1.075 ± 0.046 cc $0_2/(g \cdot h)$)							
Among toads	10	0.3730	0.0373	6.80	$\sigma_W^2 + \sigma_A^2$ (2)	$\sigma_A^2 = 0.0159$	74.4
Within toads	11	0.0604	0.0055	$p < 0.005$	σ_W^2	$\sigma_W^2 = 0.0055$	25.6
7 males and 7 females of matched body size (males: $\bar{x} = 34.2$ g; females: $\bar{x} = 33.5$ g) ($\bar{x}$ oxygen consumption ± 1 s.e. [cc $0_2/g \cdot h$)]: males 1.036 ± 0.061; females 0.806 ± 0.087)							
Between sexes	1	0.1840	0.1840	4.7	$\sigma_B^2 + \sigma_W^2$	$\sigma_B^2 = 0.0207$	34.6
Within toads	12	0.4689	0.0391	$p = 0.05$	σ_W^2	$\sigma_W^2 = 0.0391$	65.4

SOURCE: Data from T. L. Taigen, personal communication.

the relationships of a reptile or amphibian with its physical and biological surroundings can be completely reversed during ontogeny. As in the case of *Ameiva leptophrys*, the structural habitats available to a juvenile ectotherm may be quite different from those of adults of its species because of the differences in the routes of thermal energy exchange of large and small organisms (Bakken and Gates, 1975).

The importance of ectothermy in allowing juvenile amphibians and reptiles to accommodate themselves to enormous changes in body size by adjusting metabolic demands to the availability of suitable prey species is obvious. When food is abundant the low resting metabolic rates of the ectotherms allow rapid conversion of assimilated prey into biomass. The gecko *Coleonyx* can increase its body mass by 50% in 4 days of ad libitum feeding and by 90% in 10 days (Bustard, 1967). Juvenile toads manipulated their body temperatures in relation to their nutritional status by moving to warm places when they were fed, thereby facilitating digestion, and to cold areas when they were unfed, thus reducing the rate of utilization of their energy stores (Lillywhite et al., 1973).

Although the basic morphological features of juvenile amphibians and reptiles duplicate those of the adults, there is a degree of allometric change in some structures and organs. In addition there are profound ontogenetic changes in physiology that appear to be directly reflected by some features of behavior and ecology. These ontogenetic shifts offer an opportunity to investigate the interactions of physiology, ecology, and behavior without the complications of interspecific comparisons.

The best-studied ontogenetic physiological changes among reptiles affect the oxygen transport capacity of the cardiovascular system (Pough, 1980b). An increase in the oxygen capacity of the blood from birth to adulthood appears to be a widespread feature of reptiles, and it may be accompanied by changes in the hemoglobin molecule, intracellular modifiers of oxygen affinity, hematocrit, and blood viscosity. In garter snakes (*Thamnophis sirtalis*) the capacity of a unit volume of blood to transport oxygen more than doubles between birth and adult body size (Pough, 1977a). This change results from an increase in the hematocrit and a reduction in the quantity of inactive hemoglobin (Pough, 1977b). A concomitant reduction in the oxygen affinity of the blood facilitates oxygen delivery to the tissues of adult garter snakes. Similar ontogenetic changes in the properties of blood have been described in other snakes (Pough, 1977c, 1980b).

The low hematocrits (and hence low oxygen capacities) of the bloods of juvenile snakes may reflect a specialization of the cardiovascular system for low blood viscosity and low resistance to flow, thereby reducing the work of the heart. Specialization of juveniles as extremely low energy systems might allow an increase in their efficiency of secondary production and thus in rapid growth in the first weeks or months of life. If this is the case, the energy-saving characteristics of juvenile reptiles or amphibians would duplicate and extend to intraspecific levels the features that distinguish adult ectotherms from endotherms.

If these features of juveniles are specializations that reduce energy demand, they exact a price from their possessors. The low oxygen transport capacity of the bloods of juvenile snakes is reflected by poor endurance for sustained activity. Newborn garter snakes are exhausted in 3–5 min of activity (fig. 8). Endurance increases with increasing body mass, and adults are capable of 25 min of continuous activity (Pough, 1977a). A similar increase in endurance occurs in five other species of snakes that have been tested (fig. 9). The slopes of increasing endurance approximate 1 min/cm snout-vent length in all six species.

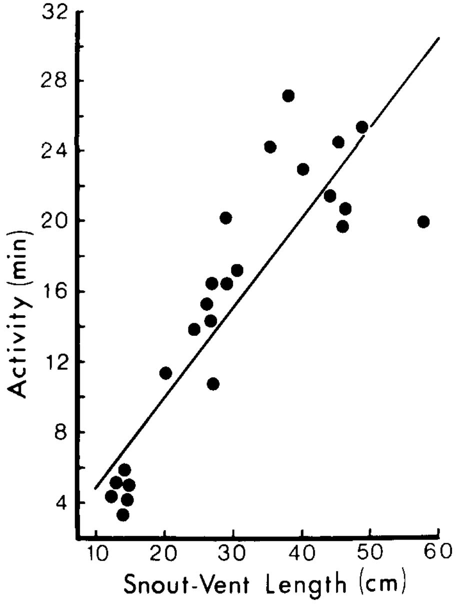

Fig. 8. Duration of activity before exhaustion at 25° C as a function of body size for garter snakes, *Thamnophis sirtalis*. From Pough (1977a); reprinted by permission.

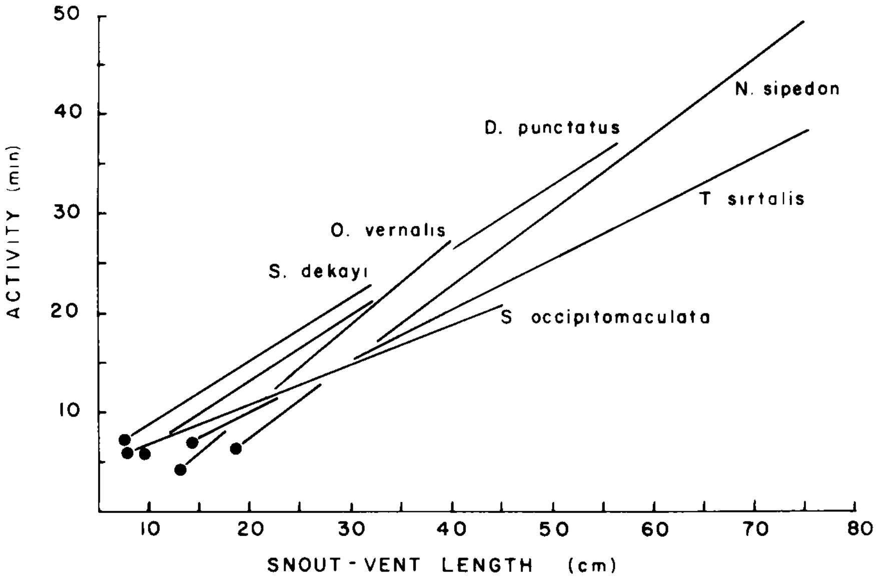

Fig. 9. Duration of activity before exhaustion at 25° C as a function of body size for six sympatric species of snakes. The dots show the body size and endurance of each species at birth or hatching. Data from Pough (1977a, 1978, unpublished).

The limited endurance of juvenile snakes should affect various features of their lives including the modes of foraging they can use and the sorts of prey they can subdue. Garter snakes swallow their prey without immobilizing it by constriction or envenomation, and the process appears to strain the aerobic metabolic capacities of both the predator and the prey. Elevated lactic acid concentrations have been measured in garter snakes and salamanders when the snakes were allowed to capture the salamanders in laboratory experiments (Feder and Arnold, 1982). The concentrations of lactic acid in the half-grown snakes used for those experiments sometimes reached the levels associated with exhaustion in juvenile snakes. It appears that the salamanders might have been able to resist a smaller snake until the snake was incapable of sustaining the attack.

There is an ontogenetic increase in the size of prey eaten by garter snakes relative to the size of the snake (table 3). The smallest snakes eat primarily earthworms that are less than 4% of the snakes' body masses and are probably relatively easy to subdue. The next size class of snakes preys chiefly on small anurans (5–6% of the snakes' masses) that are able to kick and struggle. Still larger snakes feed on frogs that

TABLE 3

ONTOGENETIC CHANGE IN DIET AND BLOOD OXYGEN CAPACITY OF GARTER SNAKES

Size Class (cm [sv])	Primary Prey	Mass of Prey (% Snake Mass)	Blood Oxygen Capacity (% Adult Value)
20–29	Earthworms	3.8	67
30–39	Small anurans	5.6	84
40–49	Large anurans	94	95
≥ 50	Mice	50	100

SOURCE: Fitch (1965) and Pough (1977a).

are nearly as large as the snakes themselves. (These frogs remain a mainstay of the snakes' diets throughout life and decrease in relative size as the snakes continue to grow.) Adult dietary habits are adopted at approximately the same body size at which adult blood oxygen capacity is achieved. Only the largest snakes feed on rodents. These are more formidable prey than frogs of the same size. Not only do the rodents have teeth and claws with which to defend themselves, but they are not subject to the rapid exhaustion during activity that characterizes the frogs.

The similarity of the ontogenetic increase in endurance among six species of snakes found in overlapping habitats in eastern North America (fig. 9) suggests that ontogenetic changes in physiological characteristics may have important ecological consequences. To the extent that the spectrum of potential prey for a species of snake is determined by the snake's endurance, the ecological relationships of the different species of snakes may be very complex. A small individual of a large species may function in its ecosystem more like an adult of a small species than like the much larger adult of its own species. The ecological consequences of ontogenetic changes in the physiology of amphibians and reptiles may introduce complications into the interspecific relationships of these taxa that are not encountered among endotherms where juveniles vicariously draw upon the same resources as adults.

For amphibians that have an aquatic larval stage, metamorphosis to the adult body form is a clear and dramatic shift that affects all the functional aspects of an individual. Metamorphosis is not the only abrupt ecological change during the ontogeny of some species, however. The behavior and ecology of newly metamophosed toads (*Bufo americanus*) are entirely different from those of adults, and the juvenile pattern persists while the animals increase in body mass by an order of magnitude (Taigen and Pough, 1981). Toad tadpoles mature rapidly and metamorphose sooner than most species of anurans. Newly metamorphosed *B. americanus* are tiny creatures, as small as 50 mg. These minute toads assemble in large groups on the shores of their natal ponds, where they are active by day and bask in the sun. This behavior is entirely different from that of the solitary, nocturnal adults, which are residents of fields and meadows.

Adult toads have high aerobic metabolic capacity (fig. 6) and can sustain activity indefinitely. Newly metamorphosed toads, in contrast, are exhausted by 15 sec of forced activity (Taigen and Pough, 1981). The endurance of the baby toads increases linearly with increasing body mass. Toads larger than 0.5 g cannot be exhausted by exercise. The maximum rate of oxygen consumption of newly metamorphosed toads is less than half that of adults (fig. 10). This rate increases with increasing body mass and reaches the adult rate in toads weighing

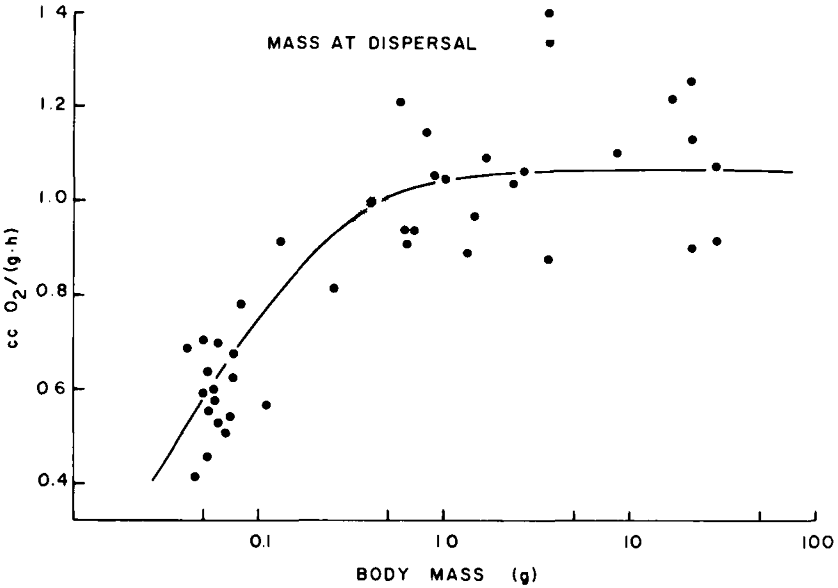

Fig. 10. Ontogenetic increase in the maximum rate of oxygen consumption of toads (*Bufo americanus*). Small toads disperse from their natal ponds at body masses of 0.35–0.50 g. This is approximately the size at which adult rates of maximum oxygen consumption are achieved. The animals were exercised in a rotating chamber for 10 min at 20° C at the highest speeds they could sustain. Gas volumes were corrected to STPD. Modified from Taigen and Pough (1981).

about 0.5 g. Thus the endurance and maximum rates of oxygen consumption increase in parallel during the ontogeny of juvenile toads and they reach values typical of adults at the same point. In contrast, the energy input from anaerobic metabolism does not change ontogenetically. As a consequence of these relationships, the juvenile toads rely to a greater extent on anaerobiosis during activity than do adults.

The change in the behavior of the toads from diurnal juveniles to nocturnal adults begins at body masses between 0.3 and 0.4 g and is completed by the time a mass of 0.5 g has been attained. Toads larger than that are not found on the shores of the breeding ponds, and the smallest individuals found in the adults' habitat are larger than 0.8 g.

Both biological and physical factors probably shape the behavioral differences between juvenile and adult toads. The adults are protected from many predators by skin glands that produce toxic substances, but newly metamorphosed toads are vulnerable, and their dense aggregations may provide a measure of protection from predation (Arnold and Wassersug, 1978). The elevated body temperatures that the small toads achieve by basking presumably accelerate growth past the size at which the animals are at high risk. An ancillary benefit of basking may be an elevated capacity for aerobic metabolism resulting from a high body temperature. If the Q_{10} for oxygen consumption is 2 and the body temperature of basking toads is 27° C (Lillywhite et al., 1973), the maximum rate of aerobic metabolism of a juvenile toad on a pond bank on a sunny day would approximate that of an adult toad foraging with a body temperature of 17° C on a cool summer night. This equality of the capacity for aerobic energy input is ecologically defined and cannot be attained by juvenile and adult toads at the same time and place. Newly metamorphosed toads have body sizes small enough to allow them to remain in the sun without overheating. Consequently they may be able to reduce their vulnerability to predation and simultaneously enhance their ability to capture prey items by increasing their capacity for aerobic energy generation by basking. To accomplish this end they must occupy a different temporal, spatial, and thermal niche from that of the adults of their species.

Green frogs (*Rana clamitans*) breed in the same ponds as the toads, but the frogs do not have an ontogenetic change in their capacity for activity (T. L. Taigen and F. H. Pough, MS). Juvenile and adult green frogs are exhausted by 2–3 min of activity, and there is no ontogenetic change in oxygen consumption (fig. 11). The frogs are larger than the toads at metamorphosis, both in absolute terms and in proportion to the size of adults of their species. Newly metamorphosed green frogs

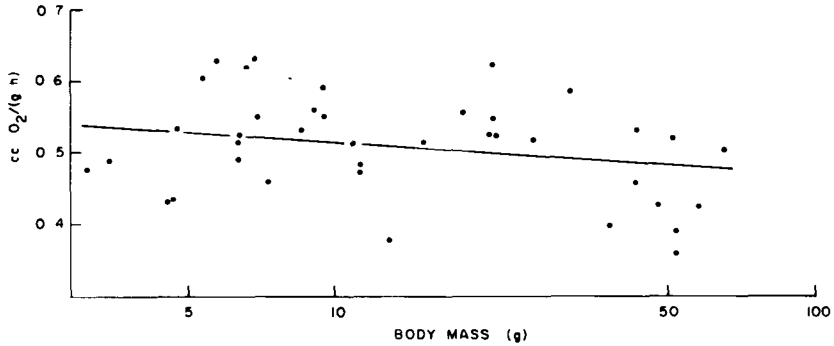

Fig. 11. Maximum rates of oxygen consumption of green frogs (*Rana clamitans*) as a function of body size. Unlike toads (fig. 10), the frogs have no ontogenetic increase in the maximum rate of oxygen consumption. The animals were exercised in a rotating chamber at 20° C for 4 min at the highest speeds they could sustain. Gas volumes were corrected to STPD. Data from T.L. Taigen and F.H. Pough (MS).

do not spend prolonged periods in aggregations on the shores of their natal ponds as the toads do.

These physiological and behavioral differences between the toads and frogs are probably aspects of their very different life histories. Toads lay their eggs and complete larval development in the shallows, where high spring water levels have inundated pond banks. This is an ephemeral habitat that disappears as water levels recede in the summer. The green frogs use deeper water for egg deposition and larval development. The short aquatic stage of the toads appears to be related to the transient nature of the resources they utilize. Metamorphosis itself is a stressful period for amphibians, and selection appears to have favored making that period as short as possible (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978). Apparently as a consequence of these two selective forces, both favoring rapid development through metamorphosis, juvenile toads emerge from their ponds as very incomplete animals. The heart, liver, and lungs of a newly metamorphosed toad are exceedingly small, and these organs undergo allometric growth during juvenile development. In contrast, the green frog tadpoles in the same ponds utilize more stable habitats, require several months to reach metamorphosis, are larger than the toads when they do metamorphose, and do not exhibit the extreme allometric growth of internal organs that is characteristic of the toads. Thus the physiological changes that occur during the ontogeny of anurans may simultaneously reflect the influences of different life histories and shape the ecology and behavior of the young animals.

SUMMARY

The general adaptation of amphibians and reptiles is to low energy flow and high efficiency of biomass production. That adaptation rests on two physiological features in which amphibians and reptiles differ from birds and mammals: ectothermy and a dichotomous system of energy generation during high levels of activity. The ways in which amphibians and reptiles differ in ecology and behavior from birds and mammals are directly related to those physiological differences. Patterns of habitat partitioning, resource utilization, and interspecific competition among the ectotherms may be different from those of the endotherms.

Some of these patterns reappear in comparisons among amphibians and reptiles. Because the energy requirements of all amphibians and reptiles are low, there appears to be less scope for adaptations that reduce the cost of living in these groups than there is among birds and mammals. Specialization for especially low energy flow, where it does occur, involves extensive modifications of life style and life history. Intraspecific comparisons avoid the difficulties of interpretation that are inherent in comparing different species. The thermoregulatory flexibility of some species of reptiles and the widespread occurrence of ontogenetic changes in physiological performance in both classes of ectothermal tetrapods offer opportunities to define the relationships among physiology, ecology, and behavior.

ACKNOWLEDGMENTS

I am grateful to Robin Andrews, Stevan Arnold, Carol Beuchat, Sharon Emerson, Martin Feder, Peter Hillman, William Mautz, and especially Theodore Taigen for permission to use unpublished data from their experiments. Carol Beuchat, Winifred Hallwachs, Alan Savitzky, and Theodore Taigen kindly read the manuscript, corrected errors, called my attention to pertinent citations, and made many other helpful suggestions. To a large extent the ideas in this paper were generated, extended, and refined in discussions with those individuals and other vertebrate biologists at Cornell, and I am greatly in their debt.

DISCUSSION FOLLOWING DR. POUGH'S PRESENTATION

Unfortunately, the recording equipment malfunctioned or speakers did not use the microphones during the discussion following Dr. Pough's presentation.

LITERATURE CITED

Andrews, R. M. 1979. The lizard *Corytophanes cristatus*: an extreme "sit-and-wait" predator. Biotropica 11:126–39.

Andrews, R. M. 1982. Energetics of sit-and-wait and widely-searching lizard predators. *In* Vertebrate ecology and systematics: a tribute to Henry S. Fitch. Special Publication, University of Kansas Museum of Natural History, Lawrence (forthcoming).

Arnold, S. J., and R. J. Wassersug. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. Ecology 59: 1014–22.

Avery, R. A. 1982. Field studies of body temperatures and thermoregulation. *In* C. Gans and F. H. Pough (eds.), Biology of the Reptilia: physiological ecology, 12:93–166. Academic Press, London.

Bajger, J. 1980. Diversity of defensive responses in populations of fire toads (*Bombina bombina* and *Bombina variegata*). Herpetologica 36:133–37.

Bakken, G. S., and D. M. Gates. 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. *In* D. M. Gates and R. B. Schmerl (eds.), Perspective of biophysical ecology. Ecological Studies 12, Springer-Verlag, New York.

Banta, A. M. 1914. Sex recognition and mating in the wood frog, *Rana sylvatica*. Biol. Bull. 26:171–83.

Bartholomew, G. A. 1982. Physiological control of body temperature. *In* C. Gans and F. H. Pough (eds.), Biology of the Reptilia: physiological ecology, 12:167–211. Academic Press, London.

Bennett, A. F. 1978. Activity metabolism of the lower vertebrates. Ann. Rev. Physiol. 400:447–69.

Bennett, A. F. 1982, The energetics of reptilian activity. *In* C. Gans and F. H. Pough (eds.), Biology of the Reptilia: physiological ecology, 13:155–99. Academic Press, London.

Bennett, A. F., and W. R. Dawson. 1976. Metabolism. *In* C. Gans and W. R. Dawson (eds.), Biology of the Reptilia, 5:127–223. Academic Press, London.

Bennett, A. F., and T. T. Gleeson. 1979. Metabolic expenditure and the cost of foraging in the lizard *Cnemidophorus murinus*. Copeia 1979:573–77.

Bennett, A. F., and G. C. Gorman. 1979. Population density and energetics of lizards on a tropical island. Oecologia 42:339–58.

Bennett, A. F., and P. Licht. 1974. Anaerobic metabolism during activity in amphibians. Comp. Biochem. Physiol. 48A:319–27.

Bennett, A. F., and K. A. Nagy. 1977. Energy expenditure of free-ranging lizards. Ecology 58(3):697–700.

Brattstrom, B. H. 1965. Body temperatures of reptiles. Amer. Midl. Natur. 73:376–422.

Brattstrom, B. H. 1970. Amphibia. *In* G. C. Whittow (ed.), Comparative physiology of thermoregulation, 1:135–66. Academic Press, New York.

Brown, J. H., and R. C. Lasiewski. 1972. Metabolism of weasels: the cost of being long and thin. Ecology 53(5):939–43.

Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. Ann. Rev. Ecol. Syst. 10:201–28.

Burton, T. M., and G. E. Likens. 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 58:1068–80.

Bustard. H. R. 1967. Gekkonid lizards adapt fat storage to desert environments. Science 158:1197–98.

Carroll, R. L. 1969. Origin of reptiles. *In* C. Gans, D. d'A. Bellairs, and T. S. Parsons (eds.), Biology of the Reptilia, 1:1–44. Academic Press, London.

Carroll, R. L. 1977a. Patterns of amphibian evolution: an extended example of the incompleteness of the fossil record. *In* A. Hallam (ed.), Patterns of evolution, pp. 405–37. Elsevier, Amsterdam.

Carroll, R. L. 1977b. The origin of lizards. *In* S. M. Andrews, R. S. Miles, and A. D. Walker (eds.), Problems in vertebrate evolution, pp. 359–96. Linnean Society Symposium Series No. 4.

Carroll, R. L., and R. Holmes. 1980. The skull and jaw musculature as guides to the ancestry of salamanders. Zool. J. Linn. Soc. 68:1–40.

Cowles, R. B. 1958. Possible origin of dermal temperature regulation. Evolution 12:347–57.

Cowles, R. B. 1962. Semantics in biothermal studies. Science 135:670.

Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 83:261–96.

Dawson, W. R. 1967. Interspecific variation in physiological responses of lizards to temperature. *In* W. W. Milstead (ed.), Lizard ecology: a symposium, pp. 230–57. University of Missouri Press, Columbia.

Dawson, W. R. 1975. On the physiological significance of the preferred body temperatures of reptiles. *In* D. M. Gates and R. B. Schmerl (eds.), Perspectives of biophysical ecology, pp. 443–73. Springer-Verlag, New York.

Dmi'el, R., and D. Rappeport. 1976. Effect of temperature on metabolism during running in the lizard *Uromastix aegyptius*. Physiol. Zool. 49:77–84.

Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains, Ecol. Monogr. 49:129–49.

Emerson, S. B. 1976. Burrowing in frogs. J. Morphol. 149:437–58.

Feaver, P. A. 1977. The demography of the Michigan population of *Natrix sipedon* with discussions of ophidian growth and reproduction. Ph.D. thesis, University of Michigan.

Feder, M. E. 1976. Oxygen consumption and body temperature in neotropical and temperate zone lungless salamanders (Amphibia: Plethodontidae). J. comp. Physiol. 110:197–208.

Feder, M. E., and S. J. Arnold. 1982. Anaerobic metabolism and behavior during predatory encounters between snakes (*Thamnophis elegans*) and salamanders (*Plethodon jordani*). Oecologia (in press).

Fitch, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. University of Kansas Publications, Mus. Nat. Hist. 15(10):493–564.

Gans, C. 1952. The functional morphology of the egg-eating adaptations in the snake genus *Dasypeltis*. Zoologica 37:209–44.

Gans, C. 1960. Studies on amphisbaenids (Amphisbaenia, Reptilia). Bull. Amer. Mus. Nat. Hist. 119(3):129–204.

Gleeson, T. T. 1979. Foraging and transport costs in the Galapagos marine iguana, *Amblyrhynchus cristatus*. Physiol. Zool. 52:549–57.

Grant, P. R. 1972. Interspecific competition among rodents. Ann. Rev. Ecol. Syst. 3:79–106.

Gratz, R. K., and V. H. Hutchison. 1977. Energetics for activity in the diamond-back water snake, *Natrix rhombifera*. Physiol. Zool. 50:99–114.

Hillman, P. E. 1969. Habitat specificity in three sympatric species of *Ameiva* (Reptilia: Teiidae). Ecology 50:478–81.

Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. *In* C. Gans and F. H. Pough (eds.), Biology of the Reptilia: physiological ecology, 12:25–91. Academic Press, London.

Huey, R. B., and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. Quart. Rev. Biol. 51(3):363–84.

Huey, R. B., and T. P. Webster. 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *cristatellus* group of Puerto Rico. Ecology 57:985–94.

Hutchison, V. H., and K. Miller. 1979. Anaerobic capacity of amphibians. Comp. Biochem. Physiol. 63A:213–16.

Hutchison, V. H., L. D. Turney, and R. K. Gratz. 1977. Aerobic and anaerobic metabolism during activity in the salamander *Ambystoma tigrinum*. Physiol. Zool. 50:189–202.

Iverson, J. A. 1972. Basal energy metabolism of mustelids. J. comp. Physiol. 81:341–44.

Iverson, J. B. 1980. Colic modifications in iguanine lizards. J. Morphol. 163:79–93.

Iverson, J. B. 1982. Adaptations to herbivory in iguanine lizards. *In* G. M. Burghardt and A. S. Rand (eds.), Iguanas of the world: behavior, ecology, and conservation. Noyes Publishing Co., Parkridge, N.J. (forthcoming).

Jaeger, R. G. 1980. Fluctuations in prey availability and food limitation for a terrestrial salamander. Oecologia 44:335–41.

John-Alder, H., and A. F. Bennett. 1981. Thermal dependence of endurance, oxygen consumption, and cost of locomotion in a lizard. Amer. J. Physiol. (Reg. Integ. Comp. Physiol.) R342–R349.

Landres, P. B., and J. A. MacMahon. 1980. Guilds and community organization: analysis of an oak woodland avifauna in Sonora, Mexico. Auk 97:351–65.

Lang, J. W. 1979. Thermophilic response of the American alligator and the American crocodile to feeding. Copeia (1979):48–59.

Lillywhite, H. B. 1970. Behavioral temperature regulation in the bullfrog, *Rana catesbeiana*. Copeia (1970):158–68.

Lillywhite, H. B., P. Licht, and P. Chelgren, 1973. The role of behavioral thermoregulation in the growth energetics of the toad, *Bufo boreas*. Ecology 54:375–83.

Marchisin, A., and J. Anderson. 1978. Strategies employed by frogs and toads to avoid predation by snakes. J. Herpetol. 12:151–55.

Mautz, W. J. 1979. Thermoregulation, metabolism, water loss, and microhabitat selection in xantusiid lizards. Ph.D. thesis, Cornell University.

Mautz, W. J., and T. J. Case. 1974. A diurnal activity cycle in the granite night lizard, *Xantusia henshawi*. Copeia (1974):243–51.

Mautz, W. J., and W. Lopez-Forment. 1978. Observations on the activity and diet of the cavernicolous lizard *Lepidophyma smithii* (Sauria: Xantusiidae). Herpetologica 34: 311–13.

Mayhew, W. W. 1963. Some food preferences of captive *Sauromalus obesus*. Herpetologica 19:10–16.

McNab, B. K. 1969. The economics of temperature regulation in neotropical bats. Comp. Biochem. Physiol. 31:227–68.

McNab, B. K. 1973. The rate of metabolism of the spiny rat, *Proechimys semispinosis*, with comments on the ecological factors that influence the basal rate of metabolism in rodents and lagomorphs. Bol. Zool. e Biol. Mar. (São Paolo), 30:93–103.

McNab, B. K. 1974. The energetics of endotherms. Ohio J. Sci. 74:370–80.

McNab, B. K. 1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. *In* G. G. Montgomery (ed.), The ecology of arboreal folivores. Smithsonian Institution Press, Washington, D.C.

McNab, B. K. 1980. Food habits, energetics, and the population biology of mammals. Amer. Natur. 116:106–24.

Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution 31:370–86.

Moberly, W. R. 1968. The metabolic responses of the common iguana, *Iguana iguana*, to walking and diving. Comp. Biochem. Physiol. 27:21–32.

Nagy, K. A. 1972. Water and electrolyte budgets of a free-living desert lizard, *Sauromalus obesus*. J. comp. Physiol. 79:39–62.

Nevo, E. 1979. Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst. 109:269–308.

Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. Ecology 45: 736–45.

Parker, W. S. 1972. Notes on *Dipsosaurus dorsalis* in Arizona. Herpetologica 28:226–29.

Parsons, T. S., and E. E. Williams 1963. The relationships of the modern Amphibia: a re-examination. Biol. Rev. 38:26–53.

Pough, F. H. 1973. Lizard energetics and diet. Ecology 54:837–44.

Pough, F. H. 1977a. Ontogenetic change in blood oxygen capacity and maximum activity in garter snakes (*Thamnophis sirtalis*). J. comp. Physiol. 116:337–45.

Pough, F. H. 1977b. Ontogenetic change in molecular and functional properties of blood of garter snakes, *Thamnophis sirtalis*. J. Exp. Zool. 201:47–56.

Pough, F. H. 1977c. The relationship between body size and blood oxygen affinity in snakes. Physiol. Zool. 50:77–87.

Pough, F. H. 1980a. The advantages of ectothermy for tetrapods. Amer. Natur. 115:92–112.

Pough, F. H. 1980b. Blood oxygen transport and delivery in reptiles. Amer. Zool. 20: 173–85.

Pough, F. H. 1983. Feeding mechanisms, body size, and the ecology and evolution of snakes. Amer. Zool. 23(2) (in press).

Regal, P. J. 1978. Behavioral differences between reptiles and mammals: an analysis of activity and mental capabilities. *In* N. Greenberg and P. McLean (eds.), The behavior and neurology of lizards. National Institute of Health, U.S. Government Printing Office, Washington, D.C.

Regal, P. J. 1980. Temperature and light requirements of captive reptiles. *In* J. B. Murphy and J. T. Collins (eds.), Reproductive biology and diseases of captive reptiles. Contribution to Herpetology, no. 1. Society for the study of Amphibians and Reptiles.

Romer, A. S. 1966. Vertebrate paleontology. 3d ed. University of Chicago Press, Chicago.

Rose, W. 1962. The reptiles and amphibians of Southern Africa. Maskew Miller, Ltd., Cape Town. 494 pp.

Ruben, J. A. 1977. Some correlates of cranial and cervical morphology with predatory modes in snakes. J. Morphol. 152:89–100.

Ruben, J. A., and D. E. Battalia. 1979. Aerobic and anaerobic metabolism during activity in small rodents. J. Exp. Zool. 208:73–76.

Ruibal, R., and R. Philibosian. 1970. Eurythermy and niche expansion in lizards. Copeia (1970):645–53.

Sergeyev, A. 1939. The body temperature of reptiles in natural surroundings. Dokl. Akad. Nauk SSSR 22(1):49–52.

Seymour, R. S. 1973. Physiological correlates of forced activity and burrowing in the spadefoot toad, *Scaphiopus hammondii.* Copeia 1973:103–15.

Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979: 297–306.

Stanley, S. M. 1979. Macroevolution. Freeman, San Francisco.

Stewart, M. M. 1967. Amphibians of Malawi. State University of New York Press, Albany. 163 pp.

Taigen, T. L., and C. A. Beuchat. 1982. Anaerobic threshold of anuran amphibians. Physiol. Zool. (in press).

Taigen, T. L., S. B. Emerson, and F. H. Pough. 1982. Ecological correlates of amphibian exercise physiology. Oecologia 52:49–56.

Taigen, T. L., and F. H. Pough. 1981. Activity metabolism of the toad (*Bufo americanus*): ecological consequences on ontogenetic change. J. Comp. Physiol. B. 144: 247–52.

Toft, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. Oecologia 45:131–41.

Tracy, C. R. 1977. Minimum size of mammalian homeotherms: role of thermal environment. Science 198:1034–35.

Turner, F. B., P. A. Medica, and B. W. Kowalewsky. 1976. Energy utilization by a desert lizard (*Uta stansburiana*). US/IBP Monogr. No. 1. Utah State University Press, Logan.

Wager, V. A. 1965. The frogs of South Africa. Purnell & Sons, Cape Town. 242 pp.

Wake, D. 1970. Aspects of vertebral evolution in the modern Amphibia. Forma et Functio 3:33–60.

Wassersug, R. J., and D. G. Sperry. 1977. The relation of locomotion to differential predation on *Pseudacris triseriata* (Anura: Hylidae). Ecology 58:830–39.

Wells, K. D. 1976. Territorial behavior of the green frog (*Rana clamitans*). Ph.D. thesis, Cornell University.

Wells, K. D. 1977a. The social behaviour of anuran amphibians. Anim. Behav. 25:666–93.

Wells, K. D. 1977b. Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology 58:750–62.

Well, K. D. 1978. Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic behaviour. Anim. Behav. 26:1051–63.

Wells, K. D. 1979. Reproductive behaviour and male mating success in a neotropical toad, *Bufo typhonius*. Biotropica 11:301–7.

White, F. N. 1973. Temperature and the Galapagos marine iguana—insights into reptilian thermoregulation. Comp. Biochem. Physiol. 45A:503–13.

White, F. N. 1976. Circulation. *In* C. Gans and W. R. Dawson (eds.), Biology of the Reptilia, 5:275–334. Academic Press, London.

LARRY B. CROWDER AND JOHN J. MAGNUSON

Cost-Benefit Analysis of Temperature and Food Resource Use: A Synthesis with Examples from the Fishes

7

The net energy balance of ectothermic animals, such as fishes, is dependent on a number of environmental variables. In particular, temperature and food are closely tied to the net energy gain and growth of fishes. Optimal use of food resources and behavioral thermoregulation each contribute to greater growth rates and fitness under a limited set of conditions. Our purpose is to review and integrate cost-benefit approaches to temperature and food resource use, to demonstrate the use of a bioenergetics model that predicts fish foraging behavior in a heterothermal environment, and to examine some recent field data on the joint use of food and thermal habitat by fishes. The available data suggest that fishes often respond to both temperature and food according to bioenergetic expectations and do not strictly follow the predictions of behavioral thermoregulation or optimal foraging.

COST-BENEFIT ANALYSES OF RESOURCE USE

Food and temperature are intimately linked in the behavioral energetics of fishes. The amount of food eaten (benefits) per unit energy or time spent (cost) in capturing that food has been treated in a series of hypotheses known as optimal foraging theory (Pyke et al., 1977). An important assumption of this theory is that the overall fitness of an

Laboratory of Limnology, Department of Zoology, University of Wisconsin-Madison, Madison, Wisconsin 53706

animal increases as a function of the net rate of energy intake. Growth and fitness are also closely tied to water temperatures that fishes occupy (Beitinger and Fitzpatrick, 1979; Magnuson et al., 1979). Most physiological functions related to consumption and conversion of energy to growth are temperature dependent. Huey and Slatkin (1976) have developed a cost-benefit model for behavioral thermoregulation in lizards. An important assumption of this model is that thermoregulation will maximize the net rate of energy gain, which would presumably maximize fitness.

