

EXPLORING MIGRATION AND LIFE HISTORIES

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Abstract

Questions: What traits define migration and what sorts of life history syndromes are found among migrants.

Organisms: Seed bugs, grasshoppers, and Southern Hemisphere birds.

Data description: In seed bugs (*Oncopeltus*, *Jadera*) there are migration syndromes that involve genetic correlations among behavioral, morphological, physiological, and life history traits. These syndromes include flight polymorphisms and polyphenisms. In cases where host plants provide strong selection, these bugs can evolve syndromes that include life history, morphological, and other adaptations in less than 100 generations. Studies of grasshoppers reveal that microhabitat choice and behavior may allow individual insects considerable control over their own life history traits. Southern Hemisphere bird migration is particularly responsive to aridity and relatively mild climates. It displays a variety of patterns and processes other than classic round-trips that may provide insight into the evolution of migration and migration ecology.

Search method: A lifetime of experimental and field study of migratory animals.

Conclusions: A full understanding of migration and its implications requires knowledge of diverse taxa and contributions from several biological disciplines. Such understanding is not served well by overspecialization with respect to either taxon or field of study.

Incipient Ecologist

Larry is quite right that much research in ecology is born of a fascination with nature. My own fascination began very early and in the tropics. I was born in 1936 on the island of Penang, then one of the Straits Settlements (with Melaka and Singapore) of the British Crown Colony of Malaya. My parents had met in Bangkok, where my mother, an American born in India, was head of the nursing school at the Royal Siriraj Hospital, and my father, an Englishman from Derby, worked for Shell Oil. My mother had been posted to Bangkok from the University of Michigan Hospital where she was the head nurse in pediatrics and helping to support her younger brother who was working toward a degree in Botany. When my father was transferred by Shell to Penang, my mother resigned her position to marry and join him. There was no feminist movement in those days, but Mother always made it clear that this was her choice. She was very independent. And to the extent that I bear the independence Larry attributes to me, I have no doubt it comes from her.

Penang and Malaya were attractive and cosmopolitan in those days, in spite of the flaws inherent in even a benign colonialism. Both the charm and the flaws have been captured well by Margaret Shennan (2000) in her book on the era. I was too young to remember my first three years spent in Penang, with a six month “home leave” to Britain, but photos of me at the time do reveal what is perhaps euphemistically called an “independent streak.” My first firm memories are as a late three and early four year old when we lived in Kuala Lumpur. There two tortoises roamed the large tropical garden on their long leashes, tadpoles in the ditch across the road were a source of fascination, and a bull mastiff mix and a seal point Siamese provided domestic company. A few months

before my fifth birthday we moved to another large colonial house and garden in Melaka accompanied by the transportable menagerie. The property was located across the road from miles of beach on the Straits of Melaka, regularly patrolled by fishermen with their throw nets. For a near five year old addicted to anything living this was a paradise. I spent my days roaming the beach begging ikan (fish in Malay) too small to be edible from the fisherman and exploring nearby forested pools where freshwater fish were harvested. I soon acquired two large outdoor tubs filled, respectively, with fresh- and salt water fish and delighted in watching them while sitting on the kitchen steps with a glass of fresh limeade and in the company of two pet ducklings.

The predilection for keeping animals has lasted throughout my life and has been inherited by our three daughters. Notable examples were an American badger and two sets of African bush babies or galagos. The badger we acquired for a summer when our oldest daughter agreed to tame it for a neighbor who was a wildlife photographer for Disney. It made a wonderful pet and would follow us around the neighborhood. It had a major drawback, however, because it could dig up the entire garden in about 10 minutes. Eventually we had to donate it to the Des Moines, Iowa Zoo. The bush babies were endlessly entertaining when we let them loose in the house in the evening (they are nocturnal). They loved visitors, including Larry when he came to Iowa City for a seminar. To the delight of us all, our bush baby bounced onto Larry's shoulder, urinated on its hands in bush baby fashion, and proceeded happily and intensely to groom Larry's ear.

Our pleasant tropical life in Melaka ended when the tsunami of World War II rolled over Malaya. My father had joined the Straits Settlement Volunteers and was

posted to Singapore shortly after my fifth birthday in November, 1941. At the end of the month my mother and I left Melaka to join him, feeling horribly guilty and depressed at leaving our household staff who had been fiercely loyal to my parents since the first days in Penang. Scarcely had we arrived in Singapore and billeted with friends when the Japanese invaded Malaya. For us this was signaled by a bombing raid in the pre-dawn of 8 December, a few hours after the bombing of Pearl Harbor on the other side of the International Dateline. For the first few nights of Japanese bombing we had no air raid shelter but repaired to a cement lined ditch infested with biting ants. We later had a proper shelter dug in the back of the garden and roofed over.

