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COMMENTS ON THE NATURE AND ORIGINS OF MIGRATIONS OF LEPIDOPTERA TO BERMUDA

Additional key words: evolution, migratory cues.

"The Lepidoptera of Bermuda" (Ferguson, Hilburn & Wright 1991), which I recently reviewed for this Journal (Gaskin 1993), includes an interesting essay in the Appendix which, for brevity, I refer to below as Ferguson (1991). In this, he discussed a number of problems and paradoxes concerning the nature and origins of the long-distance migrations of Lepidoptera to Bermuda, stimulating the additional thoughts and comments presented in this note.

I will start by summarizing the general findings of Ferguson et al. (1991): Bermuda is an oceanic archipelago, dominated by one large island, that caps a seamount with no earlier geological connections to the North American mainland. This archipelago supports a disparate, super-saturated lepidopterous fauna, assembled by over-water dispersal at various times during the last five hundred thousand years, from southeastern North America and the northeastern Caribbean. A small number of endemic species are recognized, derived from ancestors in these two regions. The remaining members of the Bermudian fauna are morphologically and probably genetically, similar to their source populations.

The biomass, diversity, and composition of the Bermudian fauna must have undergone dramatic increases and reductions during the Quaternary concomitant with several radical fluctuations in the surface area of the archipelago.

It was not the primary purpose of Ferguson and his co-workers to develop hypotheses concerning the role that interactions of environmental stimuli, physiology, and behavior might have played in the evolution of long distance migrations of Lepidoptera to Bermuda. Certainly, the phenomenon appears to pose problems for the evolutionary geneticist. If there is no demonstrable return flight, then there seems to be no way for the trait to be fed back into the source population, and no cumulative selection from one generation to the next (Ehrlich 1984). Some of the Lepidoptera which migrate frequently to Bermuda have near-global ranges, and are found also on other oceanic islands. Others have close relatives in widely distant regions with similar migratory behavior. Ferguson estimates

that the migrants to Bermuda make nonstop flights of more than 1000 km, often using lower altitude elements of the jet stream. A number of species from the southeastern United States found on Bermuda also make well-documented annual migrations into the northern states and Canada. Overwintering is unlikely in such cases because these species do not exhibit diapause. Ferguson speculates that many of these make return southern flights within continental North America that have not yet been detected. Presently the best known two-way migration within North America of course, is that of the monarch butterfly (*Danaus plexippus* L.; Nymphalidae). The movements have been copiously documented and the basic elements of the migration have been known for many years (Urquhart and Urquhart 1978). Northward spring flights in North America by species of *Vanessa* are also well known (Scott 1986). In 1992, for example, I counted about 125 *V. cardui* and *V. virginiensis* moving through one small part of Guelph, Ontario, Canada within about 4–5 hours on 26 April, pausing to nectar at clumps of spring dandelions on small patches of waste ground. Weaker southward return flights by *V. cardui* have been observed during late summer and fall in various parts of the United States (Scott 1986). There are also recent reports of consistent southerly autumn movements of *V. atalanta* in the United Kingdom (Riley & Riley 1992). Naturally, these observations may reflect only the prevailing wind direction at the time. Without resorting to mass alar tagging, it is exceedingly difficult to prove conclusively that observed movements of butterflies are in fact part of a large-scale migration rather than periodic local activity. It is, alas, quite unlikely that the kind of observer effort generated for the monarch butterfly programs could be duplicated for large-scale tagging of cutworm moths.

Recent advances in methods to identify and trace specific combinations of isotopes through food chains may give us an additional indirect way of detecting long-distance migrations. Systematic sampling of mtDNA and nDNA in given species at different localities also may provide insight into population structure and movements. Unfortunately, absolute methods for satisfactorily distinguishing sampled entities at the population level have yet to be perfected for animal species, despite great success in individual DNA "fingerprinting."