Fishes have well-defined behavioral responses to both temperature and food. Hypotheses of optimal foraging and behavioral thermoregulation both predict behaviors that should lead to maximized fitness or growth (fig. 1). The predicted behaviors and growth can be compared with observed patterns of behavior or growth as a test of these ideas, at least in the laboratory. In the field, temperature occupancy can be observed but ration is difficult to estimate and growth tends to integrate longer-term experiences. A fish foraging in a heterothermal environment may behave according to the predictions of either optimal foraging or behavioral thermoregulation but will only satisfy both hypotheses if similar behaviors are predicted.

Though optimal foraging theory and behavioral thermoregulation are useful cost-benefit analyses, the general orientation of these analyses to a single niche axis may well be inappropriate for fishes that forage and live in a heterothermal environment. We believe that the appropriate objective function for cost-benefit analyses of resource use in fishes is the net rate of energy gain expressed as growth and reproduction. This function is clearly dependent on both temperature and food. By considering the bioenergetics of fishes, one can predict behaviors of fish foraging in a heterothermal environment (fig. 1). Again, predictions of optimal growth and expected behaviors of fishes can be tested experimentally in the laboratory. Since field distributions of fishes are dependent on both temperature and food (among other factors), these distributions may be examined to see if fishes tend to respond most closely to the predictions of a bioenergetics optimization rather than behavioral thermoregulation or optimal foraging.

Animals have a series of choices to make regarding foraging and behavioral thermoregulation. Animals must first choose a habitat patch from among the available patches. Second, they must determine how long to remain in that patch. Within each habitat patch choices may be made on various prey or on various thermally heterogeneous microenvironments. Finally, animals may move at various speeds or over various paths between and within habitat patches. Costs and benefits

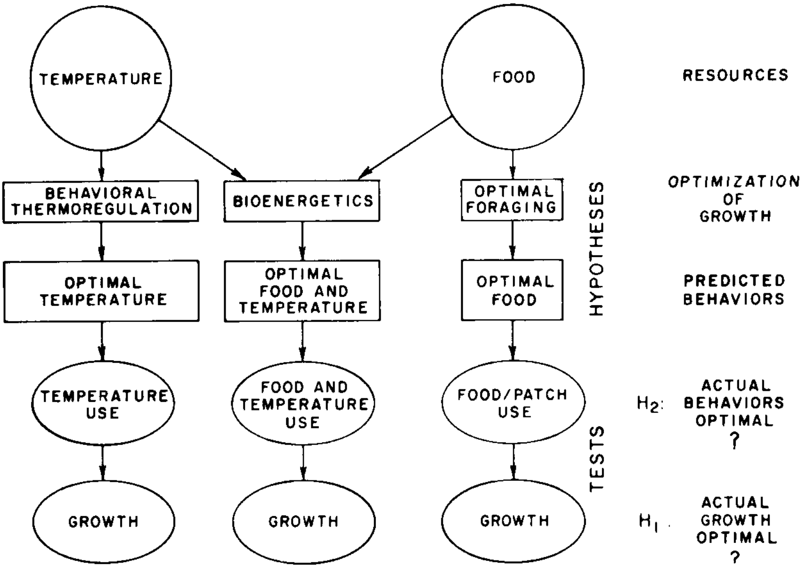

Fig. 1. Hypotheses and tests for use of food and temperature resources by fishes.

of making these choices (either behaviorally or evolutionarily) form the basis for a large body of literature. We provide here a selective review with special reference to examples from the fishes.

Choosing a Habitat Patch

Little experimental work has been done on fishes with regard to patch choice based on optimal foraging models (Pyke, 1979). Theoretically, at least, animals should allocate time to patches in an ordered fashion based on their benefits (net energy intake rate) relative to the costs of visiting those patches (Pyke et al., 1977). If an animal can in some way locate and assess the quality (in terms of costs and benefits) of each patch without actually sampling the prey resources to establish cost-benefit rankings, then foraging movements could be made directly between the "best" patch types. Both theoretical and empirical work are necessary on how fishes might sample an area to establish cost-benefit rankings of patches in which food is spatially and temporally dynamic.

How fishes select thermal habitats is better known than patch choice based on foraging. Fishes can detect small changes in temperature (about 0.1° C; Steffel et al., 1976). The range of temperatures occupied averages about 10° C and the standard deviation averages about 4° C for fishes, whether their temperature preferences are cold, cool, or warm (Magnuson et al., 1979). This range of temperatures is often closely related to optimal physiological benefits for the same species (Magnuson et al., 1979). In sockeye salmon (*Oncorhynchus nerka*), 11 physiological processes are maximized at or near their final temperature preferendum (Brett, 1971). These processes include active metabolism, metabolic scope, sustained swimming speed, and growth. Temperatures of maximum growth in fishes often correlate well with preferred temperatures (Magnuson et al., 1979; McCauley and Casselman, 1980). Physiological costs and benefits of selecting a "profitable" thermal habitat are obvious, since they directly affect physiological rates such as food consumption, food conversion, and ultimately growth.

How Long to Remain in a Habitat Patch

Optimal foraging theory deals explicitly with the problem of how long to remain in a patch, but no empirical examples are available from fishes. As an animal spends more and more time in a patch, food is depleted and capture rates decline until remaining in the patch is no longer profitable. The mathematical theory results in a relatively simple prediction: an animal should leave a patch when its food intake rate drops to the average rate for the habitat as a whole (Pyke et al., 1977). Also, this "marginal" capture rate should be equalized over all patches within the habitat (Charnov, 1976; cf. Oaten, 1977). Just how animals estimate marginal capture rates with any reliability is questionable. Krebs, Ryan, and Charnov (1974) studied patch foraging in birds and hypothesized that the birds have a giving-up time. If no food was obtained in a certain period of time since the last capture, the bird was assumed to move to another patch. These assumptions led to the predictions that the giving-up time should be constant for all patches in the same habitat and that it should be longer in the habitats with higher capture rates. Indeed, their results agreed with their predictions (Krebs et al., 1974), though the mathematical theory (Charnov, 1976) does not directly apply, since search was discrete and nonrandom.

Given ad libitum food and limited behavioral interactions, fishes should remain in a habitat delimited by their preferred temperatures for long periods of time. In the field, however, they do not always occupy their preferred temperatures. Often this results because preferred temperatures are not available. However, depletion of food, other habitat requirements, and interactions with competitors or predators may also prevent long-term occupancy of the thermally "best" patches

(Stuntz, 1975; Magnuson and Beitinger, 1978; Medvick et al., 1981). How temperature differences influence giving-up time in a food patch is unknown.

Within-Patch Choices

Once an animal has chosen where to feed, the question of what types of prey to eat arises. Optimal foraging theory predicts which prey to choose, and some experimental work has been done with fishes (Pyke et al., 1977; Pyke, 1979). The optimal diet should include the prey with the highest value of benefit/cost ratio (food value/handling time); items should then be added to the diet, in the rank order of their benefit/cost ratio, until the ratio of the next lower items exceeds that for the diet without the addition.

Three properties follow logically from the theory of optimal diets. First, ingestion of a food type is independent of the abundance of that food type but instead depends only on the abundance of more highly ranked foods. Second, as the abundance of more highly ranked food types increases, the number of lower ranked items in the diet will decline. Furthermore, items should drop out of the diet in rank order, with lower ranks of benefit/cost ratios going first. Third, if a food type is included in the diet, it should always be consumed if encountered; if excluded from the diet it should never be eaten (Pyke et al., 1977).

Ivlev (1961) was the first to show that increasing food abundance leads to increased food specialization. This expected result of optimal foraging has been shown often with data from fishes (Eggers, 1977). These data cannot directly test optimal diet predictions because information is seldom available regarding costs and benefits for various prey (Pyke, 1979).

Werner and Hall (1974) provided a quantitative test of an optimal diet hypothesis. Bluegill sunfish (*Lepomis macrochirus*), allowed to feed on *Daphnia* of three size classes, took prey according to predictions. At low prey densities little selectivity occurred. At higher prey densities smaller prey dropped from the diet in their order of profitability and frequencies in the diet agreed well with predictions. In a critique of Werner and Hall (1974), O'Brien et al. (1976) pointed out that fish may be responding directly to the visible size of *Daphnia* in Werner and Hall's (1974) experiments.

A model of behavioral thermoregulation in terrestrial ectotherms (Huey and Slatkin, 1976) yields predictions for resource use strikingly similar to those of optimal foraging theory (Magnuson et al., 1979). This model may not be directly applicable to fishes because temperature in water does not typically characterize microhabitats, as can be the case in terrestrial environments. For fishes thermoregulation is essentially in the realm of patch choice rather than within patch choices. Often when fishes move to different temperatures they encounter a completely different mix of prey resources.

Regardless, the model for behavioral thermoregulation by lizards (Huey and Slatkin, 1976) has remarkable parallels to models for optimum diet. Lizards thermoregulate effectively by basking in the sun to warm and by moving to the shade to cool. The model assumes that "an individual lizard acts to maximize its net energy gain" (Huey and Slatkin, 1976). The basis for temperature choice is similar to that for optimal foraging theory: natural selection acts to maximize fitness, which is assumed to be directly related to net energy gain. Benefits of thermoregulation are physiological: net energy gain is maximized if the lizard is actively feeding at its optimal body temperatures. Costs of thermoregulation are those associated with movement; both physiological expenditures and risk of predation are increased. Also, lizard thermoregulation depends on a number of factors in addition to physiological benefits, including foraging, social interaction, or other activities. The predictions similar to those of optimal foraging theory (Huey and Slatkin, 1976; Magnuson et al., 1979) are as follows:

1. If costs of thermoregulation are low in a particular environment, lizards may be expected to thermoregulate carefully.
2. Lizards will also thermoregulate more carefully if the productivity of the habitat is raised.
3. If thermal generalists or specialists occur, generalists will undergo greater body temperature changes and specialists will tend to live either in the low-cost habitats or where optimal temperatures are readily available.
4. Competition and predation will influence the degree of thermoregulation depending on the degree of thermal similarity between interacting species.

Optimal Movement Patterns

Feeding paths and speed of movement by animals have also been examined via cost-benefit analysis (Pyke et al., 1977). Most study of foraging paths has concentrated on insects and birds (Cody, 1974; Pyke, 1978a,b). However, three-spined sticklebacks (*Gasterosteus aculeatus*) were observed to search 2–3 times more efficiently than expected by chance (Beukema, 1968). The sticklebacks maintained a constant direction of movement through the environment but when a prey was found, the probability of turning doubled and often led to increased capture rates on clumped prey. Anchovy larvae (*Engraulis mordax*) swam more slowly and turned more frequently in response to dense aggregations of food (Hunter and Thomas, 1974).

Speed of movement by fishes while foraging has been elegantly analyzed by Ware (1975). He examined data on movement speed of bleak (*Alburnus alburnus*) collected by Ivlev (1960). Speed of movement was close to that expected from an optimal foraging strategy based on net energy gain and growth. From Ware's model the expected swimming speed to maximize net rate of energy gain was calculated to be 3.08 cm/sec; the observed speed was 2.97 cm/sec. Ware (1978) has also argued that many fishes in the wild swim at speeds that correspond with speeds predicted from optimal foraging theory; fishes appear to search for prey in ways that maximize their growth rate (Ware, 1978).

Models of behavioral thermoregulation have been proposed to simulate the movement and distribution of fishes in the thermal gradients (Neill, 1976, 1979; DeAngelis, 1978) In DeAngelis's (1978) two-dimensional model, fish movement is dependent on temperature, dissolved oxygen, food availability, and habitat preference. Fishes move a "step" at a time in a random direction biased by the above factors. DeAngelis (1978) limited himself to temperature since thermal preferences are known and the influences of the other variables are less well known.

Neill (1979) used model simulations of thermoregulation in one dimension to explore the mechanisms that underlie the distribution of fishes in heterothermal environments. He argues that "a successfully thermoregulating fish moves through its habitat in such a way as to maximize time spent at temperatures favorable for the joint conduct of its life processes." Fishes may thermoregulate via predictive mechanisms; movements are based on the fishes' thermal expectations based on individual or evolutionary "experience." This often leads to "simple" rules for thermoregulation, such as: to find warmer water, move upward or inshore. Neill (1979) points out the difficulties with a thermoregulatory mechanism based only on predictive mechanisms. Fishes may also react to recent thermal experience so that their movements are biased toward the thermal preferendum. One reactive strategy for thermoregulation could involve an increased rate of changing directions by 180° whenever recent experience indicates that thermal conditions are becoming worse (Neill, 1979).

As both DeAngelis (1978) and Neill (1979) readily admit, little experimental evidence exists to test their models. The qualitative patterns in field data appear to fit the models well, but the details of how fish move through heterothermal environments remain to be worked out.

COSTS AND BENEFITS OF FORAGING IN A HETEROTHERMAL ENVIRONMENT

Foraging and thermoregulatory behaviors in fishes have been subjected to independently developed cost-benefit analyses that are often strikingly similar. Students of foraging behaviors and behavioral thermoregulation have assumed that animals behave in ways that maximize fitness. In general, growth is assumed to correlate with fitness. But optimal foraging predicts feeding behavior based on maximizing the net rate of energy intake. Behavioral thermoregulation often assumes ad libitum feeding and predicts what temperatures fishes should occupy based on net rate of energy gain.

We propose that fishes foraging in heterothermal environments are balancing an energy budget and are behaving optimally in simultaneous response to both food and temperature. Unfortunately, consideration of the multivariate nature of fish bioenergetics has been infrequent. We will make the multivariate analogue of the arguments for optimal foraging theory and behavioral thermoregulation outlined in figure 1. Namely, fishes are expected to allocate time for food and temperature resource use in ways that maximize growth (and reproduction).

Schoener (1971) described the procedure for finding optimal behaviors as follows: (1) choosing the currency, (2) choosing the appropriate cost-benefit functions and establishing the constraints, and (3) solving for the optimum. Students of foraging and thermoregulation agree that energy is likely to be an appropriate and useful currency (Huey and Slatkin, 1976; Pyke et al., 1977; Neill, 1979; Pyke, 1979). Pyke et al. (1977) have pointed out that "it will always be the job of the naturalist to understand the biology of the animal sufficiently well to know which currency is being optimized." For fish feeding in heterothermal environments we believe that an appropriate cost-benefit function is *net rate of energy gain* convertible to growth. We will solve for the optimum using a bioenergetics model of fish growth (Kitchell et al., 1977; Breck and Kitchell, 1979).

Bioenergetics Model

Kitchell et al. (1977) have developed a bioenergetics model for simulations of fish growth. Model predictions derive from a simple energy budget equation based on fish body size, activity levels, ration levels, food quality, and water temperature. Growth is sensitive—it shows highly plastic responses to environmental changes and adjusts population biomass more quickly than does change in population numbers (Hall et al., 1970; Kerr, 1971). The model has been tested and used with several species of fish (Kitchell et al., 1977, 1978; Megrey, 1978; Weininger, 1978; Breck and Kitchell, 1979; Kitchell, 1979; Kitchell and Breck, 1980). We have used a version of the model parameterized for bluegill sunfish (*Lepomis macrochirus*). Specifics are presented in Breck and Kitchell (1979).

We held fish size, activity, and food quality constant in our simulations (cf. Breck and Kitchell, 1979); ration and temperature were varied to predict the growth response surface for a 10 g bluegill (fig. 2). Obviously, bluegills grow best feeding near maximum rates of 9% of body weight per day near their thermal optimum of 31° C. As fish move away from optimal temperatures, consumption, egestion, and excretion are reduced and growth declines (cf. Kitchell et al., 1977, fig. 1). Increases in metabolic costs with increases in temperature cause growth rate to decline at each ration level. The zero growth line (fig. 2) represents maintenance rations, which vary with temperature from 1% at 15° C to over 5% at 35° C.

If natural selection has shaped the behavior of fishes to select habitats in which they can maximize net energy gain, then the bioenergetics model should be useful to solve for the expected optimum behavior (Kitchell, 1979). For example, from the response surface (fig. 2), a 10 g bluegill in a 25° C habitat should seek out a food patch sufficient to provide a ration of 7% of body weight per day. Similarly, in an environment that provides a ration of 5% of body weight per day, the fish should seek out a habitat at about 20° C. The optimum habitat distribution of fishes foraging in an environment varying in both food and temperature may differ dramatically from predictions based on optimal foraging or behavioral thermoregulation alone.

Patch Choice Based on Food and Temperature

Assuming that fishes behave optimally, interactions between food and temperature distributions can be integrated through the bioenergetics model to predict the distribution of fishes. First, we examine the consequences of equal food patches distributed along a thermal gradient at temperatures varying from 14° to 36° C. Second, we examine the predictions in a more complex environment varying in its distribution of food and temperature. Our question here is whether predictions of fish distribution via the bioenergetics model differ from those based on

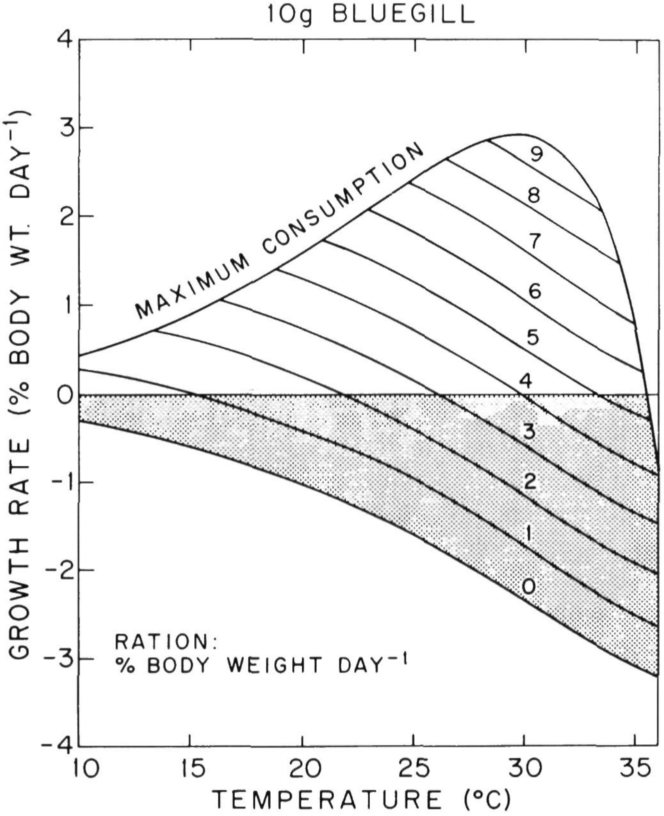

Fig. 2. Growth response of 10 g bluegill to temperature and food ration predicted by the bioenergetics model (model from Kitchell et al., 1977; bluegill data from Breck and Kitchell, 1979).

food and temperature alone or on a simple summation of food and temperature predictions.

For our first simulation food patches of equal size and quality were distributed across a thermal gradient (fig. 3, left) and the bluegill growth model was used to predict growth based on both food and temperature. Growth isopleths from model predictions (fig. 3, right) show that a greater area of the food patches may be used for positive growth at cooler temperatures even though the food patches are identical. Maximum growth occurs near preferred temperatures (~ 31° C) (Beitinger, 1974), but higher growth rates can be achieved over a larger area of the food patch at slightly cooler temperatures. Optimum temperatures for growth appear to be 1–2° C cooler than preferred tem-

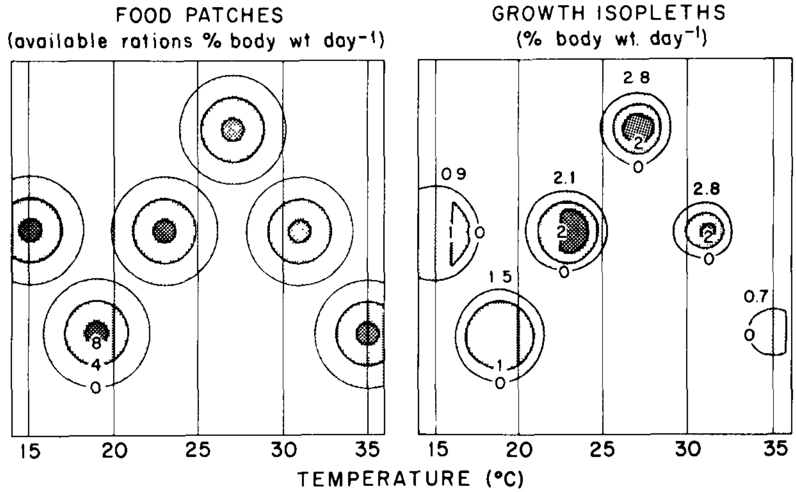

Fig. 3. *Left*, distribution of food patches and *right*, expected growth rates of 10 g bluegill in a two-dimensional habitat that includes a temperature gradient. Maximum growth is given above each food patch in the right panel.

peratures (McCauley and Casselman, 1980). At high temperatures (33–36° C) growth is reduced due to metabolic costs, even though food is abundant. At lower temperatures growth is often truncated (fig. 3, right) due to reduced consumption rates, even though food is available.

Our second set of simulations (fig. 4) was for a more complex distribution of food and temperature resources. The purpose was to determine whether the expected fish distributions, in this case 10 g bluegills, would differ markedly if our predictions were based on behavioral thermoregulation, optimal foraging, or some combination of the two including bioenergetic optimization. The growth rates (fig. 4, right) can be interpolated directly from figure 2 using temperature and achievable ration in a food patch (fig. 4, left).

When food is available ad libitum and temperature varies (fig. 4, top), growth is excellent over much of the habitat. Even so, fishes would be expected to distribute in respect to their thermal preferences (fig. 4, top left). Fishes violating their temperature preferences would grow somewhat more slowly, but on the cool side the costs would be slight. Those behaviorally thermoregulating under ad libitum conditions will have maximum growth.

When temperature is optimum and food varies (fig. 4, center), growth only occurs in food patches. Fishes would be expected to travel among food patches but distribute in respect to their food distribution

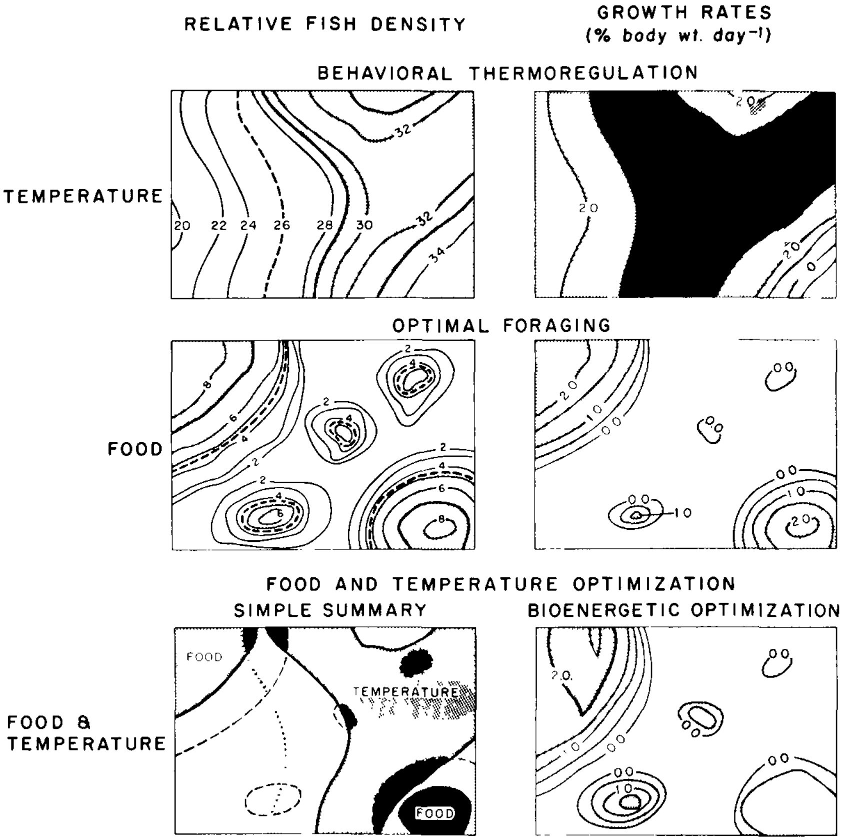

Fig. 4. Hypothetical spatial distribution of a 10 g bluegill in respect to (*top*) temperature, (*center*) food, and (*bottom*) food and temperature combined. *Left:* expected fish distributions based on behavioral response to temperature and food independently; *right:* expected growth rates based on the bioenergetic growth model. *Top*: expected fish density based on a preference of 31° C ± 2° C (dark) and 31° C ± 5° C (light), and growth based on maximum ration. *Center:* fish are assumed behaviorally to respond directly to food density in patches expressed at % body wt day^{-1} of achievable ration, and growth is computed for optimum temperature of 31° C. *Bottom left:* a simple intersection of the direct response to food and temperature independently; *bottom right:* the computed growth predictions of the bioenergetics model with both temperatures and achievable ration as inputs.

(fig. 4, center left). We assumed that fishes would distribute in a manner that produced positive growth, i.e., in patches with food available to produce rations greater than 4.5% body weight·day^{-1} or the maintenance ration at 31° C. Growth is clearly food-dependent; fishes consuming the greatest rations (e.g., > 8% body weight per day) grew fastest (> 2% of body weight per day). Growth declines rapidly given the "steep" food gradients in this hypothetical environment. At optimal temperatures fishes that achieve the highest net rate of energy intake grow best—optimally foraging fishes should achieve the highest growth rates. Of course, as food is depleted in a patch or as other factors intervene, fishes may be expected to move among patches. Where the fishes should move next could be predicted from a modified marginal value theorem (Charnov, 1976); an animal should leave a patch when its net rate of energy gain convertible to growth drops to the average rate for the habitat. The marginal rate of energy gain should tend to be equalized over all food × temperature patches in the habitat.

Finally, we compared the predictions for patch occupancy based on food and temperature alone with model predictions of growth when food and temperature both vary (fig. 4, bottom). What is the expected distribution of fishes in this habitat, which is patchy with respect to both temperature and food? Theoretically, at least, fishes should behave in ways to maximize growth rate. The greatest growth rates based on the bioenergetic combination of food and temperature do not strongly overlap the zones of best growth based on food or temperature taken alone. The same rations available at different temperatures yield different growth results; for example, fishes achieving 7% rations at 25° C grew 2.5% in body weight per day, and those consuming 8% rations at 34° C grew less than 1% per day. The expectations for fish distribution from bioenergetic optimization also differ from predictions based on a simple summation of responses to temperature and food (fig. 4, bottom left). Fishes that can distribute in respect to bioenergetic optimization in a heterogeneous environment will grow faster than those that optimize their distributions in respect to food alone, to temperature alone, or to a simple summation of food and temperature optimization.

Limitations of the Model

We have presented a static analysis to predict daily growth, assuming that the fishes remain within the same temperature and food patch. The proximal cues by which a fish could sense if it is growing at a higher rate have not been incorporated into the model. Various proximal cues may provide information on prey capture rate and temperature. In order for fishes to maximize growth in a heterothermal environment, they must be able to integrate these cues into some predictor of growth rate. Are fishes able to integrate information on food and temperature to solve the bioenergetics equation? Fishes performing this integration will grow at faster rates and will likely leave more offspring. Selection is expected to favor those with such capabilities.

USE OF FOOD AND THERMAL HABITAT BY FISHES

An extensive body of theory exists to predict foraging behaviors in fishes, but experimental evidence is limited (Pyke et al., 1977; Pyke, 1979). Empirical data on thermal preference of fishes in the laboratory and thermal experiences of fishes in the field are abundant (Coutant, 1977; Magnuson and Beitinger, 1978), but no strong, unifying theoretical framework integrates these observations (cf. Magnuson et al., 1979). The questions have been: (1) Do fishes respond behaviorally to food in ways that maximize growth? (2) Do fishes respond behaviorally to temperature in ways that maximize growth? We have presented a third alternative—fishes integrate their responses to both food and temperature so as to maximize growth. Below we examine some studies on how fishes' joint use of food and temperature may help test this idea.

Fish Distributions with Respect to Temperature and Food Availability

Four field examples are considered. In three of these a thermal gradient is provided from waters used in once-through cooling in condensers used to generate electricity. The other is a natural vertical temperature gradient in a northern lake. The examples include fishes with relatively abundant food (e.g., bluegill in Lake Monona, cisco in Pallette Lake); those with limited food (e.g., coho in Pallette Lake, ictalurids in the Connecticut River); and those that respond to the warm and cool edge of the thermal niches.

In Lake Monona, Wisconsin (Neill, 1971; Neill and Magnuson, 1974), many warm-water fish species concentrated in the outfall area relative to similar but unheated reference areas. Bluegill were captured most frequently in the outfall area, which provided not only warm water in the preferred temperature range but also a rich food source for these planktivorous fishes. Water intakes were limnetic and thus brought abundant large zooplankters into the littoral zone (Brauer et al., 1974).

To contrast distributional responses to food and temperature, a series of fish collections taken in the littoral zone and across the thermal gradients were reanalyzed for bluegill distribution with respect to temperature and food (fig. 5). Intermediate-sized bluegills (76–100 mm) were used because they are relatively the most frequent size

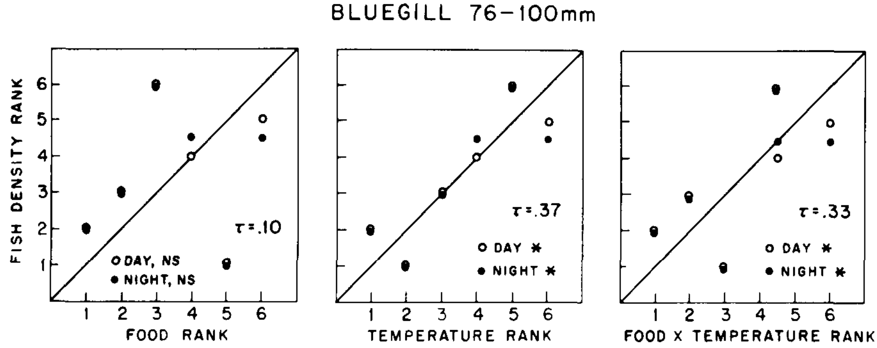

Fig. 5. Rank correlations of bluegill (76–100 mm) density at six sites in a thermal outfall, Lake Monona, Wisconsin, with food abundance, proximity to preferred temperature, and the average of food and temperature ranks. Data on fish density and temperature from Neill (1971) and Neill and Magnuson (1974) and on food density from Brauer et al. (1974). These statistics were ranked for August and September data with 1 being the highest density of bluegill (76–100 mm long) and 6 the lowest, 1 being the closest temperature to the preferred 31° C and 6 the farthest from it and 1 being high zooplankton densities and 6 low. A combined food × temperature rank for each location was the average for food and temperature alone.

class of bluegill in the outfall (Magnuson et al., 1980). Their catches were significantly correlated with temperature and food × temperature (Kendall rank correlation coefficient, $p < 0.05$, fig. 5). Their distribution was not significantly related to food rank, and adding food did not increase the ability to predict fish distribution. In this environment with high densities of food, intermediate-sized bluegill were distributed with respect to temperature.

In Lake Monona larger bluegills (> 100 mm) were less concentrated in the outfall than intermediate-sized fishes. Larger bluegills also moved out of the heated area at night and seemed to prefer larger prey—their distribution was uncorrelated with temperature and food within the outfall area. Smaller bluegills (< 75 mm) were somewhat more abundant in the outfall than in reference areas, but their density was unrelated to food or temperature within the outfall area. These data suggest that, in a zone of abundant food, fishes are often most concentrated at temperatures near their preferred temperatures, and size class–related behaviors may differ.

Kromrey (1976) examined the distribution and feeding of two centrarchid species (pumpkinseed *Lepomis gibbosus*, black crappie *Pomoxis nigromaculatus*) in Lake Columbia, a power plant cooling lake at Portage, Wisconsin (Lozano et al., 1978). Water temperatures are raised approximately 15° C by movement through the cooling system of the plant and exponentially decline to ambient along the 5 km length of the U-shaped lake. The lake is relatively homogeneous in all major characteristics except food distribution and water temperature (Kromrey, 1976).

Black crappie distribution during summer corresponded to expectations based on laboratory-determined temperature preference (fig. 6). During spring and fall, however, the fish occupied cooler than pre-

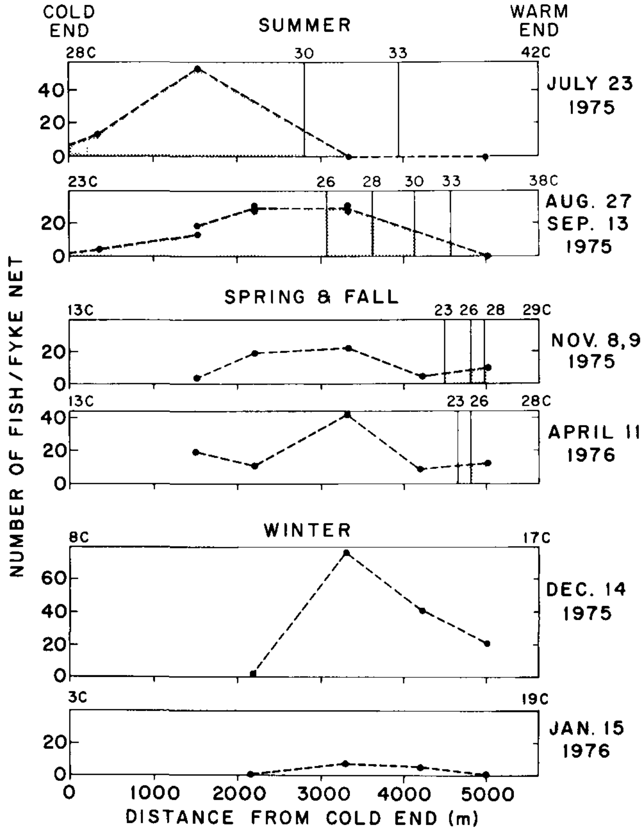

Fig. 6. Distribution of black crappie along a 5000 m temperature gradient in Lake Columbia, Wisconsin, in summer, spring and fall, and winter. The overlap between fish distribution and the thermal niche of black crappie is indicated by shaded area (± 2° C, ± 5° C). Graph is based on a reanalysis of Kromrey (1976). Each data point is the catch from a single fyke net set for 24 h. Temperature preference of black crappie is approximately 28° C (Coutant 1977). The temperatures along the lake's length were interpolated between the measured temperature at each end and a model we derived to describe the change in temperature (figs. 3 and 2, respectively, in Lozano et al., 1978).

ferred temperatures. In winter, preferred temperatures were not available and the black crappie occupied the warmer half of the lake. These results are consistent with a bioenergetic optimization of growth. Growth declines rapidly with increasing temperature at the warm side of the thermal niche (fig. 2). Black crappie during summer did not surpass the warm edge (33° C) of their thermal niche, even though temperatures up to 42° C were available. In contrast to these results, black crappie in spring and fall were distributed past the cool edge (23° C) of their thermal niche and did not crowd into the areas with preferred temperatures. Since growth does not decline sharply at the cool edge of the thermal niche, this distribution in cool water would not have been costly bioenergetically. Prey density indices (Kromrey, 1976) also suggested that food was somewhat more abundant at these cooler temperatures and perhaps increased the benefits associated with this cool distribution pattern. In winter, growth would be higher at the warmest temperatures available, assuming that food was present. Fish in Columbia Lake were in good condition in all seasons and grew well (Kromrey, 1976). These data demonstrate that black crappie will distribute themselves outside of their thermal niche and suggest that when they do, it is consistent with predictions based on bioenergetic optimization of growth.

The thermal distribution and feeding ecology of ciscoes (*Coregonus artedii*) and coho salmon (*Oncorhynchus kisutch*) were examined in Pallette Lake, Wisconsin (Engel and Magnuson, 1971, 1976; Engel, 1972, 1976). Both species are cold-water fishes and would not be expected to be in the surface waters by late summer. Data were available on the vertical temperature profile, the vertical distribution of fishes from vertical gill nets, the vertical distribution of zooplankton from Clarke-Bumpus net tows, and the food based on stomach content analyses. Ciscoes have fine gill rakers and consume primarily zooplankton. Coho salmon have coarse rakers and feed more often on larger particles, such as terrestrial insects on the surface in Pallette Lake, or, more commonly, on fishes.