My father then made what had to be the most agonizing decision to get my mother and me out of Singapore as soon as possible. I still remember driving to the docks as dawn streaked the sky on 15 January 1942 and, too young to fully understand, the sense of adventure when our ship, the P & O liner Narkunda, set sail. We found out only after departing that we were bound for Fremantle, Australia where we arrived a week later. Singapore fell on 15 February, and my father was captured along with the thousands of other British, Australian and colonial troops. He died on the Burma Railway in 1943.

When we heard from friends who had escaped from Singapore that my father was a prisoner, my mother decided we should spend the war in America. This was possible because her American passport allowed us to board the SS Island Mail, returning to the U.S. after arriving in Australia with Task Force 6814, the first American military and supply convoy to Australia following the outbreak of the war. My grandfather and two of my aunts were in Wooster, Ohio, and we made our way there from San Francisco where

we landed from Australia. A year later we moved to Cleveland where my mother took a job as a live-in nurse at University School, a private K-12 boys school in the suburb of Shaker Heights.

The school had an arboretum on its large property, and I would go there to play other boys and often on my own to watch the birds and small mammals that occurred there. I identified birds like Baltimore orioles and rose-breasted grosbeaks easily enough, but one spring when I was 11, a small black, yellow, and white bird was beyond my capabilities. On making inquiries, I was directed to the 5th grade master who produced a Peterson Field Guide. I described the bird, we leafed through the pages, and there it was – a magnolia warbler. I have been hooked on birdwatching ever since, and at least since that day I have wanted to be what I later discovered was an ecologist.

We remained in Cleveland until 1949 when we moved to Princeton, New Jersey where I completed high school. There were two highlights of the Princeton years with respect to my growing biological interests. First, through my high school biology teacher, Bill Alston, I met Charles H. Rogers, who was semi-retired at Princeton University after a career with the pioneering ornithology group at the American Museum of Natural History in New York. He took me with him on Christmas bird counts and introduced me to long-term studies of populations. The second highlight was my introduction to the American West in the summer of 1952 on a driving trip with my mother. We traveled over Wyoming and Colorado and visited Gordon Alexander and his family and my uncle Ted Porter, Aunt Marj and my cousins. Gordon was an old friend from Thailand and was head of the Biology Department at the University of Colorado, and my Uncle Ted was a

Botany professor at the University of Wyoming. Both introduced me to aspects of the fauna and flora of the West and the topography of the Rocky Mountains and the Basin and Range country.

My formal education in biology began when I went to Cornell in the autumn of 1954. My Honors adviser at Cornell was LaMont Cole who was in the process of producing his two best known papers (Cole, 1954, 1957). “Cole’s result” (1954) that age at first reproduction had a greater impact than increasing fecundity on population increase has reverberated through population biology and my own studies to this day. The “biological clock” in the unicorn (1957) was a cautionary tale about manipulating and analyzing data. My honors project on the effect of UV radiation on countershaded animals was notable only in showing me that good research required care and thought. One of my summers at Cornell was spent tending the bird menagerie of the ornithologist Charles Sibley, and the work convinced me that given what was known at the time about rearing in captivity, birds were not the best animals for experimental studies, especially if large sample sizes were required. Their value for field studies was then, and is now, undeniable. In my senior year Bill van der Kloot taught me that studying behavior and evolution was worthwhile, and my intellectual life began to come together.

Becoming a behavioral ecologist

LaMont Cole suggested two graduate programs to me, Yale and Michigan. I visited each, had a delightful chat with Evelyn Hutchinson at Yale, but a meeting with Larry over coffee in Ann Arbor convinced me that Michigan was where I wanted to go. It would be too glib to point to a single factor in my decision, but I was impressed and a bit

dazzled by Larry's ability to put problems in a fresh and imaginative way. My PhD thesis was on orientation in boxelder bugs, *Boisea (Leptocoris) trivittatus*, as Larry has outlined. I also dabbled in some other problems like locomotory reflexes in water bugs (Dingle, 1961) and in a summer at Woods Hole, the color responses of marine planktonic crustaceans (Dingle, 1962), in searching for ways to combine behavior, ecology, and evolution into a career. Larry's notions on movement in hydras and his elucidation of the implications of Fisher's "reproductive value" for evolving life histories were stored in my growing arsenal of developing ideas to re-surface later. The summer after the completion of my PhD in 1962, I spent at the Bermuda Biological Station with Don Maynard. This gave me the chance to begin studying the agonistic behavior of stomatopod crustaceans which continued for 20 years. These are fascinating animals with interesting behavior, movable eyestalks, complex vision based on 12 types of color receptors, and communication by fluorescent pigments (Caldwell and Dingle, 1976; Dingle, 1983; Marshall et al., 2003). In the interest of reasonable length I'll say no more about them here. Research on their behavior and vision continues in the capable hands of my student and colleague Roy Caldwell of UC Berkeley and his students and co-workers.