There are other ways of viewing the problems posed by Ferguson, however. It is rarely clear what proportion of any insect population migrates. We probably have more data on the migration of *D. plexippus* than for any other butterfly or moth, but some aspects are still unclear. Although huge numbers of monarch butterflies migrate from the southern wintering grounds into the northern United States and Canada in normal years, some still can be found even in southwestern Texas in the summer months. It seems unlikely that the migratory instinct is based on an "all or nothing" response in an entire population (Ehrlich 1984). Obviously long-distance return migrations, especially when two generations are involved as in the case of the monarch, demand the transfer of quite sophisticated cue recognition and navigational programming (Baker 1984, Douglas 1986). We have no clear idea of the time scale necessary for such developments.

Ferguson's second puzzle is that the monarch butterflies of Bermuda are now residential, and no longer migrate. The migratory impulse presumably can be over-ridden in some way by internal systems that can recognize specific environmental cues or stimuli of immediate importance to the organism, attention to which will benefit the individual in the short-term and increase its chances of passing on its genetic heritage to offspring. Ignoring for a moment the fact that Bermudian monarchs are on an oceanic island, the question can be seen as part of the more general one "why don't colonial butterflies migrate?" Presumably, the majority tends to remain in the area through repeated exposure to local cues, such as the presence of specific microclimatic conditions or food plants that are absent for some distance around the colony. Statistically, relatively weak fliers carrying out short-distance search movements (random walks) will usually end up back in the locality where the cues are strongest or most repetitive. It is quite normal, however, for some individuals to disperse up to tens of kilometers from a colony. This happens in the case of the European large copper, *Lycaena dispar* (f. *batavus*), for example (Pullin et al. 1993). If such wanderers fail to find their way back and the colony is effectively isolated by unfavorable habitat, then this behavior could potentially threaten the viability of the colony. In other seasons the same behavior might enhance its survival by reducing

pressure on limited food resources. Under normal circumstances, however, in the absence of significant vagility (capacity for dispersal at least to the nearest suitable habitat site), local colonies of a few hundred individuals are certain to be extirpated in the long run by environmental events, often simple density-independent occurrences such as flood, drought, or unseasonable hard frost at some critical point in the life cycle. Stochastic events probably play a greater role in colony extinctions than inbreeding. Dempster (1989) argued that vagility, as a basic attribute, is vital for survival even for butterflies well-adapted to highly specific habitats, because unless isolated colonies are "topped up" at intervals by surplus production from adjacent neighboring units experiencing "good years," they ultimately will disappear. Colonial butterflies in many parts of North America and Western and Eastern Europe have undergone dramatic declines in recent decades (Kudrna 1986). The endangered or threatened species are usually those with rather low vagility, often staying close to localized food plants. This was not such a problem before the advent of drastic modifications to northern temperate ecosystems by the activities of humanity, which have greatly reduced and fragmented previously widespread habitats. Of course, there always were extirpations of colonies by natural processes, with eradications of whole systems during the cold Pleistocene stadials, and some recolonizations in the mild interstadials (Dennis 1976). In the case of species with low vagility, recolonizations of areas were simply a function of expansion of a particular habitat or biotope. Nevertheless, the greater the innate vagility of a butterfly species, the greater the chances of recolonizations, recovery in numbers, and increased opportunities for individuals to perpetuate their genes. Dempster (1989) argued that it was no accident that the butterflies which did not seem to be on the decline in the United Kingdom comprised largely species with high vagility, such as the orange tip, *Anthocharis cardamines*.

In somewhat oversimplified terms, vagility is a basic characteristic of all organisms, providing individuals with options as burgeoning numbers at source increase competition for food supplies. It also improves the chances of meeting and mating with an individual from another parent stock and increasing the heterozygosity of the gene base of the offspring. (To take this any further would lead to a discussion of the value of sexual reproduction.) The ability of individuals on the move to respond to certain environmental cues of immediate importance, such as a change in air temperature, "land in sight," "food in sight," "mate in sight," can over-ride the general stimulus to keep moving. The actual mechanisms that both initiate and cease migration are probably hormonal in nature, even if the basis is genetic.