Ciscoes fed on prey that were more abundant in warmer waters than they prefer to occupy (fig. 7). But the median distribution of ciscoes did not exceed the bounds of their thermal niche; ciscoes were most common within their preferred temperature range. The zooplankton that ciscoes preferred were broadly distributed across temperatures and were relatively abundant within their thermal niche. Coho salmon ate prey near the surface (terrestrial insects) in May, June, and July and occupied water warmer than expected. In August surface waters apparently became so warm (23° C) that coho switched to large plankton prey (*Leptodora*, *Holopedium*, and *Chaoborus*) at somewhat cooler temperatures but still above their preferred range. Coho continued to occupy warmer temperatures and to exploit these food resources. Both coho salmon and ciscoes occasionally moved well outside their preferred range (fig. 7). Food abundance apparently overrides thermal preference for coho salmon, but the associated bioenergetic costs may

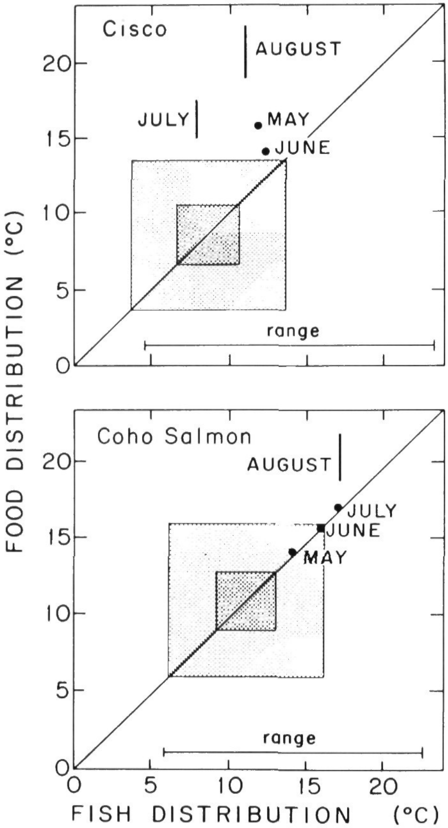

Fig. 7. A comparison of the temperature distribution of cisco and coho salmon with the temperature distribution of their preferred food during summer months in Pallette Lake, Wisconsin, based on a reanalysis of results in Engel (1972). The thermal niche of each fish is indicated by shading (± 2° C, ± 5° C) on both the fish distribution and the food distribution axes. The total range of temperature at which fish were caught is indicated along the *x*-axis. For both fish and their food, the temperature of their median distribution is plotted as estimated from figure 23, tables 18 and 19, and appendix table 2 in Engel (1972).

have contributed to the poor success of coho introductions into Pallette Lake. Maximum size obtained averaged 188 mm (35 g; Engel, 1972). In better environments, such as Lake Michigan, this species can reach 700 mm (4.5 kg; Borgeson, 1970). Ciscoes maintained their thermal preferences in spite of somewhat greater abundances of preferred foods outside this thermal range. They had a moderate-to-slow growth rate in oligotrophic Pallette Lake (Engel, 1972).

These data suggest that when food is not abundant, cold-water fishes will occupy temperatures on the warm edge of their thermal niche. The extent to which they do this is limited and is directly related to the scarcity of food. Also, many of the movements into warmer water appear to be feeding forays rather than permanent occupation (Engel and Magnuson, 1976).

Fish distributions with respect to temperature and food often make sense bioenergetically. Occasionally, however, exceptions arise. In a study of fish distribution near a power plant on the Connecticut River, Merriman and Thorpe (1976) found that brown bullheads (*Ictalurus nebulosus*) and white catfish (*I. catus*) were both abundant in a heated effluent channel during winter. Individuals of both species experienced 20–30% weight losses relative to fishes in cooler overwintering areas outside the canal. Apparently these fishes incur greater metabolic costs due to occupying warmer temperatures and, perhaps, reduced food intake and greater competition for limited food due to overcrowding in the channel (Merriman and Thorpe, 1976). The apparently disadvantageous behavior of these fishes in this particular modified habitat cannot be explained on the basis of bioenergetic optimization of growth.

Bioenergetics and Diel Fish Migrations

Young sockeye salmon (*Oncorhynchus nerka*) actively feed in the zone of peak food abundance during the night near their preferred temperatures (15° C) but vertically migrate down at dawn and spend the day in the cold hypolimnion (6° C) (Narver, 1970; McDonald, 1973). Why do these sockeyes leave the depth of preferred temperature and maximal food during the day? Following the lead of McLaren (1963), Brett (1971) suggested that this migration could lead to the most efficient conversion of food to growth. Since food conversion efficiency remains high and maintenance metabolism is much reduced at cool temperatures, it could well be bioenergetically advantageous to migrate vertically during nonfeeding times. An increasing number of examples concur with Brett's (1971) bioenergetic hypothesis.

Caulton (1978) analyzed the bioenergetic advantage of inshore-offshore migrations to tilapia (*Tilapia rendalli*). Tilapia move inshore to warm, preferred temperatures (approximately 30° C; Coutant, 1977) during the day and feed on abundant aquatic vegetation. At night they move offshore to cooler temperatures. Caulton's (1978) experiments and model simulations suggest that this behavior is also bioenergetically advantageous.

Alewives (*Alosa pseudoharengus*) feed in the thermocline at night in Lake Michigan and return to cooler, hypolimnetic waters during the day (Brandt, 1978; Janssen and Brandt, 1980). Using a bioenergetics model for alewives, Stewart (1980) has shown that a growth advantage may be obtained through diel vertical migration when the lake is thermally stratified.

In the laboratory juvenile rainbow trout (*Salmo gairdneri*) often grow better in fluctuating temperatures than in constant temperatures (Hokanson et al., 1977). These trout grew best at 15 ± 3.8° C in a diel fluctuating temperature regime. Fish growth in constant temperature tanks (17°, 19° C) near preferred temperatures (cf. Coutant, 1977) did not differ significantly from that of fishes in fluctuating temperature systems with mean temperatures 2–4° C lower (Hokanson et al., 1977). It appeared that diel temperature fluctuations below optimal temperature for growth were physiologically advantageous; fluctuations above optimal temperatures led to lower growth rates.

In lab experiments underyearling sockeye salmon fed intermediate rations grew as well in cyclic temperatures (4.5–17.5° C) as, or better than, at constant temperatures (Biette and Geen, 1980). Fish given excess rations grew best at constant temperatures near preferred (15.3–15.9° C). Those fed low rations grew best at constant low temperatures (6.2° C), where energy is best conserved. This most recent test of Brett's (1971) hypothesis suggests that under conditions occupied by underyearling sockeye salmon in Babine Lake, salmon are likely to grow more rapidly than if they did not vertically migrate (Biette and Geen, 1980). The results also suggest that behavioral patterns of fishes may change in response to both food and temperature in ways that maximize bioenergetic advantage.

Though the bioenergetic hypothesis (Brett, 1971) still needs testing (Biette and Geen, 1980), the accumulating evidence supports the hypothesis. Some fishes feed near their preferred temperature, where maximum consumption rates are possible, and move to cooler temperatures, where metabolic costs are lower, for food digestion and conversion. Since diel vertical migration and diel on- and offshore migration are common in fishes, this hypothesis warrants further research effort.

Ration, Temperature, and Fish Growth

The growth response surface of the bluegill bioenergetics model (fig. 2) suggests that as available ration declines, fish could achieve better growth rates by occupying cooler temperatures. Two of the three salmonids analyzed by Jarvaid and Anderson (1967) reduced their preferred temperatures when starved. Bluegill sunfish fed 2% daily rations lost weight and steadily reduced their preferred temperature over a 6-day period (Stuntz and Magnuson, 1976). Bluegills on 4% and 6% daily rations grew and occupied the predicted thermal range; bluegills starved for 6 days did not show declining thermal preferences, but daily median temperature was lower than preferred (Stuntz and Magnuson, 1976). Reynolds and Casterlin (1979) also tested the effects of starvation on preferred temperatures in bluegills. Two bluegills were tested over a 22-day period. Starving fish showed an almost immediate and continuous decline in preferred temperature. Upon feeding, preferred temperature increased in both individuals. Ration apparently can influence temperature selection in ways that would tend to maximize growth if food were limited.

Species Interactions

Up to this point we have examined the behavior of individual species as if they do not interact with other species in the use of food or thermal habitat. Recent reviews of resource partitioning based on food, temperature, and other habitat variables (Magnuson et al., 1979; Moermond, 1979; Sale, 1979; Werner, 1979) indicate that interactions within and among species will often influence the use of resources. Magnuson and Beitinger (1978) pointed out that biotic interactions altered behavioral thermoregulation more than did changes in habitat variables. To elaborate on the use of food and temperature, we will relate our recent experiences with Lake Michigan fishes.

Thermal distributions of Lake Michigan fishes were determined with aimed bottom trawling along temperature isotherms (3–20° C) in a region where the thermocline intersected the bottom off Grand Haven, Michigan, during late summer in 1977 (Brandt et al., 1980) and again in 1979. In 1977 alewives, rainbow smelt (*Osmerus mordax*), spottail shiners (*Notropis hudsonius*), and trout-perch (*Percopsis omiscomaycus*) comprised 94% of the catch by numbers. Species segregated along temperature gradients, despite rapid oscillations in thermocline location (Brandt et al., 1980). In general, species appeared to occupy temperatures near those preferred in the laboratory.

When diets of fishes caught in 1977 were compared (Crowder et al., 1981), an interesting pattern emerged (fig. 8). Fishes with the most similar diets (alewife, rainbow smelt) had dissimilar thermal habitat distributions. Young-of-the-year alewives, spottail shiners, and yellow perch have almost completely overlapping thermal habitats, but they have dissimilar food habits. The observed pattern of complementarity in diet and thermal habitat suggests that competition has been important in determining the structure of the Lake Michigan fish community (Crowder et al., 1981).

Between 1977 and 1979 a native coregonine chub (*Coregonus hoyi*) known as the bloater increased in abundance from less than 1% of our trawl catch to over 42%. Results of this "natural experiment" indicate

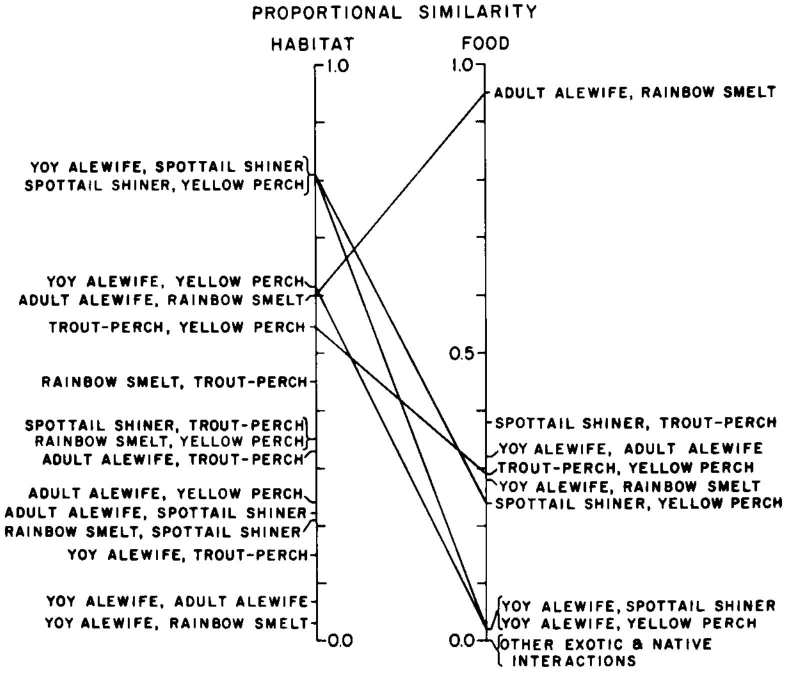

Fig. 8. Daytime proportional similarity (Hurlburt, 1978) in food and thermal habitat use by common Lake Michigan fishes taken in bottom trawls off Grand Haven, Michigan, in September 1977. Adapted from Crowder et al., 1981.

that bloaters have dramatically altered the late-summer distribution of adult alewives. In 1979 chubs were numerically the most abundant species caught in trawls from 5° to 16° C. Alewives have shifted from their preferred temperature (11–15° C) to 4–8° C, placing them outside of their preferred thermal niche and possibly at a physiological disadvantage. Competition for food or thermal habitat or both may have caused the observed shift in alewife distribution. Bloaters appear to be superior interference competitors in small lab systems (F. Binkowski, University of Wisconsin-Milwaukee, personal communication) and they also eat the larger benthic and pelagic invertebrates (*Mysis relicta, Pontoporeia hoyi*) more efficiently than do alewives (Janssen, 1978; L. B. Crowder, unpublished data). This niche shift is not unlike that in experimental ponds for centrarchid fishes described by Werner and Hall (1976, 1977, 1979).

Further analysis of the bioenergetic implications of these interactions in Lake Michigan fishes is in progress. We are also examining prey availability or patchiness as it may alter fish distributions in the highly dynamic Lake Michigan system. Both food and temperature appear to play key roles in this system, and the use of food and temperature resources appears central to understanding species interactions.

HYPOTHESES AND RESEARCH NEEDS

Behavioral thermoregulation and optimal foraging theory may be used as predictors of fish behavior by assuming that fishes thermoregulate or forage in ways that maximize growth rate and thus fitness (fig. 1). Predictions from these two cost-benefit approaches may differ dramatically. An alternative cost-benefit analysis using a bioenergetics model of fish growth predicts fish behaviors based on both temperature and food (fig. 1). We conclude that fishes likely evaluate both food and temperature. Available data suggest that fishes often behave in bioenergetically "sensible" ways and do not strictly follow the predictions of behavioral thermoregulation or optimal foraging alone.

We perceive a need for further research on patch choice in fishes. No experimental evidence exists from fishes to support the optimal foraging hypothesis for patch choice. Abundant lab evidence suggests that fishes will volitionally choose more profitable thermal habitats. But in the field fishes have a multivariate patch choice problem—food and temperature vary both temporally and spatially. The bioenergetics approach outlined here looks promising but will probably have to be made more dynamic. Predators, cover, and other variables are not explicitly included in the current model but are known to be important. Exceptions to the bioenergetic optimization patterns should lead to an incorporation of other factors.

As we seek to understand the influence of natural selection on the behaviors of fishes, we must attempt to include the major relevant variables that determine or constrain the fitness of individuals. We think that temperature and food are two such variables for fishes that forage in heterothermal environments. Much less is known about other variables that affect overall fitness, but this does not limit their potential importance.

ACKNOWLEDGMENTS

We thank Wayne Aspey and Shelly Lustick for inviting us to present a paper in Columbus. Jim Kitchell provided valuable discussion and encouragement throughout the development of this paper, and he and Jim Breck commented on an earlier draft. Cheryle Hughes drew the figures. The research on Lake Michigan and this synthesis were supported by the National Oceanic and Atmospheric Administration's Office of Sea Grant through an institutional grant to the University of Wisconsin-Madison.

DISCUSSION FOLLOWING DR. MAGNUSON'S PRESENTATION

Question: I want to ask about the Atlantic salmon. I agree with your approach and applaud you for integrating more than one variable in an attempt to understand the biology of what is happening. However, there are some exceptions to your model. It may help to identify where those exceptions occur. If you calculate, or try to predict, the possible location of the animal and yet do not observe the animal at that location, that tends to lead to a third complication. That is, what causes animals not to be where you expect them? People usually attribute this to predation and other causes. Also, there might be some value to a model such as this that not only is deterministic, in the sense that it is based on average growth rates, but also tries to incorporate some of the variance you observed. I've always been struck with the growth rate curve's function with temperature to give them food ration. If this can be relatively flat and can be observed as averages at one location, that may or may not be different from averages at another temperature location. Are the animals responding not only to the average but also to the variance?

Answer: The first thing that it obliges us to do is to provide a couple of the exceptions to our predictions. We are familiar with at least three exceptions and there are probably some others. There are some fish that when you reduce the ration their temperature preference doesn't decline. An example is the Atlantic salmon case that you presented. There are also fish in the Connecticut River power plants situation that aggregate around a long channel near the power plant; they become very skinny. Perhaps we could ask, Why didn't they move out of that high-cost environment and move to someplace where they could balance their energy budget? I don't know the answer to that now. We also have some *Tilapia* species from Africa that migrate on- and offshore. These species survive in a lake where there are thermal springs in deep water. During periods of dryness, the lake has gotten smaller, and so those *Tilapia* species feeding inshore in cool water migrate offshore into hot water, thus losing weight. Again, this is maladaptive from this kind of hypothesis. At the moment the examples that we have been able to find have tended to be eliminated primarily on the idea that they are doing both.

Now, you have questioned the optimizing temperature and food, but there are some exceptions. We don't know whether we can explain those exceptions on the basis of temperature and food based on more information, or evolutionary history of the species, or engendering a new factor such as current speed, predators, or light.

For the variance question, I'm not sure if I understand exactly what you are asking. We think that the temperature preference function, which includes temperature preferences not as a point but as a variance, is good. We think the same approach for collecting food items or patches of food as a variance would be a good idea. But I don't believe that's the point you are seeking.

Question: I have a question that relates to what you have been discussing. With brown trout, I have seen cohorts of the same group literally approach an asymtotic growth rate and then an entirely new growth rate. I would assume, under your system, that you would have to assume a different base for food, and you would consider that cohort as an entirely different population because it certainly would not be average in that system. Do you understand what I mean?

Answer: Over time, is this the same individual growing one way and asymptoting, and then a short time later growing at a new, faster rate?

Question: Yes, at the same slope as the original growth. Then the same cohort individuals in that population transfer to a fish foraging behavior rather than staying with the invertebrates. The two species within the two groups could be readily identified, and yet they were all marked the same. I've also seen this in freshwater drum.

Answer: I think most people would tend to explain that by an optimal foraging strategy in which the animal, once it became large enough to prey on the fishes, could prey at a lower cost-benefit function than when it was feeding on smaller prey. We could try to introduce the idea of thermal factors as a possibility when it got larger, although this idea is not usually engendered to explain this occurrence. So, when it got larger, another more optimal thermal environment was available to it, only with some competitive interaction with another species. Usually we use optimum foraging differences to explain that phenomenon.

Question: It is well known that the temperatures that fishes select vary seasonally with the temperatures that they are acclimated to. Could you address how that was taken care of in your studies.

Answer: Well, first of all, I'm not attacking you, but I don't believe the first statement, that the temperature preferences vary seasonally. I think temperature occupations vary seasonally, and I have reviewed the literature on the effects of photoperiod and temperature acclimation on temperature preference. In most cases where I see a seasonal variation, I find that the numbers were averaged in time with the day-to-day temperature occupation in the experiment. These were changing each day and were averaged over a period. What we find with the bluegill, where we have most of our data, is that with short photoperiods and long photoperiods, the fish prefers temperatures within 1° or 2° of each other. So, I personally have yet to be convinced that there are seasonal changes in temperature preference. On temperature acclimation, we ran an experiment where we acclimated bluegills to very cold temperatures and winter photoperiods and then put them in a temperature gradient without changing the photoperiod. They ran the temperature of the system up and killed themselves, so we said we made a mistake. We ran it again, but this time stopped the temperature from getting warmer at 20°, gave the fish 1 day to acclimate to 20°, gave them control of the temperature preference apparatus again, and immediately after that they ran it up to within 2° of their summer preference. Those were fish that were acclimated within 4° of winter temperature preferences. Now, if you look at acclimation and temperature preference, my feeling is that temperature acclimation and photoperiod have only minimal effects on preference, and that the seasonal differences in temperature occupation are primarily those of opportunity.

Question: There are times of the year, for instance in the breeding season, when breeding activities may become more important than selecting on the basis of temperature and things like that. Did you account for seasonality in your studies?

Answer: We accounted for seasonality in a couple of ways. We looked at different seasons, if that accounts for it. In terms of adding a new element, like a spawning migration or something of that nature, I think the orientation presentation (see chap. 1) would provide a good example. At a certain time of year, these birds suddenly have an urge to migrate to a different location. With spawning migration, obviously, the habitat preferences of a returning sockeye salmon in the sea are not the same as the habitat preferences of a sockeye smelt migrating to the sea. Salinity preferences vary over ontogeny as do temperature preferences. The alewife situation is an example of an ontogenetic preference change in temperature between young-of-the-year and adult alewives. We would expect these things to vary ontogenetically. These may occur simultaneously in certain seasons of the year. I have yet to be convinced that there are seasonal changes; I think that there are ontogenetic changes.

Question: I would like to compliment you on your synthesis of these different approaches. My question relates to the Lake Michigan example. The Great Lakes have had a long history of multiple perturbation. We have lost a lot of native species. It seems like the present feeling is that the prospect of recovery of many of the native species is not good in face of the exotics that now dominate some of those systems. However, some of your examples show one system in which a native species has been able to at least start recovery in face of competition with exotic species. Does that give you any hope for any of the other species that are presently at low levels?

Answer: That system really surprised me just by this species coming back in large numbers right in the center of the distribution of the two exotics, which were described to have pushed it out of the system anyway, along with some commercial fishing. So that was an unexpected result. It is possible that here we could have our cake and eat it too. It is possible that the alewife or the smelt contributed to the demise of the deep-water chub. At the same time, the adult chub could be displacing them physically along this thermal gradient. For example, the alewife and the smelt, as we have described in this paper, may have caused a demise of chubs due to predation on the eggs and larvae. And there may be interactions at other life history stages. It may be that the reduced fishing pressure took enough pressure off the chub's mortality that it was able to handle other competition with the two exotics. We even have some evidence that there are mechanisms by which the returning chubs could have physically displaced these two exotic species. Considering aggressive interactions, if you look at who pecks whom (classical peck order), the chubs at this size are socially dominant over both the smelt and the alewife. It suggests that interference competition at this size class could have resulted in displacement. We are presently looking at the idea of whether exploitation competition could have caused this displacement; we are just collecting the data to analyze at the present time. Anybody who has worked on the Great Lakes knows that just when you learn the population biology of a particular species, it disappears from the system. And all of our predecessors on the Great Lakes continue to be surprised by which dominates next. I think that we will be surprised by which is dominant next. I don't know what is going to happen.

Question: Since you seem to indicate that the smelt were getting the worst end of the deal in being displaced in the warmer temperatures, did you do any analysis as to the condition of size? Could you demonstrate a loss that these fish were experiencing?

Answer: We haven't done that yet. With both approaches it would be interesting to look at the condition factor and the annual growth rate of those animals from scales. It would be a good thing to see. I beg to differ with your belief that there are seasonal effects on temperature preferences. We did some work where it was shown that despite long-term acclimation in the laboratory, temperature tolerances were significantly different under a long photoperiod with regard to season. In other words, seasonal rhythms persisted regardless of whether we put them under a different photoperiod regime for extended periods of time. I would like to hold my rebuttle to temperature changes. I may be wrong. You know that all generalizations may be wrong and somebody is going to shoot us down. I would like to see the data.

Question: This question is in reference to your bluegill acclimation and preference studies. If we can accept Hammel model for a temperature setpoint, isn't it so that your bluegill data would indicate that bluegills are incapable of resetting their hypothalamic temperature setpoint with acclimation? If in fact you acclimate them, they still will cruise into temperatures where they will now die?

Answer: It would suggest that they didn't.

LITERATURE CITED

Beitinger, T. L. 1974. Thermoregulatory behavior and diel activity patterns of bluegill, *Lepomis macrochirus*, following thermal shock. Fish. Bull. 72:1087–93.

Beitinger, T. L., and L. C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. Amer. Zool. 19:319–30.

Beukema, J. J. 1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): the influence of hunger and experience. Behaviour 30:1–126.

Biette, R. M., and G. H. Geen. 1980. Growth of underyearling sockeye salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquat. Sci. 37:203–10.

Borgeson, D. P. (ed.). 1970. Coho salmon status report, 1967–1968. Mich. Dept. Nat. Res., Fish. Manag. Rep. No. 3. 31 pp.

Brandt, S. B. 1978. Thermal ecology and abundance of alewife (*Alosa pseudoharengus*) in Lake Michigan. Ph.D. thesis, University of Wisconsin, Madison. 226 pp.

Brandt, S. B., J. J. Magnuson, and L. B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Can. J. Fish. Aquat. Sci. 37:1557–64.

Brauer, G. A., W. H. Neill, and J. J. Magnuson. 1974. Effects of a power plant on zooplankton distribution and abundance near plant's effluent. Water Res. 8:485–89.

Breck, J. E., and J. F. Kitchell. 1979. Effects of macrophyte harvesting on simulated predator-prey interactions. *In* J. E. Breck et al. (eds.), Aquatic plants, lake management, and ecosystem consequences of lake harvesting, pp. 211–28. Institute of Environmental Studies, University of Wisconsin, Madison. 435 pp.

Brett, J. R. 1971. Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Amer. Zool. 11:99–113.

Caulton, M. S. 1978. The importance of habitat temperatures for growth in the tropical cichlid *Tilapia rendalli* Boulenger. J. Fish Biol. 13:99–112.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theoret. Popul. Biol. 9:129–36.

Cody, M. L. 1974. Optimization in ecology. Science 183:1156–64.

Coutant, C. C. 1977. Compilation of temperature preference data. J. Fish. Res. Bd. Can. 34:739–45.

Crowder, L. B., J. J. Magnuson, and S. B. Brandt. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can. J. Fish. Aquat. Sci. 38:662–68.

DeAngelis, D. L. 1978. A model for the movement and distribution of fish in a body of water. ORNL/TM-6310. Oak Ridge National Laboratory, Oak Ridge, Tenn. 78 pp.

Eggers, D. M. 1977. The nature of prey selection by planktivorous fish. Ecology 58:46–59.

Engel, S. 1972. Utilization of food and space by cisco, yellow perch, and introduced coho salmon with notes on other species, in Pallette Lake, Wisconsin. Ph.D. thesis, University of Wisconsin, Madison.

Engel, S. 1976. Food habits and prey selection of coho salmon (*Oncorhynchus kisutch*) and cisco (*Coregonus artedii*) in relation to zooplankton dynamics in Pallette Lake, Wisconsin. Trans. Amer. Fish. Soc. 105:607–14.

Engel, S., and J. J. Magnuson. 1971. Ecological interactions between coho salmon and native fishes in a small lake. Proc. 14th Conf. Great Lakes Res., pp. 14–20. International Association of Great Lakes Research.

Engel, S., and J. J. Magnuson. 1976. Vertical and horizontal distributions of coho salmon (*Oncorhynchus kisutch*), yellow perch (*Perca flavescens*), and cisco (*Coregonus artedii*) in Pallette Lake, Wisconsin. J. Fish. Res. Bd. Can. 33:2710–15.

Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15:839–926.

Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. J. Fish. Res. Bd. Can. 34:639–48.

Huey, R. B., and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. Quart. Rev. Biol. 51:363–84.

Hunter, J. R., and G. L. Thomas. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy, *Engraulis mordax* Girard. *In* J. H. S. Blaxter (ed.), The early life history of fish, pp. 559–74. Springer-Verlag, New York.

Hurlburt, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59:62–77.

Ivlev, V. S. 1960. On the utilization of food by planktophage fishes. Bull. Math. Biophys. 22:371–89.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.

Janssen, J. 1978. Feeding behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes *Coregonus hoyi* and *C. artedii*. J. Fish. Res. Bd. Can. 35:249–53.

Janssen, J., and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 37(2): 177–84.

Jarvaid, M. Y., and J. M. Anderson. 1967. Influence of starvation on selected temperature of some salmonids. J. Fish. Res. Bd. Can. 24:1515–19.

Kerr, S. R. 1971. Prediction of fish growth efficiency in nature. J. Fish. Res. Bd. Can. 28:809–14.

Kitchell, J. F. 1979. In search of an optimal environment. *In* R. H. Stroud and H. Clepper (eds.), Predatory-prey systems in fisheries management, pp. 31–33. Sport Fisheries Institute, Washington, D.C. 504 pp.

Kitchell, J. F., and J. E. Breck. 1980. A bioenergetics model and foraging hypothesis for sea lamprey. Can. J. Fish. Aquat. Sci. 37:2159–68.

Kitchell, J. F., W. H. Neill, A. E. Dizon, and J. J. Magnuson. 1978. Bioenergetics spectra of skipjack and yellowfin tunas. *In* G. Sharp and A. Dizon (eds.), Physiological ecology of tunas, pp. 357–68. Academic Press, New York. 485 pp.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Bd. Can. 34:1922–35.

Krebs, J. R., J. Ryan, and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22:953–64.

Kromrey, G. 1976. Distribution and feeding of pumpkinseed (*Lepomis gibbosus*) and black crappie (*Pomoxis nigromaculatus*) in a power plant cooling lake. M.S. research report, University of Wisconsin, Madison.

Lozano, S. J., D. W. Rondorf, and J. F. Kitchell. 1978. Assessment of a cooling lake ecosystem. Tech. Rep. No. 78-08, Water Resources Center, University of Wisconsin, Madison. 108 pp.

McCauley, R. W. and J. M. Casselman. 1980. The final preferendum as an index of the temperature for optimum growth in fish. European Inland Fisheries Advisory Commission Symposium, 80/E76.

McDonald, J. G. 1973. Diel vertical movements and feeding habits of underyearling sockeye salmon (*Oncorhynchus nerka*) at Babine Lake, British Columbia. Tech. Rep. Fish. Res. Bd. Can. No. 378.

McLaren, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Bd. Can. 20:685–727.

Magnuson, J. J., and T. L. Beitinger. 1978. Stability of temperatures preferred by centrarchid fishes and terrestrial reptiles. *In* E. S. Reese and F. J. Lighter (eds.), Contrasts in behavior, pp. 181–216. John Wiley, New York.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. 19:331–43.

Magnuson, J. J., P. A. Medvick, G. W. Gallepp, R. J. Hall, P. W. Rasmussen, and J. E. Breck. 1980. Integration of biological with thermal criteria for power plant design and water resource use. Tech. Rep. No. 80-02, Water Resources Center, University of Wisconsin, Madison.

Medvick, P. A., J. J. Magnuson, and S. Sharr. 1981. Behavioral thermoregulation and social interactions of bluegill. Copeia 1:9–13.

Megrey, B. A. 1978. Applications of a bioenergetics model to gizzard shad (*Dorosoma cepedianum*): a simulation of seasonal biomass dynamics in an Ohio reservoir. M.S. thesis, Miami University, Ohio.

Merriman, D., and L. M. Thorpe. 1976. The Connecticut River ecological study. Amer. Fish. Soc. Monogr. No. 1. 252 pp.

Moermond, T. C. 1979. Resource partitioning: a dynamic competitive balance. *In* R. H. Stroud and H. Clepper (eds.), Predator-prey systems in fisheries management, pp. 303–10. Sport Fisheries Institute, Washington, D.C. 504 pp.

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Bd. Can. 27:281–316.

Neill, W. H. 1971. Distributional ecology and behavioral thermoregulation of fishes in relation to heated effluent from a steam electric power plant (Lake Monona, Wisconsin). Ph.D. thesis, University of Wisconsin, Madison.

Neill, W. H. 1976. Mechanisms of behavioral thermoregulation in fishes. *In* Sigma Research Inc. (ed.), Report of a workshop on the impact of thermal power plant cooling systems on aquatic environments, pp. 156–69. Electric Power Research Institute, Palo Alto.

Neill, W. H. 1979. Mechanisms of fish distribution in heterothermal environments. Amer. Zool. 19:305–18.

Neill, W. H., and J. J. Magnuson. 1974. Distributional ecology and behavioral thermoregulation of fishes in relation to heated effluent from a power plant at Lake Monona, Wisconsin. Trans. Amer. Fish. Soc. 103:663–710.

Oaten, A. 1977. Optimal foraging in patches: a case for stochasticity. Theoret. Popul. Biol. 12:263–85.

O'Brien, W. J., N. A. Slade, and G. L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304–10.

Pyke, G. H. 1978a. Optimal foraging: movement patterns of bumble bees between inflorescences. Theoret. Popul. Biol. 13:72–98.

Pyke, G. H. 1978b. Are animals efficient harvesters? Anim. Behav. 26:241–50.

Pyke, G. H. 1979. Optimal foraging in fish. *In* R. H. Stroud and H. Clepper (eds.), Predator-prey systems in fisheries management, pp. 199–202. Sport Fisheries Institute, Washington, D.C. 504 pp.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52:137–54.

Reynolds, W. W., and M. E. Casterlin. 1979. Behavioral thermoregulation and the "final preferendum" paradigm. Amer. Zool. 19:221–24.

Sale, P. F. 1979. Habitat partitioning and competition in fish communities. *In* R. H. Stroud and H. Clepper (eds.), Predator-prey systems in fisheries management, pp. 323–32. Sport Fisheries Institute, Washington, D.C. 504 pp.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

Steffel, S., A. E. Dizon, J. J. Magnuson, and W. H. Neill. 1976. Temperature discrimination by captive free-swimming tuna, *Euthynnus affinis*. Trans. Amer. Fish. Soc. 105: 588–91.

Stewart. D. J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics-modeling synthesis. Ph.D. thesis, University of Wisconsin, Madison.

Stuntz, W. E. 1975. Habitat selection and growth of bluegills. Ph.D. thesis, University of Wisconsin, Madison.

Stuntz, W. E., and J. J. Magnuson. 1976. Daily ration, temperature selection, and activity of bluegill. *In* G. W. Esch and R. W. McFarlane (eds.), Thermal ecology, 2:180–84. Technical Information Center, Energy Research and Development Administration, Washington, D.C. 404 pp.

Ware, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. J. Fish. Res. Bd. Can. 32:33–41.

Ware, D. M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. J. Fish. Res. Bd. Can. 35:220–28.

Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Ph.D. thesis, University of Wisconsin, Madison.

Werner, E. E. 1979. Niche partitioning by food size in fish communities. *In* R. H. Stroud and H. Clepper (eds.), Predator-prey systems in fisheries management, pp. 311–22. Sport Fisheries Institute, Washington, D.C. 504 pp..

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–52.

Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191:404–6.

Werner, E. E, and D. J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869–76.

Werner, E. E., and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60:256–64.

LARRY L. WOLF AND F. REED HAINSWORTH

Economics of Foraging Strategies in Sunbirds and Hummingbirds

8

INTRODUCTION

The maintenance of an energy balance sufficient to meet present needs of the individual and to accrue energy for future reproduction is important in the evolutionary success of a genotype. This simple restatement of the role of energy in life history tactics places emphasis on the general class of activity associated with feeding in animals and photosynthesis in green plants. The relation between feeding behavior and reproductive success (fitness) will vary among animals, but for some the relation, either directly through energy input or indirectly through released time or energy for other activities, can be very closely coupled.

In animals with a close coupling between feeding behavior and fitness, natural selection should be an important force driving the organization of feeding behavior. The coupling between feeding behavior and fitness need not always be "tight." The variation in the extent of the correspondence between feeding and fitness may relate to many environmental variables ancillary to feeding, e.g., predation and mating. However, this variation should not deflect us from the basic argument that foraging behavior in most cases ought to be influenced by selection.

The influence of selection on the organization of foraging behavior can be studied from two general approaches, mechanistic and evolutionary, that correspond to proximate and ultimate explanations of

Department of Biology, Syracuse University, Syracuse, New York 13210

behavior. Recent theoretical work has often emphasized the latter. However, this theoretical work often may assume capabilities of the organisms for which there is no empirical evidence. Moreover, theoretical treatments sometimes suffer from what we might call the "adaptationist's fallacy"—the limited facts can be made to fit one or another adaptational scenario and usually do not uniquely test alternative explanations (Gould and Lewontin, 1979).

The mechanistic approach, though not mutually exclusive from an evolutionary approach, places more emphasis on the observed mechanics of feeding and how these influence the organization and outcome of a behavioral feeding complex. The connection to ultimate factors occurs through an analysis of how these mechanics influence some important currency related to fitness. It is also possible to see if alternative uses of the mechanics might lead to a larger or smaller horde of the seemingly crucial currency, such as energy stores. The two approaches converge at this point as the theoretician attempts to discover necessary and sufficient behavioral rules leading to the largest horde and the mechanist sees how big a horde the organism can accumulate using observed rules.

This paper attempts to straddle the proximate-ultimate conceptual fence by asking mechanistic questions in the context of theoretical decisions that might be important in organizing feeding behavior in birds that specialize on nectar as their principal energy source (see also Gass and Montgomerie, 1981). We will be interested primarily in identifying possible decision points that should occur during feeding behavior and the types of decisions that apparently are made. This is a more mechanistic approach than that of some others (e.g., Krebs, 1978; Pyke, 1978a,b,c, 1980) and is perhaps reminiscent of the approach of C. S. Holling (1966) in his analysis of the attack behavior of the preying mantis.