While at Michigan fellow graduate student Adrian Wenner introduced me to a paper by J. S. Kennedy (1958) on the flight behavior of migratory aphids (*Aphis fabae*). Kennedy was a brilliant experimentalist who made several contributions to insect behavior (Brady, 199_). In the 1958 paper he used a "flight chamber" to demonstrate the behavioral interactions between take-off, flight duration, and settling behavior that determine the migratory characteristics of these aphids and demonstrated that migration is an analyzable behavioral syndrome. It was also a penetrating critique of the ethological

models then in vogue for explaining “instinctive” behavior, because it took a behavior previously “explained” with an ethological model by other workers on aphids, demonstrated the failure of that model, and demonstrated with experiments and hypotheses how an alternative model could account for the behavior. None of the other critiques of ethology, such as those by American psychologists, could make this claim. Kennedy’s paper and the more detailed experimental papers that followed (summarized in Kennedy, 1966 and Dingle, 1996) were ignored by ethologists. For me the 1958 paper was a revelation: migration could be analyzed experimentally, and its role in the life histories of individuals and the resultant consequences for the biology of populations could be assessed. Supported by an NSF Postdoctoral Fellowship, my wife Jeri, whom I had met at Michigan, our new daughter, and I set off for the U.K. in the autumn of 1962 to work with John Kennedy at Cambridge. This began a lifetime of study on migratory organisms.

Evolution of migratory syndromes

Migration can be a long distance, round trip event especially in vertebrates, and biologists have tended to focus on the spectacular nature of the phenomenon in “charismatic megafauna” (Dingle and Drake, 2007). Definitions of the behavior have often been in terms of the populations making these movements. Thus Newton (2003) defined migration “...as a large- scale return movement of a population which occurs each year between regular breeding and wintering (or non-breeding) areas.” There are problems with this view. First, migration is defined in terms of populations so that its evolution would require group selection acting on populations. Second, the definition

does not fit most migrants. Few insects display round trips and most migrate within a season. Even in birds there are species like the Queleas of Africa that breed in different places both in the same year and in different years (Cheke and Tratalos, 2007) or that migrate but once on a lifetime like African black oystercatchers (Hockey et al., 2003). Finally, many seasonal, long distance, round trip movements like those of albatrosses and petrels between nesting and feeding grounds are clearly foraging commutes and not migratory (e.g. Jouventin and Weimerskirch, 1990). What is needed is a definition of migration that incorporates a clear understanding of the phenomenon as a behavior of individuals, sets the criteria for determining whether an individual is a migrant, and excludes movements that even if extraordinary do not constitute migration. Only in this way can it become clear how natural selection will act to produce different kinds of movement (Dingle, 1996, 2006; Dingle and Drake, 2007).

The distinct nature of migratory behavior was outlined by Kennedy in a series of papers in the 1960's (summarized in Kennedy 1966, 1985; and Dingle, 1996) reporting on careful experiments with aphids. Kennedy's flight chamber allowed him to monitor and control the migratory behavior of free flying aphids. He could determine the strength and duration of flight, the factors that initiated it, the influence of flight duration and sensory inputs on strength of settling and larviposition, and the reciprocal inhibiting and priming effects of settling and migratory flight on each other. From these experiments Kennedy defined migration to consist of persistent and straightened out movement (which could be wind or current aided) combined with temporary inhibition of maintenance behaviors like feeding or mating, but with priming of the appropriate maintenance responses at the termination of migration (see Kennedy 1985; Dingle, 2006;

or Dingle and Drake, 2007 for a formal statement of the definition). The undistracted nature of migratory movement caused by the inhibition of maintenance responses has been noted for many migrants (cf. Table 17-1 in Dingle, 1996).

Kennedy's careful definition allows one to determine, at least in principle, whether a given individual is a migrant by designing the appropriate test. Thus when hydra release and float in response to crowding and low food (Lomnicki and Slobodkin, 1966), do they initially bypass an area of food, in which case they are probably migranys, or do they attach at the first detection of food or space, in which case they are likely to be foragers? The question is not trivial or merely semantic. If it is the case that crowding and low food occur over a wide area (analogous to the deterioration of a seasonal habitat for a migratory bird), natural selection should act against a response to first contact with either empty space or a food item because this would probably not signal a suitable new habitat, but rather only an atypical favorable patch in the unsuitable present one. Crowding in hydra may be a surrogate for habitat deterioration, as it is in aphids. It could therefore serve as a pre-emptive stimulus like photoperiod, a well known trigger for departure in many migrants (Dingle and Drake, 2007). Indeed pre-emption is a characteristic of most migrations. The movement of individuals results in a shift in space of the population, and this shift is an *outcome* of migration (Gatehouse, 1987), and this ecological outcome feeds back on the behavior of individuals through natural selection (Drake et al., 1995; Dingle and Drake, 2007).

