MIGRATION: MECHANISMS AND ADAPTIVE SIGNIFICANCE

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COVER PHOTOGRAPH

A group of northern shovelers (Anas clypeata) flies north along Mustang Island, Texas Gulf beach shoreline, 3 May 1983. Thousands of ducks, herons and shorebirds fly north along the coast during peak spring migration periods at the end of April and early May. Several striped mullet (Mugil cephalus) can be seen in the surf zone, where they feed throughout much of the year.

Photograph taken with a Nikon F3 and Nikon 600 mm f5.6 lens on Ektachrome 400 at 1/2000 sec, f8. [©] 1984, **A.F. Amos.** Reproduced by permission.

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EDITOR'S NOTE

This monographic volume on migration is being offered by the University of Texas at Austin as part of its Centennial Celebration.

The symposium and resulting proceedings were organized and prepared under the aegis of Dr. Mary Ann Rankin and her committee, Drs. David Checkley, John Cullen, Christopher Kitting and Peter Thomas.

The *Contributions in Marine Science* considers these papers to be a significant contribution of academic value.

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PREFACE

Organization of the Symposium

This volume represents the proceedings of a symposium held 30 October to 2 November 1983 at The University of Texas Marine Science Institute at Port Aransas, Texas. The meeting was held as a part of the centennial celebration of The University of Texas. Its purpose was twofold: to celebrate the founding of the primary research university in the great state of Texas by bringing together scientists from around the world to discuss a topic of significant general interest, and to acquaint the general scientific community with the facilities of our Marine Science Institute.

Preparation of This Volume

Manuscripts included in this volume were submitted at the time of the symposium or within ca. 2 months afterwards, were reviewed by at least two outside reviewers, and were revised according to reviewers comments. Several submitted manuscripts were not accepted after review. The symposium was organized by Drs. David Checkley, John Cullen, Christopher Kitting and Peter Thomas of the Marine Science Institute and myself in collaboration with seven convenors: Drs. Martin Angel, Hugh Dingle, Sidney Gauthreaux Jr., Ivan Heaney, William Herrnkind, William Leggett, and William Z. Lidicker Jr. The convenors each issued invitations to the invited speakers for their respective sessions, oversaw the reviewing of the proceedings manuscripts, and wrote introductions to each of the chapters in this volume as well as contributing papers of their own. Neither the symposium itself nor this volume would have been possible without their help. On behalf of the Symposium Organization Committee and The University of Texas I take this opportunity to express my deep appreciation for their efforts.

Each member of the Symposium Organization Committee contributed to the editorial and review process of at least one chapter; John Cullen co-edited the chapter on phytoplankton, David Checkley the chapter on zooplankton (these two chapters have been combined as one in this volume); Christopher Kitting co-edited the chapter on benthic invertebrates and Peter Thomas, the chapter on fish. Others who have contributed substantially to the preparation of this volume include Mr. Christopher Thompson who helped to edit the avian papers, Ms. Robin Perkins who did much of the computer work, and Mr. Boyd Merworth and Mrs. Leslie Kjellstrand who assisted us in learning and using the Unix text processing system and the phototypesetter at The University of Texas. I also wish to thank the editorial staff of the journal, *Contributions in Marine Science*, Mrs. Ruth Grundy, Mrs. Rebecca West and Dr.

Donald Wohlschlag, Editor in Chief, who were immensely helpful in the copyediti

One of the reasons the convenors and Symposium Organization Committee decided to publish this volume as a supplement to the journal, *Contributions in Marine Science*, which is published at The University of Texas Marine Science Institute, was to draw attention to the unique and excellent opportunities for research that exist at the Institute. Thus as a part of the preface to this volume, I include a brief description of the Institute and the Aransas area.

The Marine Science Institute and Its Environment

Within easy reach of the University of Texas Marine Science Institute are diverse marine and estuarine environments of interest to scientists in many areas of research. These include the open Gulf of Mexico beyond the shelf-slope break, shallow waters of the continental shelf, bays, lagunas, wind-tidal flats and fresh-to brackish-water marshes. The institute is near both the Aransas Wildlife Refuge and the Padre Island National Seashore. The area is on the major north-south flyway for many avian migrants and the monarch butterfly and is the overwintering ground for some avian species, most notably the whooping crane.

The Institute is located about 40 miles northeast of Corpus Christi, Texas on the northern end of Mustang Island, a subtropical barrier island between Corpus Christi Bay and the western Gulf of Mexico (27°50'N and 97°03'W). The climate is classified as dry subhumid with an average annual rainfall of 72 mm (28.5 inches) compared to Port Arthur's 141 mm (55.4 inches) to the north and Port Isabel's 65 mm (25.8 inches) to the south. Greatest yearly rainfall was 122 mm (48.2 inches in 1888 and least was 14 mm (5.4 inches) in 1917. Snow is a rare event. Average annual temperature (measured at nearby Corpus Christi) is 22°C with extremes seldom reaching 38°C or falling below 0°C on the coast.

The laboratory provides easy access to the rich and varied south Texas marine environments. The open Gulf of Mexico seaward of the barrier islands and bay or estuarine environments found inland of the islands are two distinctly different marine ecosystems which investigators at Port Aransas may utilize. Wide ranges of temperature, salinity and turbidity characterize the waters of the area both seasonally and geographically; consequently these waters support a diverse assemblage of plants and animals.

The Gulf of Mexico—The soft bottom of the Gulf along the continental shelf supports a variety of organisms. Off Port Aransas the shelf is broad (average width 88.5 km) and gently sloping (2.3 m/km) with sediments grading from fine sand inshore to silt and clay along the middle and outer shelf. A short 20-min trawl in the shallow, sandy inshore areas will reveal large blue crabs (*Callinectes sapidus*), several species of shrimp (*Penaeus duorarum*, *Trachypenaeus constrictus*, and *Xiphopenaeus kroyeri*), sea pansies (*Renilla mulleri*) and numerous other invertebrates. Further offshore (water depth ca. 45 m) one typically finds deepsea starfish (*Tethyaster vestitus*, *Astropecten cingulatus*), rock shrimp (*Sicyonia*) stimpsoni), frogcrabs (Raniaoides louisianensis) black sea bass (Serranus atrobranchus), batfish (Ogocephalus sp.) and frogfish (Antennariidae).

The *open waters* of the Gulf of Mexico off the southern Texas coast are of three types: (1) the highly productive inshore zone dominated by input from Texas rivers, (2) an offshore zone which receives discharge from the Mississippi River and (3) a zone of transition between the other two. Inshore phytoplankton productivity and zooplankton abundance are correlated with peaks of nutrient input from rivers which occur each spring and fall. During these peak periods, plankton biomass and density are extremely high, many times greater than in offshore waters. Water temperature, salinity, and turbidity vary seasonally inshore but are relatively constant in offshore areas. Bottom waters in all three zones are usually turbid and exhibit high phytoplankton densities.

Sargassum weed and the blue-green alga, Trichodesmium are the most conspicuous plants in these waters. The Portuguese man-of-war (Physalia physalia), the purple storm shell, (Janthina janthina), and the sailor-by-the-wind (Velella velella) are common surface floaters. Flying fish (Exocoetidae) and the Atlantic needle fish (Strongylura marina) are frequently encountered, as are sailfish (Istiophorus platypterus), bonita (Euthynnus alletteratus), kingfish (Scomberomorus cuvalla), Gulf menhaden (Brevoortia patronus) rough scad (Trachurus lathami), and pinfish (Lagodon rhomboides). Inshore bottom dwellers include the bighead sea robin (Prionotus tribulus), the Atlantic threadfin (Polydactylus octonemus), and the southern kingfish (Menticirrhus americanus). Species which only occur offshore include the Mexican sea robin (Prionotus paralatus), the wenchman (Pristoipomoides aguilonaris) and the squid Loligo pealii, which lives near the bottom during the day and feeds on the surface at night.

The Gulf *hard bottom* is the least common of the four Gulf habitats. It includes some natural rock reefs, offshore petroleum production platforms, and man-made rock jetties. The natural rock reefs are primarily in deep waters, 3 miles or more offshore, some occurring below the normal penetration of light. The steel legs of the petroleum platforms, on the other hand, extend from the surface of the water to the bottom and provide unique opportunities for the colonization of sessile marine plants and animals in the photic zone. Some of these develop communities characteristic of tropical reefs. Inshore "hard bottom" habitat, such as the granite rock jetties that line Aransas Pass, in contrast, is inhabited by organisms that can withstand great diversity in temperature and salinity. The jetty community below the water line is composed of tunicates, anemones, soft corals and macroalgae, while above the water line it is made up of organisms adapted for extended periods of exposure to air including numerous mollusks, barnacles and some crustaceans.

Bays and Estuaries—All Texas bays except the Laguna Madre are positive estuaries in which river discharge is sufficient to lower upstream salinities. In the Laguna Madre located off the coast of semi-arid land in extreme South Texas, the lack of rainfall or other fresh water input results in salinities which periodically rise well above salt concentrations in the adjacent Gulf of Mexico. The estuaries are rich with diverse marine habitats including, *Spartina* marshes, mangrove swamps, seagy beds, oyster reefs, wind tidal flats and open bays.

Open bay waters (areas in the bay where the bottom is not covered by se. beds or oyster reefs) are common in Corpus Christi, Nueces, Aransas, and Copano Bays. The temperature and salinities in these waters vary depending on the amount of stream discharge and the season. The average water depth is 2 meters but light penetration is restricted due to persistant high winds that keep muddy bottom sediments suspended and thus prevent the establishment of seagrass beds in these areas.

The nutrient-rich waters of the open bay support large numbers of diatoms (*Rhizoslenia*, Asterionella, and Cosinodiscus) in the winter and dinoflagellates in the summer which are prey for bay zooplankton (*Acartia tonsa*, Calanus, and barnacle nauplii). The larvae of many of the commercially important shellfish and finfish feed, in turn, on the rich zooplankton fauna as do Coelenterates such as the cabbagehead jellyfish (Stomolophus meleagris), the moon jellyfish (Aurelia aurita), and the Ctenophore (Beroe ovata) which are abundant in the spring and summer. The squid Lolliguncula and various fish species including the mullet (Mugil cephalus), bay anchovy (Anchoa mitchelli), and the Gulf menhaden (Brevoortia patronus) may also be found feeding in open bay waters.

The open bay bottom sediments are mud, sand or a mud/sand mixture. The predominant invertebrate species in this habitat are burrowing polychaete worms (*Mediomastus californiensis* and *Streblospio benedicti*), infaunal bivalves (*Mulinnia lateralis*, *Abra aequalis*, and *Lyonsia hyalina*) and the hemichordate *Balanoglossus* sp. Three species of *Penaeus* shrimp frequent open bay bottoms in the spring and summer. These shrimp species along with blue crabs and bottom-dwelling fish such as the southern flounder, *Paralichthys lethostigma*, croaker, *Micropogonias undulatus* and the black drum, *Pogonias cromis* are caught by small bay shrimp boats that work these waters in the warmer months.

In the shallower portions of the bays, where the water is usually less turbid, extensive *seagrass beds* occur. The largest beds are found in the Laguna Madre but smaller stands also occur in Aransas, Redfish and Corpus Christi Bays. Seagrass species found in Texas bays include turtlegrass, (*Thalassia testudium*), widgeon grass (*Ruppia maritima*), shoal grass (*Halodule wrightii*), manatee grass (*Syringodium filiforme*), and clover grass (*Halophila engelmanni*). This habitat is extremely productive. It is an important source of food for detritivores in the seagrass-based food web and provides food, shelter, and a place for attachment for many species of plants and animals. Shoalgrass is the principal food item of the redhead and pintail duck and supplements the diet of the lesser scaup in the Laguna Madre. Epiphytic micoralgae, diatoms, and serpulid polychaetes which attach to the seagrass blades, are food for small gastropod molluscs (*Bittium varium*, *Anachis avara semiplacata*) and small penaeid shrimp which, along with juvenile red drum (*Sciaenops ocellatus*) and croaker (*Micropogonias undulatus*) use the seagrass beds for refuge from predators.