GENERAL BEHAVIORAL SEQUENCE IN FORAGING

The basic outline of foraging behavior of any consumer consists of a sequential series of connected events that start and end with changes in some internal state often referred to as "hunger" (fig. 1). Once hunger levels cross an activating threshold, the next stage of the sequence, search, is initiated. Search eventually leads to detection of possible food and may be followed by capture attempts (pursuit). A successful capture can produce ingestion and assimilation of energy and nutrients; these latter activities have a more direct effect on the hunger level. Foraging behavior stops if assimilation drives the internal state below a

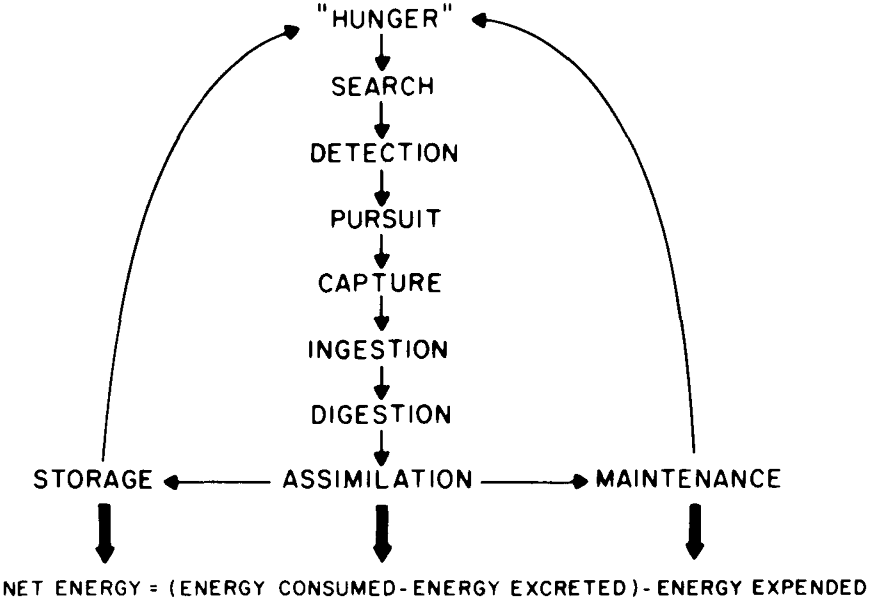

Fig. 1. Sequence of behaviors during feeding coupled with the partitioning of gross energy intake. Energy intake can either be used for maintaining the organism during and between feeding episodes or be stored for periods of enforced low intake compared with demands.

hunger threshold; foraging continues if the assimilated food is insufficient to reduce the internal hunger below a threshold. The time taken to recross a hunger threshold following a feeding event determines when the sequence starts anew.

All animals do not emphasize each stage equally. Sit-and-wait predators do not undertake active search but may search passively at all times, with hunger levels influencing detection, attack, and capture probabilities, the next stages in the sequence (Schoener, 1971). For herbivores and nectarivores, capture itself may be essentially a certainty once search and detection are successful. This is especially true of nectarivores, where the food items occur solely to be eaten as part of the tactics of the plants to enhance their own reproduction. This means that nectarivores are faced with somewhat different decisions than "classic" predators, but at a general level they can serve as model consumers for which the usual energetic currency of selective value, rate of net energy accumulation, is easily applied.

At each stage in the foraging sequence the consumer is faced with a potential series of decisions about allocating foraging effort, presumably to maximize the difference between benefits and costs per unit time. Some of the decisions are associated with the controls influencing hunger levels and ingestion, and others are involved with questions about where to feed and for how long. The possible array of decisions among alternatives probably is nearly infinite. However, we expect that only a reasonably small subset actually will be used by the foraging birds.

A useful decision, one defined in terms of maximizing the net rate of energy accumulation while feeding, depends on the reliability of the information on which the decision is based and the utility of the decision for maximizing fitness. The reliability of the information is in part a function of whether it is based on present physiological conditions or on expectations of external conditions. The information about external conditions presumably is more difficult to acquire reliably. Present physiological state can be monitored fairly directly. External conditions may be monitored through the memory system of the organism or by the correlation of past or present information with future conditions (Krebs et al., 1978).

It is our goal here to identify possible external and internal environmental information that is available to a feeding nectarivore. Then we can ask how and to what extent the information is used by a consumer. We will follow the general sequence of events in a foraging bout (fig. 1) in dealing with both the information content of the environment and the mechanics associated with using that information.

COSTS AND AVAILABLE BENEFITS OF FORAGING

Costs

The general costs of foraging and maintenance for nectarivorous birds have been reviewed extensively in the past few years (Wolf et al., 1975; Wolf and Hainsworth, 1978; Hainsworth and Wolf, 1979; Wolf and Gill, 1981). The general conclusion is that nectarivores fit fairly closely to predictions based on physiological determinants of size-related costs for a variety of birds.

Costs generally involve expenditures for temperature regulation (Lasiewski and Dawson, 1967; Calder, 1974; Brown et al., 1978) and flight (Hainsworth and Wolf, 1972b; Epting, 1980). Hummingbirds are influenced especially by their small size for thermoregulatory costs. They are relatively poorly insulated and must expend a relatively large fraction of consumed energy for maintenance. They also have relatively small storage capabilities (Calder, 1974). This leads to a requirement for high frequency of feeding as compared with animals of larger size that can store more energy relative to their demands. Although hummingbirds can enter torpor overnight, reducing thermoregulatory costs, this does not normally occur unless energy reserves are depleted to some lower threshold value, perhaps due to some risk associated with being in torpor (Carpenter, 1974; Hainsworth et al., 1977).

Hummingbirds as a group are the most thoroughly studied animals with respect to the costs of flight, primarily hovering. To date, oxygen consumption during hovering has been measured for seven species (summarized in Epting, 1980), and it is possible to make rather fine adjustments in cost estimates based on morphological factors that influence costs for lift during hovering (wing lengths and body mass).

It is possible to divide costs into detailed subsets of these general categories as exemplified by microclimatic analyses of heat exchange (e.g., King, 1974). However, there are currently few studies of the importance of these factors for foraging animals (but see Grubb, 1977; Grubb, personal communication). Moreover, some sensitivity analyses (Ettinger and King, 1980) and comparisons with independent estimates of costs (Utter and LeFebvre, 1973) suggest that this approach may not always add substantially to refinement of cost estimates. Clearly, more comparisons and information are required.

An additional, relatively unexplored area concerning foraging costs is the tactic used for feeding. Sunbirds normally perch while foraging but must fly between feeding locations. Hummingbirds are well known for their hovering mode of feeding. Some hummingbirds, such as the relatively large *Eutoxeres aquila* (Sicklebill, 11 g), regularly perch while foraging, and others may do so if an advantageous perch is available. Hover-feeding also is a facultative option, irregularly used, for small sunbirds. Perching generally is a cheaper method of foraging per unit time, although the relative difference in costs for perching versus hovering decreases with decreasing body mass (Hainsworth and Wolf, 1972b). This variation in relative costs probably is important in the evolution of the variation in foraging method among the various types of nectarivores, especially since they vary quite considerably in average size (Brown et al., 1978).

A high-cost foraging mode, such as hovering, could be favored if the consequences are a higher rate of net energy gain from more rapid feeding. Hovering could decrease the time spent maneuvering to probe a flower. If this decreased the total time between flowers, it could increase the value of hovering by providing more rapid access to flowers (fig. 2). This might be especially important when small distances between individual flowers make the time spent maneuvering at the flower a relatively large proportion of the total flying time. Long distances between flowers, where flying already comprises the majority of foraging time and energy, will make the two foraging modes more nearly energetically equivalent. We might expect, then, to see birds perching to feed most commonly when flowers are at some intermediate-to-long distance apart (fig. 2).

The characteristics of the individual flower may also be important in selecting for a particular foraging mode. The orientation and degree of clustering of flowers may represent adaptive responses by the plant to increase pollinator specificity, especially reducing the feeding efficiency of possible insect visitors. As the number of separate moves to visit *n* flowers increases, the value of hover-feeding may also increase if the postulated time penalty for landing is real. Experiments testing some of these ideas are underway with Australian honeyeaters, which can do both types of foraging (Pyke, personal communication).

Available Benefits

The available benefits of foraging by nectarivorous birds also have been reviewed in detail (Wolf et al., 1975; Gill, 1978; Pyke, 1978a; Hainsworth and Wolf, 1979). The benefits are derived from sugars in flower nectar. The energetic value of the sugars is easy to characterize (Hainsworth and Wolf, 1972a). Minor constituents of nectar, such as fats and amino acids, may be important for some nonavian nectarivores (Baker and Baker, 1975). Nectarivorous birds also catch insects, and we assume that the nectar is primarily an energy source, with other essential nutrients coming from insects (Hainsworth and Wolf, 1976; Wolf et al., 1976; Wolf and Gill, 1980). The foraging we consider in this paper is at flowers for nectar and not for insects. Generally, insect catching takes place away from flowers and at a different time. Thus, although there may be some constraints on time available for the two types of foraging, in general they can be considered as separate behaviors with exclusive organizational rules.

SEARCH AND DETECTION

During the search phase of the foraging sequence the individual generally constrains its movement to within a short distance of a local perch. However, the two extreme types of foraging behavior among nectarivorous birds, territoriality and "traplining," probably differ considerably in the amount of flying. Territory sizes are related closely to flower density and the total energy requirements of the resident individual or pair (Gill and Wolf, 1975; Gass et al., 1976; Wolf and

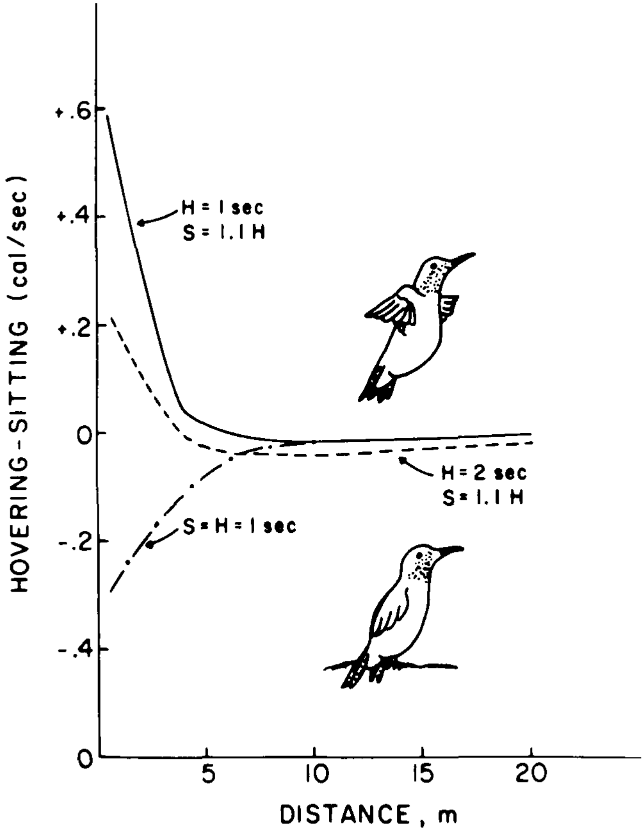

Fig. 2. The relationship between the differences in rate of net energy gain for an 8 g hummingbird sitting or hovering while feeding plotted as a function of the distance between flowers. The values assume a flight speed of 2 ms^{-1} at 85% of the cost of hovering, an ambient temperature of 20° C, a body temperature of 41° C, and a thermal conductance calculated from the equation in Hainsworth and Wolf (1972b). Functions are based on a total intake of 15 cal. The *solid line* assumes an intake rate of 15 cal/sec while hovering and 13.6 cal/sec while sitting. The *dashed line* reduces these intake rates by half for both hovering and sitting. The *dotted line* assumes that the intake rate for both sitting and hovering is 15 cal/sec. Positive values predict that hovering is energetically more efficient; negative values predict that the bird could do better by sitting while feeding.

Wolf, 1976; Kodric-Brown and Brown, 1978). Flight distances usually do not exceed the diameter of the territory.

When territoriality is not possible or is less beneficial energetically than nonterritoriality (Gill and Wolf, 1975; Carpenter and McMillen, 1976; Wolf, 1978; Brown and Kodric-Brown, 1979), the proportion of time spent locating good foraging sites increases (Montgomerie, 1982). Male long-tailed hermit hummingbirds (*Phaethornis superciliosus*) may fly up to 1 km from their lek perches to their regular feeding areas (Stiles and Wolf, 1979), whereas nonterritorial individuals of both sunbirds and hummingbirds may have to fly among foraging sites not occupied by territorial residents (Hainsworth and Wolf, 1972a; Feinsinger, 1976). However, there is very little direct evidence of the increased time spent in flight by nonterritorial birds while foraging (see Montgomerie, 1982).

Females of most hummingbirds are forced into a nonterritorial foraging technique during the breeding season by their nesting activities (Legg and Pitelka, 1956; Wolf, 1969; Wolf and Wolf, 1971; Hainsworth and Wolf, 1972a; Stiles, 1973). Female sunbirds generally reside within a territory defended by a male (Skead, 1967; Wolf and Wolf, 1976). In at least one hummingbird species this behavior has been modified so that the female uses flowers defended by the male, although the male apparently makes no direct contribution to the postmating nesting effort (Wolf and Stiles, 1970).

Search costs also are influenced by the requirements to choose among an array of available flowers offering rewards that vary in quality. Hummingbirds have a choice among several plant species, in addition to choices within a plant species. The availability of multispecific choices varies seasonally with the patterns of flowering by the plants and the population sizes of other hummingbirds (Wolf, 1970; Stiles, 1975, 1980; Feinsinger, 1976, 1980; Wolf et al., 1976; Des Granges, 1979; Montgomerie, 1982). Large birds generally are able to dominate smaller ones and intraspecifically males dominate females (Wolf, 1970; Feinsinger, 1976). These effects may restrict the choices available. In multispecific flower assemblages this generally means that the subordinate birds are forced onto plant species or particular inflorescences that would not have been their first choice in an unrestricted situation (Feinsinger, 1976; Wolf et al., 1976; Gill, 1978).

For many sunbirds and some hummingbirds, the spatial scale of the choice among plant species is enlarged, since many plant species usually grow as monospecific stands. Multiple choices force higher costs, but also may increase the uncertainty of the alternatives. As the distance among patches or the uncertainty of flowering time increases, the birds are forced to make choices with less direct information about the available alternatives. This appears to be especially important in East African sunbirds (Wolf and Gill, 1980) and may also be important among north temperate migrant hummingbirds (Brown and Kodric-Brown, 1979). The degree to which choices must be made among multispecific patches also will vary seasonally (Wolf, 1970; Feinsinger, 1976; Wolf et al., 1976; Stiles, 1980).

Even monospecific stands are patchy at one or more spatial scales for a feeding nectarivore. If we assume some initially homogeneous distribution of rewards and a constant renewal rate, the foraging activities of a bird will produce some locations that have been depleted more recently than others. Only under the unlikely condition that an organism visits all locations in it's feeding area on each feeding bout will the homogeneity be maintained. Thus, consumer-produced heterogeneity must be added to any underlying plant-related heterogeneity that is produced independently of the foraging activities. This plant-related heterogeneity might reflect genetical or physiological differences in nectar production (Teuber et al., 1980), differences in age of flowers (Carpenter, 1976), or morphological differences influencing the efficiency with which individual flowers can be visited (Wolf et al., 1972).

These morphological differences, especially interspecific ones, may be easily available cues to heterogeneity. Environmental or genetic differences among conspecific plants will require sampling, probably repeatedly, and may not be within the discriminatory abilities of the birds (Hainsworth and Wolf, 1976). Bird-generated heterogeneity is a post-hoc, plus-minus type of effect and potentially is available as useful information for a bird to bias future foraging efforts.

In some cases the foraging organism might reduce the overall heterogeneity of nectar volumes. As average nectar volumes among individuals of one plant species decline with high harvest intensity, the variance in nectar volume among randomly chosen flowers may decline (Gill and Wolf, 1975; L. L. Wolf and F. B. Gill, MS). This may follow partly from the large percentage of the total flowers visited each time or from preferential feeding at the flowers containing the highest volume. Additionally, if the consumer visits several plant species, the net reward per unit foraging time theoretically might be equalized across the plants regardless of heterogeneous production rates (Fretwell and Lucas, 1970; Tullock, 1971; Heinrich, 1976, 1978). In spite of the potential reductions in nectar heterogeneity, the variance in quality among locations can be considerable and should produce related biases in locations of feeding activity.

Search costs in a heterogeneous environment are traded off against the chance of increasing the net capture reward. The birds ought to choose among simultaneous options of interspecific or intraspecific flower types, selecting the one with the highest net energy intake rate. Thus, it is of interest to know whether the birds can discriminate among energy intake rates and, if they do, to know if the information is actually used in choice of feeding locations.

Laboratory Choices

Variables that are related directly to energy intake rate and that might be discriminated are sugar concentration, volume of fluid available, corolla morphology (especially corolla length), and the volume rate of intake (Hainsworth and Wolf, 1979). More indirect cues include any morphological traits of the plants or flowers differentiating among plant types with average rate of intake differences. We have varied volume intake rate, corolla length, and available volumes independently to ask which seem to be most important for food choice in the laboratory. These experiments held sugar concentration of the reward constant so that gross intake rate also measured net energetic reward per unit time spent feeding.

The experiment was a simple two-position choice following initial presentations where both locations had the same reward characteristics. For the choice situation, one of the two locations contained the same reward as during the initial presentations and the other location had a different reward based on volume intake rate, volume of fluid, or corolla length. The test bird was forced to sample the alternatives several times and then its subsequent choices were noted over 20 trials. We asked if there was a significant change in choice of position from the initial presentations.

The six birds tested showed significant changes in choices only when volume intake rate was varied (table 1). The birds were more likely to switch to the higher volume intake rate position when there was a difference. There was no difference in the response when volumes or corolla lengths were varied; the birds were equally likely to switch positions when there was no difference in volume or corolla length as when there was a difference. Considering all three variables simultaneously, we can say that the majority of birds, if they responded at all, were most influenced by volume intake rate (choosing the higher rate) and less by volume and corolla length. Although the choice was not always made, the experiments do indicate that the birds can and will respond differentially to the three variables, preferentially using volume intake rate as the key cue for a choice between two alternative feeding sites. Since volume intake rate is a combination of corolla length and nectar volume, the birds appear to use the cue most directly related to rate of energy gain.

TABLE 1

INFLUENCE OF VARIABLES AFFECTING RATE OF NET ENERGY GAIN ON CHOICES OF FEEDING LOCATIONS FOR FEMALE ARCHILOCHUS ALEXANDRI IN THE LABORATORY

Variable	Correct Choice	No Choice
Intake rate		
Same	37	76
Different	45	41
Volume		
Same	27	33
Different	55	84
Corola length		
Same	30	30
Different	52	87

SOURCE: Data from L. L. Wolf et al., MS.

NOTE: *Same* indicates a choice situation where that variable is the same in the two positions; *different* indicates that the variable has a different value in each position. A correct choice is to the position providing a higher rate of net energy gain, shorter corolla, or higher volume. Significant incorrect changes in position preference occurred only on 1% of the trials and are not included.

Earlier experiments with "infinite" volume feeders showed that the intake rate preference could be overridden easily by a sufficient difference in sugar concentration. The birds had a marked preference for the higher of the two sugar concentrations, even if the lower concentration offered the higher rate of net reward, due to a shorter corolla attached to that feeder (Hainsworth and Wolf, 1976). The preference for the higher concentration disappeared only when the corolla length of that feeder approximated the extreme distance that a bird could reach its tongue. A hypothesis for these observations is that in the field, volume intake rates tended to be fairly similar among some plant species so that concentration played the key role in net benefit rates. Sugar concentrations might also be a "supernormal" stimulus (Staddon, 1975), but this explanation does not seem likely since the tested concentrations are within the range normally encountered by the birds. The preference for higher sugar concentrations also might reflect the relative difficulty of monitoring the two cues. However, week-long experiments with the same choices showed no shift in preference toward the higher net intake rate. Over this time period we might expect the birds to be able to monitor the differences.

The ability of hummingbirds to detect a food with higher sugar concentration when rate of volume intake is constant depends on sugar concentration. A larger difference is required for discrimination as concentration increases (table 2). The logarithmic nature of discrimination characteristics is viewed as a compromise (trade-off) between two opposing processes (fig. 3): (1) ability to respond with high sensitivity to environmental changes at low energy values (high sensitivity line in fig. 3), and (2) a cutoff in discrimination ability at some saturation value that dictates the range of response to differences in the environment. A logarithmic function achieves relatively high sensitivity at low environmental energy values with some response but a decreasing sensitivity over a relatively extended range. A corollary suggests that if the logarithmic response curve of figure 3 can vary in slope, responses of highest sensitivity would be predicted for animals with the lowest net gains of energy during feeding and responses of lower sensitivity would be predicted for animals with higher net gains of energy during feeding.

The importance of these detection abilities to the choice of feeding locations in the field has not been studied. It seems unlikely that they could serve as finely tuned, local choice mechanisms, but they could probably operate at the level of choices between plant species or perhaps between major patches within a species (see below).

Choices between plant species, though presumably predicated on the differences in net benefit that are obtained, still require cues to signal the differences without forcing the bird to probe the flowers prior to the choice. In this case morphology and color are both reasonable cues. The color similarities among hummingbird-visited plant species in western North America suggest the importance of color as a cue (Grant, 1966). Birds that are rewarded at a sufficient rate at one plant species might be expected to return regularly to that color and be less inclined to shift to another color.

TABLE 2

MINIMUM INCREASE IN SUCROSE CONCENTRATION REQUIRED FOR DISCRIMINATION BY HUMMINGBIRDS

Sugar Concentration (molar sucrose)	Minimum Required Increase (molar sucrose)
0.25	0.05
0.50	0.10
0.80	0.20
1.00	>0.20

SOURCE: Based on Hainsworth and Wolf, 1976.

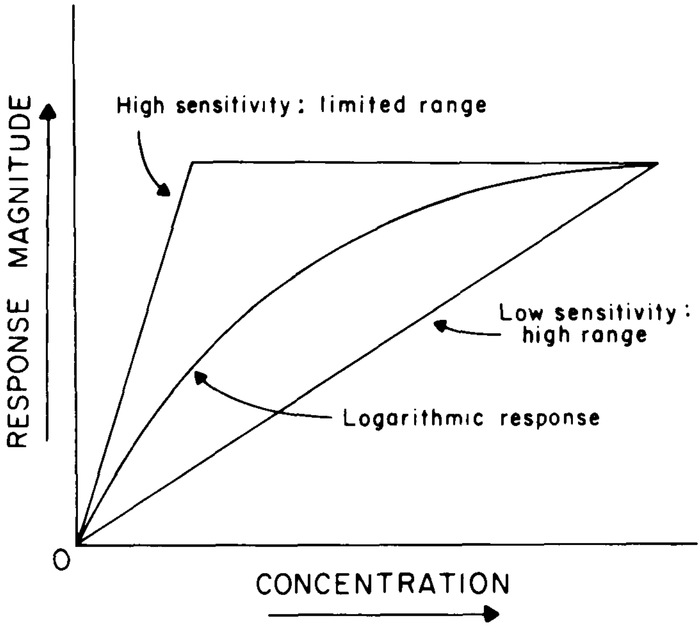

Fig. 3. Response magnitude versus energy intensity. Response magnitude depicts information input as in a receptor system (such as frequency of action potentials in an afferent neuron). The logarithmic function is viewed as a compromise between arithmetic functions with (1) high sensitivity but limited range (due to saturation) and (2) low sensitivity but extended range. Based on Hainsworth, 1981.

We have tested this hypothesis in the laboratory by asking if hummingbirds learn more quickly to return to the same color or to a different color after receiving a reward. This is a "win-stay," "win-switch" experimental paradigm (Olton, 1981). where color rather than position is the variable associated with "winning" (receiving a reward). The hummingbirds tested learned (to at least 80% correct choices over 3 successive days) to win-stay to color (return to the same color on their next visit) about twice as fast as they learned to make their next foraging visit to the alternative color (win-switch to color). This pattern is maintained whether or not the birds were trained initially to the test situation with either alternate color. The rate of learning the task seemed not to vary with training color, suggesting that, at least with yellow and blue, there was no basic color bias influencing the choice. However, we intentionally did not use red as a color cue in these experiments. The speed of learning the color-cue task (4 days to reach our criterion) suggests that inherent color biases may play at most a minor role and one that would be difficult to demonstrate experimentally using this paradigm.

The same experimental procedure was used to ask if birds were able to learn spatial cues. The birds now had to learn whether the reward would be in the same location as the initial presentation (win-stay) or the alternative position (win-switch). In this experiment the 6 birds tested each learned to win-switch more quickly than they learned to win-stay. In contrast to the rapid learning of the color cues, the birds took 3–10 times longer to learn the spatial task.

The change in which task (win-switch or win-stay) was learned more quickly in the two situations accords well with what one might expect from the biology of these nectarivores. Nectar is a slowly renewing resource that normally is depleted by a foraging bird. The usual response should be to shift to a new location for subsequent feeding efforts, shunning the recently visited locations sufficiently long to allow nectar volumes to replenish. The possible color mimicry among hummingbird flowers suggests that color is an important visual cue and that the birds should have a tendency to return to the same color on subsequent bouts. The broad spectrum of color response by the birds (Goldsmith and Goldsmith, 1979) indicates that the color red is not necessarily crucial, and in our experiments the birds simply returned to a rewarded color, with no obvious bias between the two colors tested.

Field Choices

A hungry nectarivore initiates a search for a specific foraging site by flying to a patch of flowers. Once at a patch there are several spatial scales of possible additional decisions before a flower is actually probed (Wolf and Hainsworth, 1978; Hainsworth and Wolf, 1979; Gass and Montgomerie, 1981). Except for individual flowers we have not specified any spatial scale for these decisions. Flowers are arranged on stalks, which are themselves clustered, and clusters of stalks are more or less isolated from other clusters. The potential information and decisions about foraging locations might occur at any or all of these spatial scales.

Foraging birds can enhance their net rate of energy gain by biasing visits to areas least recently visited, allowing the flowers maximum time to replenish the nectar. Decisions about where to forage could be made before the actual foraging attempt (a priori) or not until the flower is probed and potentially provides information about local conditions (a posteriori) (Hainsworth and Wolf, 1979). A priori decisions would require that the bird be able to remember locations of flowers recently visited (or ones not recently visited) and select for memory capabilities as part of the sensory apparatus of foraging (Orians, 1981).

Memory capabilities are selected in the context of the utility and cost of storing and processing information. The use of memory presumably is constrained by the length of time the information must be stored (Beatty and Shavalia, 1980) and by the specificity of the information required as a function of the total possible information that could be stored. Figure 4 indicates an optimum spatial scale for remembering information that is neither too grandiose nor too detailed. The large spatial scale simply is not sufficiently fine-grained for useful predictions of future conditions, but the very local spatial scale is too fine-grained to integrate sufficient diversity of locations in the memory store.

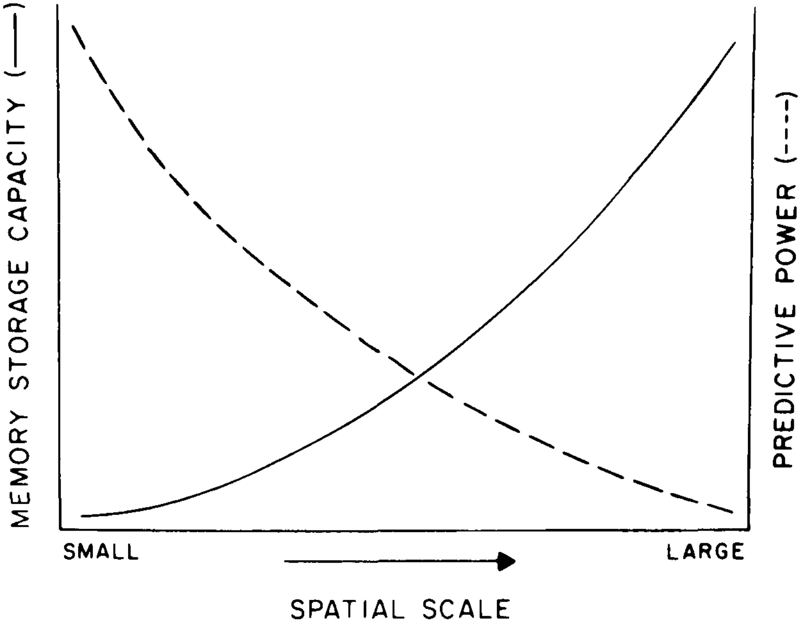

Fig. 4. The relationship between the ability to remember specific spatial locations (memory storage capacity) and the value of any particular location as a function of the spatial scale of the locations remembered. The combination of the two opposing functions suggests that use of memory to order foraging locations would occur at some intermediate spatial scale. The actual scalar dimensions would depend on the foraging range of the animal and the spatial scale of distribution of the patches. Time since the last visit would serve as another variable (a third axis) negatively related to the value of memory.

The value of the information depends on how closely it approaches reality. For feeding nectarivores a possible store of information about the external environment relates to locations of high or low amounts of nectar. Since nectar is a predictably renewing resource, this amounts to remembering which locations have been visited and when. However, the value of this information depends on whether the individual is the sole exploiter of the nectar pool, a possible advantage of territoriality (Gill and Wolf, 1975; Charnov et al., 1976). As the probability of other nectar-feeders visiting a location increases, the value of remembering the location decreases.

A Priori Information

A bird potentially could partition a foraging area into large sections that could be visited in some nonrandom sequence. The bird could either revisit the area sequentially until it has been depleted, then shift efforts to another large section, or alternate between sections. The latter tactic might be most useful if the bird visited a large proportion of each section per foraging bout or if it could not remember within-area locations of previous foraging efforts. A broad-tailed hummingbird (*Selasphorus platycercus*) in Colorado foraged in a territory containing flowering *Ipomopsis aggregata* plants in two sections separated by an area containing no flowers. The bird almost always (95% of bouts) foraged entirely within one area or the other on a single foraging bout. On 4 of 5 days the bird did not depart from random visit sequences to the two sections (L. L. Wolf and F. R. Hainsworth, MS). The lone nonrandom day was more alternation between areas than expected by chance.

The choice of foraging locations in this territory appeared to depend on perch sites. The location of the start of a foraging bout depended on which of 3 or 4 perches the bird came from, but there was no bias as to which perch was used at the end of a foraging bout as a function of the previous foraging area (table 3). What determined the location of a start perch is not clear, and the bird could change perches between foraging efforts. However, the lack of sequences of starts in either area suggests that very little, if any, information at this spatial scale was used to determine subsequent foraging locations.

Sunbirds foraging at a weedy mint (*Leonotis nepetifolia*) in East Africa may have partitioned their territories vertically (Gill and Wolf, 1977). This plant produces stalks with ball-like inflorescences (verticils) at regular intervals up the stalk (Gill and Conway, 1979). Foraging birds tend to move horizontally through a patch of flowers, rarely

TABLE 3

NUMBER OF TIMES PER PERCH BROAD-TAILED HUMMINGBIRD BEGAN OR ENDED FORAGING BOUTS IN TERRITORY OF FLOWERING IPOMOPSIS AGGREGATA PLANTS (COLORADO, JULY 1979)

TERRITORY SECTION	PERCH 1	2	3	4	5
	Bouts Started				
A	5	70	9	2	1
B	60	91	2	1	6
	Bouts Ended				
A	11	69	1	1	1
B	36	124	0	2	9

(< 20% of all moves) changing strata within a foraging bout, but regularly changing strata to start the next bout. This patterning permits fairly large-scale partitioning with a minimum of information stored, since usually only 2–4 verticils per stalk will bloom simultaneously. The birds may need to remember no more than an average of three locations—high, middle, and low—to organize the start of foraging bouts nonrandomly. This mechanism obviously works only when the vertical dimension is characterized by clearly defined strata, a result of the growth characteristics of this plant.

We can collapse the spatial scale of a territory somewhat by partitioning the two major sections of the Colorado hummingbird territory mentioned earlier into subsections. This becomes somewhat arbitrary, and the potential divisions are numerous. For now, we will use divisions created by "uninterested" persons. Employing more sophisticated techniques associated with centers of flowering probably is not warranted without some intuitive biological reason for each separation. Within each major section of the territory, A or B, the birds again tended to stay within the subsections of a foraging bout. The high probability of remaining within an area during a bout allows us to ask more easily whether there is a spatial pattern to use of subsections between foraging bouts. For only 1 of 14 data sets was there any indication that the use of a subsection was not independent of the location of the preceding foraging bout.

Another possible level of patch selection by a bird at the start of a foraging bout could be individual plants within the large patch. We do not have any information on this spatial scale for birds that were regularly using a single area.

For the hummingbirds foraging at *Ipomopsis*, it seems that there is very little use of a priori information at the start of a foraging bout. This accords with the relatively uncommon occurrence of nonrandom foraging at specific marked inflorescences during long observation periods within a day. Frequency distributions of visits per stalk generally did not depart significantly from a Poission distribution, suggesting random use of the total territory.

A Posteriori Information

Memory mistakes or a lack of utility of memory can be compensated for by predictive locational information obtained while feeding (a posteriori). The value of this information presumably increases as the correlation of quality among locations increases. In fact, spatial patches in which the resource is hidden, such as nectar in flowers or prey that are not readily visible, can probably be defined by the quality correlation of adjacent and more distant locations (Pyke, 1978a; Zimmerman, 1979). Phrased slightly differently, a patch is a spatial location bounded externally by a marked increase in variance of resource quality—a definition of patch regularly used by plant ecologists and some animal ecologists. Depending on patch size and the predictive relation within a patch, mistakes in foraging at poor locations potentially can be corrected and high-quality patches can be exploited more thoroughly.

There is very little information about the degree or scale of patchiness in areas of flowering plants visited by nectarivores (see, however, Pleasants and Zimmerman, 1979). For *Ipomopsis* we have measured nectar volumes in 10 arbitrary plants at varying distances from a focal plant and found no consistent pattern of changing variance with increasing distance from the focal plant. However, when variances are compared within and between plants, some predictive information appears. Variation in nectar volumes within each of the 10 neighbors and a focal plant is less than the variation among the plants. Similarly, the variation in average nectar volumes among one set of 11 plants is less than among all measured clusters of 11 plants. Thus, it appears that the birds know more about the flowers on a single plant than about those on nearby plants. But plants close to each other tend to be more similar than other sets of such plants scattered throughout the bird's foraging area. Birds on a foraging bout could take advantage of this patchiness by biasing length and directionality of moves between sequential foraging locations (Smith, 1974a,b; Zach and Falls, 1976a,b,c; Krebs, 1978; Pyke, 1978b).

Once feeding has started a hummingbird or sunbird moves from one clump of inflorescences to the next closest one (fig. 5). A similar pattern is usually followed between inflorescences within a clump. This foraging pattern creates local patches at the clump and inflorescence scale in what might have started as a relatively homogeneous distribution of nectar volumes. It also maximizes use of these bird-created local patches. The distance moved following a visit to a poor-quality plant averages longer than after a good one for hummingbirds and some sunbirds, moving birds farther from the area that is judged to be of poor quality. This behavior is essentially the same as that shown by bees

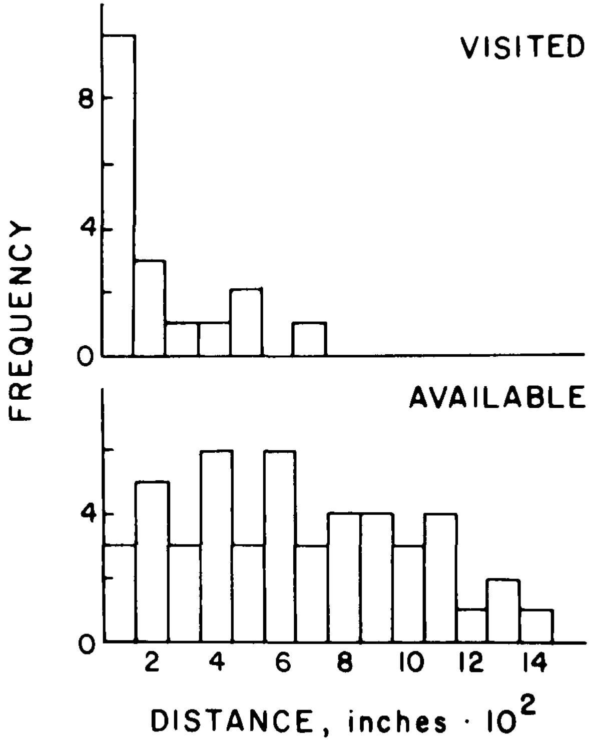

Fig. 5. Frequency distribution of distances from a single clump of flowering *Ipomopsis aggregata* plants to (*bottom*) all other clumps within a territory used by a resident broad-tailed hummingbird, and (*top*) clumps actually visited immediately subsequent to visits to the reference clump within a foraging bout. Data from Colorado, July 1979 (Wolf and Hainsworth, MS).

(Pyke, 1978b; Heinrich, 1979; Waddington, 1979; Zimmerman, 1979) and many other organisms with area-restricted search (see review in Krebs, 1978).

The directionality of foraging flights between inflorescences varies from significantly straight ahead to random directionality (fig. 6). There usually is a forward bias during any foraging bout. Variation in foraging directionality might be expected as the probability of revisits changes. Revisits should change indirectly with size of foraging area and length of foraging bout (Pyke, 1978c; Zimmerman, 1979).