When I arrived in Cambridge my first task was finding a suitable insect for the analysis of migration. Fortunately the North American milkweed bug, *Oncopeltus fasciatus*, was in culture with the V.B. Wigglesworth research group at Cambridge, and

this insect proved a superb research subject. Like most “seed bugs” it can be easily reared on the seeds of its host plants, various species of milkweeds (*Asclepias*) in this case., and otherwise takes readily to laboratory life. In the first instance it (and mealworms, *Tenebrio*) proved handy for addressing some questions emanating from my thesis (Dingle, 1964, 1965a). But what drew most of my effort at Cambridge was a successful attempt to analyze migration in milkweed bugs. A search of the available literature suggested it was probably migratory. Our later work showed this was indeed so; it has a seasonal migratory cycle similar to that of another milkweed specialist, the monarch butterfly (Brower, 1995).

I studied migration by taking advantage of an insect flight reflex. When lifted from the substrate with a thread or small stick attached to the pronotum, most insects will begin to fly (or swim in the case of aquatic species (Dingle, 1961)). Johnson (1960, 1963) had described an “öogenesis-flight syndrome” whereby insects engaged in migration post-tenerally after cuticle hardening and generally before they began to reproduce. Using tethered flight, and by rearing milkweed bugs under controlled conditions and noting age and reproduction, I was able to show that these insects dramatically increased the number of long duration flights at the end of the teneral period, and that these rapidly decreased in frequency and duration following the onset of reproduction, exactly as would be expected of a migrant (Dingle, 1965b, 1966). Later my students, postdocs, and I were able to show that migration in milkweed bugs, like that in Kennedy’s aphids, was programmed by interactions between flight and maintenance, mediated by circadian rhythms (Caldwell and Dingle, 1967; Rankin et al., 1972; Slansky, 1980; Alden et al., 1983).

The evolution of a reproductive-flight syndrome in migratory insects makes sense in terms of life history “strategies.” Most insect migrations result in colonizing an empty and favorable habitat at the termination of migratory flight. Under these circumstances selection should favor those individuals that maximize reproductive output by placing “all eggs in the new basket.” This follows from Fisher’s reproductive value (Slobodkin 1961, 2003). The relationship prompted what became a research program assessing the evolution of migration and life history syndromes.

It is a truism in evolutionary biology that traits do not evolve in isolation but in a coordinated way with other characters that may include behavior, physiology, morphology, development, and life history. These correlated traits are the targets of selection and evolve together to make adaptations “work” (Frazzetta, 1975). Syndromes may occur within one level of organization such as morphology, or across levels as is the case with migratory behavior and life history programming. They may also vary with situation as in spring or fall for a migrant (Sih et al., 2004). Syndromes have some interesting consequences. First, there may be trade-offs among traits; with migration, for example, energy for flight muscle is not available for reproduction (of which more below). Second, such trade-offs could maintain variation in both phenotype and genotype, for example by masking the expression of some traits so they are not exposed to selection. Third, selection acts on both the direction and strength of correlations among traits as well as on the traits themselves. Thus it is necessary to understand genes, genetic architecture, environments, and their interactions in molding syndromes (Sih, et al., 2004; Dingle, 2006; van Noordwijk, et al., 2006).

Studies of migration continued with my first job at the University of Iowa. I was hired as a comparative physiologist because, as Larry has indicated, ecology was still “a small, underfunded corner of biology”, and there were few jobs. The same was true for behavior, let alone behavioral ecology. I had excellent physiology training from Howard Schneidermann and Bill van der Kloot at Cornell and at Michigan from Bill Dawson and Don Maynard, in whose course I had been a teaching assistant. This training landed me the job at Iowa. With later expansion of the department, I graduated to teaching animal behavior and evolution.

The Iowa department under the chairmanship of the embryologist Jerry Kollros was a happy one, and I launched immediately into research on insect migration. Milkweed bugs were easily collected, along with the seeds of their host plants, from local fields. The first experiments at Iowa demonstrated that both genes and the environment had important influences on migration in these bugs (Dingle, 1968a,b, 1974). Rearing bugs in families revealed a large hereditary component to migratory flights. Temperatures equivalent to an Iowa summer effectively eliminated migration and promoted early and rapid reproduction; lower temperatures and short days induced a reproductive diapause that in turn helped to promote migration south in the autumn, as in monarch butterflies (Brower, 1995). In experiments initiated by my students Roy Caldwell and Mary Ann Rankin, we learned that juvenile hormone promoted migratory flight (Rankin, 1978), and that there was considerable additive genetic variation for flight duration (Caldwell and Hegmann, 1969).