In areas where the salinity is between 10-30% and plankton are abundant, oyster reefs develop built up by countless Crassostrea virginica (American oyster) individuals, living and dead. The reefs are usually formed perpendicular to the predominant current and along its edge where current-borne food (phytoplankton) is most available. Such reefs are important as attachment points for sedentary animals such as the hook mussel (Isachadium recurvum) the anemone (Aiptasiomorpha texaensis) and the slipper shell limpet (Crepidula fornicata). The reefs also provide food and shelter for numerous motile vertebrate and invertebrate species regarded as oyster pests, such as the blister worm (Polydora websteri), the boring sponge (Cliona celata), the oyster paddock (Diplyothyra smythii), and the oyster drill (Thais haemostoma). Small stone crabs (Menippe mercenaria) seek refuge between the cracks and crevices formed by the oysters growing together while adult crabs dig burrows at the base of the reef. The skillet fish (Gobiosox robustum) clings to the reef with a sucker that is formed jointly from the underside of the belly, pectoral and ventral fins.

Communities of black mangrove (Avicenna germinans), occur in the bays and estuaries along the waters edge or other areas subject to tidal inundation. In the three major passes south of Galveston, Pass Cavallo, Aransas Pass, and Brazos Santiago Pass, these plants are found in dense enough concentrations to be called *mangrove swamps*. The second largest of these swamps on the Texas coast covers 600 hectares on Harbor Island, a low barrier island located at the confluence of Aransas Pass, Lydia Ann Channel, Aransas Channel and Corpus Christi Channel. The swamp covers the majority of the land area and lines the numerous tidal channels that dissect the island. The margins of these channels are shared by *Spartina*.

Mangrove swamps are typically extremely rich in species diversity. Striped mullet (*Mugil cephalus*), red drum (*Sciaenops ocellatus*), spotted sea trout (*Cynoscion nebulosus*) and the blue crab (*Callinectes sapidus*) use this habitat as a nursery area and feeding ground. Wading birds like the least bittern (*Ixobrychus exilis*), the black crowned night heron (*Nycticorax nictiorax*), and the clapper rail (*Rallus longirostris*) hunt small fish and fiddler crabs (*Uca* sp.) among the tangled roots of the mangrove.

The major emergent aquatic vegetation along the shallow margin of South Texas bays (except the hypersaline Laguna Madre) is smooth cordgrass (*Spartina alterniflora*). This species attains its maximum growth midway between high and low tide levels and like the mangrove, is an important contributor of nutrients from upland sources to the coastal food web. Most of the animals living in the *Spartina marsh* habitat depend on the living plant as refuge and not as food.

The marsh periwinkle (*Littorina irrorata*) feeds on plant matter and detritus in the muddy bottom around the base of the *Spartina*. This small snail climbs up the grass stalk to avoid the rising water at high tide and then descends to the sediment surface to feed as the tide recedes. Fiddler crabs (*Uca* spp.) also feed on plant material and detritus exposed during the low tide and use the *Spartina* as a refuge from predators. The ribbed mussel (*Geukensia demissa granosissima*), which anchors itself in the sediment at the base of the *Spartina*, and the polychaete *Laeonereis*

cluveri are common subtidal invertebrates in this habitat. Sesarma crabs, which feed on the oldest outer leaves of the Spartina and any fiddler crabs it can catch, and a pulmonate mollusc (Melampus bidentatus) that feeds on diatoms and other algae as well as on Spartina and decayed animal matter are two species which actually consume the cordgrass.

Large portions of the south Texas bay shorelines are classified as wind tidal flats. This broad, level habitat covers hundreds of square miles of shoreline on the leeward side of the Laguna Madre. Only during extreme high tides from storms or periods when the winds blow water onto these flats is there sufficient moisture to maintain a marine ecosystem. Most of the time the flats are dry and exposed to constant winds, high temperature, and hypersalinity, and are therefore not suitable for the establishment of typical salt marsh plants. Only the hardiest species such as the filamentous green algae, Lyngbya sp. can tolerate the extremes of temperature, salinity, and periodic flooding and dessication. This microscopic alga forms a sheetlike, homogeneous, leathery mat over the surface of the tidal flat. The mat, in turn provides food and shelter for microinvertebrates (protozoans, nematodes, and harpacticoid copepods) and a variety of salt tolerant insects such as Tachys pallidus and Diplochaetus lecontei. When the flats are flooded, small fish (Cyprinodon wariegatus and Fundulus spp.) feed on the mat and the insects that have been trapped by the rising water. During this period shorebirds also come to the flats to feed on these small fish and insects. When the waters recede, the fish that have survived the bird predaton return to the Laguna Madre.

The Facilities

MSI includes 82 acres of ocean front land and 100,000 square feet of laboratory space, a 14,000 square foot physical plant, a four-acre boat basin, 17 apartments, 16 dormitory rooms and a mess hall. The Institute operates a variety of research vessels including the 85-ft LONGHORN, the 57-foot KATY, and a half dozen smaller boats for bay work. The laboratory includes both a scientific staff and a physical plant support staff; facilities are available for visiting scientists and students year-round. Inquiries regarding short- or long-term accommodations should be addressed to: Dr. Robert Jones, Director; The University of Texas Marine Science Institute; Port Aransas, Texas 78373, U.S.A.

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INTRODUCTION

The amazing feats of orientation, homing, and distance that some migrants display have awed human observers for centuries and still present exciting challenges in research. Migration is a major factor in the life history of countless organisms and draws the interest of ecologists, physiologists, geneticists, behaviorists, evolutionary biologists, and theoreticians. This symposium and its proceedings volume were organized in the spirit of this general interest. The papers in this volume are grouped along taxonomic lines and reflect the organization of the symposium. Contributions include both general reviews and research reports. In addressing the topic of migration widely and in the context of a symposium, we have not been able to cover all aspects of research in migration/dispersal in each group, but we have presented a variety of approaches and summaries of results that we feel represents current thought in the area and suggests fruitful areas for future research. Readers are encouraged to forage across chapters for work that addresses similar questions in different groups and to discern general principles, parallels, or differences for themselves.

In spite of, or perhaps because of the enduring and widespread interest that migration has elicited, there exists a history of disagreement concerning what it actually is. To the person studying movements of birds or mammals, migration usually means long-distance "round-trip" movement from a summer or wet-season range to a winter or dry-season range, while movement that takes the organism permanently away from its natal area is dispersal. Many horizontal aquatic migrations involve a return of individuals to the area of origin, but others are reminiscent of common insect movement patterns and involve passive transport on ocean currents to breeding or feeding areas with return to the point of origin being performed by a subsequent generation. To scientists studying plankton, migration is movement (usually vertical and diel) between areas rich in nutrient to areas that support photosynthesis, or movement to and from areas of high prey density but high predation risk. Although at first glance vertical migration of plankton may seem a different phenomenon from horizontal movements of other organisms, in terms of frequency during the life cycle and function served, such movements are not unlike the round-trip migrations of vertebrates. Entomologists have come to consider many types of movement migration, and it is unusual if return by the same individual to the departure area occurs. A further complicating factor in defining or even discussing migration is, as Taylor and Taylor (1983) point out, that migration in an ecological or genetic context may include quite different types of movement than would migratory behavior.

Disagreements in definition are more than semantic argument; they reflect basic differences in approach and in the kinds of questions being addressed. They may even contribute to erroneous assumptions such as the long-held belief that because many insect migrants do not precisely direct their flight path and do not, as individuals at least, return to the natal habitat or point of origin, migration in such cases must be nearly the equivalent of genetic death, favored only under the most adverse conditions

or, in group selection arguments, because of benefit to the resident, nonmigrant population. What types of movement should be considered migration, and how they may relate to one another are complex questions that form a subtle barrier to synthesis and generalization across systems. With his characteristic clarity and brilliance, John Kennedy in the first paper of this volume, attacks the definition barrier once again and sets the stage for the diverse papers in the 6 chapters that follow. He also discusses the general principles and questions that can be discerned in the wide array of movement patterns called migration and/or dispersal.

In the second paper of the volume, Hugh Dingle discusses the broad question of the role of migration in life history. Once again generalizations depend somewhat on one's definition of migration, but Dingle suggests some general principles and areas for future research. One question that emerges from Dingle's discussion and from many other papers in this volume is that of the "cost" of migration or dispersal. Some knowledge of the cost or benefit of migration is essential to understanding either its role in the life history of a species or its evolution. The long-held view that migrants incur great cost in terms of risk of death or injury en route, energetic demands of the trek, and/or delayed or diminished reproduction is being addressed in many groups both experimentally and theoretically. Papers by Denno, Palmer, Zera and Solbreck in this volume each address this question in insect systems. Zera documents actual fitness differences between winged and wingless waterstriders. The other three authors, in contrast, suggest that under some circumstances the cost of migration in insects may be less than previously supposed, particularly when the costs of staying are weighed against benefits in a new habitat; long-distance movement may form part of a colonizing life history strategy in which migration and reproductive output are both maximized. Leggett discusses the role of migration in the life history evolution of fish, suggesting that migration can and does greatly reduce the impact of environmental variance on reproductive success. Dodson, Lambert and Bernatchez assess the energetic costs of migration and reproduction in two species of anadromous coregonines. These authors find that energetic costs of migration are high in both, but neither species behaves so as to minimize that cost. Again in fish, Miller, Crowder and Moser analyze the cost/benefit ratio of migration to estuarine nursery areas. Alerstam discusses the energetic costs and benefits associated with different flight patterns in arctic and common tern migrations and shows that energy use during these amazing flights from northern tundra to Antarctic pack ice accounts for nearly one quarter of the total energy budget of the species.

A related question addressed in several chapters concerns the use of passive transport mechanisms by migrants to reduce the energetic cost of long-distance movement. For example, when fish such as plaice, sole, cod, and eel move up off the bottom and into moving tidewater according to the direction and speed of the water movement, they are exploiting the tide for passive transport and reducing the costs of movement. Similarly many fish travel long distances in ocean currents and reduce both energy and time required for long-distance travel. The currents may also provide an orientation cue on long swims. (See McCleave, Arnold, Dodson and Neill 1984 for several reviews.) These behaviors resemble the flight strategy of many insect

migrants that after take-off, fly up past their boundary layer and are carried long distances by prevailing winds. The insects are thought to determine the direction of travel by controlling altitude and time aloft and by choosing, in response to appropriate environmental cues, the appropriate day and time of day to go aloft. In this volume, McCleave and Kleckner model the passive drift of eels in ocean currents, and Heyerdahl, in a beautiful summary of his life's work, documents the movements of early civilized man across the major oceans by passive drift. Richardson discusses use of the wind and weather fronts by birds in flight, while Schmidt-Koenig, Walker, Solbreck, and Brower each address this question in insects.

Orientation mechanisms also show common trends as well as differences across systems. Certainly for passive migrants, orientation within the transporting medium to exploit but not be at the mercy of the medium is a general need; but data on the extent to which passive migrants actually accomplish this ideal and the mechanisms by which they may do so are difficult to obtain, since such studies usually require following the migrants en route. Radar studies on African locusts and other insects have provided the best information for insects (see Rankin and Singer 1984; Rainey 1978 for reviews). In this volume, Schmidt-Koenig and Walker each discuss orientation to wind by butterflies and Solbreck analyzes long-range movement and settling in a lygaeid bug and the spruce bark beetle. Richardson and Alerstam both discuss orientation of birds to prevailing winds. McCleave and Kleckner address orientation in the transport medium by eels; Hamilton describes similar behavior in molluscs. Heyerdahl gives an elegant explanation of ocean navigation by early man.