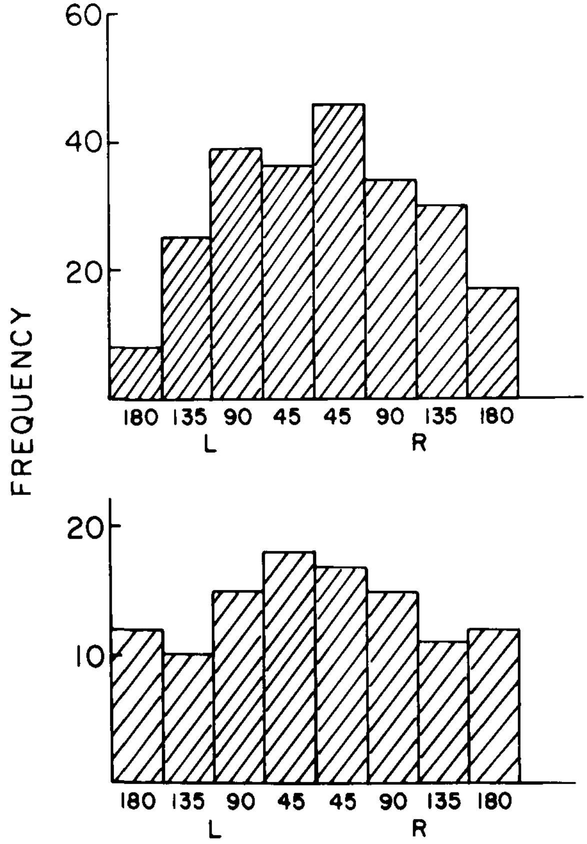

Fig. 6. Directionality of flights for hummingbirds departing from flowering *Ipomopsis aggregata* stalks during a foraging bout. The directionality was measured relative to the incoming direction. Note the change from (*top*) a markedly straightforward flight pattern (July 1979) to (*bottom*) one that approaches random directionality (July 1980). Data collected on same area in Colorado with *Selasphorus* hummingbirds.

The directionality might also reflect the assessment of local conditions by the birds in a patchy foraging area (Zach and Falls, 1976a,b,c; Pyke, 1978c). Bumblebees tend to reduce the angle of departure from a stalk that is of poor quality (Pyke, 1978b). Hummingbirds also show a higher probability of moving straight ahead following visits to fewer than expected numbers of flowers on the inflorescences. However, limited evidence indicates that sunbirds do not show similar changing directionality (Gill and Wolf, 1977).

The rules of movement within an inflorescence have been examined in some detail for inflorescences of *Ipomopsis* visited by hummingbirds (Pyke, 1978a, 1980) and to a lesser degree for *Leonotis nepetifolia* visited by sunbirds (Gill and Wolf, 1977). Birds approaching an inflorescence always have less than perfect knowledge of the quality of the inflorescence. This should select for quick assessments of expectation of future rewards on subsequent flowers on the inflorescence. The value of the information depends on the predictability of nectar volumes within an inflorescence. For both *Ipomopsis* and *Leonotis* the variance of nectar volumes within an inflorescence is less than between inflorescences. At the level of adjacent flowers on *Ipomopsis* inflorescences there is very little information from one flower about the quality of nearby flowers (Pyke, 1978a; Wolf and Hainsworth, MS). However, we expect the predictive level of the within-plant nectar volumes to vary through time as they reflect the foraging activities of the birds and the natural variation of nectar production rates.

Quick assessment of inflorescence quality would lead to two categories of plants—ones that were rejected by a forager as of poor quality and ones that exceed some threshold value and are assumed to be of sufficiently high quality to be accepted as a foraging site. Rejected plants would be characterized by visits to only a few flowers before the bird leaves (Gill and Wolf, 1977). Accepted plants that pass this initial scrutiny would be visited according to other sets of rules. Pyke (1978a, 1980) has suggested that these rules primarily reflect the increasing probability of revisiting a flower during a foraging effort, a mistake that would produce a short-term negative net benefit, although the magnitude of the effect would vary with the average environmental nectar volumes (Charnov, 1976). Our laboratory studies suggest additional contributions to rules for the bird's behavior on an accepted inflorescence from (1) flower arrangement on the inflorescence, (2) position of the start of a feeding bout at the inflorescence, and (3) the subsequent direction of foraging on the plant (Wolf et al., MS).

For sunbirds, rejection behavior increases the reward per flower visited, compared with what would be achieved if rejection had not occurred (Gill and Wolf, 1977). However, the value of the behavior varies with the mean and variance of nectar volumes, and the rate of rejection varies accordingly. The shift to less rejection as nectar volumes in the habitat decrease suggests that the birds do not have a rigid rule but may vary the rule as a function of expectations of rewards among alternative foraging sites.

Hummingbirds show similar behavior but may make incorrect assessments more often. Two *Selasphorus* species foraging at *Ipomopsis* in Colorado in 1979 showed no difference in the mean nectar volumes expected on the remaining flowers of visited and rejected inflorescences. However, the median nectar volume for rejected stalks was significantly less than for accepted stalks. The difference of the mean and median comparisons reflects several high-quality stalks that were rejected. These stalks, though of high average quality, nonetheless had empty flowers immediately adjacent to the visited area, and we assume that the visited flowers also were empty. These observations are consistent with the suggestion by Gill and Wolf (1977) that empty flowers among the first few probed stimulate rejection.

The differences between *Ipomopsis* and *Leonotis* in the efficiency of rejection behavior partly reflects the difference in foraging behavior at the two plants where a stalk is accepted. An inflorescence of *Ipomopsis* accepted by a hummingbird has a decreasing proportion of the total flowers visited as flower number increases (Pyke, 1978a; fig. 7). Sunbirds generally visited all or most of the flowers on accepted *Leonotis* verticils.

The difference between *Ipomopsis* and *Leonotis* visit patterns probably reflects the difference in floral arrangement and its effect on revisit probabilities within a foraging bout. *Leonotis* is spatially organized so that a bird can merely continue its foraging direction with little error. *Ipomopsis* requires more directional changes, both horizontal and vertical, while feeding, a condition that in the laboratory reduces total number of flowers visited on artificial arrays. The three-dimensional organization of the plants appears to have been selected to either facilitate or confuse a foraging bird on *Leonotis* and *Ipomopsis*, respectively.

The value of biased movement patterns, both within and between inflorescences, depends on the patchiness of the nectar distribution. The feeding patterns of the birds generally create patches at both spatial scales, although perhaps less so within inflorescences of *Leonotis*. These patches then act as a positive reinforcement to maintain the movement patterns on subsequent foraging bouts. However, we might expect that the patchiness would break down through time as the birds

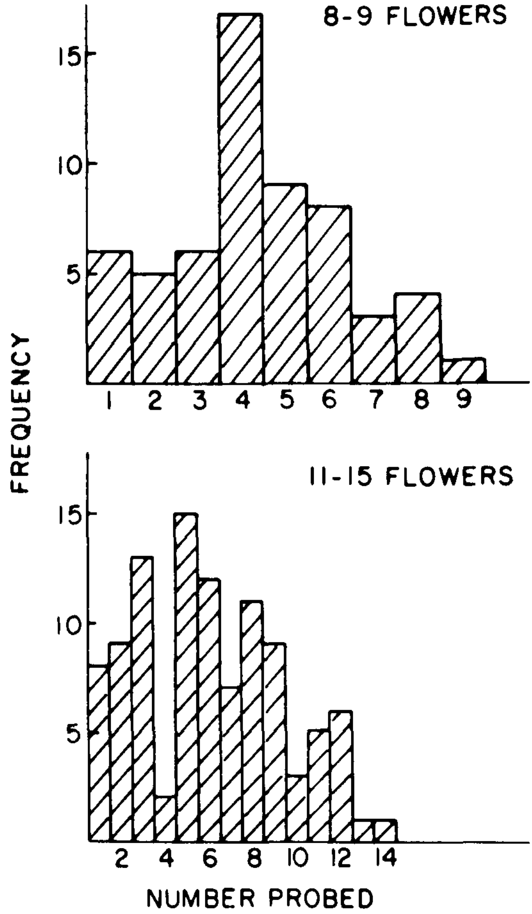

Fig. 7. Frequency distributions of number of flowers probed on single visits by a hummingbird (*Selasphorus*) to plants of *Ipomopsis aggregata* with variable numbers of flowers open. Note what appear to be several modes at slightly different flower numbers in the two distributions. Data from Colorado, July 1980 (Wolf and Hainsworth, MS).

initiated foraging in different places and as they responded with longer flights from locally poor quality patches. Only by using very regular foraging routes would the birds maintain patchiness for long periods in usual circumstances. Very high nectar volumes and high flower density might make it possible to maintain patchiness, especially with short-lived flowers that are reasonably synchronous in blooming.

INGESTION, ASSIMILATION, AND HUNGER

Amount of Nectar Consumed and Feeding Frequency

The foraging bout ends when the bird begins other major activities for an extended period of time. For most hummingbirds and sunbirds in natural situations, foraging occupies less than 50% of the daylight hours and often less than 20% (Wolf and Hainsworth, 1971; Gill and Wolf, 1975; Wolf, 1975; Wolf et al., 1975; Frost and Frost, 1980). Feeding bouts usually are short, with longer nonfeeding periods intervening. The following discussion considers the possible inputs that control amount consumed on a foraging bout and the frequency of bouts.

Gross energy intake/time is the product of amount consumed and feeding frequency (energy/meal × meals/time = energy/time). These variables, or corollaries of them, are frequently measured in studies of energy regulation through feeding (LeMagnen et al., 1973; Wolf and Hainsworth, 1977; Kissilef et al., 1979). These variables need not be the only components involved in energy regulation (see Levitsky et al., 1976; Boyle et al., 1978; and Borer et al., 1979, for circumstantial evidence for the importance of factors other than gross energy uptake/time), but there is a strong physiological foundation for viewing regulation in terms of a product of amounts and frequencies (Hainsworth, 1981).

Both meal sizes and feeding frequencies potentially could be controlled to contribute to regulation of net energy intake in animals. However, there is very little information concerning how variation in either contributes quantitatively to energy regulation. There also is very little information concerning the components of underlying control mechanisms for feeding (i.e., internal stimuli that lead to meal initiation, or hunger, and meal termination, or satiation). Among rats and some other mammals a common response to food deprivation is increased meal size coupled with increased meal frequency (Levitsky, 1970; Kanarek and Collier, 1979). However, this response is not necessary for regulation of net energy gains over long periods, as assimilation and energy expended also can vary (see Levitsky et al., 1976; Boyle et al., 1978). Some species, such as hamsters (Borer et al., 1979) and guinea pigs (Hirsch, 1973), normally do not vary either meal sizes or feeding frequencies following food deprivation, yet net energy gains restore the losses over long periods.

The traditional interpretations of central nervous system control of feeding in vertebrates involving the ventromedial and lateral areas of the hypothalamus have also been challenged recently (e.g., Friedman and Stricker, 1976), partly on the grounds that these areas may involve only pathways rather than integration centers. There also is no unanimity concerning possible internal stimuli leading to hunger or satiation other than that the stimuli should somehow index energy (Booth et al., 1976).

Studies of hummingbird feeding have suggested a possible quantitative role for feeding patterns in energy regulation. A general pattern is summarized in figure 8 (Wolf and Hainsworth, 1977). The initiation of a meal depended on prior meal size together with expenditures between meals with a relatively constant rate of energy accumulation (net gains) throughout a day. A detailed model of hummingbird energy expenditures and intakes suggested that meal size was directly related to rate of net energy gain (DeBenedictis et al. 1978; Hainsworth, 1978). The model was based on either meal-to-meal periods (DeBenedictis et al.,

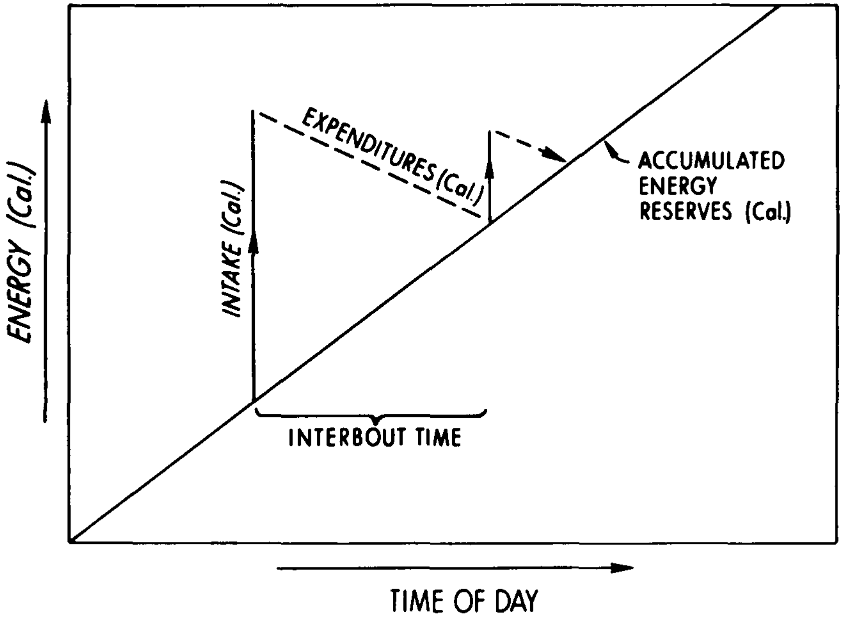

Fig. 8. A general model for the patterning of feeding bouts by hummingbirds. The line with positive slope indicates a constant rate of energy storage during the day. The model is premised on meal initiation occurring when the previous meal has been depleted due to storage and short-term expenditures for maintenance. From Wolf and Hainsworth, 1977; reproduced by permission.

1978) or these periods coupled to a daily time scale with use of stored energy to balance overnight expenditures (Hainsworth, 1978). Figure 9 shows some predictions for a set of parameters of the daily energy balance model. At a given food concentration, rate of net energy gain would be maximized at a particular meal size, due partly to the effects of the weight of a meal on energy expenditures between meals (De Benedictis et al., 1978; Hainsworth, 1978). The daily energy balance model also predicts that variation in use of energy stored (e.g., for overnight expenditures) should result primarily in adjustments in meal

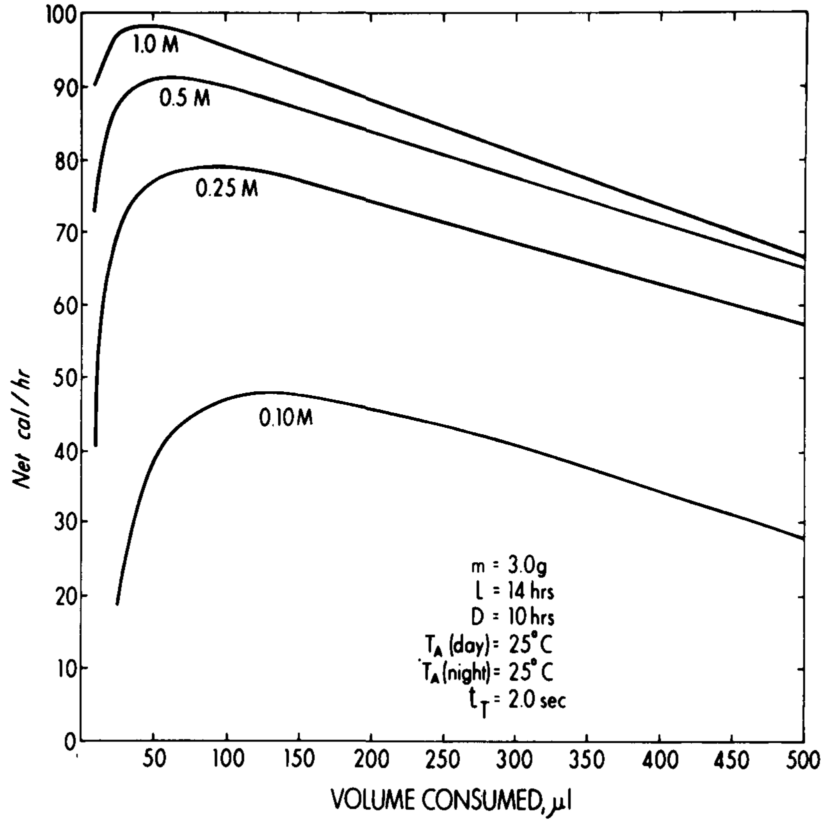

Fig. 9. Predicted relationship between rate of net energy gain and meal size based on a model of hummingbird energy expenditures and energy intakes. Calculations are for four food (sucrose) concentrations. Parameters of the calculations are: m = mass, L = light hours, D = dark hours, T_A = air temperature, t_T = round-trip transit time from perch to a feeder. From Hainsworth, 1978; reproduced by permission of the American Society of Zoologists.

size, whereas variation in maintenance expenditures between meals during a day should primarily result in adjustments in meal frequency (Hainsworth, 1978).

Despite these predictions and initial agreement between observed and predicted meal sizes (DeBenedictis et al., 1978), it currently is not clear whether the model makes good predictions in all situations. Rate of net energy gain throughout a day (slope of storage line in fig. 8) appears to vary with the amount of stored energy compared with some "set point" amount (see below). As with the selection of foods discussed earlier, this would indicate a long-term rate of net energy gain that is not always maximized. Thus, although short-term feeding may involve maximization of rate of net energy gain, hummingbirds may not always be perched at some maximum rate of net energy gain under longer-term conditions. To examine variation in meal size and frequency in more detail we have explored some of the characteristics of daily energy regulation in hummingbirds. These characteristics involve an integration of the internal processing of foods (ingestion, assimilation, and hunger), although we are not concerned here with the details of each step.

Daily Energy Storage: Characteristics of Regulation

Regulation of energy implies controls, and there are four models for general negative feedback controls applied to physiological systems (Hardy, 1965). The four models are summarized in figure 10 in terms of the nature of responses (R) to decreases in a controlled variable (V) below some reference point (V_{set}). Differences among the models depend on the nature of a response when a controlled variable changes. For energy regulation the controlled variable is net energy, and a response is any change that will tend to maintain net energy over time within certain limits. Thus, a response can be generalized as any factor that influences the rate of net energy gain.

The most common types of control mechanisms are known as on-off and proportional. On-off controls (fig. 10A) have threshold characteristics and occur where maximum and sustained responses to changes are important. This is the control mechanism equivalent suggested by maximization of rate of net energy gain in short-term feeding. Proportional controls (fig. 10B) involved a linear dependence of response on the extent of displacement of a controlled variable from a reference. These types of controls are very common in physiological systems where the magnitude of a response depends on the extent of demand to control a variable within certain limits.

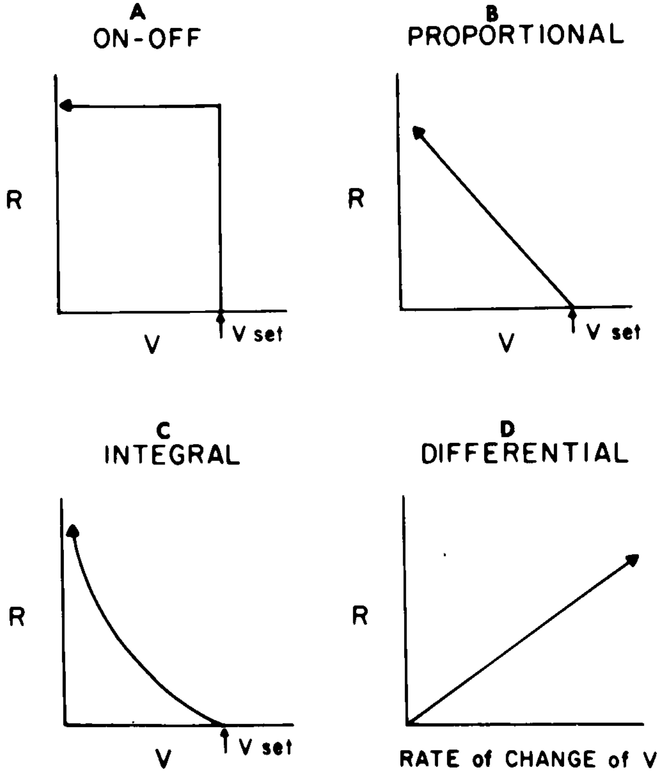

Fig. 10. Four models of control: (*A*) on-off controls produce a threshold relationship between a response (*R*) and variation in the regulated variable (*V*) below a set point (V_{set}); there is (*B*) a linear relationship for proportional controls and (*C*) an exponential relationship for integral controls (for fixed intervals), and (*D*) *R* depends on the rate of change of *V* for differential controls.

Integral and differential controls are less common in physiological systems, although some proportionally controlled systems may show integral or differential features (Hardy, 1965). In integral controls the rate of a response depends on the extent of displacement of a controlled variable from a reference (fig. 10C). Over a standard time period this generates an exponential relationship between response and displacement from a reference that minimizes the variation in response time for a range of displacements. Differential controls show an anticipatory feature, since the response depends on the instantaneous rate of change of a controlled variable (fig. 10D). Note, however, that differential controls do not involve references of set points.

The most extensive use of control models is for systems where short-term responses occur, as in respiratory regulation (Edwards and Yamamoto, 1965; Hitzig and Jackson, 1978) and body temperature regulation (Hardy, 1965; Hammel et al., 1977; Heller et al., 1978). where responses to displacement of controlled variables occur within seconds or minutes and are easily quantifiable. The control of energy regulation occurs over longer intervals, and the potential controls are more complex and less understood. Despite this, aspects of feeding and energy regulation have been examined in a control system framework, particularly for species where energy regulation occurs over seasonal time scales (Mrosovsky and Barnes, 1974; Mrosovsky and Powley, 1977).

A difficulty for characterizing energy controls in animals comes from the potentially large number of factors required to specify the controlled variable (stored energy) and responses to displacement of the controlled variable that ultimately are reflected in rates of net energy gain. Control of net energy may involve what is consumed, the amount consumed, feeding frequency, assimilation efficiency, and what must be expended from assimilated energy. Since each of these factors can vary depending on the animals and their foods, it is difficult to identify a system where all factors can be accounted for with sufficient precision. The hummingbird-nectar system provides an opportunity to examine rate of net energy gain responses to changes in net energy.

Figure 11 shows some preliminary measurements of average daily rates of net energy gain as a function of displacement of net energy downward produced by 4–5 hr food deprivations on successive days following a control day. Note that some birds show a response analogous to proportional (linear) controls; some show a response similar to integral controls (compare with the general models in fig. 10). However, none show a response similar to an on-off (sustained maximization) type of control.

Several studies of feeding suggest that animals should maximize the rate of net energy gain while they feed (on-off control) (Krebs, 1978; Pyke, 1978a) yet longer-term (daily) regulation of energy appears to be proportional to some displacement from a reference. These two views can be reconciled by considering the time periods over which they operate. For a bird that achieves a maximum possible rate of net energy gain while it is feeding, the daily pattern of energy regulation would be determined by when feeding attempts were initiated. With a given rate of net energy gain from feeding, higher frequency of feeding (within food processing limits) would generate higher daily rates of net energy gain.

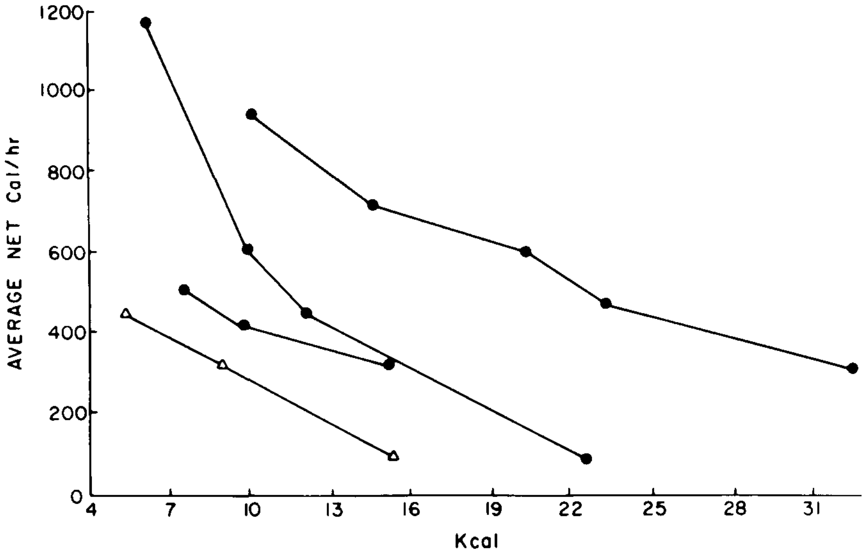

Fig. 11. Measured average daily rates of net energy gain for *Eugenes fulgens* (*solid circles*) and *Lampornis clemenciae* (*unshaded triangles*) as a function of energy reserves. Reserves were calculated from mass in excess of 7.0 g (where torpor occurs for these species) assuming 9,500 cal/g.

Figure 12 illustrates the average contributions of meal sizes and meal frequencies to daily rates of net energy gain. Note the substantial contribution of meal frequencies to rates of net energy gain ($r^2 = 0.78$). These patterns suggest that meal termination (meal sizes, or short-term satiation) contributes less to daily energy regulation than previously hypothesized (Hainsworth, 1978). Meal frequency (initiation, or short-term hunger) appears to be the major factor influencing daily rates of net energy gain.

Why should daily energy regulation show proportional control features? One possibility could be some risk associated with feeding patterns. If high-frequency feeding was associated with high risks, it would be expected to occur only when risk from starvation outweighed other risks for feeding.

Finally, note that the reference values for control of energy storage (set points) in figure 11 are variable (birds were tested at different times). This suggests a mechanism for even longer-term (seasonal) control of energy storage. If the set point for response to depletion of energy reserves varies with seasonal demands for energy (such as for molt, migration, or reproduction), it would provide a way to adjust internal energy supplies to changing demands for energy. A similar

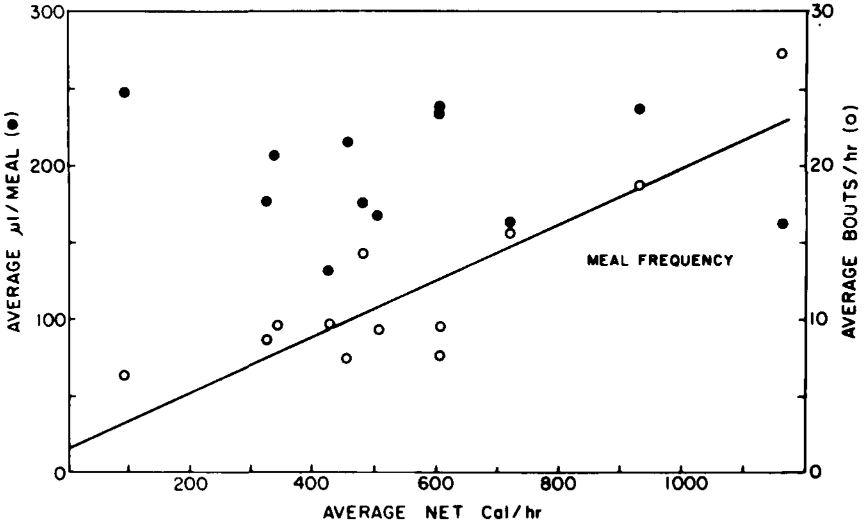

Fig. 12. Average meal size (*left, solid circles*) and frequency (*right, open circles*) versus average daily rate of net energy gain. There was no relationship between average meal size and average rate of net energy gain. There was a significant correlation, however, between average meal frequency and average rate of net energy gain ($r = 0.78$; $p > 0.01$).

type of "sliding" set point model has been postulated to operate for seasonal hibernators (Mrosovsky and Barnes, 1974; Mrosovsky and Powley, 1977).

SUMMARY

We have tried to suggest that feeding is indeed organized in ways that reflect the action of natural selection, producing individuals better able to survive and reproduce than might be achieved by a variety of alternative organizations of feeding behavior. We have not been able to show whether the birds are doing the best possible. It remains for the future to predict what they might be capable of achieving energetically, taking into account what appear to be the physiological and sensory limitations of the birds. At present we still are not sure of all the foraging rules.

The objective criterion for the outcome of the rules changes with the time scale. Individual feeding bouts appear to be organized to maximize rate of net energy intake using a variety of possible sources of information and discriminatory capabilities. At longer time scales there are important negative feedback components that work to regulate closely the total energy stores within and among days. The daily stores appear to be associated with longer-term (e.g., overnight) costs. The even longer term, seasonal stores are probably associated with periods of either high energy demand, such as migration, breeding, or molt, or perhaps with seasonal periods of low resource availability (Katz, 1974). The birds apparently deal with these variable time scales with a proportional control mechansim, based on internal feedback from available energy stores in reference to a desired set point.

The external information available to the birds is organized at several levels of patchiness. However, the character and spatial definition of these patches change through time, partly as a function of the feeding by an individual and partly from the effects of other individuals. This reduces the value of prior decisions to choose foraging locations, and the use of such information apparently varies considerably. Information gleaned from a foraging effort is more often used to make decisions about subsequent foraging efforts. The scales for this use of patchiness in a posteriori decisions range at least from individual flowers through large clumps of individual plants that bloom simultaneously.

ACKNOWLEDGMENTS

Our research is supported financially by grants from the National Science Foundation and the Senate Research Fund of Syracuse University. We would like to thank S. Cole, T. Mercier, M. Tardiff, and A. Valakas for their important technical and intellectual contributions to the research on foraging; A. Evans very capably typed the manuscript.

DISCUSSION FOLLOWING DR. WOLF'S PRESENTATION

Question: I noticed that ruby-throated hummingbirds in Michigan will feed on monarda or bee balm. This plant is very similar to the plants of the sunbird in Africa. They have their inflorescence in layers and the inflorescence is in circles. I was wondering if anybody had studied the ruby-throat in such habitat where there are patches of bee balm. And if so, do they parallel more closely the sunbird in their foraging strategy? If not, would you expect them to more closely?

Answer: The first part of the answer is very simple: nobody studied it. I would certainly be very glad for you to do it! For the second part, I think that *Leonotis* tends to be a flower that, due to its morphology, really restricts insect visitation. *Monarda*, on the other hand, I think probably is a flower that is regularly visited by insects, in addition to the birds. So the noise level in terms of environmental information that is potentially available to those birds is going to be really constrained by virtue of the fact that there is something else working out there on those flowers at the same time. My guess is that you see less of this kind of pattern just for that reason in ruby-throats, but nobody studied it so I'm safe!

Question: I wonder if you would comment on predation in hummingbirds. William Buskirk studied mixed flocks in Costa Rica. He classified these birds into guilds. One of the guilds was called the "traplining nectarivore" into which he plunked hummingbirds. He was interested in various aspects of whether they foraged in mixed species flocks and such. I remember that he said that one species of hummingbird did not forage in mixed species flocks because there was no selection pressure for behavior that would mitigate predation. That is to say, he assumed that hummingbirds had no predators worth mentioning in an evolutionary context. In your presentation you implicated that they did. I wonder if you could shed some light on that.

Answer: Let me ask you, how did I implicate that they did?

Questioner: I thought that; I might be mistaken. I thought you said at one point that some of their behavior could have been due to predation, and then you said that we always invoke predation.

Answer: One reason that it is so easy to invoke predation as an "out" is because it is so hard to measure. The general anecdotal evidence that is available suggests that there is a lot of predation on hummingbirds, but it's all in the nestling stage. It is so rare that people report in the journals when they see an instance of predation on hummingbirds. Ernst Mayr has a paper on a sharp-shinned hawk catching a ruby-throat in Massachusetts, and there was a recent picture of a roadrunner sitting on the eaves of a house near a hummingbird feeder waiting for the hummingbirds to come by, and then leaping off and snatching them out of the air. But it is probably a very rare event and probably is not all that important in organizing foraging behavior. I can't prove that. What I commented on in terms of increased predation is that if you get too heavy, if you build up weight too fast and have trouble flying for a long time, that does potentially open you to all kinds of predation. But the fact that it doesn't occur could be simply because they sort of optimize weight gain, down to the point where predation isn't all that important. I can't answer your question and neither can Doug Morse for mixed species flocks.

Question: It seems that some birds retain information, and based upon that, they forage the next day in some other area. Are there any data to show that they may also forage in a very limited area? Are there any data that might show that they sample the environment in passing through, and use that at the same time to base the next day's foraging?

Answer: What you're asking is a longer term kind of question that I was trying to avoid when we initiated this project in East Africa. One of the things that we were interested in was the organization of those nectar-feeding communities. Did they follow the same kind of general rules that hummingbird communities did in the New World, since they were presumably doing the same sorts of things out there in relation to the source? One of the very difficult things that we couldn't do, or really couldn't deal with, was movement patterns. In general, sunbird flowers occur as fairly large patches that are monospecific patches separated by a large amount of space, since they tend to be early second-growth flowers that disappear rapidly. They tend to be separated by a fair amount of space from the next patch of some other flower species. You may have a lot of sunbirds in one patch, but it is very difficult to figure out what's going on in terms of birds coming in and doing the kinds of sampling that you are talking about and making a decision as to whether this is a good place to stay or not. Now, it's pretty clear in the kinds of community organization that we've been able to study that there is a lot of aggressive interaction going on between species in these patches. If you get the right kind of colonization pattern into one of these patches that lasts on the order of 6 to 8 weeks, you get a lot of competition. The birds tend to sort out in relation to size, usually size-related interspecific dominance hierarchies. As a consequence, birds that have been there for a while pick up and leave because they are eliminated from the system by the bigger birds that are coming in, or they leave because their perception of the system was that they weren't getting much of a return for their effort so they just left. I really don't have the answer to that; I would guess that there is a fair amount of that kind of sampling, but not on the scale that you are talking about in the sense that the probability of finding a new patch is relatively low and it may take a while. So in the short term you are better off sitting around trying to build up what you can at that spot and then leaving.

Question: Have you done any work on foraging strategies at a time when a female is feeding the young and has to get proteinaceous food in addition to keeping herself going?

Answer: When you are doing this kind of foraging behavior research, the minute you have to start worrying about reproduction and all the kinds of things that are going on with that, complications of all kinds arise, just like the issues we have been talking about. So, in fact, all of the things that I have talked about are really associated with nonbreeding situations. The sunbirds form monogamous pair bonds in general, so there is a lot of this interaction going on between the male and the female. A lot of what the males and females are doing is associated with that reproductive effort. So we completely avoided the breeding season. Essentially, when I'm talking about territorial birds I am talking about a single bird occupying a territory and beating the hell out of an intruder. In the hummingbirds, on the other hand, what we look at are principally males. Females were essentially using peripheral flowers in many cases, and were kept out of the good patches unless they "paid" for it, and I recommend a paper on "prostitution behavior" in hummingbirds! So, we have essentially tried to eliminate all of those kinds of nutrient questions that you brought out. An even broader question is, What is the male going to do with his time in relation to trying to keep a hold of the female, and all that sort of thing, as opposed to foraging. More directly, I think I tried to indicate at the beginning that spatial insect foraging, which these birds do, tends to be spatially and temporally separated from the activity at the flowers. I felt that it was not unrealistic to say that we can look at organizational and decision rules associated with working the flowers, and then we can go and look if we really want to. I don't want to look at the organizational rules associated with catching insects.

Question: The other question was, Has anybody done any comparisons on these strategies with those in the hummingbird moths, which feed in somewhat the same way?

Answer: Nobody has really looked at the hummingbird moths as far as I know. There is obviously a lot of literature that is expanding quite rapidly on bees doing similar sorts of things. A student of mine is just finishing a dissertation on bee optimal foraging and is going out and trying to create the information in the environment rather than worrying about the lack of information and the changing information. He is trying to control the information of the enviroment.

Question: In relation to the earlier question on hummingbird predation, there was a paper on a very small hawk that lives in the tropics and is a hummingbird specialist, eating hummingbirds almost exclusively.

Answer: There are several species down in the tropics, and the little hawk is interesting. Gary Stiles, who is the author of that paper, got on to this when we were looking at lek behavior in hummingbirds. Leks, in general, are defined as types of nonresource mating stations so that they are not defending flowers, and they are not associated with feeding at all. It is associated with sitting on a perch waiting for the females to come by; apparently these little hawks do try traplining these lek perches, and they know where they are. The males return to the same perches day after day and sit there and call from them. You can watch a little hawk fly through these leks checking out the perches of these males. When we were doing this study we also had another type of bird hawk that used to trapline out mistnets by picking the hummingbirds out of the mistnets.

Question: I was wondering if you were aware of any of the hummingbird energetics literature in which the birds save energy by hovering at resonating frequencies in terms of both their breathing and the motion and frequencies of their wing beat? And if that is the case, one could propose that they are saving more energy by hovering at this frequency than they would by using the energy to decelerate while feeding and accelerate to get back into the air again. I don't recall whether they hover at resonating frequency or not.