If there is now no return migration to the southeastern United States by resident monarch butterflies in Bermuda, it may be that the local cues, e.g., somewhat less fluctuation in photoperiod than in New England or southern Canada, or the winter being mild enough for adult survival, may serve to suppress the instinct to leave. Perhaps the prevailing seasonal winds around Bermuda may make it a one-way journey for all immigrant Lepidoptera whatever their migratory indications. Has it been established that *all* Bermuda monarchs are now non-migratory, or is this an assumption (reasonable enough on the face of it) based on monarchs or their immature stages being found there year-round? It would be useful to clarify this point. It also would be interesting to release Bermuda monarchs in critical localities in North America and see what they would do, for example, in the face of a much reduced day-length in central Ontario in early autumn. In a few years time, developments in "wildlife technology" will make radio emitters approaching the size of a pinhead commercially available for this kind of study where mass alar tagging is not appropriate. Prototypes already have been tested.

I think it unlikely that long distance return migrations commonly evolve from long distance one-way dispersals, not just in the case of Bermuda but also on any continental mass. It seems to need too many unlikely events to occur in sequence. Initial returns probably would be accidental. Development of migration in this way would require not only that a few founders somehow find their way back carrying the behavioral trait with them, but also that over a number of generations the survival rate of their offspring should exceed that extant in the general population. In the first few generations the statistical chances of their elimination would seem to be high, unless conditions specifically favorable to the migrators developed quite rapidly in the source habitat.

More realistically, migrations can generally be considered as a survival mechanism evolved, probably during periods of climatic and/or ecological change, as a response to gradual increase in segregation or "de-coupling" of optimal zones for feeding and breeding which had been more closely adjacent in the earlier history of the population. No near-miraculous return flights need be postulated, only slowly widening, short-distance seasonal oscillations. Under these circumstances, natural selection for capacities to navigate and recognize cues could occur with plenty of opportunity for the advantageous traits to accumulate in the population. In the case of the monarch and species with a similar pattern of migration, another vital zone presumably became segregated from both optimal feeding and breeding regions, i.e., that in which the species could survive the winter in the adult stage. Perhaps the monarch already was locked into this type of life cycle, because of critical requirements of one or more of the immature stages that could not be easily modified subsequently. The fact that we see this kind of pattern in a number of the large Holarctic nymphalids suggests that there has been insufficient time for natural selection to favor alternatives other than extension of the seasonal movements and adult overwintering. If we look for distinctly warmer regimes, when the monarch might have been able to overwinter easily at significantly higher latitudes than today, there seem to be three main choices, the rather arid, warm Upper Oligocene, part of the Miocene, or the post-glacial "Warm Period" of about 6,000 years ago. In theory, 5-6,000 generations does not seem an unreasonable time for significant changes in population behaviors to occur, although probably far too short a time for significant changes in biologically important physiology or morphology. The exceptions might include wing color patterns, which often play a role in behavioral responses and recognition and could be subject to quite rapid selection.

My conclusion then, is that the probable answers to the important questions posed by Ferguson in his essay in this monograph are as follows: monarchs and many of the other butterflies and moths that reach Bermuda became long distance migrators on the mainland in response to historical changes in their habitats, much like the migratory songbirds. We don't know when this happened, because behavior does not leave a fossil record. Their original ranges may have been much the same as today latitudinally, but with the critical difference that the adults could overwinter through much of the range instead of only at the southern extremity. The overwintering stage of the life cycle may have been the most critical factor in determining which options were open to selection when conditions changed.

It would be interesting to make some experimental comparisons between the critical factors that appear to operate in such migrations in North America with those in wet-dry season and low-high altitude migrations by Lepidoptera, for example in east Africa and India.

In the case of migrations to Bermuda, the driving forces may be quite incidental; there are some species which have relatively great vagility over land. When these are swept offshore into air masses with a lower level jet stream, they can remain aloft for long periods using the same adaptations that serve when they are over the continent. Because the basic dispersal instinct can be over-ridden by immediate stimuli related to basic survival, they will surely attempt to descend to feed and rest if an oceanic island is located. Prevailing seasonal winds perhaps prevent them from ever returning to southeastern regions of the United States, but it would be exceedingly difficult to determine this conclusively. Additionally, because they have arrived somewhere with resources, the migratory instinct may be suppressed by something as simple as the act of feeding or egg-laying. We have only limited information concerning which hormonal or other physiological releasers and suppressors may be involved. It might be instructive to put aerial nets on ships passing east and north of Bermuda to see what proportion of individuals lift off to fly further. Even rather small species of Lepidoptera, such as *Nomophila* spp. have been recorded far out to sea.