Orientation to cues other than the transport medium has been studied in many different systems. Able and Cherry summarize and evaluate recent work on orientation and navigation in birds, and Bingman, Beck and Wiltschko analyze the ontogeny of migratory orientation in the pied flycatcher *Ficedula hypoleuca*, particularly implicating the earth's magnetic field as a primary source of orientational information. Baker argues that humans and other mammals can also orient via the earth's magnetic field, while Schmidt-Koenig and Brower each discuss this possibility and other orientation mechanisms for the monarch butterfly. Walker analyzes orientation of several fall-migrating butterflies in the southeastern U.S., Herrnkind reviews his work on orientation mechanisms in migrating lobster, and Hamilton describes some fascinating experiments on orientation of migrating *Aplysia*.

The adaptive significance and evolution of migration are discussed by many authors in this volume, however, Gauthreaux, and Ketterson and Nolan analyze these questions in avian systems, and Quinn addresses the evolution of homing and straying in sockeye salmon. Brandt, in an empirical study and Kiester, using a theoretical model discuss various aspects of sex-specific dispersal in small vertebrates.

The cues that induce and terminate migration have interested scientists as well as casual observers. Photoperiod, temperature, food quality or quantity, and other aspects of habitat quality have all been shown to elicit movement or settling in some systems. This general topic is addressed in different ways by many of the contributors. Angel, Kerfoot and Huntley all discuss the factors that induce migration of zooplankton; Heaney, Sommer, Klemer, and Kamykowski each analyze reasons for

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phytoplankton movements, with Kamykowski contributing some specific methodological suggestions for research in this technically difficult area. The paper by Kitting on the diel migration of a small mollusc in a seagrass community provides an interesting echo to those on plankton. Wolcott and Wolcott assess the possible causes for migration of terrestrial and intertidal crustaceans, Scheibling does the same for sea star movement, and Herrnkind analyzes proximal causes of lobster movement. Fenton and Thomas review what is known of factors involved in bat movements, while McCullough gives an excellent general summary of long-range movement of large terrestrial vertebrates. Gauthreaux, and Ketterson and Nolan discuss reasons for migrating or not migrating and cues involved in settling for birds.

Investigations of physiological changes that induce migration or dispersal have revealed some interesting parallels between small mammal dispersal and insect migration. Tendency for movement away from the natal habitat in both is frequently associated with the prereproductive period, and the suggestion that hormones involved in reproductive development may also influence migratory movements has been made in both systems (see Holekamp, Simpson and Smale; Rankin; Herman; Brower, this volume). Herrnkind briefly considers the question of probable physiological controls of lobster migration, and Berthold summarizes physiological changes associated with migration in birds.

The genetics of migratory behavior or migrant morphology is an extremely important area that has not been addressed in many systems. In this volume, Zera and Palmer in insects and Berthold in birds discuss their results in this critical area.

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MIGRATION, BEHAVIORAL AND ECOLOGICAL

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ABSTRACT

Movements called migrations vary so much in mode and scale among animals that it has proved difficult to arrive at agreed generalizations. There is now no consensus even among students of insect migration. Two different ways of escape from the prevailing confusion of concepts and terminology have recently been proposed. R.R. Baker argues that migratory behavior should be regarded as an aspect of exploratory behavior: a view here judged untenable. On the other hand L.R. and R.A.J. Taylor argue convincingly that migration as an ecological process must be defined at the ecological level: it is population re-distribution by movement, whether or not the movement is controlled by the animal through some specialized migratory behavior. A general definition of specialized migratory behavior is offered with illustrations showing that it cannot be regarded simply as extended foraging behavior. Previous definitions of migration have tried to combine ecological and behavioral criteria but failed because by no means all population-redistributing movements involve any specialized migratory behavior. Some major evolutionary factors that may explain the great diversity of migratory behaviors are briefly surveyed. Clear recognition of the distinction between the ecological and behavioral meanings of migration is enough to remove the current confusion and offers hope of eventual objective criteria for other, complementary concepts such as "habitat," "trivial movement" and "station-keeping." Quantitative comparison of track patterns inside and outside areas deemed to be units of habitat is necessary for this but has hardly begun.

INTRODUCTION: BEHAVIORAL SPECIALIZATION

Integrating the subject of migration among animals generally is not easy because perceptions of what migration is depend so much on the particular animals elected for study: their size, mode and medium of locomotion, life strategy and so on. This contribution is colored by experience of insect migration, but there is an exceptionally rich store of information on insect migration as has often been said (e.g., by Taylor and Taylor 1983, p. 187). Not the least of the insects' merits in the search for general principles is that they span the critical range of sizes from birds and mammals down to the microscopic. This variety enabled students of insect migration to make progress in the last two decades towards a consensus on what migration is, at least in behavioral terms, and many of us believed this was comprehensive enough to cover other animals too (e.g., Southwood 1981). The recognition that even the so-called dispersals of small, feeble insects are not typically accidental but adaptive (Johnson, 1969) meant that "migration" could now embrace them as well as the self-propelled traveling of larger animals, from insects to whales, for which the term was once reserved; while special terms such as *emigration* and *nomadism* could be reduced to sub-categories of the overall phenomenon, migration.

As an insect ecologist reviewing the ecology and evolution of migration in animals generally, Dingle (1980) carried the trend to its logical conclusion by stripping away all particularities to arrive at this general definition:

Migration is specialized behavior especially evolved for the displacement of the individual in space.

Dingle had started out from a particularized behavioral definition of insect migration (below) but then jettisoned it, presumably because there are many obvious exceptions to it outside the insects. Unfortunately, paring down the concept of migration to the point of complete universality in this way, although logical, leaves the definition with little substance. The resulting definition centers on behavioral specialization but can specify no more than its common outcome, spatial displacement; there is no common type of behavior that can be identified as causing migratory rather than nonmigratory spatial displacement.

A definition without exceptions is hard to find in biology and as in this case can be achieved only at the cost of content. With that is lost its usefulness as a starting point for recognition and analysis of specific cases, thus defeating the object. If a more explicit definition is generally, although not universally, applicable, then not only does it provide such a starting point but each exception to it becomes a "natural experiment," raising answerable questions about the special conditions that make it an exception and thus about the conditions for the general case too. If this reasoning (cf. Southwood 1977) is valid, we need a more particularized behavioral definition and can go back to the one from which Dingle (1980) started. It referred to insects but may also be applicable, with some exceptions and some amendment, to animals generally:

Migration is persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it. It may be effected by the insect's own locomotory exertions or by its embarkation on some transporting vehicle, and in common with diapause involves a phase of depression of "vegetative" (growthpromoting) functions as a condition for their resumption (Kennedy 1961).

On reflection, it will be apparent that each of those particular characteristics is comprehended under the single word *travel* as we apply it to our own behavior in ordinary speech. This word is used again and again without a second thought throughout the migration literature, which gives one some confidence in the general usefulness of the definition, unwieldy though it be. It does not attempt to define a watertight category with every case displaying the specified characteristics in equal degree. Rather, it attempts to define the common *direction* of specialization evident in the behavior of migrants (also Kennedy 1975, Kennedy and Way 1979).

Behaviorally, "vegetative functions" are activities that exploit the available resources for growth: somatic growth in juveniles and adults and growth of the genital and accessory products in adult sexual maturation. They include a variety of localizing, station-keeping behaviors in association with foraging (followed by feeding) and with reproductive behaviors following sexual maturation: mate-finding, mating, oviposition-site finding, nesting, oviposition or parturition, parental care, etc. Some inhibition of these responses seems to be a constant feature of migratory behavior; whereas the behavior by which the movement itself is executed is highly variable. "Vegetative stimuli" include those betokening not only food but also the associated resources required for the effective vegetative existence of the species: stimuli from shelter, resting sites, mates and other conspecifics, mating sites, nest sites, landmarks, microclimate, etc.

Note that the definition gives "some" internal inhibition of vegetative activities as a criterion of migratory behavior. Baker (1978, p. 18; likewise Taylor and Taylor 1983) dismissed that key criterion on the grounds that the inhibition of vegetative responses is neither total nor maintained for twenty-four hours a day, which suggests he must have overlooked the word "some." Feeding does of course sometimes interrupt migratory locomotion which demands fuel for the muscles. This feeding may provide material for growth as well, but that is while reproductive behaviors are inhibited, before sexual maturity, so there is again some inhibition of vegetative activity. Mating and oviposition also sometimes interrupt migratory locomotion, or occur at other times in the same day, like roosting—to mention three further types of vegetative activity mentioned by Baker. Segregation of migratory and vegetative activities into separate periods of the day (quantified, for example, by Caldwell and Rankin 1974) illustrates rather than contradicts the inhibition of vegetative activities during migratory behavior.

On the other hand Baker (1978, p. 5) brought out a serious defect in my 1961 definition of migratory behavior quoted above. Like Johnson's (1969) definition of migration, it covered only movements from one vegetative habitat site to another. It omitted movements to and from non-vegetative sites where no breeding occurs: sites of diapause, dormancy, hibernation, aestivation, etc., hereafter referred to collectively as "diapause sites." The wording of the 1961 definition implied that the responses that are more or less inhibited when the movement starts are the same as those that eventually arrest it, but this cannot be generally true of movements to and from diapause sites. Thus migration from a vegetative to a diapause site begins with some inhibition of the station-keeping responses to vegetative stimuli but it is eventually arrested, not by them, but by station-keeping responses to different, non-vegetative stimuli from the diapause site (e.g., Landin and Vepsäläinen 1977).

However, repairing that omission does not affect an important point in the 1961 definition, namely, that the migratory activity is a condition for the development of responsiveness to the stimuli that eventually arrest it (e.g., Foster 1978; other examples in Kennedy 1966 et ante, 1975). This is probably true of migrations to and from diapause sites as well as those between two vegetative sites. A classic

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illustration from applied entomology concerns coccinellid beetles that hibernate in the mountains and in the spring fly down to lowland orchards, their vegetative habitat. When beetles ready to migrate were collected from their mountain hibernacula, carried down to the orchards and released there, they refused to behave as the operators hoped. Instead of staying to prey on the aphids there, they flew away—in the same direction as they normally would have taken from the mountains (Williams 1958, p. 94).

An amended definition would then be:

Migratory behavior is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence.

INTEGRATIVE LEVELS

Meanwhile there have been two proposals for radical re-integration of the whole subject, one at the ecological level by Taylor and Taylor (1977, 1983), and one at the behavioral level by Baker (1978, 1981, 1982). Both parties maintain that migration studies have become too parochial, losing touch with the natural context and altogether too preoccupied with diverse behavioral mechanisms supposedly peculiar to migration but defying generalization. Both parties define migration in such a way as to include movements over any distance no matter how small:

A change of place between generations (Taylor and Taylor 1983);

The act of moving from one spatial unit to another (Baker 1978).

For the Taylors, migration is in the first place not an act at all but "a purely spatial concept" (1983, p. 197), not behavioral but ecological, a matter of population redistribution by movement of any kind whatsoever. It is simply

the component of movement peculiar to population dynamics, whether controlled or not (1983, p. 184).

Movements to and from diapause sites within one generation also affect population dynamics, but they are omitted if migration is a "change of place between generations" only. This omission does not seem to be an oversight since the authors repeat it ("Survival is by movement within the population and, if it separates the birthplace of generations, we call it migration" (1983, p. 199)), and Johnson (1969) had already described migration similarly as a change of breeding place. Baker (1978, p. 5) pointed out that this description excluded, inter alia, some of the most spectacular migrations of mammals and birds, which are to and from **non**-breeding places. Rather than repair the omission Baker took it as support for a major theme of his monumental book, that there is nothing definable about migration to justify distinguishing it from movement in general. This echoes Elton's (1927) view of migration and it helps to explain Baker's very unspecific definition above.