Answer: I will call on my coauthor to answer this question. He is the physiologist in this operation. I assume there is a relationship between frequency and wing length. Others have pointed this out, and there is quite a bit of information about the requirements of wing length for lifting a mass. This is assumed to be related to their requirements for generating a lot of energy per unit time. But the critical question about hovering versus perching is, as you mentioned, the amount of time you must invest to perch compared with hovering. I think that the best way to approach this, rather than trying to calculate frequencies, is to go in with a stopwatch and give a bird a perch and ask what proportion of time in excess of what would be expended in hovering would be involved in perching. If it's in the order of 10%, then it should be possible to design an experiment where you can have a bird like a hummingbird that would hover. I think the relative advantages between hovering and perching are size-dependent.

Question: But isn't it in the small bird that the differential becomes more pronounced?

Answer: But giant hummingbirds are hard to come by! So we are using a 3 or a 9 g bird. The whole thing can be modeled in terms of what the net energy is.

Question: Is there any evidence that the birds are not selecting for quantity of nectar they can get from a flower but rather for the quality of the nectar?

Answer: If you noticed that I constrained very carefully in what I was talking about to intraspecific flowers, we assume there is variation in the nectar quality, but not much. Clearly, we can build on top of that a whole set of questions associated with exactly what you are talking about. That is, qualitative differences in the flower's nectar, as well as quantitative references in the rate at which they can get that nectar out. I just chose at this time to eliminate all that. But you are quite right. It turns out in the laboratory that if you begin to ask questions like that, sugar concentration itself becomes a prime clue that birds will use, and they will select the more concentrated sugar from a pair of feeders to the detriment of their net intake rate of energy. So it seems to be a prime clue; maybe it's a monitor. In terms of making those kinds of choices, that's another level of decision making that I didn't get into at all.

Question: A question about how fast hummingbirds should accumulate energy through the day in order to make it through the following night: Have you tried to look at different situations where perhaps predation intensity varies the predictability of being able to find food late in the day? If food is quite predictable in the environment, then perhaps they should have a low accumulation rate and then cram it all in at the last few hours. That should also be the case if there is a high predation rate. And conversely, if there are not very many predators around, but strong competition, perhaps you should load up early in the morning.

Answer: You're quite right. I can't deny what you say; what I try to indicate in these studies focuses on the first question that you are interested in: Given the best possible worlds, what would they do? So you bring them into the lab and only constrain the availability of that energy. Unless one is beating on them with a club or something, there is no predation involved. So they don't have to worry about all those constraints. Certainly, I would like somebody, and you are quite welcome, to go do it. I'm certainly not going to. Go out into the environment and find out how these patterns change from what we have seen in the context of all the constraints that you have talked about. John Magnuson has already talked about some constraints that might be added into his system. Certainly you have identified some in the hummingbird system.

LITERATURE CITED

Baker, H. G., and I. Baker. 1975. Studies of nectar-constitution and pollinator-plant coevolution. *In* L. E. Gilbert and P. H. Raven (eds.), Coevolution of animals and plants. University of Texas Press, Austin.

Beatty, W. W., and D. A. Shavalia. 1980. Spatial memory in rats: time course of working memory and effect of anesthetics. Behav. Neur. Biol. 28:454–62.

Booth, D. A., F. M. Toates, and S. V. Platt. 1976. Control system for hunger and its implications in animals and man. *In* D. Novin, W. Wyrwicka, and G. A. Bray (eds.), Hunger: basic mechanisms and clinical implications. Raven Press, New York.

Borer, K. T., N. Rowland, A. Mirow, R. C. Borer, and R. P. Kelch. 1979. Physiological and behavioral responses to starvation in the golden hamster. Amer. J. Physiol. 236: E105–E112.

Boyle, P. C., L. H. Storlien, and R. E. Keesey. 1978. Increased efficiency of food utilization following weight loss. Physiol. Behav. 21:261–64.

Brown, J. H., W. A. Calder III, and A. Kodric-Brown. 1978. Correlates and consequences of body size in nectar-feeding birds. Amer. Zool. 18:687–700.

Brown, J. H., and A. Kodric-Brown. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated plants. Ecology 60:1022–35.

Calder, W. A. 1974. Consequences of body size for avian energetics. *In* R. A. Paynter, Jr. (ed.), Avian energetics. Publ. Nuttall Ornithol. Club No. 15. Cambridge, Mass.

Carpenter, F. L. 1974. Torpor in an Andean hummingbird: its ecological significance. Science 183:545–47.

Carpenter, F. L. 1976. Plant-pollinator interactions in Hawaii: pollination energetics of *Metrosideros collina* (Myrtaceae). Ecology 57:1125–44.

Carpenter, F. L., and R. E. McMillen. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639–42.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoret. Popul. Biol. 9:129–36.

Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. Amer. Natur. 110:247–59.

De Benedictis, P. A., F. B. Gill, F. R. Hainsworth, G. H. Pyke, and L. L. Wolf. 1978. Optimal meal size in hummingbirds. Amer. Natur. 112:301–16.

Des Granges, J. L. 1979. Organization of a tropical nectar feeding bird guild in a variable environment. Living Bird 17:199–236.

Edwards, M. W., Jr., and W. S. Yamamoto. 1965. Carbon dioxide balance and the control of breathing. *In* W. S. Yamamoto and J. R. Brobeck (eds.), Physiological controls and regulations. Saunders, Philadelphia.

Epting, R. J. 1980. Functional dependence of the power for hovering on wing disc loading in hummingbirds. Physiol. Zool. 53:347–57.

Ettinger, A. O., and J. R. King. 1980. Time and energy budgets of the willow flycatcher (*Empidonax traillii*) during the breeding season. Auk 97:533–46.

Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. Ecol. Monogr. 46:257–91.

Feinsinger, P. 1980. Asynchronous migration patterns and the coexistence of tropical hummingbirds. *In* A. Keast and E. S. Morton (eds.), Migrant birds in the neotropics: ecology, behavior, distribution, and conservation, pp. 411–19. Smithsonian Institution Press, Washington, D.C.

Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoret. 19:16–36.

Friedman, M. I., and E. M. Stricker. 1976. The physiological psychology of hunger: a physiological perspective. Psychol. Rev. 83:409–31.

Frost, S. K., and R. G. H. Frost. 1980. Territoriality and changes in resource use by sunbirds at *Leonotis leonurus* (Labiatae). Oecologia 45:109–16.

Gass, C. L., G. Angehr, and J. Centa. 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. Can. J. Zool. 54:2046–54.

Gass, C. L., and R. D. Montgomerie. 1981. Hummingbird foraging behavior: decision-making and energy regulation. *In* A. C. Kamil and T. D. Sargent (eds.), Foraging behavior: ecological, ethological, and psychological approaches. Garland STPM Press, New York.

Gill, F. B. 1978. Proximate costs of competition for nectar. Amer. Zool. 18:753–63.

Gill, F. B., and C. A. Conway. 1979. Floral biology of *Leonotis nepetifolia* (L.) R. Br. (Labiatae). Proc. Acad. Natur. Sci. Phil. 131:244–56.

Gill, F. B., and L. L. Wolf. 1975. Economics of territoriality in the golden-winged sunbird. Ecology 56:333–45.

Gill, F. B., and L. L. Wolf. 1977. Nonrandom foraging by sunbirds in a patch environment. Ecology 58:1284–96.

Goldsmith, T. H., and K. M. Goldsmith. 1979. Discrimination of colors by the black-chinned hummingbird, *Archilochus alexandri*. J. comp. Physiol. 130:209–20.

Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. London, B, 205:147–64.

Grant, K. S. 1966. A hypothesis concerning the prevalence of red coloration in California hummingbird flowers. Amer. Natur. 100:85–97.

Grubb, T. C., Jr. 1977. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland: horizontal adjustments. Condor 79:271–74.

Hainsworth, F. R. 1978. Feeding: models of costs and benefits in energy regulation. Amer. Zool. 18:701–14.

Hainsworth, F. R. 1981. Animal physiology: adaptations in function. Addison-Wesley, Reading, Mass.

Hainsworth, F. R., B. G. Collins, and L. L. Wolf. 1977. The function of torpor in hummingbirds. Physiol. Zool. 50:215–22.

Hainsworth, F. R., and L. L. Wolf. 1972a. Energetics of nectar extraction in a small, high altitude, tropical hummingbird. J. comp. Physiol. 80:377–87.

Hainsworth, F. R., and L. L. Wolf. 1972b. Power for hovering flight in relation to body size in hummingbirds. Amer. Natur. 106:589–96.

Hainsworth, F. R., and L. L. Wolf. 1976. Nectar characteristics and food selection by hummingbirds. Oecologia 25:101–13.

Hainsworth, F. R., and L. L. Wolf. 1979. Feeding: an ecological approach. Advances Study Behav. 9:53–96. Academic Press, New York.

Hammel, H. T., R. W. Elsner, H. C. Heller, J. A. Maggert, and C. R. Bainton. 1977. Thermoregulatory responses to altering hypothalamic temperature in the harbor seal. Amer. J. Physiol. 232: R18–R26.

Hardy, J. D. 1965. The "set-point" concept in physiological temperature regulation. *In* W. S. Yamamoto and J. R. Brobeck (eds.), Physiological controls and regulations. Saunders, Philadelphia.

Heinrich, B. 1976. The foraging specializations of individual bumblebees. Ecol. Monogr. 46:105–28.

Heinrich, B. 1978. The economics of insect sociality. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural ecology. Sinauer Associates, Sunderland, Mass.

Heinrich, B. 1979. Resource heterogeneity and patterns of movements in foraging bumblebees. Oecologia 40:235–45.

Heller, H. C., J. M. Walker, G. L. Florant, S. F. Glotzbach, and R. J. Berger. 1978. Sleep and hibernation: electrophysiological and thermoregulatory homologies. *In* L. C. H. Wang and J. Hudson (eds.), Strategies in cold: natural torpidity and thermogenesis. Academic Press, New York.

Hirsch, E. 1973. Some determinants of intake and patterns of feeding in the guinea pig. Physiol. Behav. 11:687–704.

Hitzig, B. M., and D. C. Jackson. 1978. Central chemical control of ventilation in the unanesthetized turtle. Amer. J. Physiol. 235:R257–R264.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Memo. Entom. Soc. Can. 48:5–86.

Kanarek, R. B., and G. Collier. 1979. Patterns of eating as a function of the cost of the meal. Physiol. Behav. 23:141–45.

Katz, P. L. 1974. A long-term approach to foraging optimization. Amer. Natur. 108:758–82.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. *In* R. A. Paynter, Jr. (ed.), Avian energetics, pp. 4–79. Publ. Nuttall Ornithol. Club No. 15. Cambridge, Mass.

Kissilef, H. R., R. K. Nakashima, and A. J. Stunkard. 1979. Effects of jejunoileal bypass on meal patterns in genetically obese and lean rats. Amer. J. Physiol. 237:R217–R224.

Kodric-Brown, A., and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. Ecology 59:285–96.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural ecology. Sinauer, Sunderland, Mass.

Krebs, J. R., A. Kacelnik, and P. Taylor. 1978. Test of optimal sampling by foraging great tits. Nature 275:27–31.

Lasiewski, R. C., and W. R. Dawson. 1967. A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69:13–23.

Legg, K., and F. A. Pitelka. 1956. Ecologic overlap of Allen and Anna hummingbirds nesting at Santa Cruz, California. Condor 58:393–405.

LeMagnen, J., M. Devos, J. Gaudilleire, J. Louis-Sylvestre, and S. Tallon. 1973. Role of a lipostatic mechanism in regulation by feeding of energy balance in rats. J. comp. physiol. Psychol. 84:1–23.

Levitsky, D. A. 1970. Feeding patterns of rats in response to fasts and changes in environmental conditions. Physiol. Behav. 5:291–300.

Levitsky, D. A., I. Faust, and M. Glassman. 1976. The ingestion of food and the recovery of body weight following fasting in the naive rat. Physiol. Behav. 17:575–80.

Montgomerie, R. D. 1982. Energetics and the foraging strategies of some tropical hummingbirds. Ecology (in press).

Mrosovsky, N., and D. S. Barnes. 1974. Anorexia, food deprivation, and hibernation. Physiol. Behav. 12:265–70.

Mrosovsky, N., and T. L. Powley. 1977. Set points for body weight and fat. Behav. Biol. 20:205–23.

Olton, D. S. 1981. Spatial memory and food searching strategies. *In* A. C. Kamil and T. D. Sargent (eds.), Foraging behavior: ecological, ethological, and psychological approaches. Garland STPM Press, New York.

Orians, G. H. 1981. Optimal foraging and the evolution of discriminatory behavior. *In* A. C. Kamil and T. D. Sargent (eds.), Foraging behavior: ecological, ethological, and psychological approaches. Garland STPM Press, New York.

Pleasants, J. J., and M. Zimmerman. 1979. Patchiness in the dispersion of nectar resources: evidence for hot and cold spots. Oecologia 41:283–88.

Pyke, G. H. 1978a. Optimal foraging in hummingbirds: testing the marginal value theorem. Amer. Zool. 18:739–52.

Pyke, G. H. 1978b. Optimal foraging: movement patterns of bumblebees between inflorescences. Theoret. Popul. Biol. 13:72–98.

Pyke, G. H. 1978c. Are animals efficient harvesters? Anim. Behav. 26:241–50.

Pyke, G. H. 1981. Optimal foraging in nectar-feeding animals and coevolution with their plants. *In* A. C. Kamil and T. D. Sargent (eds.), Foraging behavior: ecological, ethological, and psychological approaches. Garland STPM Press, New York.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

Skead, C. J. 1967. The sunbirds of southern Africa. A. A. Balkema, Cape Town.

Smith, J. N. M. 1974a. The food searching behaviours of two European thrushes. I. Descriptions and analysis of search paths. Behaviour 48:276–302.

Smith, J. N. M. 1974b. The food searching behaviours of two European thrushes. II. The adaptiveness of the search patterns. Behaviour 49:1–61.

Staddon, J. E. R. 1975. A note on the evolutionary significance of "supernormal" stimuli. Amer. Natur. 109:541–45.

Stiles, F. G. 1973. Food supply and the annual cycle of the Anna hummingbird. Univ. Calif. Publ. Zool. 97:1–116.

Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology 56:285–301.

Stiles, F. G. 1980. The annual cycle in a tropical wet forest hummingbird community. Ibis 122:322–43.

Stiles, F. G., and L. L. Wolf. 1979. Ecology and evolution of lek behavior in the long-tailed hermit hummingbird. Amer. Ornithol. Union, Monogr. No. 27.

Teuber, L. R., M. C. Albertsen, D. K. Barnes, and G. H. Heichel. 1980. Structure of floral nectaries of alfalfa (*Medicago sativa* L.) in relation to nectar production. Amer. J. Bot. 67:433–39.

Tullock, G. 1971. The coal tit as a careful shopper. Amer. Natur. 105:77–80.

Utter, J. M., and E. A. LeFebvre. 1973. Daily energy expenditure of purple martins (*Progne subis*) during the breeding season: estimates using D_2O^{18} and time budget methods. Ecology 54:597–604.

Waddington, K. D. 1979. Flight patterns of foraging bees relative to density of artificial flowers and distribution of nectar. Oecologia 44:199–204.

Wolf, L. L. 1969. Female territoriality in a tropical hummingbird. Auk 86:490–504.

Wolf, L. L. 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. Condor 72:1–14.

Wolf, L. L. 1975. Energy intake and expenditures in a nectar-feeding sunbird. Ecology 56:92–104.

Wolf, L. L. 1978. Aggressive social organization in nectarivorous birds. Amer. Zool. 18:765–78.

Wolf, L. L., and F. B. Gill. 1980. Resource gradients and community organization of nectarivorous birds. Act. XVII Cong. Intern. Ornithol., pp. 1105–13.

Wolf, L. L., and F. R. Hainsworth. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52:980–88.

Wolf, L. L., and F. R. Hainsworth. 1977. Temporal patterning of feeding by hummingbirds. Anim. Behav. 25:976–89.

Wolf, L. L., and F. R. Hainsworth. 1978. Energy: expenditures and intakes. *In* A. Brush (ed.), Chemical zoology, vol. 10. Academic Press, New York.

Wolf, L. L., F. R. Hainsworth, and F. B. Gill. 1975. Foraging efficiencies and time budgets of nectar feeding birds. Ecology 56:117–28.

Wolf, L. L., F. R. Hainsworth, and F. G. Stiles. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. Science 176:1351–52.

Wolf, L. L., and F. B. Stiles. 1970. Evolution of pair cooperation in a tropical hummingbird. Evolution 24:759–73.

Wolf, L. L., F. G. Stiles, and F. R. Hainsworth. 1976. Ecological organization of a tropical, highland hummingbird community. J. Anim. Ecol. 45:349–79.

Wolf, L. L., and J. S. Wolf. 1971. Nesting of the purple-throated carib hummingbird. Ibis 113:306–15.

Wolf, L. L., and J. S. Wolf. 1976. Mating system and reproductive strategy of malachite sunbirds. Condor 78:27–39.

Zach, R., and J. B. Falls. 1976a. Ovenbird (Aves: Parulidae) hunting behavior in a patchy environment: an experimental study. Can. J. Zool. 54:1863–79.

Zach, R., and J. B. Falls. 1976b. Foraging behavior, learning, and exploration by captive ovenbirds (Aves: Parulidae). Can. J. Zool. 54:1880–93.

Zach, R., and J. B. Falls. 1976c. Do ovenbirds (Aves: Parulidae) hunt by expectation? Can. J. Zool. 54:1894–803.

Zimmerman, M. 1979. Optimal foraging: a case for random movement. Oecologia 43: 261–67.

SHELDON I. LUSTICK

Cost-Benefit of Thermoregulation in Birds: Influences of Posture, Microhabitat Selection, and Color

9

INTRODUCTION

It is my purpose in this paper to discuss and evaluate some of the ways in which birds adjust to varying thermal environments. The examples used will be taken from field and laboratory studies conducted by myself and graduate students working with me. Not only do we want to look at the way in which birds adjust to their thermal environments, but I would hope that the studies presented in this paper would point out the importance of an intergraded approach to answering ecologically relevant questions. We must remember that an animal is greater than the sum of its parts and that this animal is inseparable from its environment. To obtain ecologically relevant answers one cannot remain a specialist. We need studies that combine physiology, behavior, morphology, and ecology, and though it is sometimes more difficult, our studies must deal with more than one variable at a time.

In simple terms, an animal is fit, in an evolutionary sense, if it can reproduce, obtain food, and avoid becoming someone else's food. It might be said that those animals leaving the most viable offspring at the least possible cost are the most fit. In most birds a major portion of the cost of survival is spent in maintaining a relatively high (42° C) body temperature (homeothermy). Birds respond to their thermal environment in three ways (fig. 1). There is a physiological response, a

Department of Zoology, Ohio State University, Columbus, Ohio 43210

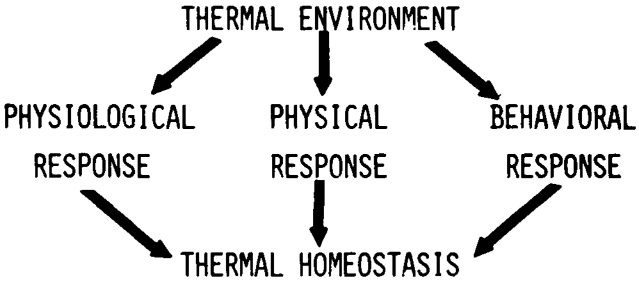

Fig. 1. Ways in which an animal can achieve thermal homeostasis.

morphological response, and a behavioral response, all three of which lead to thermal homeostasis. Vertebrates in general are in a sort of genetic trap with regard to the kinds of physiological and anatomical adjustments that they can make to environmental conditions. In contrast, most vertebrates have evolved very complex behavioral patterns, and behavioral adjustments to the environment can be rapid, precise, and highly flexible. Even more important is the fact that many of the behavioral adjustments are less costly than the physiological or anatomical adjustments.

Our study to date has embodied laboratory and field investigations to correlate the adaptiveness of coloration and environment to thermoregulation, in particular, and to relate microhabitat selection to maximized energetic efficiency, in general. The primary model has been the herring gull, *Larus argentatus*, whose color varies from dark brown (75% absorptivity) as juveniles to gray (50% absorptivity) and white (10–15% absorptivity) as adults. A secondary model has been the starling, *Sturnus vulgaris*, and blackbirds (*Molothrus ater, Agelaius phoeniceus, Quiscalus quiscula*) in general, these species being noted for their communal roosting behavior during the cold winter nights of north-temperate latitudes. A third model, the Carolina chickadee, *Parus carolinensis*, is a very small bird that overwinters in north-temperate latitudes and whose weather-dependent foraging strategies have been studied (Grubb, 1975, 1977).

SIGNIFICANCE OF COLOR TO RADIATIVE HEAT LOAD

It is patently obvious that there are many factors acting in selection for animal coloration. Burtt (1978) stresses the need for a balanced, scientifically rigorous approach to the question of the evolution of animal coloration. A priori there would seem to be a trade-off in the selection for color. Factors affecting color are precision of microhabitat selection, body size, predator-prey interaction, and individual recognition, among others. Although concealment and social interaction are the most easily recognized selective advantages of coloration pattern, researchers have long been calling attention to the overemphasis of these factors (Cartwright and Harrold, 1925; Cole, 1943; Hamilton and Heppner, 1967; Lustick, 1969). The significance of color to physiological processes of thermoregulation in endotherms is more difficult to determine. With regard to fur and feathers, there is still a question as to whether light or dark coloration is a better absorber of radiant energy. Monteith (1973) points out that "reflectivity is an important discriminant in the heat balance of animals but the relationship between coat color and radiative heat load is complex." He further points out that "radiation intercepted by the hairs of a coat is scattered forwards toward the skin, as well as being reflected away from the animals"; the amount of solar radiation reaching the skin will therefore be smaller under a dark coat than under a light one of the same structure. That light pelage and plumage seem to transfer more radiative energy than darker ones is further substantiated by theoretical studies on solar radiation transfer through fur and feathers by Davis and Birkebak (1971) and Hutchinson and Brown (1969). Harrington (1926) suggested that multiple reflections entering through the white insulatory layers may allow greater warming at the skin surface. Oritsland (1970) also found that a dark insulatory layer is warmer superficially but bright fur warms deeper layers. Krog (1955) noted how transparent hairs of Salix (willow catkins) and Lepidopteran caterpillars in the Arctic transmitted solar radiation inward but trapped longwave radiation, creating a greenhouse effect. Marder (1973) found that though black plumage heats more than white, skin temperatures were similar. Walsberg et al. (1978) stated that convective cooling differentially affects the radiative heating of dark and light plumages, so that at very low wind speeds black plumages acquire a greater radiative heat load than do white plumages, but the heat loads of black and white plumages rapidly converge as wind speed is increased. It should be pointed out that this effect was observed best when the feathers were erected and not when they were smooth. It has also been demonstrated that darker colors absorb more solar radiation. Blum (1961) found that the skins of blacks would absorb 30% more sunlight than the skins of whites. Other important studies with insects (Hill and Taylor, 1933; Digby, 1955; Dudley, 1964; Cena and Clark, 1972) and lizards (Klauber, 1939; Cole, 1943; Norris, 1967; Pearson, 1977), as well as mammals and birds (Hamilton and Heppner, 1967; Lustick, 1969; Heppner, 1970; Lustick et al., 1970; Neal and Lustick, 1975; DeJong, 1976; Finch and Western, 1977), verify the substantial difference in energy uptake by variously colored animals. Lustick (1969) and Heppner (1970) show that dark birds had a significantly greater reduction in metabolism at air temperatures below the lower critical temperature than did white birds when receiving radiation. More recently Chappell (1980b), working with white and dark pelage from winter and summer acclimatized ermine and mink, and Finch et al. (1980), working with light and dark desert goats, showed dark pigmentation to be a better absorber of solar energy than light pigmentation.

Based on the studies to date, one could conclude that barring the erection of light-colored feathers or hair (which allows the solar radiation to be reflected inward), dark pigmentation is a better absorber of solar energy. As soon as one makes this statement the question arises of why one finds black birds in the desert and white birds in the Arctic. One could state this question another way: is thermoregulation a major selecting factor in the evolution of color?

ENERGY BALANCE IN THE HERRING GULL

Using the herring gull as a model, let's investigate how color, posture, and orientation influence the thermal balance of these birds, keeping in mind the question of whether thermal regulation is a major factor in the evolution of color.

We chose the herring gull as a model for two reasons: (1) its color varies between juvenile (brown, 75% absorptivity) and bicolored adult (white, 10%, and gray, 50% absorptivity); (2) it is tied to land in open areas during the nesting season. We studied a herring gull colony during the 1977 and 1978 breeding seasons at the U.S. Steel calcite quarry in Rogers City, Michigan. The adults maintained a territory from April through July. Assuming that the herring gull is a good homeotherm, the heat balance can be expressed by the following equation:

$$\Delta T_B = R_s \pm R \pm C \pm K + MR - EWL \qquad (1)$$

where

ΔT_B = change in body temperature
R_s = direct solar radiation
R = thermal radiation
C = thermal conduction
K = convection
MR = metabolic rate
EWL = heat lost by evaporation

In order to calculate the effects that color, posture, and orientation might have on the energy balance of the gull, we combined laboratory studies dealing with (1) the effects of air temperature on metabolic rate, (2) the effects of temperature on evaporative water loss, and (3) field studies in which we monitored various environmental parameters (table 1).

TABLE 1

ENVIRONMENTAL PARAMETERS MONITORED IN THE FIELD

R_s	direct solar radiation
R_d	diffuse solar radiation
R_a	atmospheric radiation
R_g	ground radiation
R_r	reflected radiation
V	wind velocity
T_a	ambient temperature
T_{sky}	sky temperature
W	surface temperature of white plumage exposed to R_s
D	surface temperature of gray plumage exposed to R_s

In this study we asked three basic questions:

1. What effect does solar radiation have on the gulls?
2. How does color affect the use of solar radiation?
3. What behavioral mechanisms might the gulls use to overcome thermal stress?

In previous studies (Lustick, 1969; Lustick et al., 1970, 1979) we had shown that below their lower critical temperature dark-colored birds can use solar radiation to alleviate thermal stress, whereas above the lower critical temperature solar radiation adds to thermal stress. Thus, it is necessary to determine the thermal neutral zone of the adult gulls under standard conditions (no sun or wind) (fig. 2).

The adult gulls maintained a relatively constant body temperature over a 40° C range of ambient temperature (−10–30° C) (fig. 2). Thermal neutrality, though not sharply defined, lies between 5° and 30° C. Adult gulls (1000 g) seem well adapted to a cold climate and should be able to maintain their body temperature at air temperatures of −50° C.

The air temperatures that the gulls were exposed to while on territory during April, May, and June ranged between 0° and 15° C. Birds sitting on the nest in direct sunlight were observed to pant, which indicates that there was a net heat flow into the bird. Birds standing at air temperatures between 5° and 15° C were not observed to pant. This can partially be explained by the fact that the feet are important ave-

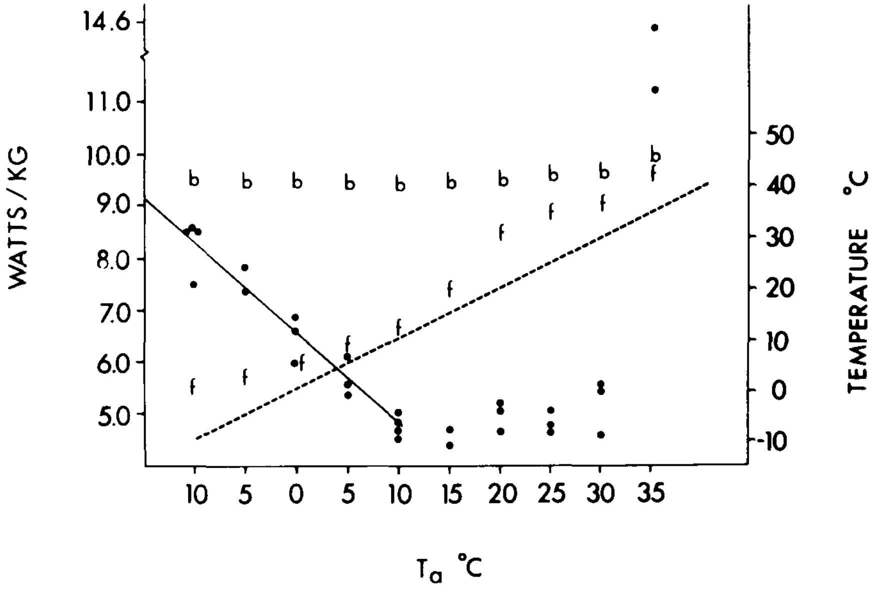

Fig. 2. The relationship of metabolic rate (*shaded circles*), mean foot temperature (*f*), and mean body temperature (*b*) to ambient temperature (T_a). The regression line relating metabolism to T_a was fitted by the method of least squares (w/kg = 6.63–0.174 T_a). *Dashed line* shows temperature equilibrium. N = 6. From Lustick et al., 1978. Reprinted by permission from *Science*, vol. 200, pp. 81–83, 7 April 1978. Copyright 1978 by the American Association for the Advancement of Science.

nues of heat loss (Steen and Steen, 1965; Lustick et al., 1979); the foot temperature exceeded the T_a at all temperatures above the lower critical (fig. 2). If we accept the general conclusion that dark-pigmented feathers are a better absorber of solar energy than light-pigmented feathers, we would predict that if the gulls exposed their gray back to the sun they would absorb more solar radiation than if they exposed their white surfaces to the sun.

In direct sunlight, with wind velocities of 0.3 m/sec, the surface temperature of the gray plumage increased to as much as 15° C above the air temperature, compared to 4° C above T_a for the white plumage (fig. 3). The temperatures of surfaces not receiving direct sunlight approximated the air temperature. When wind velocities were higher than 2.2–3 m/sec, the gull faced into the wind at T_a's between 0° and 15° C.

What behavioral mechanisms are there to minimize heat stress from intense solar radiation? It is difficult for a bird the size of the herring gull to seek cover, although the juveniles do (Lustick et al., 1979). As

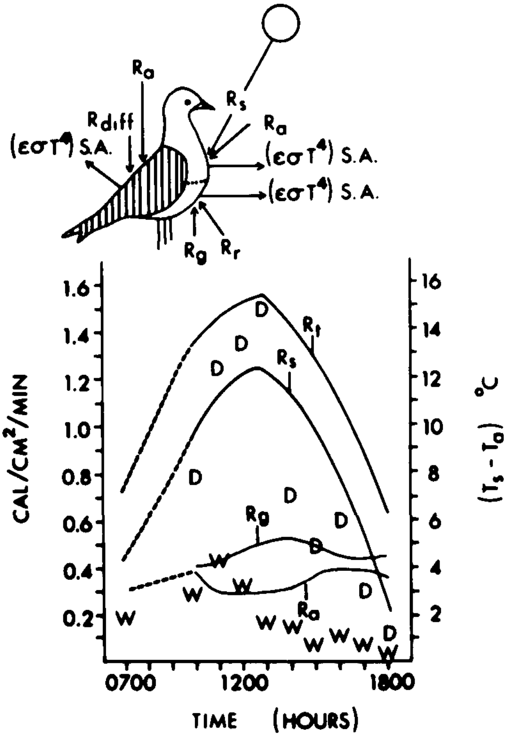

Fig. 3. The total down radiation (R_t), the solar radiation (R_s), the total ground radiation (R_g longwave plus R_r reflected shortwave), the atmospheric radiation (R_a), and the difference between surface and ambient temperature ($T_s - T_a$) when the bird faces the sun with white surface (*W*) and gray back (*D*). In calculating the net radiation, the radiation intensities were multiplied by the surface area (*S.A.*) receiving that radiation and in the case of R_s by the proper absorptivity. Radiation loss from the bird was determined by ($\epsilon\sigma T^4$) *S.A.*, where ϵ is the emissivity of the surface, σ is the Stefan-Boltzman constant, and T is the surface temperature in degrees Kelvin. Data obtained in Rogers City, Michigan, on 14 April 1977; 93 surface temperatures were monitored. Adapted from Lustick et al., 1978.

mentioned previously, they can stand and lose heat through the feet (fig. 2) or they could enter the water and increase the rate of heat loss through the feet. When not on territory the birds will be found in the water on hot sunny days. Another behavioral pattern used by the adult gulls to minimize heat stress was orientation toward the sun (fig. 4). On days with low wind velocities and air temperatures between 5° C and 15° C, the birds actually rotated 180° during the day, always facing the sun. When facing the sun their posture is such that the darker dorsal surface is exposed to R_d and R_a and the white ventral surface is ex-

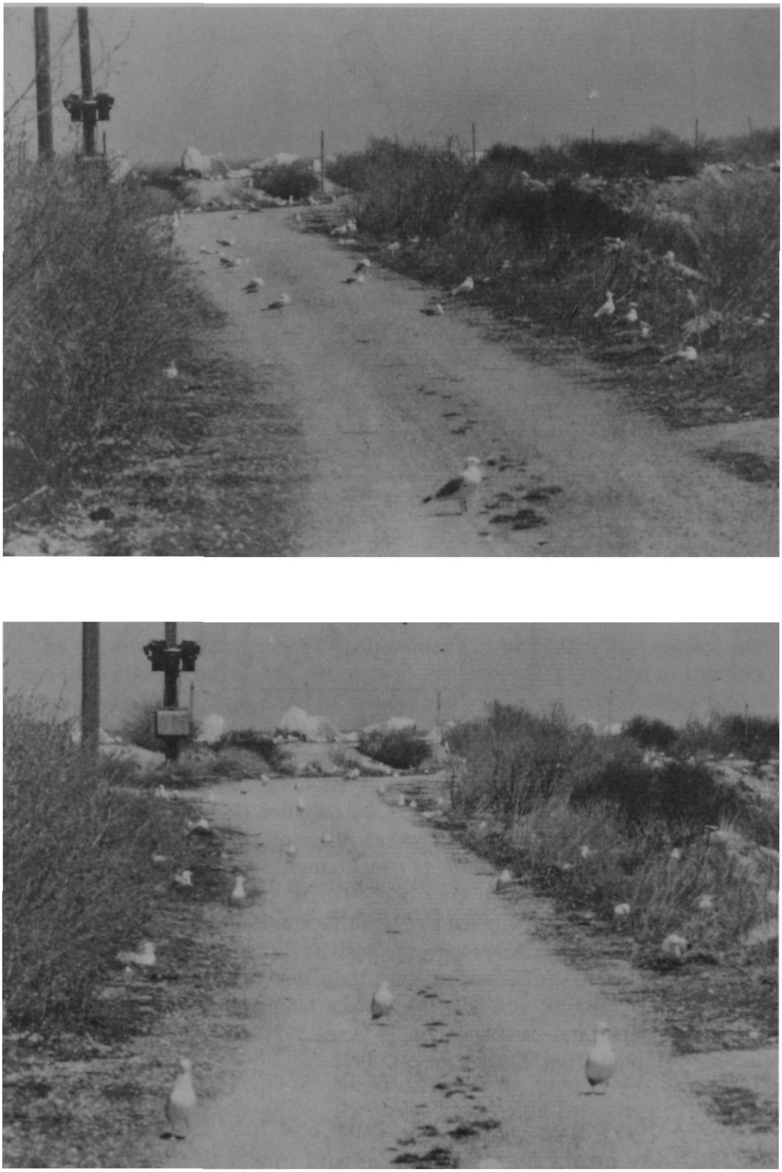

Fig. 4. Orientation toward the sun by herring gulls at noon (*top*) and 3:00 P.M. (*bottom*).

posed to R_a, R_s, R_r, and R_g (fig. 3). Orientation toward the sun and postural adjustments to vary the angle of incidence of solar radiation can minimize radiative heat gain by (1) reducing the exposed surface area to approximately one-fourth the total surface area and (2) exposing the less absorptive white surfaces to direct solar radiation. The skin temperature of gulls receiving direct and long-wave radiation (697 w/m^2 and 348 w/m^2, respectively) was 38.11 ± 0.25° C under their white plumages and 40.6 ± 1.03° C under their gray plumages (measured in lab). The higher skin temperature under the dark plumages suggests that dark plumages acquire (or transmit) a greater radiative heat load than do white plumages. It should be pointed out that the white breast plumage has the greater insulative quality, and this might account for some of the difference in skin temperature between white and gray plumage.