The addition of Joe Hegmann to the Iowa faculty in 1968 brought quantitative genetics into the analysis of migration syndromes. By fortuitous circumstance Joe was

looking for ways to apply quantitative genetics beyond laboratory mice, and my lab was looking for methods to analyze the genetics of migration and life history syndromes. A massive cooperative series of experiments produced several interesting results concerning genetic and environmental influences. Not surprisingly we found considerable variation within and between species of seed bugs with respect to the adaptive nature of life cycles, both migratory and sedentary (Dingle et al., 1980a,b; Derr et al., 1981; Dingle and Baldwin, 1983; Baldwin and Dingle, 1986). Using various genetic designs we were able to show that not only was there considerable genetic variation in life history traits like diapause, but there were also patterns of genetic correlations suggesting adaptive and evolving life history syndromes. There was a further major influence of adaptive maternal effects (Dingle et al., 1977; Hegmann and Dingle, 1982; Dingle et al., 1982; Leslie and Dingle, 1983a, b; Groeters and Dingle, 1987; Hayes et al., 1987). Maternal effects were particularly interesting because through these, diapausing and migrant autumn mothers suppress diapause and therefore cause earlier reproduction in their largely non-migratory offspring of the subsequent early spring generation. The latter initiates the spring/summer period of population expansion.

To assess migratory syndromes specifically, my postdocs Jim Palmer (at Iowa), Ken Evans (at UC Davis after I moved there in 1982), and I used artificial selection and took advantage of the fact that both migratory (Iowa) and sedentary (Puerto Rico) populations of milkweed bugs occur (Palmer and Dingle, 1986, 1989; Dingle and Evans, 1987; Dingle et al., 1988; Dingle, 1994). We first selected for wing length, a character known to be associated with migration in insects and birds. In bugs from both populations, we produced replicate long and short winged lines. Both responded readily

to selection, and in both there was a positive correlated response for body size, demonstrating shared genes for these two traits.

In other traits the Iowa and Puerto Rico bugs responded differently to wing length selection. In the migratory bugs early fecundity and flight duration both correlated positively with wing length, but there were no such correlations in the non-migratory bugs. These results suggested a migratory syndrome involving flight, fecundity, and wing length based on shared genes present only in the Iowa population. Natural selection had evidently produced the syndrome by acting on the strength and direction of the genetic correlations among the individual traits.

Subsequent selection on the duration of flight confirmed the syndrome in the migratory bugs (Palmer and Dingle, 1989). Even though selection for long and short flights was carried over only two generations, there was strong divergent response. This brief selection also produced positive genetic correlations for wing length and early fecundity. Direct selection on flight thus produced the same syndrome as selection on wing length. The rapid responses produced indicated much genetic variation (variance and covariance) upon which selection could act to produce an adaptive syndrome.

In addition to demonstrating the genetic basis for migratory syndromes, it is important to explore the proximate causes of the genetic correlations. Hormones mediate between genes and behavioral and life history outcomes with important fitness implications (Ketterson and Nolan, 1992; Dingle, 2002). C.G. Johnson (1969), especially, had suggested that the insect oögenesis-flight syndrome was coordinated by juvenile hormone (JH) because of its role in the development of the reproductive system in adult female insects. This suggestion was followed up by my student, Mary Ann Rankin. Using

a combination of topical applications of JH mimics plus ablation and transplants of the corpora allata, the source of JH, she was able to show that JH stimulates migratory flight in pre-reproductive milkweed bugs (Rankin and Riddiford, 1978). Through imaginative use of artificial selection, she also demonstrated that it was intermediate titers of JH that stimulated migratory flight; once high titers were reached, reproduction kicked in and migratory flight ceased (Rankin, 1978). She and her students went on to show that JH was a factor in the migrations of other insects as well (Rankin et al., 1986; Rankin, 1991).

Contemporary evolution of syndromes in soapberry bugs

In 1990 Scott Carroll from the University of Utah joined my lab at UC Davis as a postdoc. Scott's PhD thesis was a study of the soapberry bug, *Jadera hematoloma*, so called because it feeds on the seeds of the Sapindaceae, or soapberry family. In different parts of its range these bugs feed almost exclusively on the seeds of a single host. Fruits of these hosts vary in size, but in all cases seeds occur at the center of a fruit capsule at different distances from the capsule wall, depending on host species and fruit size. The length of the mouthpart stylets (the "beaks") across populations is a positive function of the distance between fruit wall and seed in the various hosts (Carroll and Boyd, 1992).