The Taylors are accustomed to studying actual populations on maps (e.g., Taylor and Taylor 1979) in accordance with their sound principle of looking at the whole population when considering population dynamics, and elsewhere in the 1983 article (p. 197) they describe migration as

the persisting change that is left over when all other, minor excursions are removed, whatever their cause or function.

So it appears that in practice they do not treat minor movements as migrations, and at first sight this amended version would be more generally acceptable. But the definition has now lost its rigor: the criterion of "minor" is subjective, for it depends on the scale of one's map. Moreover it is of course impossible to ascertain solely from a series of maps the extent to which a redistribution is in fact due to movement, as distinct from natality and mortality.

Nevertheless the Taylors' main thesis is valid. Migration is an ecological process and "an ecological property can only be defined ecologically" (1983, p. 200). Their corollary that "migration can be *characterized* behaviorally, physiologically, or genetically for individuals or species, but not *defined* at lower levels of organization" may be less convincing, but their main point that these different levels must be distinguished is compelling and new. Rogers (1983) is confident that the Taylors' approach can lead on to major advances at the ecological level since it stems from their previous achievement in breaking with the tradition of considering only time in population dynamics, neglecting space. It is now generally acknowledged that a real population "forms a continuum in space and time": the famous fern stele model of Taylor and Taylor (1977).

Their new theory of migratory *behavior* (the Delta Model of Taylor 1961; Taylor and Taylor 1977, 1978, 1979, 1983) is another matter. It states in effect that the movements involved in population re-distributions result from density-dependent, alternating, mutual attraction and repulsion between conspecifics (1983, pp. 202 and 207). While there is no doubt that those intraspecific locomotory reactions are real and important, the theory that they explain L.R. Taylor's ecological Power Law relating population density and spatial variance, confounds the behavioral and ecological levels. For in attributing redistributive movements in general to those particular locomotory reactions, the theory contradicts the Taylors' own point (below) that many of these movements involve no special behavior. Also, the Power Law holds for plants (Taylor, Woiwod and Perry 1978) which do not locomote. Some other objections and alternatives to the Delta Model are summarized by Dye (1983).

There is indeed widespread confusion in the literature between the ecological and behavioral levels. It is epitomized by the continual bracketing together of migration and dispersal as if these were complementary categories on the same level, or even synonyms. Southwood (1981) set out the objective relationship between these two different processes in a lucid diagram showing that dispersal, being an increase in the mean distance between individuals, is something that only a population can do; whereas migration, being movement beyond the habitat, is something an individual also can do, a behavioral process. But the reason why people so often speak of "dispersal" instead of migration seems to be historical: they are anxious to avoid any of the old, restricted, behavioral connotations of the word migration, such as self-propulsion, unidirectionality, or regular returns, where these do not apply or are not known to apply. It is to be hoped that with the recent broadening of the behavioral meaning of migration this anxiety will be allayed and the term dispersal dropped. It is redundant at the behavioral level, and it leads again and again to the absurdity of an individual being described as dispersing, as Baker (1978) justly says. One cannot help wondering how this heroic, dismembered individual still manages to arrive in one piece.

The Taylors give a more compelling reason for keeping clear the distinction between the ecological and behavioral levels of migration:

The definition of migration in ecology...has no equivalent in behavior or physiology (1983, p. 200).

They point out (p. 197) that at the ecological level it is impossible to draw any line between displacements during accidental or trivial movements and displacements that are "controlled," i.e., due to some special migratory behavior. Although the former are excluded from the behavioral definition of migration they must be included under the ecological definition of it: re-distribution by movement "whether controlled or not." Ecologically, migration "does not exclude 'accidental' migrants such as a foraging bee that is blown off course and unable to recover" (1983, p. 197), although this is patently not migratory behavior. A vivid example of migration by trivial movements that is quoted by both Southwood (1981) and the Taylors (1983) is the rapid and repeated re-colonization of islands that have been de-populated by flooding, which has been observed in a behaviorally nonmigrant species of beetle. Ecologically, this is undeniably migration. Moreover, no general limit can be set on the time-span of a migration in the ecological sense (Elton 1958), whereas in the behavioral sense each migration is completed in less than one life-span. Thus migration at the behavioral level is not co-extensive with migration at the ecological level; it covers a smaller class of movements.

EXTENDED FORAGING?

Baker (1978, 1981, 1982), by contrast, focuses on migratory behavior. The context into which he wishes us to re-integrate it is *exploratory* behavior. Exploratory behavior consists of movements during which the animal acquires and stores topographical information about the resources in its environment, and it may not stop to exploit any of them at the time, returning later for this. The proposition that long-range migrants that are found colonizing a fresh habitat area have done the trip beforehand on a non-colonizing, exploratory visit seems far-fetched. It seems incredible, too, that natural selection could allow such a laborious performance to persist when less costly options are open. Baker (1982, pp. 163-194) recognizes two groups of exceptions to the rule of prior exploration, all among invertebrates, and

explains that the first group "base their way of life" on "a sense of direction" instead of the "sense of location" achieved by exploring, while the second group are "automatons" with no sense of either. The first group includes well-known butterfly migrants and the locusts, and the second, well-known aphids and the phoretic mites (see Binns 1982). Perhaps it is not pure coincidence that these supposedly exceptional arthropods are also those whose migratory behavior is better documented than usual.

For all the other migrants, Baker stands by the exploratory theory of migratory behavior. There is no good evidence for it in long-range migrants, and as Baker says, the evidence would be very hard to obtain, whereas there is experimental evidence against it. For example, birds that have never been outside the laboratory show the seasonally "right" compass orientation on first seeing the natural starry sky (see Schmidt-Koenig 1979), and birds can be induced, by prior exposure to the appropriate seasonal daylengths, to orient their movements in opposite directions under a planetarium "sky" in conformity with the seasonally opposite directions of their migrations (Emlen 1969). The best documented case of migration among the insects and probably among all animals is that of the desert locust. This enabled Draper (1980) to check Baker's (1978) interpretations of their movements one by one: they were not borne out.

If one wishes to integrate migratory behavior into a wider behavioral context, then that surely would be *foraging* behavior—provided one is permitted to stretch that term to cover the locomotory maneuvers used in finding not only food but any kind of resource item: mate, oviposition site, resting place, refuge, display site, nest site, warmth and so on. For lack of a better term "foraging behavior" will be used here inclusively for all those behaviors, as Prokopy and Roitberg (1984) have recently used it. Likewise foraging for food items and searching for oviposition sites (hosts of parasitoids) are so similar that they are already often treated together (Hassell 1978).

Admittedly the term' that has long been used for behaviors of that kind is *searching*. But this term, also, would need re-defining to make it more apt than foraging, and it is too entrenched for that now. Searching can be done with a vertebrate eye or arthropod antenna or any other independently movable receptor organ, by itself, scanning the environment without any locomotion by the animal, whereas foraging clearly means locomotion. Locomotion is the common feature that can be observed in all behaviors of this kind (de Ruiter 1967) and needs to be conveyed by their name, above all in any study of spatial displacement. "Searching" certainly implies some form of scanning (ibid.) but fails to specify locomotion. For what searching really describes is not observed behavior but a human, subjective, cerebral activity that is not observable in animals.

Foraging as therefore used here, in the context of spatial displacement, may be defined objectively as:

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Reiterative locomotory activity that is readily interrupted by an encounter with a resource item of one particular kind.

That is to say, the animal's threshold of response to stimuli from one kind of resource item is particularly low at that particular time, so that when these specific stimuli are received, they readily inhibit the locomotion, replacing it by some other behavior, say eating. If the encountered resource item then disappears for some reason, such as being eaten by the animal or preempted by a rival, the locomotion is normally resumed. But if now another similar resource item is not encountered within a certain time, for the given animal, the foraging movement is again replaced by some different behavior, say resting, or emigration (e.g., Roitberg, van Lenteren, van Alphen, Galis and Prokopy 1982). If the intervals between the encounters remain shorter than that, the activity may be called "local foraging," typical of behavior within the habitat; if longer, it will be called "extended foraging" as defined strictly below.

Foraging behavior, in the inclusive sense defined above, appears to be what the Taylors have in mind as migratory behavior, for they describe desert locust migration as "basically a prolonged oviposition flight, terminated by environmental cues that anticipate improved prospects for survival of the offspring" (1983, p. 199). But the behavior of swarming desert locusts is not like that (e.g., Popov 1958, Kennedy 1951). When they reach sexual maturation their migratory flying is indeed somewhat reduced, but it is not terminated by the moist soil that is the cue for oviposition, or even by oviposition in it. They fly on, often within the day, laying eggs in widely separated places, and the places where they settle when ready to lay are not related to the suitability of the soil for laying. While they are still sexually immature, they fly more persistently and their mating and oviposition responses are totally inhibited.

If there were no phase of inhibition of responses to vegetative stimuli with their arresting, detaining effect, animals would not be able to leave a habitat until it ceased to supply enough of these stimuli. It is this inhibition of vegetative responses that underlies the impression of "undistractededness" (Johnson 1969) that migrating animals often give to an observer. If animals could never emigrate in anticipation of deterioration of the habitat, which is signaled by the decrease of vegetative sensory inputs, then behavioral migration would always be facultative, in other words always due to "current adversity," which it certainly is not (e.g., Southwood 1962).

Migration cannot be called simply extended foraging, although there is a continuous spectrum here. The sequential changes of responsiveness to conflicting environmental stimuli seen in migratory behavior, are also observable, although more frequent, during trivial foraging movements within the habitat. The female small cabbage white butterfly, for example, interrupts (inhibits) her egg-laying response to a host plant after laying only one egg on it and takes off on a brief flight. After that she becomes responsive to host plants again and therefore orients her flight to a neighboring plant, lands and lays another egg on it. The duration of the bouts of inhibition of those three vegetative responses to host plants governs the spacing out of the eggs through the habitat and is somewhat more extended in the Australian than in the Canadian habitats of the species (Jones 1977). Migratory behavior would involve

still further extension of the inhibition.

Temporary inhibition of the response to one kind of orienting stimulus in favor of another occurs repeatedly when animals are not migrating and becomes prolonged when they are. Taking desert locusts as a well-known example again, the nonmigratory, non-gregarious nymphs are attracted to vertical silhouettes and thus to the plant clumps of their desert habitat sites. This response is inhibited for periods of minutes while they leave the plants and bask in the sun on adjacent patches of bare ground. When they turn into the migratory, gregarious form, the attraction to plants is inhibited for hours every day (reappearing whenever the day becomes excessively hot). The consequent tendency to avoid obstacles facilitates their sustained traveling. The orienting stimuli to which they become most responsive on the march are the sun (as a compass) and the sight of their moving fellows in the crowd, both of which have some stabilizing effect on their direction of march (Ellis and Ashall 1957; Kennedy 1939, 1945).

It is of course the long-range orientation mechanisms that have always been the most striking and most studied component of behavioral specialization in migrants. The common characteristic here is that directional cues emanating directly from resources cease to play the dominant role in the animal's orientation behavior, a role taken over by directional cues from ubiquitous environmental features like the sun, the stars, the geomagnetic field or the wind. Being ubiquitous, these alone can provide a traveler with continuous guidance. Steering by them may serve only to stabilize the ground track, thus tending to straighten it out. This increases the animal's net displacement in space and hence its coverage of new ground. With further behavioral sophistication, migrants use those ubiquitous cues as signposts with the aid of their internal "maps," in navigating towards distant resources, as much elegant recent work has shown (this volume).