By incorporating the field and laboratory data into the heat balance equation:

$$MR + H_r - H_c - H_e = T_B \qquad (2)$$

where

MR = standard metabolism
H_r = net radiation
H_c = convective heat loss
H_e = evaporative heat loss,

we were able to calculate the thermal energy exchange between the gulls and their environment when they face the sun and when they had their backs to the sun (table 2). Since wind velocity at the level of the bird varied between 0 and 0.6 m/sec, we estimated the forced convective heat loss at a mean wind speed of 0.3 m/sec using the equation from Calder and King (1974). The mean heat loss by evaporation determined in the laboratory at 10° C was found to be 5.5 w/m^2. When summing all the factors influencing the energy balance except thermal conductance, we find that birds facing the sun are in closer thermal balance (heat gain more closely approximating heat loss) than birds with their backs in the sun. We now know that adustments in posture and orientation can minimize the exposed surface area and absorptivity in adult bicolored gulls. It is obvious that a solid-colored dark bird could also minimize the radiative gain from solar radiation by orientation and posture changes that in turn minimize surface area and could possibly increase reflection by increasing the angle of incidence. Skuldt et al. (1975) have shown the angle of incidence to be extremely

TABLE 2

ESTIMATES OF MEAN NET RADIATION EXCHANGE WHEN HERRING GULLS ARE FACING TOWARD OR AWAY FROM THE SUN

14 April 1977 Time (hours)	Dorsal Surface in Sun H_r in w/m^2	Ventral Surface in Sun H_r in w/m^2	T_A °C	Dorsal Surface in Sun $MR + H_r - H_c - H_e$ in w/m^2	Ventral Surface in Sun $MR + H_r - H_c - H_e$ in w/m^2
1000	97.6	27.9	4	117.0	59.0
1100	62.7	−31.4	3	77.7	4.5
1200	92.7	−47.4	3	105.6	−10.8
1300	85.8	−54.4	5	82.1	−28.1
1400	101.1	−43.9	5	114.8	−16.6
1500	71.1	−62.1	5	89.7	−33.6
1600	55.8	−11.2	5	71.7	16.2
1700	38.4	−27.9	6	55.3	−5.9
1800	−10.5	−31.3	5	15.8	−2.8

SOURCE: From Lustick et al. (1978). Reprinted by permission from *Science*, vol. 200, pp. 81–83, 7 April 1978. Copyright 1978 by the American Association for the Advancement of Science.

Radiation calculations are based on 93 surface temperature measurements.

MR = metabolic rate derived from figure 2; H_r = net radiation; H_e = evaporative heat loss at 10_C; and H_C = forced convective heat loss.

important to the penetration of solar radiation in fur. Radiation physicists have long known that as the angle of incidence increases above 45°, the reflectivity of natural surfaces increases regardless of color (Monteith, 1973). Reflectance in cattle coats increases with increased angle of incidence (Riemerschmid and Elder, 1945).

It is obvious from an energy balance standpoint that it would be advantageous to be dark in cold climates and light in hot climates. Why then do we find white birds in the Arctic and black birds in the desert (is thermoregulation important in the selection of color)? Color as a physical response to environmental temperature stress is in a genetic trap—that is to say, it changes very slowly—whereas vertebrates in general and birds in particular have evolved complex behavior patterns and possess great learning capabilities. Thus, they adjust to thermal stress behaviorally (orientation and postural adjustment to minimize or maximize reflectance and surface area or feather erection to modify the absorptivity of radiant energy), removing the selective pressure to evolve the appropriate color for thermoregulation. It will be interesting to look at birds that change color with the seasons (reflective in summer to absorptive in winter). The same sort of discussion existed in the mid 1950s between Scholander (1956), Irving (1956), and Mayr (1956) concerning the climatic rules of Bergmann and Allen, with Mayr supporting the importance of the climatic rules to homeothermy (increased size in northern latitudes being selected for) while Scholander and Irving pointed out the exceptions to these climatic rules and demonstrated the importance of physiological and behavioral adaptations. Large size, like dark color, is advantageous in a cold climate but not necessary because of the many physiological and behavioral adjustments animals can make.

If a thermal balance cannot be achieved by the interaction between color, orientation, feather erection, and posture adjustments, the organism must seek the proper microclimate or, as Porter and Gates (1969) stated, find a more suitable climate space with regard to radiation, wind, air temperature, and humidity.

IMPORTANCE OF MICROCLIMATE TO ENERGY BALANCE AND SURVIVAL

Failure of birds to adjust successfully to one or more factors of the climate space (Porter and Gates, 1969) may result in death. Accounts of large-scale mortality in birds are prevalent in the literature. Several reports suggest that periods of severe weather are directly responsible for mortality. A study of bird mortality by Odum and Pitelka (1939) cites high winds up to 77.3 km/h, coupled with driving rain and a sharp drop in temperature, as the cause for 4% mortality in a roost of 25,000 birds. Similar conditions, which resulted in soaked birds, caused the death of 8,046 cowbirds in Columbus, Ohio (Kessler et al., 1967).

Lack of sufficient food or the ability to forage coupled with severe weather may also result in mortality, either directly, through depletion of fat stores and subsequent starvation, or by causing weakened birds, which may then be more susceptible to the effects of severe weather. Jogi (1968) found 4,500 dead house and sand martins, many of which were juveniles. Many of these birds appeared to have died of starvation due to a lack of food or an inability to forage during a period of severe weather. Many were found huddled together in an apparent effort to conserve body heat. Graber and Graber (1979) noted that heavy snowfall and extreme cold in Illinois resulted in a mortality rate higher among ground foragers and smaller species. This presumably indicates that the ground foragers were unable to find sufficient food.

Should severe weather not result in mortality, it can nevertheless serve to limit foraging rates and alter foraging substrate. Grubb (1978) found that wintering woodland birds in central Ohio decreased foraging rates with increasing wind velocities and decreasing temperatures, in an apparent effort to conserve energy by reducing convective heat loss. In addition, several species changed the foraging substrate as well by moving to substrates that appeared to offer greater protection from the wind. Nuthatches and woodpeckers switched to larger branches and the trunks of trees, and chickadees and titmice switched from the twigs of trees to twigs of shrubs.

The above studies indicate the importance of weather in the survival of birds. An important means for birds to adjust to weather variables in an effort to survive is to seek favorable microclimates. Especially illustrative of this fact is a study by Stewart (1978) in which he found that the mortality rate among starlings roosting in trees was 15% from two nights of very cold (−24.4° and −17.2° C) temperatures. In a nearby barn used by 2,500 starlings, the mortality figure for the same period was 0.4%. Many other studies point to birds that seek favorable microclimates. This has been demonstrated for the pygmy nuthatch (*Sitta canadensis*) (Knorr, 1957), eastern bluebirds (*Sialia sialis*) (Frazier and Nolan, 1959), house sparrows (*Passer domesticus*) (Kendeigh, 1961), redwing blackbirds (*Agelaius phoeniceus*), common grackles (*Quiscalus quiscula*), brownheaded cowbirds (*Molothrus ater*) (Francis, 1976), starlings (*Sturnus vulgaris*) (Kelty and Lustick, 1977; Yom-Tov et al., 1977), monk parakeets (*Myiopsitta monachus*) (Caccamise and Weathers, 1977), juvenile herring gulls (*Larus argentatus*) (Lustick et al., 1979), and black-billed magpies (*Pica pica hudsonia*) (Reese et al., 1980).

Favorable microclimates serve to reduce the energetic requirements of birds through alteration of the four factors comprising the climate space. Energetic requirements may be reduced through a reduction of wind velocity in the roost (Francis, 1976; Kelty and Lustick, 1977); a decrease in the radiation of thermal energy to the environment by increasing percentage of cover (Calder, 1973, 1974; Kelty, 1977); a decrease in incoming shortwave solar radiation to birds at moderate temperatures (Lustick et al., 1979); and an increase in local temperature above ambient temperature due to local effects of roost location in protected areas (Yom-Tov et al., 1977), temperature inversions in mountainous areas (Reese et al., 1980), or enclosed roosting or nesting cavities (Kendeigh, 1961; Caccamise and Weathers, 1977).

In a stressful environment it may be necessary for birds to maximize their energetic efficiency through conservation of energy stores in order to survive. Use of a favorable microclimate that alters one or more of the factors making up the climate space will add significantly to this conservation of energy.

Although three of the elements of the climate space—radiation, humidity, and ambient temperature—have been extensively studied with regard to their effects on avian energetics, the effects of wind velocity, or forced convection, have been examined primarily through utilization of heat transfer theory (Calder and King, 1974; Bakken, 1976; Walsberg and King, 1980). Use of heat transfer theory to determine the effect of the roost on avian energetics may lead to an underestimate of the energetic significance of the roost to the bird. This may in part be due to a lack of specific information on the effect of wind on the bird's metabolic rate. For example, Walsberg and King (1980) conclude that the roosting behavior of the American robin (*Turdus migratorius*) in dense vegetation during winter nights in eastern Washington produces only a slight thermoregulatory savings (3–5%) over birds roosting in the open. Studies by Kelty and Lustick (1977), based on experimental data derived by using a wind tunnel to measure metabolic rates of starlings, suggest a greater savings (12–38%) for birds roosting in well-protected versus open sites.

In experimental studies of the effects of wind velocity on birds by Gessaman (1973) on the snowy owl (*Nyctea scandiaca*), Robinson et al. (1976) on the white-crowned sparrow (*Zonotrichia leucophrys gambelii*), and Kelty and Lustick (1977), the metabolic rate was found to increase linearly with the square root of the wind velocity. Kelty and Lustick found, however, that at 15.1 km/h the metabolic rate of starlings increased abruptly in a nonlinear fashion. Robinson did not use wind velocities of this magnitude.

In addition to the above studies with live birds, Chappell (1980a) reports that thermal conductance in heated, skin-covered metal casts of arctic shorebirds in a wind tunnel also increased with the square root of the wind velocity. Using the same technique with arctic mammals resulted in a more accurate prediction when regressions of heat loss were made on the wind velocity (Chappell, 1980b).

In an effort to ascertain more accurately the energetic savings realized by blackbirds utilizing various roost sites and to compare the thermoregulatory benefits afforded by different types of roosts, this study utilizes data on the metabolic rates of blackbirds and starlings while in a wind tunnel (table 3). Measurements of the percentage of cover and the wind velocity in several roost types are used to compare and contrast the energetic requirements of blackbirds and starlings using these various roost sites at night. Energy budgets for blackbirds are based on measured metabolic rates and certain assumptions concerning radiative heat loss derived from earlier studies by Kelty (1977) and Kelty and Lustick (1977). These energy budgets are used to illustrate the relative value of each roost type in reducing energetic expenditures.

Wind velocity was measured simultaneously inside and outside on the windward side of several deciduous roosts, one cattail roost, a

TABLE 3

REGRESSION EQUATIONS FOR METABOLIC RATE ON THE SQUARE ROOT OF WIND VELOCITY AT FIVE TEMPERATURES

Species	Temperature (°C)	Equation*	r	N
Cowbirds	10	a $17.53 + 3.628V^{1/2}$	0.834	40
	5	b $20.08 + 3.457V^{1/2}$	0.822	40
	0	c $23.67 + 3.765V^{1/2}$	0.760	40
	−5	d $28.61 + 3.085V^{1/2}$	0.730	40
	−10	e $30.38 + 3.294V^{1/2}$	0.714	40
Male redwings	10	a $19.35 + 2.316V^{1/2}$	0.558	28
	5	a $21.36 + 1.916V^{1/2}$	0.511	28
	0	a $20.05 + 2.622V^{1/2}$	0.619	28
	−5	b $23.10 + 2.681V^{1/2}$	0.606	28
	−10	c $24.54 + 3.458V^{1/2}$	0.786	28
	10,5,0	$20.25 + 2.285V^{1/2}$	0.562	84
Female redwings	10	a $25.82 + 2.939V^{1/2}$	0.533	24
	5	ab $28.41 + 3.158V^{1/2}$	0.687	24
	0	b $30.76 + 3.347V^{1/2}$	0.684	24
	−5	c $36.96 + 2.725V^{1/2}$	0.517	24
	−10	d $38.06 + 4.785V^{1/2}$	0.660	24
Male grackles	10	a $14.23 + 1.983V^{1/2}$	0.697	22
	5	a $15.56 + 2.250V^{1/2}$	0.719	24
	0	b $18.74 + 2.709V^{1/2}$	0.785	21
	−5	b $17.87 + 3.226V^{1/2}$	0.885	16
	−10	b $18.66 + 3.445V^{1/2}$	0.733	21
	−10,−5,0	$18.52 + 3.091V^{1/2}$	0.773	58
Female grackles	10	a $14.66 + 2.196V^{1/2}$	0.698	24
	5	b $15.52 + 2.789V^{1/2}$	0.875	24
	0	c $17.37 + 3.919V^{1/2}$	0.845	22
	−5	d $22.17 + 2.826V^{1/2}$	0.718	18
	−10	e $23.03 + 3.817V^{1/2}$	0.883	16
	5,10	$14.92 + 2.125V^{1/2}$	0.694	46
Starlings†	0,5	a $13.78 + 2.680V^{1/2}$	0.980	...
	−10	b $16.80 + 3.010V^{1/2}$	0.700	...

*Equations denoted by the same letter are not significantly different ($P > 0.05$).
†0–7.3 km/h

single eastern red cedar tree, and a pine roost. Wind velocity within the roost was then recorded as a percentage of the velocity recorded outside the roost. This percentage remained essentially constant down to very low wind velocities. Measurements were made between 2 and 3 m above the ground with a hand-held anemometer (starting speed 0.15 m/sec; Central Scientific Co., model 13B-1064) and two Field Recording Wind Monitors (R. M. Young Co., model 6101 anemometer and chart recorder).

Measurements of sky, ground, tree, and bird surface temperatures were made inside deciduous and pine roosts during January and February. Temperatures of the ground, air, and trees were determined with a thermocouple connected to a Bailey Instruments (Model Bat Four) thermometer, and bird and sky temperatures were determined with a Mikron 44 infrared thermometer. To measure bird surface temperatures birds were tethered to a tree and allowed to settle for 20 min before measurements were made. Tethered birds could assume normal postural positions.

Energy budgets for the five groupings of birds were calculated by adding the net radiative heat loss to the convective heat loss determined in the wind tunnel. Net radiative heat loss was calculated according to Kelty (1977) and represents the net radiation exchange between the bird and the ground, trees, and sky. For birds roosting in the open the equation was:

$$H_r = (\epsilon_b \sigma T_r^4)\ (S.A.) - ((\epsilon_g \sigma T_g^4)\ (0.5\ S.A.) + (\epsilon_s \sigma T_s^4)\ (0.5\ S.A.)) \tag{3}$$

and in the roost:

$$H_r = (\epsilon_b \sigma T_r^4)\ (S.A.) - ((\epsilon_g \sigma T_g^4)\ (0.5\ S.A.) + (\epsilon_t \sigma T_t^4)\ (0.5\ S.A.)Z + (\epsilon_s \sigma T_s^4)\ (0.5\ S.A.)1-Z) \tag{4}$$

where:

H_r = net radiation exchange (W bird^{-1})
ϵ = infrared emissivity of radiating surface, where:
  $\epsilon_b = \epsilon_{bird} = 1.00$ (Calder, 1975)
  $\epsilon_t = \epsilon_{tree} = 0.90$ (Sellers, 1974)
  $\epsilon_g = \epsilon_{ground} = 0.97$ (Sellers, 1974)
  $\epsilon_s = \epsilon_{sky} = 1.20 - 171/\sigma T_a^4)$ for clear sky (Montieth, 1975)
  $= 1.00$ for completely overcast sky
T = temperature of radiating surfaces (°K), where:
  $T_r = T_{bird\ surface}$
  $T_t = T_{tree}$
  $T_g = T_{ground}$
  $T_s = T_{sky}$
σ = Stefan-Boltzman constant (5.67×10^{-8} Wm^{-2}°K^{-4})
$S.A.$ = bird surface area (m^2), calculated according to Walsberg and King (1978)
Z = percentage of vegetative cover in the roost to which the bird is exposed above the horizontal

Convective heat loss was determined by subtracting the net radiative heat loss under complete cloud cover from the metabolic rates determined in the wind tunnel. Assuming that bird surface temperatures in the wind tunnel are similar to those of birds on cloudy nights, radiant heat loss on cloudy nights should approximate the radiant heat loss in the wind tunnel (tree, ground, and sky temperatures approximate the air temperature).

In order to calculate the energy budgets it was necessary to make several assumptions. Birds were assumed to have a surface temperature (T_r) constant over the entire body surface. In reality the surface temperature varies somewhat over the body surface. However, with passerines of the sizes used in this study the variation is small. The surface temperature of a gray jay (*Perisoreus canadensis pacificus* Gmelin) determined by radiometric analysis by Veghte and Herreid (1965) at a T_a of −8° C varied from 3.5° to 6.8° C. Smaller species show less variation and larger species show greater variation.

The T_r at each T_a was assumed to be the same as that of the redwing blackbird. At a T_a of −10° C the T_r in the open was −3° C and in all roosts was 0° C. At a T_a of 0° C the T_r in the open was 6° C and in all roosts was 8° C. These T_r's fall between values calculated from Calder (1973) for a hummingbird (T_r of 3° C and 10.4° C at a T_a of −10° C and 0° C respectively) and Moen (1973) for a sharp-tailed grouse (*Pedioecetes phasianellus*) (T_r of −2.6° C and 6.0° C at −10° C and 0° C respectively). The gray jay used by Veghte and Herreid had a T_r of 4.59° C at −8° C and −4.88° C averaged for the entire body surface area but making no adjustment for the area of each separate part. The male and female redwings used in this study had a T_r or 2.5° C and −2.0° C respectively at a T_a of −7° C.

Sky temperatures (T_s) of −30° C at a T_a of −10° C and −25° C at 0° C were used for the calculations. Under complete overcast conditions $T_s = T_a$, as suggested by Monteith (1975).

ROOST MICROMETEOROLOGY

The percentage of vegetative cover measured during the winter in several roost types may be seen in table 4. In deciduous roosts cover varied from a low of 9% in the Brand Road roost to a high of 22.3% in the McGowen Road roost. Three roosts measured again during July varied from 51% cover in the R and F roost to 94% in the Airport roost. A cattail roost measured during the winter contained 61.6% cover. A single eastern red cedar tree gave 81.3% cover, and a pine woods ranged from 75–96% cover (table 4).

The wind velocity measured in the deciduous roosts varied from a low of 25% of the velocity measured outside the roost in the Airport and McGowen Road roosts to a high of 73% in the Henderson Road roost. Wind velocity 0.5 m above the water surface in the cattail roost

TABLE 4

PERCENTAGE OF COVER AND WIND VELOCITY FOR SEVERAL ROOST TYPES

Roost	Percentage of Cover	Percentage of Wind Velocity outside Roost
Henderson Road	13	63–73
Roost #2	11–16	50–60
Kitzmiller Road	21.7	55–58
Worthington	16.6	50–58
R and F roost	winter 18 summer 51–80	50
Brand Road	winter 9 summer 88	42
Airport	winter 13–16 summer 87–94	43 @ 100 m 25 @ 200 m
Morse Road	10.8	35–38
McGowen Road	22.3	25–28
Cattail marsh	61.6	10–16
Cedar tree	81.3	15
Pine roost	75–96	0

was 10–16% of the velocity 2.5 m above the water surface. In the red cedar tree the velocity was 15% of that outside the tree's cover, whereas 100 m inside the pine woods was 0% of the velocity recorded outside (at the level of birds). The wind velocity outside the pine roost reached a maximum of 48.6 km/h during recording.

Wind velocity in the roosts was affected not only by the density of growth within the roost but also by the surrounding topography. Roosts located in open areas were less effective in reducing the effects of the wind than roosts located in low spots or near buildings. In addition, the size of the roost was an important factor in cutting the wind velocity. In the Airport roost the wind velocity recorded 100 m inside the roost was 43% of the velocity recorded outside but the velocity 200 m inside the roost was only 25% of that outside. If the outside velocity was 15.1 km/h, this represents a difference of 2.7 km/h between the two recording locations.

Measurements of the surface temperatures of the ground, trees, and birds and sky temperature were made in the R and F deciduous roost on two clear nights in January and February 1980 and in the pine roost by Kelty (1977) (table 5).

TABLE 5

MEASURED TEMPERATURES AT NIGHT
(IN °C)

Roost Type	T_a	T_g	T_t	T_s	T_r	$T_r - T_a$	N
Deciduous	−8.0	−8.0	−8.0	−37.0	−5.0 to −4.0*	3.0 to 4.0	2 redwing blackbirds
Deciduous	−7.0	−6.0	−7.0	−26.0	+2.5*	9.5	2 redwing blackbirds
					−2.0	5.0	2 redwing blackbirds
Pine	−10.0	−10.0	−10.0	−24.4 ± 2.5	−7.8*	2.2	10 starlings
Pine	0.0	0.0	0.0	−24.3 ± 2.7	+3.2	3.3	9 starlings

*Surface temperature inside roost.

NOTE: T_a = ambient temperature, T_g = ground temperature, T_t = tree temperature, T_s = sky temperature, and T_r = bird surface temperature.

ENERGY BUDGETS

At −10° C the metabolic rate increased linearly with the square root of the wind velocity in three species studied—cowbird, common grackle, and redwing blackbird. This agrees with Gessaman's (1973) work on the snowy owl and Robinson and others' (1976) work on sparrows. Over a range of wind velocities from 0 to 7.5 km/h, the starling followed this same relationship; above 7.5 km/h the increase in metabolism was no longer linear, being 45.3 ± 0.7 mWg^{-1} at km/h (table 3).

Net radiative exchange decreased with increasing percentage of canopy cover or increased cloud cover (table 6). The radiative energy loss in a pine roost with 96% cover is only 32% of the value in the open at −10° C. Radiative energy loss when cloud cover is complete varies from 14% of the radiative loss when skies are clear and birds are in the open to 91% of the loss from a pine roost with 96% cover at −10° C. This is due to the fact that under heavily overcast conditions the clouds are often in thermal equilibrium with bird surface temperatures and the emissivity of the sky increases to one (Monteith, 1973). Thus the sky and the bird are in approximate thermal equilibrium.

The calculated net radiative heat losses and energy budgets reveal the importance of the roost to the birds using it to reduce total energy expenditures. For all birds the net radiative heat loss in a pine roost with 75–96% cover under clear skies is reduced 35–54% over the net radiative heat loss in the open. This is due solely to the increase in cover that the roost provides. This figure corresponds closely to the savings calculated by Calder (1974) for a hummingbird moving under branches to nest. When the additional effect of the roost in reducing the wind velocity is taken into consideration, the total energy losses at −10° C in the pine roost are reduced 43–64% from those in the open. This percentage would increase at higher wind velocities (wind velocities greater than 15 km/h, the maximum we could generate in a wind tunnel).

In all birds tested except the brown-headed cowbirds, the rate of heat loss exceeded their peak heat production capabilities on clear nights at −10° C in the open (table 7). In fact, in the brown-headed cowbird, heat production barely exceeds heat loss in the open at −10° C (table 7). The redwing blackbird is the only bird tested that could not survive in a deciduous roost with 18% cover at −10° C. The starling was the bird best suited to overwinter in the Columbus, Ohio, area. This is probably due to the fact that the winter acclimated starlings have a much higher heat production (Lustick and Adam, 1977) than expected and their surface temperatures were lower than those of

TABLE 6

CALCULATED NET RADIATIVE HEAT LOSS (W BIRD^{-1}) FOR BIRDS

Species	Roost Type		Percentage of Cover	H_r at 0° C	H_r at −10° C
Cowbirds	Open	c*	0	1.390	1.420
		o		0.503	0.547
	Deciduous	c	18	1.360	1.330
		o		0.536	0.575
	Pine	c	75	0.892	0.895
		o		0.640	0.665
	Pine	c	96	0.719	0.734
		o		0.679	0.698
Male redwings	Open	c	0	1.700	1.740
		o		0.615	0.678
	Deciduous	c	18	1.660	1.640
		o		0.655	0.713
	Pine	c	75	1.090	1.100
		o		0.783	0.823
	Pine	c	96	0.879	0.908
		o		0.829	0.867
Female redwings	Open	c	0	1.350	1.380
		o		0.512	0.557
	Deciduous	c	18	1.320	1.300
		o		0.542	0.583
	Pine	c	75	0.880	0.887
		o		0.642	0.669
	Pine	c	96	0.716	0.735
		o		0.678	0.699
Male grackles	Open	c	0	2.440	2.520
		o		0.892	0.983
	Deciduous	c	18	2.410	2.370
		o		0.951	1.030
	Pine	c	75	1.580	1.600
		o		1.140	1.190
	Pine	c	96	1.270	1.320
		o		1.200	1.250
Female grackles	Open	c	0	1.980	2.030
		o		0.692	0.771
	Deciduous	c	18	1.930	1.900
		o		0.739	0.812
	Pine	c	75	1.250	1.270
		o		0.890	0.942
	Pine	c	96	1.000	1.040
		o		0.946	0.989
Starlings	Open	c		....	2.050
	Deciduous		18	....	2.000
	Deciduous	c	30	....	1.820
	Pine	c	75	....	1.240
	Pine	c	96	....	0.930
	Cedar tree	c	81	....	1.150

*c = clear sky, o = overcast sky

the other birds tested, thus decreasing radiative heat loss. The energetics of the birds in the various roost types agree with the winter distribution of these species: 90% of the birds overwintering in the Columbus, Ohio, area are starlings, and, as pointed out, they roost in

TABLE 7

COMPARISON OF HEAT LOSS (W BIRD^{-1}) FROM BIRDS BY RADIATION AND CONVECTION

Species	Roost Type	Percentage of Cover	Wind Velocity (km/h)	MR^{1*}	MR^{2*}	Peak MR
Cowbirds	Open	0	15.2	2.89	2.01	2.94 ± 0.15
	Deciduous	18	7.6	2.60	1.85	
	Pine	75	0.0	1.66	1.43	
	Pine	96	0.0	1.46	1.42	
Male redwings	Open	0	15.2	3.46	2.40	2.99 ± 0.44
	Deciduous	18	7.6	3.08	2.15	
	Pine	75	0.0	1.83	1.55	
	Pine	96	0.0	1.58	1.56	
Female redwings	Open	0	15.2	3.30	2.48	2.12 ± 0.29
	Deciduous	18	7.6	2.97	2.25	
	Pine	75	0.0	1.89	1.67	
	Pine	96	0.0	1.71	1.68	
Male grackles	Open	0	15.2	4.91	3.37	4.61 ± 1.69
	Deciduous	18	7.6	4.35	3.01	
	Pine	75	0.0	2.45	2.04	
	Pine	96	0.0	2.11	2.04	
Female grackles	Open	0	15.2	4.32	3.06	3.83 ± 1.24
	Deciduous	18	7.6	3.80	2.61	
	Pine	75	0.0	2.19	1.86	
	Pine	96	0.0	1.91	1.86	
Starlings†	Open	0	15.2	5.67	......	5.14
	Deciduous	18	7.6	3.92	......	
	Pine	75	0.0	2.36	......	
	Pine	96	0.0	2.05	......	

Heat loss was measured at −10° C in four roost types at a wind velocity of 15.2 km/h in the open under clear and fully overcast skies.

*MR^1 = metabolic rate under clear sky; MR^2 = metabolic rate under fully overcast sky.

†Adapted from Kelty (1977).

pines during the winter. The redwing blackbirds that are stressed the most migrate south, where they choose wetland areas in which to roost but also make use of deciduous thickets, pines, canebrakes, and sugarcane fields (Meanley, 1965). In Tennessee and Kentucky winter roosts of blackbirds and starlings are often composed of loblolly pine (*Pinus taeda*) (Francis, 1976; Robertson et al., 1978; Dolbeer et al., 1978) and in Ohio, *Pinus strobus* (Kelty and Lustick, 1977); and in Washington robins utilize Douglas fir (*Pseudotsuga menziesii*) (Walsberg and King, 1980).

In late summer and early fall, blackbirds and starlings roost in deciduous roosts which at this time of year provide a great deal of cover (51–94%) (table 4). However, abandonment of deciduous roosts for pine roosts occurs in late November in mid-Ohio. In a roost in Olean, New York (Cattaragus County), this abandonment coincided with the dropping of leaves and air temperatures of 0.5° C on clear nights.

Not only do birds switch from a deciduous to a pine roost in the winter but within a pine roost they show vertical displacement depending on weather conditions. On cold, clear, windless nights the birds roost under the canopy; on cold, cloudy, windless nights they roost nearer the top of the canopy; whereas on cold, cloudy, windy nights they roost down below the canopy out of the wind (Kelty and Lustick, 1977).

It is obvious from table 7 that all birds tested except redwing blackbirds could survive in a deciduous roost, yet they make the move to pines. Here one must remember that to survive, the energy budget must be balanced; input must equal output. The reduction in output afforded them by the pine roost means that they need less input to maintain an energy balance. This will be of great importance where food supplies are limited due to snow cover. Birds in general are opportunistic, and one would expect them to maximize their energetic efficiency by microhabitat selection.

ENERGETIC CONTROL OF BEHAVIOR: FORAGING IN CAROLINA CHICKADEES

The major question asked in the study on the Carolina chickadee was, Can physiological data collected in the laboratory be used to explain foraging strategies of the Carolina chickadee in a winter woodlot? To answer this question we (Mayer et al., 1979) looked at the interaction of wind and air temperature on the metabolic rate of the chickadee over a range of air temperatures from 5° to −10° C and at wind velocities of from 0 to 7.3 km/h.

The standard metabolic rate of the Carolina chickadee increased from 51.6 w/kg at 5° C to 72 w/kg at an air temperature of −10° C (fig. 5) and may be expressed by the equation $Y = 58.42 - 1.34X$. Over an air temperature range of from 5° to −10° C there was a significant increase (over standard metabolic rate) in metabolic rate at each of the three wind speeds tested (fig. 5). At air temperatures of from 0° to −10° C there was no significant difference in metabolism between the birds exposed to each of the three wind speeds (1.4, 2.9, and 7.3 km/h), indicating that below 0° C metabolism peaked at the lowest wind speed tested (fig. 5). At −10° C only birds exposed to wind speeds of 1.4 km/h or lower could survive the 90 min test period. As metabolism increases with wind and low ambient temperature, the body temperature of the bird decreases (fig. 6). The maximum meta-

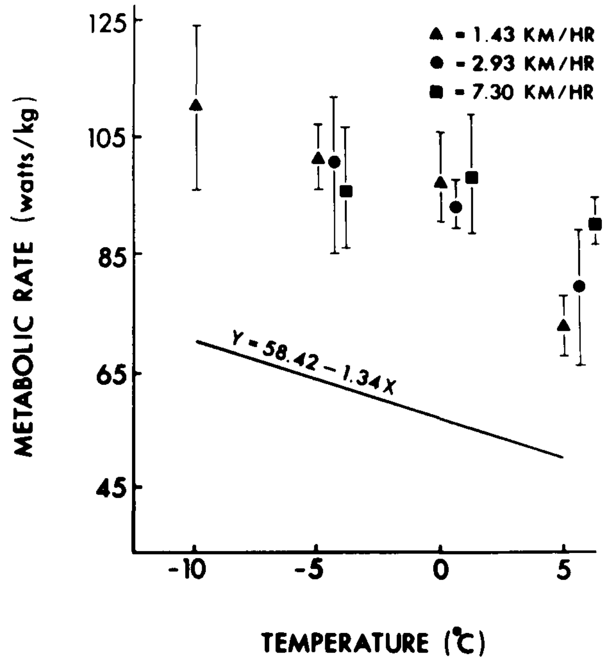

Fig. 5. Metabolic rate of the Carolina chickadee (*Parus carolinensis*) as a function of temperature and wind. *Solid line* represents zero wind speed. N = 50. From Mayer et al., 1979. Reprinted with permission from *Comparative Biochemistry and Physiology*, vol. 63A, L. S. Mayer, S. I. Lustick, and T. C. Grubb, Jr., "Energetic Control of Behavior: Foraging in Carolina Chickadees," Copyright 1979, Pergamon Press, Ltd.

bolic rate attainable for a Carolina chickadee is approximately 106 w/kg and is 4.2 times the 25.1 w/kg metabolic rate in thermal neutrality (Munzinger, 1974). That the birds could not maintain their body temperature at peak metabolic rates indicates that heat loss was greater than heat production under all combinations of wind speeds of at least 1.4 km/h at the air temperatures tested. Munzinger (1974) has shown that roosting Carolina chickadees become hypothermic at low air temperatures (5° C), their body temperatures dropping to near 30° C but not below.

When the standard metabolic rate is extrapolated it reaches the mean peak metabolic rate of 106 w/kg at −35° C without wind, suggesting that the Carolina chickadee could survive −35° C by seeking the proper microhabitat. We would predict from our laboratory studies that on days characterized by low temperature (below 0° C) and wind, the activity of the Carolina chickadee would be restricted to windless

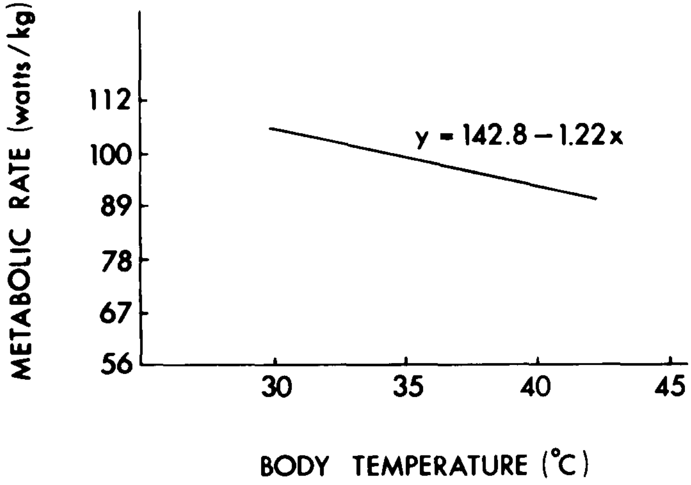

Fig. 6. Metabolic rate of the Carolina chickadee as a function of body temperature. N = 47. From Mayer et al., 1979. Reprinted with permission from *Comparative Biochemistry and Physiology*, vol. 63A, L. S. Mayer, S. I. Lustick, and T. C. Grubb, Jr., "Energetic Control of Behavior: Foraging in Carolina Chickadees," Copyright 1979, Pergamon Press, Ltd.

microclimates. Grubb (1978) has presented data on weather-dependent foraging of the Carolina chickadee that substantiate our laboratory predictions. He found that both the number of sightings per hour and the foraging rate (m/min) decreased with decreasing temperature to approximately zero between −20° and −29° C when sun was occluded and wind velocities were between 0.36 and 3.6 km/h (fig. 7). From our data on the effects of wind on metabolism it can be seen that metabolic rate peaks at 5° C (fig. 4), depending on the wind speed instead of −35° C, indicating that foraging rate and conspicuousness would be reduced or modified at higher air temperatures with wind. Grubb (1975, 1977, 1978) found the Carolina chickadee to use different foraging strategies—downward displacement from the canopy, feeding restricted to the leeward side of tree trunks, movements to the leeward side of woodlots, increases in the time spent stationary, or retreat from the woodlots to dense, early successional vegetation, where wind velocity would be minimal.

It is highly probable that thermal benefits from solar radiation could negate some of the effects of low air temperature and wind (Lustick, 1969; Neal and Lustick, 1975; Neal, 1976), again modifying foraging strategies. Carolina chickadees have been observed sunbathing, and

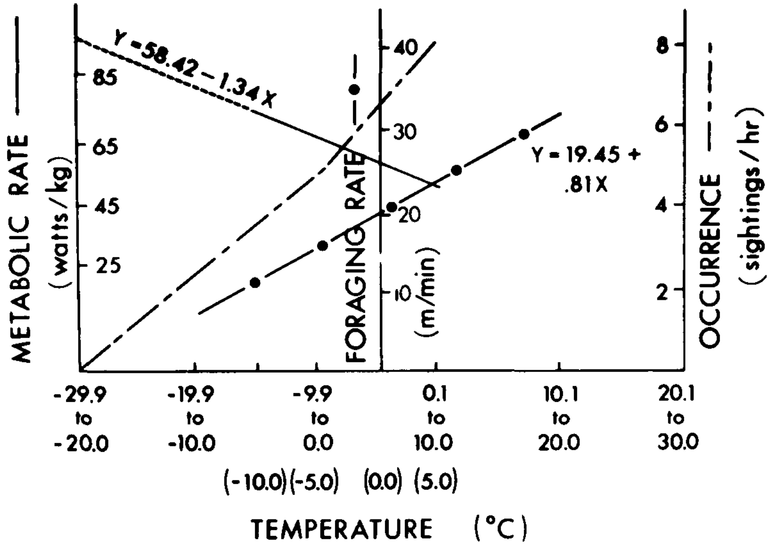

Fig. 7. Standard metabolic rate (*solid line* extrapolated to −29° C), foraging rate (m/min, *dashed line*), and occurrence (*dotted line*) of the Carolina chickadee as functions of air temperature. From Mayer et al., 1979. Reprinted with permission from *Comparative Biochemistry and Physiology*, vol. 63A, L. S. Mayer, S. I. Lustick, and T. C. Grubb, Jr., "Energetic Control of Behavior: Foraging in Carolina Chickadees," Copyright 1979, Pergamon Press, Ltd.