In parts of the range of *Jadera* in the southern U.S. exotic sapindaceous plants have been introduced, and the bug has switched to these, especially the goldenrain trees, *Koelreuteria elegans* and *K. paniculata*. Horticultural records allow determination of the dates these trees were introduced, and Scott showed that the beaks of the bugs converged in about 40 years or about 100 generations on the size of the fruits of the new hosts. The convergence involved changes in beak length of as much as two standard deviations from

ancestral populations. This contemporary evolution was further shown in museum specimens which served as a “fossil record” of the changes; transitions in beak length occurred in bugs in the collections very soon after goldenrain tree introductions (Carroll and Boyd, 1992). Experiments in my lab demonstrated that both additive genetic variation and epistatic effects contributed to this evolution and that other changes in adaptations occurred along with beak length shifts (Carroll et al., 1997, 1998, 2001, 2003a).

The fruiting phenologies and fruit crop sizes of the native and introduced hosts select, respectively, for migratory and sedentary races of soapberry bugs. In Florida, for example, the asynchronously fruiting native balloon vine (*Cardiospermum*), a large fruited host, produces far less fruit than the introduced goldenrain trees that also fruit synchronously (Carroll et al., 2003b). Consequently, at any given time fruit may or may not be present on a vine or in a local population of vines. To track fruiting bugs must be able to move between hosts or patches. Recent immigrants to patches of vines are pre-reproductive, fly readily, and have a silvery sheen characteristic of migrants. In contrast, the small fruited goldenrain trees set fruit synchronously and copiously minimizing the benefits to movement. The bugs feeding on these trees show none of the signs of migratory activity present in balloon vine bugs, and a higher frequency of flightlessness due to a flight polymorphism (Carroll et al., 2003b).

I had encountered flight polymorphisms and polyphenisms when studying migration in cotton stainer bugs (*Dysdercus spp.*) during a sabbatical year in Kenya (Dingle and Arora, 1973) and in water striders (Gerridae) with post doc Arja Kaitala (Kaitala and Dingle, 1992). Females of cotton stainers histolyze the flight muscles at the

termination of migratory flight, and the protein from these muscles is converted to yolk proteins to supply an early boost to reproduction (Nair and Prabhu, 1985). Histolysis occurs in soapberry bugs as well, but here it is part of a four morph syndrome: (1) a fully winged form that retains wing muscles and flies throughout life; (2) a fully winged form that histolyzes the wing muscles prior to reproduction; (3) a fully winged form that never develops flight muscles; and (4) a short winged form also lacking in flight muscle. Laboratory crosses within and between morphs reveal a complex genetic architecture that differs between migratory and sedentary populations. There are additional differences between populations in response to environmental factors and to JH, both of which differentially influence morph frequencies (Dingle and Winchell, 1997).

There are also a number of other differences between ancestral long beaked balloon vine bugs and derived short beaked goldenrain tree bugs (Carroll et al., 2003b; Dingle, 2006). First, the frequencies of the wing morph differed. For example, among long winged bugs the proportion of females possessing flight muscles prior to reproduction was 76% in the migrant balloon vine sample but only 56% in the sedentary derived race (84% vs 58% in males). Muscle histolysis was also more frequent in the recently evolved race. In both populations age at first reproduction was later in the long winged individuals, but the difference was much greater in the ancestral migrants, presumably reflecting a trade-off between reproduction and migration (cf Roff and Fairbairn, 2007). There were no differences among morphs in egg production in either population, but the non-migrants produced greater numbers of smaller eggs in all morphs, possibly reflecting a weaker trade-off between reproduction and flight as a consequence of the abundant synchronous fruit production of the host goldenrain trees. My student,

Ruth Winchell, showed that population differences extended to the level of muscle enzymes responsible for oxidative metabolism. In bugs with flight muscle and flight capability, levels of these enzymes were higher in the migratory population than in the sedentary one (Winchell et al., 2000).

What is particularly interesting is a relation between beak length and the flight polymorphism in soapberry bugs, a relation that was unexpected. To further assess the genetic basis for beak length and the structure of genetic correlations with other traits, we performed replicated bi-directional selection for beak length in each of our soapberry bug populations. We started each line with externally identifiable long winged bugs, although we could not determine without sacrificing individuals which of the three long winged morphs they were. Over the course of selection the short winged form kept appearing in the selected lines. This allowed us to compute correlations between beak length and the frequency of the wing morphs using a threshold model (Roff and Fairbairn, 2007 give a good summary of the method). There were strong and significant genetic correlations in both populations with log beaks and the frequency of long wings positively correlated (H. Dingle, S.P. Carroll and T.R. Famula, ms. In prep.). This means beak length is part of a migratory syndrome in these insects. Thus selection for long beaks on the native balloon vine host also selects for long wings and presumably flight, allowing the bugs to move between asynchronously fruiting plants. Via its action on beak length, host fruit size influences migration in addition to the influence on flight of the distribution of hosts over space. These results suggest that answering important questions about which traits will be selected to form syndromes and under what conditions, will require analyses at multiple levels from genes to enzymes to ecology.