The light from the sky likewise does not come from any resource but functions as a vertical "signpost." It is no doubt involved in local foraging when that includes brief flights between landings as in the small cabbage white butterfly, and it takes over as the dominating orientation cue for numerous insect migrants that use it phototactically in embarking on their transporting vehicle, the upper wind which then straightens and stretches out their movement horizontally (Johnson 1969; Riley, Reynolds and Farmery 1983). When the insect has entered the migratory state, this climbing response to the sky light may be triggered by particular weather stimuli received on the ground, which helps to ensure that the wind vehicle will be going the "right" way at the time of embarkation (e.g., Brown, Betts and Rainey 1969; Schaefer 1976; Riordan 1979). Analogous mechanisms have been described in birds (Keeton 1981), fishes (Arnold 1981, Harden Jones 1981) and marine larvae (see Baker 1978; Angel, this volume).

Thus migratory behavior embodies in exaggerated form the basic pattern of behavioral sequencing that already operates during local foraging. Nevertheless these examples show that migratory behavior is more than extended foraging. That is to say, it is more than a simple extension, when resources are spaced further apart, of the unchanged temporal pattern of local foraging behavior. Because *dis*inhibition of vegetative responses sets in quickly during each bout of locomotion in local foraging, the animal is ready to respond to a new vegetative stimulus very soon. If such a stimulus is received equally soon, then the animal is arrested again within a short distance, thus tending to stay within a habitat locality where such stimuli abound. Migratory behavior is different: disinhibition of the vegetative responses during locomotion is slow, and their prolonged inhibition prevents the animal from being promptly re-arrested by another vegetative stimulus, so it keeps going.

With "obligatory" migration where the prolonged inhibition of the stationkeeping responses arises from genetic causes, it is obvious that the migration is not extended foraging. This is not so obvious with "facultative" migration since the latter is due to the "current adversity" of habitat deterioration, over-crowding included. The deterioration will mean that arresting stimuli from local resources are weakening and coming in less often, or being nullified by opposing stimuli. Nevertheless, the emigration could be equated with extended foraging only if these sensory inputs, increasingly antagonistic to vegetative responses, had no cumulative effect on the animal's responsiveness to vegetative as against locomotory stimuli. That is hardly conceivable. Locomotory excitability will increase together with inhibition of the station-keeping responses, as demonstrated in the field (e.g., Turnbull 1964, Smith 1974, Waddington and Heinrich 1981, Roitberg et al. 1982) and in laboratory experiments (e.g., Thomas 1974, Traynier 1979, Chapman 1982, Kennedy 1966 et ante, Kennedy and Ludlow 1974).

Migratory behavior has differentiated and diversified so much through the animal kingdom and even within the insects that the Taylors described it as "a multiplicity of specific mechanisms" (1983, p. 201), implying that the mechanisms have little in common. But there does appear to be a recognizably common direction of specialization, and it is this that provides the much-needed starting point and frame of reference for the behavioral analysis of each particular case. Given these, it is possible to set about identifying which responses to which stimuli are relatively inhibited and which are enhanced to the point of dominating the animal's behavior for the time being.

This has yet to be done for most cases of ecologically known movements. We lack the information needed to assess whether the movement does involve special migratory behavior. The problem is acute with what is called "nomadism," where the resource itself moves—like the prey of wolves and seals, or the plankton food of fishes, or the vegetation produced by shifting local rainfall in the desert or savannah for many ungulates, birds and insects. The locomotory activity of an animal that is exploiting such a mobile resource can be notably persistent (although discontinuous), but it may look as if this is simply because it is pursuing the resource: not migrating but engaged in shifting foraging. To the extent that the pursuing animals manage to keep in contact with such a mobile resource, one might not expect to find any prolonged inhibition of the animal's responses to it or any special use of long-range "signpost" stimuli.

An instance where both of these characteristics of special migratory behavior are in fact present concerns wolves tracking their mobile caribou prey in northern Canada (see Sinclair 1983). There comes a time in the spring when the wolves cease preying on the caribou herd, although it is still at their mercy, and run ahead of it to raise families where the caribou will arrive later to raise their own families. In this way the wolves gain a richer resource in the shape of easily caught caribou young. (Somebody could have warned Little Red Riding Hood about wolves!). There are many more cases where special migratory behavior is involved in the pursuit of mobile resources, and still more are likely to be discovered if sought.

EVOLUTIONARY FACTORS

A number of factors have been identified which, it is inferred, have influenced what particular kind of behavioral specialization has occurred during the evolution of migrants. They explain why students of the migratory behavior of different animal groups have perceived and defined migration in such different ways. A major factor is the animal's power. The effects of this factor have been encapsulated in another lucid diagram of Southwood's (1981). The less locomotive power the animal has relative to that of its medium—air or water—the more the animal must rely on the movement of that medium for its traveling. Vice versa, the greater the animal's power, the more the animal can rely on its own controlled locomotion and orientation reactions and make sophisticated use of long-range "signpost" stimuli. Animals of intermediate power (large insects, small-to-medium fishes and birds) tend to combine the two techniques of directional travel, heading as well as drifting downstream thus adding their own appreciable speed to that of the current, like downstream canoeists in Southwood's (1978) analogy.

Power goes, in general, with size, making it easy to understand why small animals of insect size or less rely so much on currents of air or water. But another factor also favors this: for any given shape, the smaller the animal the more buoyant it is and the less energy it need expend on simply keeping itself aloft in the current. Energy expenditure on that is also saved by some migrant birds and insects that have acquired the arts of gliding and soaring (Alerstam 1981); these activities of course occur also in nonmigratory, foraging behavior, notably in birds of prey.

Another factor for animals big and strong enough not to rely entirely on a transporting vehicle for migration, is their locomotory mode. Swimming is energetically the cheapest mode of travel, and out of water, flying is cheaper than running (Schmidt-Nielsen 1972). The insects were the first to invent flight and not surprisingly use it for migration in the great majority of cases (Johnson 1969), shifting into a specialized, steady, cruising mode of flight when migrating (e.g., Ward and Baker 1982).

Unlike the situation in vertebrates, flight is confined to the adult stage in insects as a whole, whether they be migrants or not, and this stage (unless flightless) is also behaviorally the most sophisticated one in the life-history, being equipped with the most elaborated receptors, CNS and effectors. That kind of morphological and physiological specialization serves the adult's exacting behavioral tasks of mating and oviposition, i.e., the correct *placing* (not growth) of the genital products. It was therefore dubbed "sensorimotor" specialization in contradistinction to the "vegetative" specialization of insect juveniles ("adults find growth resources, while juveniles exploit them": Kennedy 1956, p. 362; 1961). The adult insect is preadapted for further specialization into migratory behavior, which is also exacting, and was therefore described as "super-adult" by analogy with the "super-adults" produced by endocrine manipulation (ibid.). Presumably that is why it is at the adult stage that migratory behavior has differentiated in the great majority of insects.

Surprisingly at first sight, the minority of insects with flightless adult females have gone to the opposite extreme, differentiating migratory behavior at the earliest, smallest stage rather than any intermediate one: mealy-bugs, for example, and gypsy and winter moths whose first-instar larvae let themselves go on long silken threads somewhat like gossamer spiders. Here it is the earliest instar that is best fitted for migration on the grounds of size, power and energetics above-mentioned (and see Rogers 1983).

The adult is again typically a migratory stage among vertebrates, but here (Amphibia aside) there is no switch-over between juvenile and adult like that in the insects to a different morph with a different locomotory mode better fitted for migratory specialization, and vertebrates are generally larger and stronger. Accordingly, the immature stages often migrate as well. But departure from the usual insect pattern of a migrant adult and a nonmigrant juvenile goes as far as complete reversal in numerous marine invertebrates. Here the bottom-living adults are non-migratory, whereas the larvae rise (again, apparently phototactically: see Baker 1978, pp. 483-4) and migrate, at any rate in the ecological sense, in the form of plankton on horizontal currents. This rise amounts to "active embarkation on a transporting vehicle." But it surely cannot be assumed to have evolved solely, if at all, as specialized migratory behavior because the medium that transports them also carries the food supply on which they grow: it is their vegetative habitat. They can travel without any inhibition of their vegetative responses.

This is quite untrue of aerial migrants—a point oddly missed by A.C. Hardy when he invented the term "aeroplankton" for the insects that he netted high in the air, although they were entirely out of their habitat for the time being, quite unlike the marine plankton which was his primary concern. Given a habitat that also transports them, the marine animals in question are able to do their migrating as juveniles, often with even less specialization than the small migratory larvae of flightless insects. They undoubtedly migrate in the ecological sense, horizontally as well as vertically. The question of whether they migrate horizontally in the behavioral sense, as well, cannot be given a general answer; it is a matter that requires investigation in each separate case, like nomadism. In some cases they apparently do show specialized migratory behavior, adjusting their level in the water in such a way as to be carried by profitable currents at a certain stage of their development, as already mentioned. Cases where their migration is not accompanied by any inhibition of vegetative responses, however, constitute obvious exceptions to the "rule" that migratory behavior includes such inhibition. They are exceptions that could be said to "prove the rule" for other migrants whose vegetative habitat is not at the same time a transporting vehicle.

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SPATIAL BEHAVIOR AND SPATIAL POPULATION DYNAMICS

Foregoing sections have attempted to illustrate the proposed definition of migration in the behavioral sense as a category distinct from migration in the ecological sense, and of lesser scope. The Taylors have highlighted this distinction and presented a strictly ecological definition of migration: population re-distribution by movement. But their treatment of migratory behavior still seems to confuse the two levels. The definition of migratory behavior proposed here does not refer solely to the movement itself, which varies greatly in mechanism, but invokes also the more constant, negative feature: inhibition of vegetative responses.

Confounding of the ecological and behavioral levels has led students into more and more conceptual and hence terminological difficulties, chronicled by Baker (1978, 1982) and the Taylors (1983). Thus Johnson (1969) concluded from his exhaustive survey of insect migration that definitions of it based only on behavior could be no more than partial, and Baker (1978, p. 18) took this as an early sign of the failure of Johnson's and other entomologists' whole approach to the subject. But that conclusion of Johnson's was the direct result of the vain attempt to find a definition that combined the ecological and behavioral levels as if they were coextensive and any criteria should apply to both. Dingle (1980) made a fresh attempt to do the same thing, and the result was a bare, noncommittal definition as we have seen. Southwood (1962) had defined insect migration in line with the Oxford English Dictionary definition of "migrate": "to move from one place of abode to another"; but Southwood (1981) agreed with Baker (1978) that defining migration did present problems and refrained from doing so again. Nevertheless he could not accept Baker's very broad definition, and confusion was worse confounded.

Pointing to the existing confusion in terminology and the concepts it conveys, Baker offered an escape from the impasse by means of a "major semantic purge" of the field (1982, p. 7) to accommodate his entirely new view of it which he says is a product of "the behavioural ecology revolution" (1982, pp. 1-4). This refers to evolutionary behavioral ecology which he says is "the new establishment for behavioural theorists" (ibid. p. 1), a "new regime" superseding ethology which saw animals "only as bundles of innate reflexes traveling from one automatic response to another" (ibid., pp. v-vi). Behavioral ecology is on the contrary an "anthropomorphic concept of animals" (p. v). The animal is "a sentient creature attempting as an individual to solve the spatial and temporal problems created for it by its environment" (ibid., p. 14) "in much the same way as Man" (p. v). On this basis, migration is identified with exploratory behavior and defined accordingly as any movement from one place to another.