Grubb (1977) has shown that the intensity of solar radiation in nature can dictate the degree to which a bird species uses a given habitat for foraging. In a recent study by Weathers and Nagy (1980) comparing doubly labeled water and time-budget estimates of daily energy expenditure, the potential sources of error in the time-budget method were attributed to the lack of the incorporation of the influence of solar radiation on metabolism of free-living birds.

Our studies emphasize the interactions between physiological demands and their behavioral and ecological consequences. Further, the interactions between behavior, physiology, and ecology suggest that ecological phenomena can be predicted accurately from laboratory studies dealing with the energetic efficiency of animals.

The interaction between behavior and physiology is even more important as one realizes that behavioral adjustment can occur rapidly and at less cost to the animal than most physiological adjustments, allowing the animal to get food, reproduce, and avoid becoming someone else's food at minimal cost.

DISCUSSION FOLLOWING DR. LUSTICK'S PRESENTATION

Question: Why don't gulls go in the shade?

Answer: For two reasons: (1) there is very little in the way of shade, and (2) with their large wingspan it would be difficult for them to take off from under thick brush in an emergency.

Question: Lots of birds have variations in plumage within a species, and it seems to me that you might be able to use your approach to predict differences between males and females where they have different breeding plumages. The question I'm really interested in is, In males that are polimorphic with respect to coloration, such as the European ruff, can you make some predictions concerning differences or limits on the behavior they would have?

Answer: Larry is smiling from ear to ear, because that is exactly what he is trying to do right now using the goldfinch, in which the male changes from bright yellow (which has a very high reflectance) in the summer to an olive green in the winter. We are doing that now comparing the difference in microhabitat between male goldfinches out in the open all the time and the female, who sits on the nest 97% of the time, has tremendous cover, and, of course, is dark in coloration.

Question: On the feather lipid issue, in many species, particularly marine species, birds have prominent orbital glands like harderian glands, and they also have specialized preen glands at the base of the tail. Many of the secretions themselves are pigmented. Have you looked at the possible role of absorbance-reflection and insulated properties as a function of preen gland secretions?

Answer: Not at all, mainly because most of our absorption-reflectance work must be done somewhere else. We could do things like that, but we haven't tried. When I first started all this, I thought color was probably the most important thing there was as far as thermal regulation goes. Now, after 16 years, it's nice if you are dark in a cold climate and white in a hot climate, but it's sort of like Bergmann's rule—within a species if you go north the animal gets larger, and it increases its insulation and loses less heat. That holds only in 33% of the animals looked at. The same thing is true of color. I don't know what percentage it holds in, but the animals have such a tremendous array of behaviors and can use the microclimate so well that they can overcome being the wrong color. So now I don't think color is as important as I used to. It's nice if you happen to be the right color.

Question: In your chickadee data you showed a decrease in body temperature with some fairly dramatic decreases in ambient temperature. I was wondering if they were in fact losing control at that point, or if one waited long enough, they would equilibrate at a lower body temperature. In other words, did your chickadees ever show adaptive hyperthermia?

Answer: We studied the energetics of both Carolina and black-capped two years ago. They can withstand 10° hypothermia. They can drop their body temperature to 30°. We never took a body temperature below 30° C; we were afraid of losing them. They will recover from a 30° C body temperature on their own. I would think that is how black-capped chickadees make it in the Arctic. Of course from our comparative study we can conclude that there really wasn't a physiological difference between Carolina and black-capped chickadees. But again, we studied them from Cincinnati and Akron, and we should have studied them from Alaska and Florida.

LITERATURE CITED

Bakken, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. J. Theoret. Biol. 60:337–84.

Blum, H. F. 1961. Does the melanin pigment of human skin have adaptive value? Quart. Rev. Biol. 36:50–63.

Burtt, E. H., Jr. (ed). 1978. The behavioral significance of color. Garland Press, New York. 456 pp.

Caccamise, D. F., and W. W. Weathers. 1977. Winter nest microclimate of monk parakeets. Wilson Bull. 89(2):346–49.

Calder, W. A. 1973. An estimate of the heat balance of a nesting hummingbird in a chilling climate. Comp. Biochem. Physiol. 46A:291–300.

Calder, W. A. 1974. The thermal and radiant environment of a winter hummingbird nest. Condor 76:268–73.

Calder, W. A. 1975. Factors in the energy budget of mountain hummingbirds. *In* D. M. Gates and R. B. Schmerl (eds.), Perspectives of biophysical ecology. Springer-Verlag, New York. 609 pp.

Calder, W. A., and King, J. R. 1974. Thermal and caloric relations in birds. *In* D. S. Farner and J. R. King (eds.), Avian biology, 4:259–413. Academic Press, New York.

Cartwright, B. W., and C. G. Harrold. 1925. An outline of the principles of the natural selective absorption of radiant energy. Auk 42:94–108.

Cena, K., and J. A. Clark. 1972. Effect of solar radiation on temperatures of working honeybees. Nature New Biology 236:222–23.

Chappell, M. A. 1980a. Thermal energetics of chicks of arctic-breeding shorebirds. Comp. Biochem. Physiol. 65(A):311–17.

Chappell, M. A. 1980b. Insulation, radiation, and convection in small arctic mammals. J. Mammal. 61(2):268–77.

Cole, L. C. 1943. Experiments on toleration of high temperatures in lizard with reference to adaptive coloration. Ecology 24:94–108.

Davis, L. B., and R. C. Birkebak. 1971. An analysis of energy transfer through fur, feathers, and other fibrous materials. University of Kentucky High Temp. and Thermal Rad. Lab., HTL-TR5.

DeJong, A. A. 1976. The influence of simulated solar radiation on the metabolic rate of white-crowned sparrows. Condor 78:174–79.

Digby, P. S. B. 1955. Factors affecting the temperature excess of insects in sunshine. J. Explr. Biol. 32:279–98.

Dolbeer, R. A., A. R. Stickley, S. B. White, and P. P. Woroneck. 1978. Agricultural impact of a winter population of blackbirds and starlings. Wilson Bull. 90(1):31–44.

Dudley, B. 1964. The effects of temperature and humidity upon certain morphometric and colour characters of desert locust (*Schistocere gregaria* Forkskol) reared under controlled conditions. Trans. Roy. Entol. Soc., London, 116:115–29.

Finch, V. A., and D. Western. 1977. Cattle colors in pastoral herds: natural selection or social preference? Ecology 58:1384–92.

Finch, V. A., R. Dmi'el, R. Boxman, A. Shkolnik, and C. R. Taylor. 1980. Why black goats in hot deserts? Effects of coat color on heat exchanges of wild and domestic goats. Physiol. Zool. 53(1):19–25.

Francis, W. J. 1976. Micrometerorology of a blackbird roost. J. Wildl. Manag. 40(1):132–36.

Frazier, A., and V. Nolan. 1959. Communal roosting by the eastern bluebird in winter. Bird-Band. 30:219–26.

Gessaman, J. A. 1973. Ecological energetics of homeotherms: a view compatible with ecological modeling. Monogr. Ser., vol. 20. Utah State University Press, Logan. 155 pp.

Graber, J. W., and R. R. Graber. 1979. Severe winter weather and bird populations in southern Illinois. Wilson Bull. 91(1):88–103.

Grubb, T. C., Jr. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodlot. Condor 77:175–182.

Grubb, T. C., Jr. 1977. Weather-dependent foraging behavior of birds wintering in a deciduous woodlot: horizontal adjustments. Condor 79:271–74.

Grubb, T. C., Jr. 1978. Weather-dependent foraging rates of wintering woodland birds. Auk 95:370–76.

Hamilton, W. J., II, and F. Heppner. 1967. Radiant solar energy and the function of black homeotherm pigmentation: an hypothesis. Science 155:196–97.

Harrington, E. L. 1926. Protective value of hair. J. Heredity 17:461.

Heppner, F. 1970. The metabolic significance of differential absorption of radiant energy by black and white birds. Condor 72:50–54.

Hill, L., and H. J. Taylor. 1933. Locusts in sunlight. Nature 132:276.

Hutchinson, J. C. D., and G. D. Brown. 1969. Penetrance of cattle coats by radiation. J. Appl. Physiol. 26:454.

Irving, L. 1956. The usefulness of Scholander's views on adaptive insulation of animals. Evolution 10:257–59.

Jogi, A. I. 1968. Mass death of swallows in Estonia at the end of August 1959. *In* Z. D. Spurin, Y. Y. Lusis, E. J. Taurins, and E. K. Vilka (eds.), Birds of the Baltic region: ecology and migrations, pp. 154–59. Israel Program for Scientific Translations.

Kelty, M. P. 1977. Interaction of physiology, behavior, and environment on the seasonal energetics of the starling, *Sturnus vulgaris*. Ph.D. thesis, Ohio State University, Columbus. 66 pp.

Kelty, M. P., and S. I. Lustick. 1977. Energetics of the starling (*Sturnus vulgaris*) in a pine woods. Ecology 58(5):1181–85.

Kendeigh, S. C. 1961. Energy of birds conserved by roosting in cavities. Wilson Bull. 73(2):140–47.

Kessler, F., M. L. Giltz, and H. E. Burtt. 1967. High mortality of a population of cowbirds wintering at Columbus, Ohio. Ohio J. Sci. 67(1):46–50.

Klauber, L. M. 1939. Studies of reptile life in the arid southwest. II: Speculations on protective coloration and protective reflectivity. Bull. Zool. Soc. San Diego 14:65–79.

Knorr, O. A. 1957. Communal roosting of the pygmy nuthatch. Condor 59:398.

Krog, J. 1955. Notes on temperature measurements indicative of special organization in arctic and subarctic plants for utilization of radiated energy from the sun. Physiologia Pl. 8:836–59.

Lustick, S. I. 1969. Bird energetics: effects of artifical radiation. Science 163:387–90.

Lustick, S. I., and J. Adam. 1977. Seasonal variation in the effects of wetting on the energetics and survival of starlings, *Sturnus vulgaris*. Comp. Biochem. Physiol. 56A: 173–77.

Lustick, S., B. Battersby, and M. Kelty. 1978. Behavioral thermoregulation: orientation toward the sun in herring gulls. Science 200:81–83.

Lustick, S., B. Battersby, and M. Kelty. 1979. Effects of insolation on juvenile herring gull energetics and behavior. Ecology 60(4):673–78.

Lustick, S., S. Talbot, and E. L. Fox. 1970. Absorption of radiant energy in redwinged blackbirds (*Agelaius phoeniceus*). Condor 72:471–73.

Marder, J. 1973. Body temperature regulation in the brown-necked raven (*Corvus corax ruficollis*) II. Thermal changes in the plumage of ravens exposed to solar radiations. Comp. Biochem. Physiol. 45(A):431–40.

Mayer, L. S., S. I. Lustick, and T. C. Grubb, Jr. 1979. Energetic control of behavior: foraging in Carolina chickadees. Comp. Biochem. Physiol. 63(A):577–79.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10:105–8.

Meanley, B. 1965. The roosting behavior of the red-winged blackbird in the southern United States. Wilson Bull. 77:217–28.

Moen, A. N. 1973. Wildlife ecology: an analytical approach. W. H. Freeman & Co., San Francisco. 458 pp.

Monteith, J. L. 1973. Principles of environmental physics. American Elsevier Publishing Co., New York. 241 pp.

Munzinger, J. S. 1974. A comparative study on the energetics of the black-capped and Carolina chickadees, *Parus atricapilles* and *carolinensis*. Ph.D. thesis, Ohio State University, Columbus.

Neal, C. M. 1976. Energy budget of the eastern chipmunk (*Tamias striatus*): convective heat loss. Comp. Biochem. Physiol. 54:157–60.

Neal, C. M., and S. I. Lustick. 1975. Energy budget of the eastern chipmunk (*Tamias striatus*): artificial radiation. Comp. Biochem. Physiol. 50(A):233–36.

Norris, K. S. 1967. Color adaptation in desert reptiles and its thermal relationships. *In* W. W. Milstead (ed.), Lizard ecology: a symposium, pp. 162–229. University of Missouri Press, Columbia.

Odum, E. P., and F. A. Pitelka. 1939. Storm mortality in a winter starling roost. Auk 56:451–55.

Oritsland, N. A. 1970. Energetic significance of absorption of solar radiation in polar homeotherms. *In* M. W. Holdgate (ed.), Antarctic ecology, 1:464–70. Academic Press, New York.

Pearson, O. P. 1977. The effect of substrate and of skin color on thermoregulation of a lizard. Comp. Biochem. Physiol. 58(A):353–58.

Porter, W. P., and D. M. Gates. 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39:227–44.

Reese, K. P., D. F. Balph, and M. H. Balph. 1980. Why do some black-billed magpies roost high on the side of a mountain? Abstracts, A.O.U. 98th Stated Meeting. Colorado State University, Fort Collins.

Riemerschmid, G., and J. S. Elder. 1945. The absorptivity for solar radiation of different coloured hairy coats of cattle. Onderstepoort J. of Vet. Sci. and Anim. Ind. 20(2):223–34.

Robertson, R. J., P. J. Weatherhead, F. J. S. Phelan, G. L. Holroyd, and N. Lester. 1978. On assessing the economic and ecological impact of winter blackbird flocks. J. Wildl. Manag. 42(1):53–60.

Robinson, D. E., G. S. Campbell, and J. R. King. 1976. An evaluation of heat exchange in small birds. J. comp. Physiol. 105:153–66.

Scholander, P. F. 1956. Climatic rules. Evolution 10:339–440.

Sellers, W. D. 1974. Physical climatology. University of Chicago Press, Chicago. 272 pp.

Skuldt, D. J., W. A. Beckman, J. W. Mitchell, and W. P. Porter. 1975. Conduction and radiation in artificial fur. *In* D. M. Gates and R. B. Schmerl (eds.), Perspectives of biophysical ecology, pp. 549–58. Springer-Verlag, New York. 609 pp.

Steen, J., and I. B. Steen. 1965. The importance of the legs in the thermoregulation of birds. Acta Physiol. Scand. 63:285–91.

Stewart, P. A. 1978. Weather-related mortality of blackbirds in a Kentucky roosting congregation. Wilson Bull. 90(4):655–56.

Veghte, J. H., and C. F. Herreid. 1965. Radiometric determination of feather insulation and metabolism of arctic birds. Physiol. Zool. 38:267–75.

Walsberg, G. E., G. S. Campbell, and J. R. King. 1978. Animal coat color and radiative heat gain: a re-evaluation. J. comp. Physiol. 126:211–22.

Walsberg, G. E., and J. R. King. 1980. The thermoregulatory significance of winter roost sites selected by robins in eastern Washington. Wilson Bull. 92:33–39.

Weathers, W. W., and K. A. Nagy. 1980. Simultaneous doubly labeled water ($^{3}\mathrm{H}\ \mathrm{H}\ ^{18}\mathrm{O}$) and time-budget estimates of daily energy expenditure in *Phainopepla nitens*. Auk 97:861–67.

Yom-Tov, Y., Y. A. Imber, and J. Otterman. 1977. Microclimate of winter roosts of starlings (*Sturnus vulgaris*). Ibis 119(3):366–68.

Index

Absorbance-reflection, 290
Acclimation, 214, 216
Acoustic beacons, 19, 22
Activating threshold, 224
Active escape behavior, 169, 171. *See also* Static escape behavior
Active foraging, 171, 173
Activity level, 32, 72–73, 76, 77
Adaptive radiation, 153
"Adaptive syndrome," 161
Adaptive zone, 158
Adaptive coloration, 266
Aerobic energy generation, 150, 180
Aerobic metabolism, 163, 166–67, 173, 177, 179–80
Aerobic power input, 172–73
Agalychnis callidryas, 172
Agelaius phoeniceus, 266, 276
Agamids, 155
Aggressive behavior, 91, 93, 107, 117, 118–21, 124–25, 133–34, 135, 171, 216
Alaskan gyre, 43–44, 46
Alburnus alburnus, 195
Alewives, 208–11, 215, 216
Alosa pseudoharengus. *See* Alewives
Alpha male fishes, 118–21, 124, 126, 128–29, 131, 133, 137; pupfish, 126, 133; trout, 121, 124
Alternate reproductive strategies, 90, 104–6
Amargosa, 126, 128–29, 131
Ameiva, 144–45, 162, 175
Amphisbaenians, 152–54
Anaerobic energy input, 167–68, 172, 180
Anaerobic metabolism, 142, 149–50, 165–66, 180
Anolis, 162, 165
Animal coloration, 266
Anurans, 151, 161, 166, 167–68, 171–73, 177, 181
Australian honeyeaters, 228
Averett, R. C., 33

Babine Lake, 30, 40–42, 49
Babine River, 30, 49, 59
Baboons, 67–88
Basiliscus, 157
Behavioral polymorphisms, 104–05
Behavioral thermoregulation, 189–90, 193–97, 199, 209, 211
Benefit/cost ratio, 93, 193
Bioenergetics, 134, 190, 196, 207; efficiency, 40; expectations, 189; hypothesis, 40, 208; optimization, 190, 199, 201, 205, 207, 212; approach, 211; model, 189, 196–97, 208–9, 211
Blackbird, redwinged, 90, 280, 283, 285
Blackpoll warblers, 7
Blue jay, 23
Bluegill sunfish, 108, 193, 197, 199, 202–3, 209, 214, 216; growth model, 198
Body size: and energy requirement, 150–53; and food habits, 155–57, 158–59; and metabolic rate, 32, 152, 173, 175; and temperature, 144–45
Bogert, C. M., 145
Breeding activities: and aggressive behavior, 89–111 passim, 124–26; and temperature, 215
Brett, J. R., 39, 40, 52–53, 207
British Columbia, 30, 43–44, 47. *See also* Babine Lake, Babine River
Brownheaded cowbird, 276, 283
Bufo, 171–73, 178–79
Burtt, E. H., Jr., 266
Buss, D. H., and O. M. Reed, 74–75

Caecilians, 152–53
Calder, W. A. III, 283
Caloric intake, 70, 118
Carnivores, 154–57, 159
Carolina chickadee, 266, 276, 286–88, 290
Catfish, white, 207
Caulton, M. S., 208
Centrarchid fishes, 203, 211
Chaoborus, 206
Chappell, M. A., 268
Ciscoes, 202, 205–7
Cnemidophorus, 126, 130, 143, 162–3, 165
Colyeonyx, 175
Color, 268–69, 274–75, 290: mimicry, 236; vision, 17; pattern, 267
Common grackle, 276, 283
Competition, 32, 106, 145, 153, 194, 207, 210–11, 214, 216
Conception, 68, 78–79
Convective cooling, 267
Convective heat loss, 275, 279
Conversion efficiency, 57, 142
Coregonus hoyi, 210
Coregonus artedii, 205
Corucia zebrata, 157
Corytophanes cristatus, 148
Cost benefit analyses, 190, 194, 196, 211: approaches, 211; function, 214; model, 190; rankings, 191
Cowbird, brownheaded. *See* Brown-headed cowbird
Cowles, R. B., and C. M. Bogert, 145
Cruising foragers, 161–63, 165
Current velocity, 118–20, 125, 128, 135

Dasypeltis, 148
DeAngelis, D. L., 195
Deciduous roosts, 277, 280–81, 285
Defensive behavior, 161, 166, 171
Desert goats, 268
Dietary habits, 154, 156–57
Dipsosaurus, 157, 163, 166
Dominance, 89, 122: hierarchy, 72, 91, 93, 117–18, 120, 122, 133; rank, 72
Dominant fishes, 119, 124, 126, 133–34, 137
Dominant males, 93, 96, 98–102, 105–7, 111, 124–25, 133

Ectotherms, 144–51, 153, 155, 159–60, 166, 173, 175–76, 182, 189, 193
Ectothermy, 142–44, 146, 148, 150, 155, 175, 182
Edwards, R. R. C., et al., 33–34
Elasmobranch fishes, 23
Elephant seals, northern, 89–111
Eleutherodactylus coqui, 171–72
Elliott, J. M., 37
Emlen, S. T., 4
Endothermy, 144, 145, 147–49, 150–53, 155, 159–61, 173, 176, 178, 182
Energy: and aggressive or holding behaviors, 117-38, 171–73; and animal coloration, 266–75; and body forms, 150–53; and diet, 153–61, 189–216; and ectothermy, 150; external sources of, 143–49; and food production, 162–63, 223–59, 286–89; and growth, 43–49, 57–58; and infant care, 71–81; and juveniles, 173–82; and metabolic rate, 32–36, 153–60; and microclimate, 275–82; and migration, 40–42, 49–53; and partitioning of input, 165–73; and predation, 36, 78, 161–65, 168–71; and reproduction, 49–50, 67–86, 89–111; and thermoregulation, 145–49, 265–91; yolk sac as, 38
Energy balance, 223–59 passim, 286
Energy budgets, 31–33, 57–58, 148, 166, 213, 277, 279, 283–86
Energy flow, 142, 159–60, 182
Epilimnion, 39–40
Engraulis mordax, 195
Environment: heterogeneous, 201; heterothermal, 189–90, 195–96, 201, 212
Euphausids, 45–46, 51, 53
European ruff, 290
Eutoxeres aquila, 227
Excretion, 31–32, 37, 58

Feathers: erection of, 267, 275
Feeding, 75–76, 209; behavior, 196; competition, 71; ecology, 205; efficiency, 72, 77, 80; forays, 207; nectarivore, 226, 231, 238; patterns, 247; rate, 34–35, 122, 134; sites, 1; time, 72, 76
Fence lizard, 148
Fingerlings, 35, 39, 57
Fitness, 190, 194, 196, 211–12, 223–24, 228
Food, 189, 200; acquisition, 80; availability, 84; conversion efficiency, 39, 57; habits, 154–55, 159; intake rate, 192; patches, 197–99; resources, 154, 160
Foragers, types of, 161
Foraging, 18, 76, 161–65, 171, 173, 177, 180, 190–91, 193–94, 196–97, 211–12, 225; behaviors, 189, 196, 202, 214, 223–224; bout, 226, 239; paths, 194; rate, 288; sequence, 228; strategies, 266, 286
French, R., et al., 30, 51

Frogs, green, 180–81
Fry, 33, 36, 38–39, 50, 57
Fur seals, Alaskan, 90

Gadgil, M., and W. H. Bossert, 104
Gadus morhua, 33
Garter snakes, 175, 177
Gasterosteus aculeatus, 194
Gekkonids, 155
Gessaman, J. A., 277, 283
Gestation, 67, 69–70
Golden plover, 23
Goldfinch, 290
Gorillas, 68–69
Graber, J. W., and R. R. Graber, 275
Griffin, D. R., 22
Grooming, 71, 77, 79–80
Groot, C. et al., 40
Groves, T. D. D., 36
Growth, 32, 34–35, 39, 40, 43, 45, 47, 57, 190, 192, 195–97, 199–202, 205, 207–09, 211: model, 40, 43; growth optimal, 190; growth rates, 34–35, 47–48, 51, 53, 160, 189, 195, 197–99, 201, 207, 209, 211–12, 216; rate curve's, 212; metabolism tank, 30, 35
Grubb, T. C., Jr., 275, 288–289

Habitats, 144–45, 160, 162, 165, 192: open, 144–45; partitioning, 145, 182; patch, 190–92; preferences, 215; stressful, 145; utilization, 144–45
Harrington, E. L., 267
Hausfater, G., 68
Hawk, sharp-shinned, 255
Heat: balance, 267; exchange, 146; flow, 269; loss, 153; stress, 271; transfer, 277
Herbivores, 154–57, 159, 225
Herring gull, 266, 268, 270, 276
Holding, 118–22, 129–30, 132, 135, 138: behavior, 122, 128; positions, 118, 119–20, 124, 135; territories, 133
Holling, C. S., 224
Holopedium, 206
Homing, 7; flights, 1; pigeons, 7, 9, 17–18, 20, 23
Honey bees, 18
Hubbard Brook Ecosystem, 142
Huey, R. B., and M. Slatkin, 190
Hummingbirds, 226–27, 230, 241, 244, 280, 283: broad-tailed, 238; ruby-throated, 254
Hutchinson, J. C. D., and G. D. Brown, 267
Hyla crucifer, 172
Hyperolius viridiflavus, 172
Hypothermia, 291

Ictalurids, 202
Ictalurus nebulosus, 207
Idler, D. R., and W. A. Clemens, 49
Iguana, 156, 163: iguanidae, 165; iguanids, 155; iguanine lizards, 157
Indigo birds, 90
Infant care, costs of, 68–86
Infrasound, 19–20, 22
Ingestion, 32, 37, 155, 224
Interbirth intervals, 69–70, 78–79, 81
Interference competition, 211, 216
Interspecific competition, 144, 182
Intraspecific competition, 89, 171–73
Ipomopsis, 238, 240, 243–44
Irving, L., 274–75
Ivlev, V. S., 195

Jarvaid, M. Y., and J. M. Anderson, 209, 218
Jogi, A. I., 275
Juveniles, 39–40, 69, 85, 129–31

Keeton, W. T., 1, 7, 8, 9, 11–12, 22
Kelty, M. P., 277, 281
Kelty, M. P., and S. I. Lustick, 277
Kitchell, J. F., et al., 196–97
Klauberina, 162
Klein, D., 77
Kodric-Brown, A., 125, 131
Kramer, G., 7, 14
Krog, J., 267
Kromrey, G., 203–5

Lactation, 71–72, 76–77, 79, 82, 149, 165–66, 168, 171: increment, 73; period, 73, 77
Lactic acid, 165, 167–68, 177
Larus argentatus, 266, 276
LeBoeuf, B. J., 90, 104, 109
Lee, R. B., 77
Leiocephalus schreibersi, 162
Leonotis, 238, 243–44, 254
Lepomis. See Bluegill sunfish
Leptodora, 206
Low-protein diet, 75
Lustick, S. I., 268

Macaques, 68
Mackerel shark, 36
McLaren, I. A., 39, 207
McNab, B. K., 160

Magnetite: in pigeons, 12
Magnets: and pigeons, 12, 15
Marder, J., 267
Marmosets, 85
Marmots, 90
Martins, 275
Maternal care among baboons: costs of, 69–81; hypoglycemia, 83; lactation, 73; mortality, 80–81; nutritional strain, 77; weight maintenance, 73
Matthews, G. V. T., 9
Mayr, E., 255, 274
Menstrual cycle: in baboons, 69–70
Merriman, D., and L. M. Thorpe, 207
Metabolism, 31–33, 36, 40, 70, 154, 268; capacities, 172–73; costs, 117–18, 125, 128–29, 132–33, 162, 166, 197, 199, 207–8; demands, 172, 175; efficiency, 46, nitrogen, 37; processes, 58, 146
Metabolic rates, 32–35, 37, 40, 42, 48, 51, 53, 118–19, 132, 136, 151–52, 154–55, 157–60, 162, 269, 277, 283, 286–88; active, 31, 33–35, 49, 192; basal, 35, 73, 153–54, 159; feeding, 33–36, 42; high, 160; hourly, 40; resting, 32, 124, 130, 144, 146–47, 149–50, 154, 162–63, 165–66, 175; standard rate, 33–34, 59, 286–87;
Microclimates, 288; heat exchange, 227
Microhabitats, 144–45, 266; selection, 286
Migration/migratory, 7, 215; animals, 1; birds, 19; cycle, 4; flights, 1; on- and off-shore, 208, 213, routes, 7; season, 4; vertical, 39, 45–46, 57, 207–8
Millar, J. S., 151
Mink, 168
Mirounga angustirostris, 90
Moen, A. N., 280
Molothrus ater, 266, 276
Monkeys, vervet, 77
Monteith, J. L., 267, 280
Myiopsitta monachus, 276
Myotis lucifugus, 40
Mysis relicta, 211

Naismith, D. J. and Ritchie, C. D., 76, 88
Natural selection, 111, 197, 212, 223
Navigational systems. *See* Orientation
Nectar, 18, 224, 228, 236
Nectarivores, 154, 223–59
Nerodia sipedon, 148
Nicolson, N., 70, 75, 80
Notropis hudsonius. *See* Shiner, spottail
Nuthatch, 276
Nyctea scandiaca, 277

O'Brien, W. J., et al., 193
Odum, E. P., and F. A. Pitelka, 275
Oncorhynchus, 29, 30, 192, 205, 207
Optimal foraging, 189–91, 196–97, 199, 201, 211, 214; strategy, 195, 214; theory, 189, 192–96, 211
Orientation, 4, 8, 14, 21, 215, 228, 268–69, 273–74; behavior, 17, mechanisms, 12; strategies, 9; toward the sun, 271
Oritsland, N. A., 267
Osmerus mordax, 209
Owl, snowy, 283
Oxygen consumption, 118–19, 125, 149, 155, 171

Packer, C. 75,
Papi, F., et al., 12
Papio cynocephalus, 68
Parus carolinensis, 266
Passer domesticus, 276
Passeriformes, 4
Patch(es), 190–93, 200, 231, 245, 254: choice, 191, 194, 197, 211; selection, 239; types, 191; of food, 213
Pedioecetes phasianellus, 280
Perch, yellow, 210
Percopsis omiscomaycus, 209
Perisoreus canadensis pacificus, 280
Phaethornis superciliosus, 230
Photoperiod, 4, 214, 216
Phrynosoma m'calli, 158
Physignathus, 157
Physiological conditions, 226: costs and benefits, 192; rates, 192; state, 226
Pica hudsonia, 276
Pine roost, 278, 281, 283
Pinus, 285
Plethodon cinereus, 142, 148
Pomoxis nigromaculatus, 203
Pontoporeia hoyi, 211
Post, D. G., 68
Postpartum amenorrhea, 70, 79–80
Postural adjustment, 268–69, 271, 273–75
Pough, F. H., 150–53, 155–58, 163, 175–78, 180–81, 186
Prairie chickens, 90
Predation, 145, 194, 212, 216, 223; on hummingbirds, 255
Predator, 78, 86, 225; avoidance of, 129, 169, detection of, 78; protection from, 71; risk, 194
Preying mantis, 224
Pseudotsuga menziesii, 285
Pupfish, 117, 124–26, 128–31, 133–37

Q_{10}, 33, 147, 180
Quiscalus quiscula, 266, 276

Radiative heating, 267, 273
Rana, 171–72, 180
Reindeer, 90
Reproduction/reproductive, 68, 129, 190: behavior, 107, 125; biology, 171; effort, 67–68, 79–80, 100, 102, 104, 107–08; maturation, 75; parameters, 68; phases, 69; potentials, 160; senescence, 70; status, 77; strategies, 81; success, 78, 80–81, 90, 92, 96, 100, 104–05, 107, 125, 223; territory, 133; value, 81
Resting, 75, 79–80: rates, 149, 162; time, 77
Reynolds, W. W., and M. E. Casterlin, 209
Ricker, W. E., 47
Roadrunner, 255
Robinson, D. E., et al., 277
Salmo, 37, 117–18, 120, 208. *See also* Salmon
Salmon: Atlantic, 212–13; Babine sockeye, 49, 53, 59; Bristol Bay sockeye, 51; chinook, 36; coho, 33, 202, 205–06, 207; growth model of, 34; Pacific, 30, 36, 58; sockeye, 29–59. *See also Salmo*
Satellite males (pupfish), 124, 126, 129–33
Sauer, E. G. F., 4
Saunders, R. L., 33
Sauromalus obesus, 148, 157
Sceloporus, 148, 162
Schlichte, H. J., 9
Schmidt-Koenig, K., 9
Scholander, P. F., 274–75
Seals, Weddell, 90
Selasphorus, 238, 244
Shiner, spottail, 209, 210
Sialia sialis, 276
Sicklebill, 227
Sitta canadensis. See Nuthatch
Skinks, 155, 157
Skuldt, D. J., et al., 273–74
Smelt, rainbow, 209–10
Smolts, 35, 39–42, 50, 53, 57
Snakes, water, 148
Snow, C. C., 75
Social: grooming interactions, 71, 75–76; groups, 67; reproductive hierarchy, 133; pressures, 71; time, 77; dominance, 216
Sockeye. *See* Salmon, sockeye
Solar radiation, 267–70, 273, 288
Soltz, D., 124, 131
Sparrows, 283
Squid, 37, 46, 51, 53
Squirrel, ground, 90
Starlings, 266, 276–77, 283, 285
Stasko, A. B., 51
Static escape behavior, 169, 171, 173
Stewart, D. J., 276
Stickleback, 194
Stress, 70, 78, 84
Sturnus vulgaris, 266, 276
Subordinate fishes, 118–19, 121, 124, 133, 134, 137–38
Subordinate elephant seal males, 90, 100–102, 105
Sunbirds, 227, 230, 241, 243
Swimming speed, 118–22, 125–26, 128, 131, 135–36, 192

Tail-beat frequency, 118–19, 121
Tamarins, 85
Teiid lizards, 162–63, 165
Temperature: acclimation to, 214; and activity, 32, 146–48, 155, 163, 165; ambient, 153; body, 46, 144–47, 152, 155, 160, 162, 163, 165–66, 175, 180, 265, 269; environmental, 46; and equilibrium, 144–45; gradients in, 145; and hypothalamic set point, 216; lethal, 145; lower critical, 268–69; optimal, 197, 208; preferred, 192, 194, 198–99, 202, 203–5, 207–9, 211, 213–15; regulation, 163; skin, 273; sky, 280; surface, 270, 280, 283
Territory/territorial, 1, 117, 119, 124–26, 128–33, 228–30; behavior, 117, 119, 124, 126, 133; birds, 257; defense, 118, 126, 128–29, 132–33; fish, 133; maintenance, 132, 137; males, 125, 130, 131; size, 130
Tetrapods, 144, 151, 160
Thamnophis sirtalis, 175
Thermal: balance, 268, 273; benefits, 288; conductance, 273, 277; energy exchange, 175, 273; environments, 265; equilibrium, 283; generalists, 194; habitats, 189, 191–92; homeostasis, 266; micro-environments, 190; neutrality, 269, 287; niche, 180, 205, 207; optimum, 197; preference, 195, 199, 202, 206–7; range, 209; stratification, 39–40; stress, 269, 274; tolerance, 33; patches, 192
Thermocline, 39, 44, 46–47
Thermoneutral zones, 150, 155
Thermoregulation, 144–46, 165, 190, 194–96, 211, 266, 40
Thermoregulatory, 182: behavior, 144–46, 196; costs, 226–27; mechanism, 146, 195

Thrush, Swainson's, 23
Tilapia, 208, 213
Tiliqua, 156
Time budgets, 68, 71, 75–76, 83, 289
Titmice, 276
Tortoises (*Testudinidae*), 154
Trachydosaurus, 156
Trout, 117–18, 122, 124, 133, 135–37, 208; brook, 108; brown, 37, 120, 213; dominant, 133, perch, 209; rainbow, 118–20. *See also Salmo*
Tuatara, 154
Tupinambis, 156
Turdus migratorius, 277

Ungulates, 159
Uromastyx, 156–57, 163
Uta stansburiana, 143

VO_2, 135, 137
Varanus, 156
Veghte, J. H., and C. F. Herreid, 280
Verticils, 238–39, 244

Walcott, C., 9
Waldvogel, J. A., 13–14
Walsberg, G. E., and J. R. King, 277
Walsberg, G. E., et al., 267
Warblers, 4
Ware, D. M., 195
Weaning, 77, 80, 82, 84
Weathers, W. W., and K. A. Nagy, 289
Werner, E. E., and D. J. Hall, 193, 211
Williams, G. C., 104
Wind velocity, 270–71, 273, 276–78, 280–81, 286–88
Woodpeckers, 276

Xantusiidae, 160

Zonotrichia leucophrys gambelii, 277
Zooplankton, 39, 205

(Continued from front flap)

Wayne P. Aspey is assistant professor of zoology and coordinator of general biology at Ohio State University. Sheldon I. Lustick is professor of zoology and director of the Environmental Biology Graduate Program at Ohio State.

Hummingbird illustration by David Dennis

Book and jacket design by Harold M. Stevens

Ohio State University Biosciences Colloquia

No. 1: Genetics and Biogenesis of Mitochondria and Chloroplasts, *edited by C. William Birky, Jr., Philip S. Perlman, and Thomas J. Byers* $15.00

No. 2: Regulatory Biology, *edited by James C. Copeland and George A. Marzluf* $20.00

No. 4: Plant Cell and Tissue Culture: Principles and Applications, *edited by W. R. Sharp. P. O. Larsen, E. F. Paddock, and V. Raghavan* $37.50

No. 5: Cellular Interactions in Symbiosis and Parasitism, *edited by Clayton B. Cook, Peter W. Pappas, and Emanuel D. Rudolph* $25.00

Ohio State University Press
2070 Neil Avenue
Columbus, Ohio 43210