On a sabbatical in Australia in 1997, I discovered that this island continent also has soapberry bugs (*Leptocoris spp.*) that feed on the seeds of native Sapindaceae, exotic goldenrain trees, and exotic balloon vines. As in North America, some of the bugs have evolved to match fruit sizes even in the face of apparent gene flow (Carroll et al., 2005a, b). We don't know yet whether these bug species are migratory, but they fly readily so it seems likely. In any event they provide the rare opportunity to compare similar invasion events on two continents, a study that is ongoing in cooperation with colleagues at the University of Queensland.

Altitude and grasshopper seasonal life cycles

Residence at UC Davis in the Central Valley of California prompted a study of life cycle plasticity in the grasshopper, *Melanoplus sanguinipes*. This species is distributed in California from the coast to the crest of the Sierra Nevada. All populations are univoltine and display an egg diapause that occurs over the winter, and populations in the Central Valley exhibit an adult reproductive diapause during the heat of the summer when eggs would likely desiccate. In conjunction with postdocs Susan Scott, Tim Mousseau, and Joerg Samietz and students Matt Orr and Mark Salser, were studied over the altitudinal range throughout much of California.

The egg diapause of this species turned out to be particularly interesting (Dingle et al., 1990; Dingle and Mousseau, 1994; Orr, 1996). The eggs, which are deposited just below the soil surface, pass through a number of identifiable stages during embryogenesis, and diapause can occur at any of several later stages. At high altitudes with short seasons diapause occurs in almost all eggs and in the final embryonic stage, so

that in the spring hatching occurs as soon as snow melts and the soil warms up. At the coast most eggs also diapause, preventing premature hatching on warm winter days, but diapause can occur over several stages of embryonic development. This latter characteristic seems to serve as a bet-hedging strategy because it means that hatching occurs over several days. Newly hatched nymphs are highly susceptible to drowning in rain drops, and the pattern of emergence means not all new nymphs would be caught by an unpredictable heavy spring rainfall. At intermediate altitudes only about half of the eggs diapause. At these altitudes low temperatures and snow prevent winter hatch in nondiapause eggs, but these hatch in the first warm days of spring and get an early start in a relatively short growing season. They are, however, likely to suffer heavy mortality if there is a late snowfall, as in fact we saw happen. The diapause eggs hatch later after the time of potential late snow, but the trade-off is a late start on the growing season.

Temperature and photoperiod exert varying influences on the life cycles over the altitudinal range. As heterotherms grasshoppers develop faster at higher temperatures, but in *M. sanguinipes* the effect is modified by altitude. At all temperatures over a physiological range high altitude populations develop more rapidly, in keeping with their short growing seasons, but the trade-off is smaller adult size (Dingle et al., 1990).

Development rate is also accelerated in short days, insuring that adulthood and reproductive capability are reached before the season ends. We have observed in controlled experiments that high altitude grasshoppers actively increase body temperature over ambient to a greater degree than those from lower altitudes, again in keeping with promoting more rapid development in a shorter season. In the field they achieve these higher body temperatures by moving into sunlight, where they can absorb heat, and by

spending more time basking in those areas. Selection thus favors more up-regulation of body temperatures under cooler conditions (Samietz, et al., 2005). These grasshoppers are not simply responding passively to temperature, but rather are behaviorally choosing temperature to optimize their seasonal life histories.

These grasshoppers optimize in one further way. Like many grasshoppers, *Melanoplus spp*, respond developmentally to crowding (like locusts). In this case rearing nymphs in isolation can result in the insertion of an extra instar during development and a larger adult (Dingle and Haskell, 1967). Along the altitudinal gradient in California populations from lower altitudes display the ability to insert this extra instar when isolated, while at higher altitudes this ability is lost (Salser, 2003). There is a reproductive advantage to larger size in that more eggs are produced, but the extra instar delays adult eclosion. In the valley and foothills with a long season, this delay matters little, but the short seasons on the Sierra crest cancel the advantage of size-associated higher fecundity. Subtle and some not so subtle adjustments thus mold the evolution of these seasonal life cycle syndromes that incorporate behavior, development, morphology, and patterns of reproduction.