The argument is bewildering. Neither Tinbergen (1951) as a founder of Ethology nor his scientific descendants have ever regarded the study of the function or "survival value" of behavior (its evolutionary, ultimate causes) and the study of its present (proximate) causes as rival "regimes," one of which could supersede the other as the scientifically legitimate "establishment." The surge of interest in ultimate causes since Hamilton (1964) is not that kind of scientific revolution: the complementary study of proximate causes remains as legitimate and necessary as the evolutionary half of Behavioral Ecology. Nor do ethologists or evolutionary behavioral ecologists (e.g., Krebs and Davies 1981) regard the study of function as anthropomorphism. They would be astonished, too, at Baker's identification of proximately causal ethology with inflexible, push-button reflexology, and would repudiate his charge (Baker 1982, p. 1) that they have "seen an animal as an automaton, a very simple machine." That was precisely the view they have always rejected, from Lorenz (1950) and Tinbergen (1951) through to Halliday and Slater (1983), and have managed to supersede. Indeed Baker has reintroduced the very confusion of approaches that Tinbergen (1951, p. 5) effectively warned them against. Altogether, it seems just as well that there do remain as Baker says (1982, p. 4) some "pockets of resistance" to his revolution.

Maintaining a clear distinction between the behavioral and ecological levels seems to be a better way out of the existing conceptual muddle. It opens the way towards the objective criteria which the Taylors find so deplorably lacking in existing mixed definitions. It should now be possible, for example, to separate out the behavioral content from Southwood's (1981) definition of habitat:

The area that provides the resource requirements for a discrete phase of an animal's life.

The habitat, as so defined, is also the area traversed by the animal's trivial movements, that is those within its sensory range where it forages.

Note first that "a discrete phase of an animal's life" could be a nonbreeding phase. A habitat is not necessarily vegetative; it can be a non-vegetative, diapause site—the viewpoint taken here but not by the Taylors (p. 500). At the same time this definition of habitat combines criteria from the ecological and behavioral levels, and the Taylors (1983, p. 201) predictably rejected it on account of the "untenable qualifications" added to the ecological content. "Untenable," because they contain "subjectively selected" units such as habitat "for which no criteria can usually be given" (1983, p. 207). Even if no criterion of habitat has usually been given, the question for the future is whether in principle one could be.

In the context of the "spatial dynamics" of populations (to borrow the Taylors' useful term, presumably designed to remind us that "population dynamics" has for too long meant only temporal dynamics), a habitat is a spatial unit, an area (or volume). In the first, environmental or ecological part of Southwood's definition of habitat above, the criterion is the presence of required resources. But as Hassell and Southwood (1978) pointed out, the presence of required resources in an area does not

of itself make that area a spatial unit of habitat. The animal's station-keeping behavior in the presence of those resources is what makes it one. Clearly, the density of the resource items in the area must be sufficient to have that localizing, station-keeping effect, but the criterion still lies in the behavior.

The second part of the definition specifies "trivial" movements within the area as an additional, now behavioral, criterion of habitat. It does not say explicitly that they play any part in delimiting the habitat area; indeed it seems to say that the movements are trivial because required resources elsewhere are beyond the foraging animal's sensory range. This would beg the question of why its foraging is confined to that area, anyway. The answer can only be that the stimuli received from the resources and associated features *within* its sensory range, within the area, keep its movements trivial. Their triviality, meaning small range, will act together with any repellent effects of stimuli from non-resource features, to keep the animal within the area and thereby set the bounds of the area as a spatial unit of habitat.

Thus the first, ecological part of Southwood's definition of habitat depends entirely on the second, behavioral part. This is precisely the Taylors' complaint, but all it means is that the criterion of a habitat as a spatial unit lies at the behavioral rather than the ecological level. A given area becomes a habitat only because it does trivialize the animals' movements. But "trivial movement" in turn lacks an objective criterion or even quantification. Nor do we know how in practice these movements add up to station-keeping and thus turn the area into a trap. The idea of trivial movement as opposed to migration goes back to the turn of the century (for this history, see Johnson 1969, Taylor and Taylor 1983), and yet in all these years there seem to have been remarkably few attempts to quantify the spatial pattern of trivial movements in the field, let alone identify the causal mechanisms.

The recent extensive descriptions and modeling of foraging behavior have been directed to the temporal rather than the spatial patterning of movements within the habitat. Spatial considerations including turning responses have received some attention, notably in Hassell and May (1974), but the purpose of these studies has been to answer questions about population stability over time (Hassell and May 1973, Hassell 1978, Hassell and Southwood 1978) or evolutionary, "ultimate" questions about the allocation of time between more and less rewarding patches of the habitat (Krebs and Davies 1978, 1981). Moreover foraging movements are only part of the behavioral system that makes the habitat area a trap. Reactions to other resources such as conspecifics, shelter, resting places, mating places, learned landmarks, etc., all add to the trapping effect.

What is needed for the purposes of quantifying spatial dynamics is the recording and analysis of the patterns of actual tracks in the field. Those in an area that has been identified as a habitat (as distinct from territorial or other subunits of habitat) on other criteria—population density, presence of resources—need to be compared with those in adjacent nonhabitat areas. No such information is to be found in ecology textbooks and symposia; the need for it was probably not felt so long as "population dynamics" neglected spatial dynamics. This lacuna is confirmed by the lack of any techniques for recording these tracks in the field and analyzing them afterwards, in "the ecologist's Bible," Southwood's (1978) *Ecological Methods*. No doubt there are more cases in the literature, but I have come across just six published attempts to make such field measurements *comparing habitats with nonhabitats* (not just rich and poor parts of the habitat): two on birds (Smith 1974, 1977) and four on insects (Smit 1960, Douwes 1968, Zalucki and Kitching 1982, Kennedy 1939). Much more is needed in order to quantify spatial dynamics and understand its mechanisms.

The type of spatial maneuver best known to ecologists as a station-keeping mechanism, is klinokinesis, where the reaction is a change simply in the rate or frequency of self-steered turning (Havukkala 1980, 1984; Havukkala and Kennedy 1984). But klinokinesis figures large in the literature of population ecology in only one of its variety of forms: the temporary increase of turning by a parasite or predator after it has contacted and "handled" a host or prey (Hassell and May 1974, Hassell and Southwood 1978, Hassell 1978, Roitberg et al. 1982). The result of this is closer scanning of the immediate vicinity, the area-restricted search of Tinbergen, Impekoven and Franck (1967). This in turn causes aggregation of the animals on a local patch where hosts or prey are concentrated within the larger habitat. The reaction has a small-scale, short-term (up to minutes) station-keeping effect on the individual, but frequent contacts prolong it. Perhaps more important for stationkeeping on the habitat scale is the orthokinetic arresting effect of meeting many hosts or prey, both the literal arrest while "handling" each resource item and virtual arrestment through the reduction of each intervening bout of locomotory activity (e.g., Zach and Falls 1958, Thomas 1974, Waddington and Heinrich 1981, Kennedy 1966 et ante).

However, there are also other forms of the klinokinetic reaction, some of which operate on a larger scale than that well-known klinokinetic after-effect of direct contact with a resource item, the aggregating consequence of which in any case depends on how much these items are themselves aggregated (Murdie and Hassell 1973, Eveleigh and Chant 1982, Waage 1983). Diffuse stimuli such as odors or air humidity can increase turning without any interruption of the locomotion (see Bell and Tobin 1982, Kennedy 1978, Havukkala 1985, Havukkala and Kennedy 1984). Moreover the sudden cessation of such stimuli from a patch or habitat when an animal moves out can cause it to turn more, and even to turn directly back into it (ibid.). But these unlearned, self-steered reactions that help to trap the animal in any habitat area are overlaid by reactions to features specific to a given area, especially but by no means only in vertebrates. The latter are learned during exploratory behavior and have a similar trapping effect in a habitat, home range or territory. This important learned component is thoroughly documented in Baker's (1978) survey and constitutes what he calls the animal's "sense of location." The station-keeping effect of all these turning reactions to resource-associated stimuli is of special interest for spatial population dynamics because they are all evidently more or less inhibited when the straightened-out movement characteristic of migratory behavior supervenes.

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It would be an illuminating exercise to tease apart all these station-keeping responses in the field in specific cases, but perhaps not a necessary one for the immediate end in view. That would be to establish quantitative movement-pattern criteria which will distinguish station-keeping behavior from migratory behavior, and migratory behavior from re-distributive movements during nonmigratory, "trivial" behavior—expecting no hard-and-fast categories, but looking out for bimodalities. Along these lines there may be some hope of finding objective behavioral criteria for the presently vague but ecologically necessary categories of habitat, trivial movement, foraging, station-keeping, etc.—and, of course, for their obverses which make up the subject of migration.

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MIGRATION AND LIFE HISTORIES

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ABSTRACT

Migration confers flexibility on life histories and allows choices of where and when to breed. It thus has profound influences on life history "strategies." Genetic and phenotypic studies of a number of insects suggest the possibility of distinct migration—life history syndromes programmed by natural selection and involving positive correlations among migratory characteristics and aspects of reproduction and survival. The correlation structure suggests adaptation for colonization. In fish there is also evidence for migration syndromes which include reproductive characters, and these may evolve relatively rapidly. In birds there is evidence for considerable genetic variation in dispersal and reproductive characters indicating that correlation structures would be worth investigating. The variation seen in migratory patterns in general can best be understood in the context of the genetic and phenotypic "architecture" of life histories.

INTRODUCTION

Migration is an important component of the life histories of many organisms as the papers in this symposium attest. Not only does it permit escape from unfavorable conditions, but it also allows exploitation of habitats created by successional, seasonal or, as in the case of plankton, even daily changes in the environment. The migrant can thus make use of resources patchy in space and time and determine via its behavior where and when to breed. The latter in turn involves reproduction and survival and hence fitness. The advantage of migration to fitness can be considerable (Solbreck, this volume). It is this relationship between migration and life histories that I wish to explore here. The problem is an important one because the involvement with fitness places the study of migration-life history "strategies" directly in the mainstream of evolutionary biology (Bell 1980; Dingle 1984, in press).

The question I shall address is just how the relationship between migration and other life history traits is constructed to form a "strategy." Specifically we wish to know if there is a characterizable migration-life history syndrome (or syndromes) with identifiable sets of connections among the relevant ecological, physiological and genetic factors. Such connections would imply a complex adaptation (Frazetta 1975) with traits tied together and organized to make the adaptation function appropriately. The presence of such a complex adaptation is implied by Kennedy (1961, 1975 and this volume) when he identifies migration as specialized behavior involving the enhancement of locomotory reflexes which temporarily inhibit "station-keeping" responses, i.e., those involved in keeping the organism in the habitat where it feeds and reproduces, but promote their later recurrence. Rankin and Herman (this volume) have documented the hormonal control of this physiological syndrome in very diverse insects, and Meier and Fivizzani (1980) have discussed the association between reproductive hormones and migration in birds. Physiological ties between migration and life histories are thus established. I shall therefore concentrate here on ecology and genetics and review some of the ways these might influence migration and life cycle patterns.

A life cycle syndrome which includes migration would be expected to display certain attributes. Since migration allows escape from uncertain or unfavorable habitats and the colonization of favorable ones, selection should produce a suite of life history traits that coevolve with migratory behavior to promote (1) flexibility in the face of uncertainty and (2) the ability to successfully colonize (Safriel and Ritte 1980, Simberloff 1981, Dingle 1984). Such a suite might include larger size which seems to be selected for when environments are heterogeneous (Roff 1978; Dingle, Blakley and Miller 1980; Fairbairn 1984), more rapid development to adulthood to minimize the possibility of being trapped in a poor habitat, the potential for early reproduction in the new habitat, higher fecundity to further promote colonization, and appropriate life history responses to environmental cues which signal changing conditions. A good example of the latter is photoperiod. The molding of suites into adaptive syndromes by selection requires that the traits be organized genetically by the appropriate sets of genetic correlations (Hegmann and Dingle 1982, Rose 1983, Dingle 1984). A reasonable prediction concerning the above traits would be an array of positive genetic correlations tying them together into a migration-life history strategy or syndrome. In this paper I shall survey data relevant to this prediction and to the relationship between migration and other life history characters which promote flexibility such as diapause and wing polymorphism. Most of the data will be from insects because they have proved the most amenable to studies of migration and life histories, but I shall also consider some selected vertebrates and try to point out directions further studies might take.