Ferguson's suggestion, that the current high population levels of species such as *Spodoptera* spp. and *Pseudaletia unipuncta* probably result from the relatively recent massive vegetation changes in North America, seems very reasonable. Despite pesticide use, our techniques of crop monoculture assist population growth of some of these insects, and

almost guarantee periodic explosive outbreaks. As these huge populations reduce local resources, dispersal is strongly favored. Even in moderately r-selected organisms such as cutworm moths (cf. herring, with eggs in the tens of thousands), traits for dispersal are probably so universal that further intensive selection may not be necessary. The long-term survival problem for these moths, however, is not over when they reach new food sources on a small, isolated island group such as Bermuda. The century or so of change in North American vegetation is clearly not enough time for selection to work in favor of significant decrease in individual fecundity, or the kinds of specialized behaviors evolved in *Heliconius* species in resource-limited tropical habitats (Gilbert 1983). The sedentary island populations of recent origin are still going to be prone to periodic, chaotic population outbreaks and subsequent crashes at times when sources of natural mortality diminish, simply because of their potential fecundity.

This does raise interesting possibilities for other types of research using island Lepidoptera, in addition to the kinds of studies made by Ferguson on migration. Someone might like to examine other aspects of the situation. For example, by looking at related species and genera on islands with biotas of different and preferably known ages, could we test the hypothesis that endemic island Lepidoptera may have evolved lower fecundity rates over time than comparable migrant species, becoming more adapted to the limitations of their food plant and nectaring resources? Alternatively, do the island immigrant populations begin to show more diversity in food plant selection than their continental counterparts?

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CORRECTIONS TO "CHECK LIST OF THE OLD WORLD
EPIPASCHIIINAE AND THE RELATED NEW WORLD GENERA
MACALLA AND EPIPASCHIA (PYRALIDAE)"

Additional key words: *Lepidogma latifasciata*, *Locastra*, *Stericta kiensis*, *Teliphasa dibelana*, *Trichotophysa*.

The following are corrections to a list of Old World Epipaschiinae (Solis 1992) discovered after publication. The corrections are listed in alphabetical order as in the original work. Included are several corrections pertaining to the Japanese fauna identified by Inoue (1993). In addition to the corrections listed below, the valid name for the host plant *Eugenia jambolana* Lamarck (Solis 1992:281) should be *Syzygium cumini* (Linn.) (G. Robinson pers. comm.).

Coenodomus hampsoni West, 1931: misspelled locality name, should be Palali, not Palili.
Epilepta dentatum (Matsumura and Shibuya, 1927): country should be Japan, not Formosa.

Lepidogma latifasciata (Wileman, 1911): it is a **new combination**.

Lista plinthochroa West, 1931: misspelled locality name, should be Palali, not Palili.

Locastra maimonalis (Walker, [1859] 1859): years are [1859] 1858, and it is a junior synonym of *L. crassipennis* (Walker).

Locastra crassipennis (Walker, 1857): senior synonym of *L. maimonalis*.

Neopaschia nigromarginata Viette, 1953: locality should be Madagascar Est: Fianarantsoa, not Madagascar, Saigon.

Odontopaschia economia Turner, 1913: misspelled species name, should be *ecnomia*.

Orthaga durranti West, 1931: misspelled locality, should be Philippine Islands, not Philippines Islands.

Salma nyctizonalis (Hampson, 1916a): misspelled locality, should be Philippine Islands, not Philippines.

Shoutedenidea Ghesquière, 1942: misspelled genus name, should be *Schoutendenidea*.

Stericta angulosa de Joannis, 1929: misspelled locality, should be Vietnam, not Vitenam.

Stericta angulosa de Joannis, 1929: misspelled locality, should be Vietnam, not Vitenam.

Stericta kiensis (Marumo, 1920): valid species; is not a junior synonym of *Stericta rufescens* (Marumo, 1920), should be placed after *Stericta indistincta*.

Termioptycha elegans (Butler, 1881): species belongs in *Teliphasa*, should be placed after *Teliphasa dibelana*.