Final comments

Migration is one of several kinds of movements in organisms, but one that is distinct both quantitatively and qualitatively. Briefly, movements can be divided between those that keep organisms in place (“station-keeping”) like foraging and those that result in a change in place like moving to a new home range (“ranging”) in the same habitat or shifting habitats often, but not necessarily dramatically (migration) (Dingle, 1996). What

is often not distinguished in the movement literature is that specific behaviors lead to *outcomes* of populations staying in place or settling in a new place. The population outcomes, including round trips, do not define the movements, but they do provide the natural selection that determines what kinds of syndromes, migration or station keeping, will occur (Dingle and Drake, 2007). Furthermore, migration is a general phenomenon among organisms and is not confined only to certain groups (Dingle, 1996). This fact was evident once migration was clearly defined behaviorally.

Failure to distinguish between behaviors and outcomes and among the different kinds of movement is systemic across the fields of ecology and behavior, and I would argue, is hindering the development of the conceptual framework needed to advance understanding and to design experiments and field studies (Dingle and Drake, 2007). Such is the case with the term “dispersal”, and its use in describing both animal and plant movements. It seems to have come into use in place of “migration” in many instances because the movements under observation were not round trips. It is now used to indicate a number of different types of movement from the transitive “wind dispersal” to the intransitive “dispersal” of young mammals to the “dispersal ability” of biogeography. Lost is one of the original meanings of increase in distance among individuals (Southwood, 1981), an important component of population dynamics, as is its opposite, aggregation. Nor is it apparent what behaviors or related traits selection is acting upon to produce the displacements, or lack of them, observed. Furthermore the term is frequently used as if the movement involves a single trait which clearly it does not. Unless one has a clear definition that distinguishes one movement syndrome from another and does not conflate behavior with its outcome, one cannot determine the action of selection, and

confusion and confounding will result. Both Kennedy (1985) and I (Dingle 1996; Dingle and Drake, 1997) have emphasized these points, as have others from a more population perspective (Watson, 1992; Turchin, 1998).

One further comment. In 1961 Larry Slobodkin wrote a charming piece in the journal "Etc." titled "Every daffodil has eight letters" (Slobodkin, 1961). In it he pointed out that literary scholars often had little idea of what the living organisms described in prose or poetry actually looked like. I fear we may have a similar phenomenon among biologists, even ecologists. Many times biologists studying a particular taxon have told me with certainty how a behavior they were studying was unique or definitive, when I could readily cite an example from another taxon which falsified their claim. I also worry that specialization within fields like physiology and ecology leads to C. P. Snow's "Two Cultures" between disciplines. As I hope I have made evident, to understand migration and seasonal life histories as syndromes in all their ramifications requires knowledge of many organisms and at least a passing acquaintance with fields of biology outside one's own. Mathematical sophistication is valuable and often necessary, but not at the expense of knowing organisms. This is not unique to migration. There are many more organisms than those "which are furry things that are wild and usually noble" (Slobodkin, 1961), and it behooves us to avail ourselves of the richness and diversity in nature that so many of us appreciated as children and of the diversity of methods we now have available to study them. We owe it to our students to teach them to do likewise. Like Larry's mentor, Evelyn Hutchinson (1953), we should make no apologies for the complexities of nature.

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Table 1. Comparisons of the “migration syndromes” of ancestral (feeding on balloon vine) and derived (feeding on goldenrain tree) soapberry bugs (*Jadera hematoloma*). Data are from Carroll and Boyd 1992; Dingle 2001; and Dingle, Carroll and Famula in prep.). LW = long wing; SW = short wing; 6 day eggs are total eggs laid by 6th day of reproduction; heritabilities are for beak length; genetic correlations are between beak length and wing morph frequency.

Trait	Ancestral	Derived
Beak length (mm x 100)	735	660
LW with flight muscle	76%	56%
LW egg weight (mg)	7.2	5.6
LW 6 day eggs	142	264
LW age first reproduction	23	7.3
Heritability LW	0.51	0.68
Heritability SW	0.60	0.87
Genetic correlation	-0.68	-0.84

Table 2. Some avian migratory patterns on Southern Hemisphere continents. Data are from Dingle (2004, 2008).

Group	Number of species in:		
	Africa	Australasia	South America
Northern migrants (1)	42	10	28
Northern migrant raptors (2)	15	0	4 (5?)
Austral raptors (migrants)	53(4)	17(5)	54(8)
Austral rallids (migrants)	15(8)	14(3)	43(7)
Austral cuckoos (migrants)	12(11)	11(10)	21(5)
Nectarivores (migrants) (3)	21(3)	74(25)	223(7)

(1) Exclusive of shorebirds; (2) raptors = Accipitridae and Falconidae; (3) nectarivores are sunbirds in Africa, honeyeaters in Australasia, and hummingbirds in South America.