MIGRATION AND DIAPAUSE

Many insects which breed in the temperate zone overwinter by entering a state of developmental arrest known as diapause which is usually cued by photoperiod. In some species such as the coccinellid beetle *Hippodamia convergens* there may also be a quiescent period over a summer dry season. In either case the inactive state is passed in a protected site, and there are often migratory movements to and from such sites so that migration and diapause combine for added life cycle flexibility. These movements may be quite local or, as in the case of *Hippodamia* (Hagen 1962), the milkweed bug *Oncopeltus fasciatus* (Dingle 1978) and the monarch butterfly *Danaus plexippus*, they may cover considerable distances. The extreme case of migration to a diapause site is that of the northeastern North American population of the monarch butterfly which may migrate several thousands of kilometers to overwinter in the volcanic plateau of central Mexico (Brower, this volume).

Whether movement occurs over short or long distances, the pattern of the migration-diapause relationship is generally similar. An example is the well-studied case of the seed bug Lygaeus equestris on the Baltic island of Gotland (Solbreck 1972, 1976, this volume; Solbreck and Sillèn-Tullberg 1981). In the fall, adults migrate to diapause sites in sheltered rock out-croppings and around stone buildings. During the overwintering period, energy is provided from an enlarged fat body which shrinks as reserves are metabolized, and the ovaries are undeveloped. As the winter progresses, the insects become more susceptible to stimulation of the reproductive system by warm temperatures, and diapause is essentially ended by January with the insects remaining dormant as a consequence of the extreme cold. The bugs also become more sensitive to stimuli inducing flight as has also been found in the ladybird beetle Coleomegilla maculata (Solbreck 1974). With spring warming in May, there is emergence from the diapause site and migration to host plants in the surrounding terrain. Under the stimulus of feeding, the ovaries mature, and the bugs produce the new generation which will diapause the following winter, although in warm years a partial second generation can be produced. The "decision" to diapause involves a delay in reproduction but results in the benefit of winter survival. There are thus lifecycle trade-offs which involve migration, diapause and reproduction.

A direct relationship between migration and diapause has been demonstrated for the milkweed bug Oncopeltus fasciatus (Dingle 1978). Like the monarch butterfly, O. fasciatus invades northern latitudes in the spring and produces up to three summer generations depending on location and climate. The bugs are unable to tolerate temperate zone winters with long periods of subfreezing temperatures; rather, the evidence suggests that they return south (Dingle 1981). This return movement is facilitated by a short-day diapause which occurs in the adult (Dingle 1974) and results in the cessation of reproduction. Using tethered flight, we have demonstrated that the bugs can migrate throughout the diapause period, whereas under summer conditions, migration ceases 2-3 weeks after adult eclosion when reproduction is initiated (Dingle 1978). Diapause may last 60 days or more at 23°C, giving the insects ample time to migrate considerable distances. As with the monarch butterfly and L. equestris, migration and diapause result in delayed reproduction, but with the alternative gain of escape to more favorable conditions for overwintering (and in O. fasciatus, reproduction). The monarch and O. fasciatus are each the only members of tropical groups to invade the temperate zone, and it seems likely that the evolution of a migration-diapause system made this possible (Tauber and Tauber 1976; Dingle 1978; Brower, this volume). If so, this is an important link between the two behaviors and further emphasizes the importance of overall life-history pattern.

A further case of an intimate relation between an adult reproductive diapause and migration occurs in the cotton stainer bugs *Dysdercus* spp. which migrate entirely within the tropics. These insects feed on the seeds of various Malvales and undertake migrations to exploit seasonally available resources, usually at the beginning of the dry season (Dingle and Arora 1973; Derr 1980a, b; Dingle 1982). Migrations occur during periods of food or water shortage, when females delay reproduction (diapause) and retain wing muscles; when a suitable host plant with ripe seeds is found, feeding commences, wing muscles are histolyzed and egg development is initiated. The more migratory species are larger and show more rapid early reproduction (Derr, Alden and Dingle 1981) which suggests a life history strategy adapted for colonization.

The nature of life history variation in the New World Dysdercus bimaculatus was examined by Derr (1980b) under conditions of plentiful food and water and under water stress. The latter was chosen as an environmental variable, since water is necessary for feeding in these seed-sucking bugs, and its availability determines whether the bugs migrate or histolyze wing muscles and reproduce locally. The level of environmental moisture stress varies among the host trees (Sterculia), and response to stress varies among females. Individuals thus face considerable uncertainty and a number of options for reproduction in time and space. In the nonstressful environment, heritability estimates for characters having to do with timing (age at first reproduction, inter-clutch interval) were not significantly different from zero, while those relating to fecundity (e.g., clutch size) were estimated at around 0.30 (i.e., about 30% of the variance for the trait was additive genetic variance or that variance contributing directly to parent-offspring resemblance and hence sensitive to selection). In the stressful and more uncertain environment, heritability for age at first reproduction was also around 0.30; in contrast to favorable environments, the environmental uncertainty associated with water stress seemed to maintain greater additive genetic variance. Even more interesting, age at first reproduction was not associated with other life history traits in any predictable way; division of the females into early and late reproducers did not result in division on the basis of any other traits. I shall return to this lack of association between age at first reproduction and other life history traits below. It will suffice to note here that the association between the starvation diapause of Dysdercus and migration involves both phenotypic and genetic complexity (see review in Dingle 1984).

MIGRATION AND WING FORM

Many insects have evolved wing polymorphism (genetic) or wing polyphenism (environmental) in response to habitat variation (see Dingle 1980 for review and Zera, this volume, for a discussion of the genetics). In general, species or populations from isolated sites (e.g., mountaintops, bogs) and lusher more stable habitats are brachypterous or apterous, while those from harsher or more temporary conditions are macropterous. In a well-studied example, Vepsäläinen (1978) has shown that European gerrid bugs (Hemiptera: Gerridae) run the gamut from fully winged to wingless with a range of intermediate populations and species displaying polymorphic

and/or polyphenic combinations. An interesting exception to the general rule seems to be the absence of wing morph variation in many of the temperate zone arboreal phytophagous Hemiptera (Waloff 1983). These are fully winged even in lush permanent habitats, probably because flight provides the most efficient locomotory mechanism for moving about in trees, which are large and architecturally complex.

The advantage of flight to escape unfavorable habitats and to colonize favorable ones is obvious, but what are the advantages of winglessness given that it forces the insect to remain sedentary? The reasonable consensus seems to be that in the absence of wings and associated flight muscles, more energy can be channeled to reproduction (see also Zera, this volume). The occurrence of post-flight wing muscle histolysis in many species is consistent with this view. For some species, however, the evidence is not always obvious. Denno (this volume), for example, finds little difference in the life histories of the two morphs of the planthopper *Prokelisia marginata*, and there are similar results from other insects (Dingle 1982).

In the species where there is reproductive benefit, this seems to take two forms (Dingle 1982; Zera, this volume). First, flightless individuals are more fecund, and secondly, they also reproduce earlier (note that there is some tendency for earlier reproduction in Denno's *Prokelisia*). The latter trait especially allows more rapid population growth and a greater contribution by the individual female to future generations (Stearns 1976). An example of the generally greater fecundity of apterous aphids is shown in Figure 1 which compares morphs in *Sitobion avenae* and *Metapolophium dirhodum* studied by Wratten (1977). In both cases, there is greater production of nymphs by apterae of these viviparous aphids across all age classes. Apterae tend to be larger than alates, but the differences hold even when the data are corrected for size. In some cases apterae can produce almost double the number of young when compared to alates, so that production of alates does indeed involve life history trade-offs.

In aphids the switch to alate production generally results from crowding and is thus an environmental effect. But in the pea aphid *Acyrthosiphon pisum* (Lamb and MacKay 1979) and undoubtedly others, there are genetic influences which arise from differences among clones. These differences occur in the proportion of winged forms produced under a standard crowding stimulus. Clones sampled from the periphery of alfalfa fields or from isolated fields produced a smaller proportion of alates than those sampled from the centers of fields, probably because they lost more migrants than they received. Clonal differences were consistent across generations. The varying degrees of selection for migration on aphid clones produce populations that are both genetically and phenotypically flexible with respect to migration, and the two morphs provide specialization for the productive and migratory aspects of life histories, respectively. Similar strategies are also evident in other wing polymorphic or polyphenic insects (Dingle 1982).



Figure 1

Reproduction (means \pm s.e.) in the aphids Sitobion avenae and Metapolophium dirhodum over the major portion of adult life. Open bars are apterae, hatched bars alatae. Note greater nymph production by apterae of both species. Data from Wratten (1977).

MIGRATION-LIFE HISTORY SYNDROMES

Since migration is likely to involve colonization of new habitats (or empty habitats in the case of return to breeding areas), selection should produce complex adaptations which include both the ability to migrate and the ability to colonize, and which persist in the new environment (Simberloff 1981). The life history characters which best promote colonization and persistence are early and rapid reproduction (Safriel and Ritte 1980), and indeed migrant colonizers are often described as "r-selected" as a consequence of these characteristics (Stearns 1976). These traits are phenotypically correlated with migration, but the important issue for evolutionary biologists is the extent to which the phenotypic correlations contributing to successful colonization are genetically based (Dingle 1984, in press).

We (Hegmann and Dingle 1982) undertook a three year study of half-sib and full-sib families in milkweed bugs (*Oncopeltus fasciatus*) to examine this issue. The genetic correlation matrix resulting from that study indicated strong positive genetic correlations among size, fecundity, and development rates. In other words the syndrome of large, rapidly developing and fecund bugs was based on genes shared by these traits. A further interesting result was the failure to demonstrate a correlation between age at first reproduction and any of the other characters (see Derr's results for *Dysdercus* discussed above). The follow-up study, using selection for wing length to assess genetic correlation structure, is reported by Palmer elsewhere in this volume. Palmer's results confirm the results of the sib-analysis and also demonstrate a positive genetic correlation between flight and the size and fecundity measures, supporting predictions concerning a migration-life history syndrome.

A life history syndrome involving migration has similarly been demonstrated in *Tribolium castaneum* by Lavie and Ritte (1978) and Wu (1981). They used movement between vials of flour in laboratory experiments as an index of migration ("dispersal" in their terminology). In both cases "dispersing" and "nondispersing" lines of beetles were generated by selection and examined for correlated life history traits. The summary of the results in Table 1 clearly shows the existence of positive correlations between migration and production characteristics as might be expected for colonizers. The "high dispersal" line consisted of larger beetles which produced more and larger eggs after developing more rapidly. Wu also selected successfully for high and low "dispersal" in the related *T. confusum*, a more sedentary species. In the latter case Wu was unable to demonstrate positive correlations between production and migration, suggesting that the colonization syndrome was characteristic only of the more migratory species, *T. castaneum*.

The migration-colonization syndrome in some insects may also involve a direct influence of flight on reproduction (Dingle 1985). In alates of the black bean aphid Aphis fabae for example, flight induces settling and larvi-position responses (Kennedy and Booth 1963a, b). In this species reproduction by alates is greatly delayed if no flight occurs. In the frit fly Oscinella frit, flight shortened the pre-oviposition period by as much as three days, with the effect more pronounced in younger females (Rygg 1966). Similarly the pre-oviposition period was shortened by approximately five days in Oncopeltus fasciatus by bouts of tethered flight (Slansky 1980). In an interesting experimental study of the relation between wing polymorphism and egg production in the cricket Pteronemobius taprobanensis, Tanaka (1976) found that micropters began laying eggs earlier and produced more eggs than macropters. But macropters of this insect frequently lose the wings after flight. Tanaka also found that artificially dealating macropters resulted in increased egg production. There is thus apparently feedback from the wing form to the ovary, although just how this is mediated remains to be discovered. Suffice to say that there is a significant behavior component (phenotypic) to the enhanced reproduction that occurs in migratory populations or species.

VERTEBRATE MIGRATION AND LIFE HISTORIES

With their relatively large sizes and long generation times, vertebrates have not proved as amenable to the study of migration-life history patterns as have insects, but there has been considerable recent progress (reviewed in Dingle 1980). This progress has been most evident in studies of fish and some of the important current work is summarized in papers in this volume (e.g., Dodson, Leggett, Quinn). Fish migration from the sea to fresh water rivers in particular is apt to involve considerable energy expenditure with concomitant trade-offs which involve reproduction. Schaffer and Elson (1975) examined migration in the Atlantic salmon (*Salmo salar*) from an energetic and life history perspective and made several predictions. The first of these was that long, fast rivers in which high energy expenditure is required to reach

Table 1

Comparison of life history traits in the flour beetle *Tribolium castaneum* between lines selected for high and low migration rates. Data from Wu (1981); egg production data from Lavie and Ritte (1978). All differences between lines are statistically significant.

Character	High migration line	Low migration line	
Migration rate ¹	6.83	1.59	
Development time ²	29.03	30.51	
Egg production in 4 day period	47.8 ± 1.8	42.2 ± 1.8	
Egg length (mm)	0.601	0.586	
Body weight (mg)	22.6	19.7	

¹ Mean number of vials traversed in generation 17

² Median number of days from egg to adult

spawning grounds would select for a longer feeding period at sea to provide energy for the spawning run and delayed reproduction as a consequence. Secondly, they predicted that rapid growth at sea subsequent to the age at first possible spawning (increased growth and future return per unit effort) should be characterized by relatively delayed spawning. Finally, high year-to-year variation in juvenile survival should result in selection for adults spawning at different ages, i.e., individuals should "bet-hedge" by producing offspring with high variances for age at first reproduction. These predictions generally held for rivers in eastern Canada and demonstrated the importance of phenotypic correlations between migration and life table characters.

Life histories with respect to migration have also been studied in the American shad *Alosa sapidissima* (Carscadden and Leggett 1975, Shoubridge 1977). In the St. John's River in Florida, environmental variance is low with relatively high temperatures optimal for juvenile survival over a long period. The high temperatures are, however, a stress for adults because they result in high energy expenditure during the upriver spawning migration. This population is semelparous with a high fecundity of 412,000 eggs per spawning. In contrast in the Miramichi River in New Brunswick, environmental variance is high and the generally low temperatures reduce the energetic cost of migration but increase mortality of juveniles. Here iteroparity is the rule with delayed age at first reproduction and total fecundities of only some 266,000 eggs per lifetime. Variation was also noted as a function of river length; longer rivers create greater risks for adults and tend to select for semelparity. Long Pacific rivers may have been a major factor selecting for the general pattern of semelparity seen in Pacific salmon (*Oncorhynchus* spp.; see also Quinn, this volume).

Region	Ratio Adult/Juvenile Survival	Reproduction	Environmental Variance*	Maturity	Fecundity
North					
Atlantic	High	Iteroparous	High	Delayed	Low
South					
Atlantic	Low	Semelparous	Low	Early	High
Pacific					
(Introduced)	High	Iteroparous	Low	Early	High

 Table 2

 Life histories of migratory shad (Alosa sapidissima) in North American rivers.

 Data from Shoubridge (1977).

*Primary effect is on juvenile survival

On the west coast of North America, shad were introduced in the late 19th century, and there has been rapid evolution of migration and life history patterns. These shad came from the Hudson, Potomac and Susquehanna Rivers where 20 to 40% of the adults are repeat spawners, age at maturity is about 4 years for males and 4.6 years for females, and lifetime fecundity is on the order of 300,000 to 350,000 eggs. The Pacific Rivers where these fish were introduced display a much wider range of conditions, reflected in the life histories of the respective populations. Here 32 to 77% of the females are repeat spawners, age at maturity is from 3.3 to 3.8 years for males and 4.0 to 4.5 for females, and lifetime fecundities range from 321,000 to 500,000 eggs. The life histories of Atlantic and Pacific shad are briefly compared in Table 2. The rapid evolution of differences suggests strong local selection pressures and considerable genetic variance for the traits. We do not know the extent of possible genetic, developmental or environmental correlations, and these would be well worth studying.

There are also some recent efforts to analyze bird migration and its relation to life histories. Andersson (1980) examined the occurrence of nomadism which he defined as the tendency for both adults and juveniles to wander widely in search of food and for the adults to settle and breed where food is locally abundant. This behavior contrasts to the more usual case where breeding occurs at the same location from year to year. Both theoretical considerations and empirical data suggest that nomadism is more likely with cyclic rather than random fluctuations in food abundance. Given cyclic food production, nomadism is favored in birds with large clutches and a higher ratio of juvenile to adult survival. Birds with large clutches also tend to mature earlier and the combination of the two factors constitutes a good colonization "strategy," as described above for insects. The pattern is characteristic of, for example, snowy owls which also depend on cyclic food resources (lemmings) and are well known for their irruptive movements. A summary of Andersson's

Factors	Examples
Cyclic resource fluctuation	High arctic, Australian deserts
Long intervals between good years	Seed crops of boreal trees
High Juvenile : adult survival ratio	
Large clutches	Snowy and short-eared owls 8–10 eggs) vs. jaegers (2 eggs)

 Table 3

 Factors favoring adult nomadism in birds (after Andersson 1980).

conclusions, with some examples, is given in Table 3.

A second example from bird life histories comes from long-term studies of populations of the European great tit (Parus major) in England and Holland (summarized in Table 4). These populations were nonmigratory, but the young do disperse to breed away from the territories on which they were raised. Heritability estimates of an array of life history traits (Table 4) indicate relatively high proportions of additive genetic variance, suggesting that these traits would respond quite rapidly to selection. About 60% of the variance for dispersal, for example, is the result of additive genetic influences; offspring, in other words, display dispersal patterns very similar to those of their parents. As in the case of fish discussed above, what we do not know is the genetic correlation structure. However, the heritability estimates certainly suggest that they would repay study. Are the high genetic variances observed (see also Berthold, this volume) associated with high genetic covariances? If so, which traits are involved, and does the covariance structure suggest a life history-dispersal syndrome (in the tits) or a migration-life history syndrome in migrants? If the insect data are any guide, we might predict a positive association between migration and clutch size (see also Andersson's analysis in Table 3) since this would be a good colonizing strategy, but no association between migration and onset of laying, indicating behavioral flexibility in the face of environmental variance (see below). Data on the extent of these covariances should give a new perspective to the "why" questions of bird migration (Dingle 1980). The apparent presence of large genetic components of migratory behavior in "true" migrants (Biebach 1983; Berthold, this volume) suggests that questions about migratory strategies in birds, although by no means easy to answer, are now tractable.

Similar studies of life history syndromes should also be profitable with small mammals. Certainly there is a genetic component to dispersal behavior (Krebs, Gaínes, Keller, Myers and Tamarin 1973; Rasmuson, Rasmuson and Nygren 1977), and life history differences occur between migratory ("dispersing") and nonmigratory populations (Sullivan 1977; Tamarin 1977a,b). For a full analysis, what we now need to know is whether the phenotypic associations have a basis in a genetic correlation structure.

Trait	Heritability (h^2)	Source
Body weight	0.59-0.72	van Noordwijk et al. 1980
Clutch size	0.37-0.38 0.48	van Noordwijk et al. 1980 Perrins and Jones 1974
Onset of laying	0.14 0.30 0.18-0.45	Jones 1973 van Noordwijk et al. 1980 van Noordwijk et al. 1981
Dispersal distance	0.56-0.62	Greenwood et al. 1979

 Table 4

 Heritability estimates for various life history traits in British and Dutch populations of the great tit (*Parus major*).

DISCUSSION AND CONCLUSIONS

The importance of migration to life histories means that a complete understanding of *why* animals migrate must place migratory behavior in the context of overall fitness. This in turn means consideration of reproduction and survival characteristics associated with migration. The data I have cited imply that the association may have a particular structure based on an array of genetic and phenotypic correlations with other traits of the life history. The net result is a "syndrome" or "strategy" adapted, within the constraints imposed by environment, development and phylogeny, for migration and colonization. Migration brings flexibility to life histories and fitness functions and is important to the continuum which connects proximate and ultimate aspects of adaptation (Leggett, this volume).

The evolution of migration strategies depends on both the environment, which determines selection pressures, and on the underlying genetic and developmental structures, which determine the response to selection. While not ignoring the former, my focus here has been on the latter. The presence of significant components of additive genetic variance for migration and life history traits, e.g., Table 4, indicates that considerable response to selection in these traits is possible. But more importantly, genetic correlations among traits, e.g., Table 1 and Palmer (this volume), indicate that responses do not occur in isolation, but rather that selection on one trait can also result in responses in others. In other words clusters of traits will evolve together producing complex adaptations or "strategies." I have focused on correlations with life histories, but there are other potentially important correlations as well. What, for example, is the genetic basis for orientation and navigation, and does it contribute to the structure of migration syndromes as outlined here?

One particularly interesting aspect of insect life history strategies revealed by the available studies is the apparent lack of correlation between age at first reproduction and other traits as seen in *Oncopeltus* (Hegmann and Dingle 1982, Dingle 1984) and *Dysdercus* (Derr 1980b). Age at first reproduction (α) has repeatedly been shown to

display high proportions of additive genetic variance in uncertain environments (review in Dingle 1984) allowing a range of responses which function like a "genetic rheostat" (Dingle, Brown and Hegmann 1977). To understand why a good migration strategy might not include correlation of a variable α with other traits, consider the consequences of strong genetic correlations. If these were present, variation in α could cause detrimental variation in the traits with which it was correlated (whether positively or negatively). Conversely, α might be prevented from varying (and hence from responding flexibly) if a large negative correlation with another character made it impossible for natural selection to alter both in the same direction. This would represent a cost in terms of flexibility (a "cost of correlation"), and might select for independence of α from other traits. A number of traits such as the timing of migratory movement might similarly be independent. The possible generality of such relationships across taxa seems very much an area ripe for investigation. These points are elaborated further in Dingle (1984).

A second interesting aspect of insect life histories is the maintenance of wing polymorphism. In the usual situation apterous or brachypterous morphs of low mobility and high reproductive potential are present under stable conditions, while macropterous forms of high mortality and lower reproductive performance serve for migration to different habitats when conditions deteriorate. Life cycle trade-offs are partitioned between the morphs. Gene differences occur in the thresholds for wing production (Lamb and McKay 1979; Zera, this volume), but we know essentially nothing of the association of thresholds with other life history traits either phenotypically or genetically. Are there, for example, trait associations with low threshold for macroptery similar to associations between migration and life history characters in other insects (e.g., *Oncopeltus*), or are there differences in the wing polymorphic species? The presence of such clear alternative strategies would seem to make insects particularly attractive organisms for probing the "why questions" of migration.

An important task for the evolutionary ecologist is the determination of the structure or "architecture" of genetic and phenotypic correlations and the prediction of the course evolution will take. Studies of migration are thus fertile fields for analysis of important evolutionary questions as I suggested at the beginning of this paper. It is a mark of our progress in studies of migration that the questions have been defined; it is a measure of our task that their analysis has barely begun.

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