

Monarch sex: ancient rites, or recent wrongs?

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Sponsored by the RES, British Ecological Society, Linnean Society and Natural History Museum (Entomology), Lincoln Brower will give presentations about Monarch conservation on 27th June (at the NHM) and about Monarch biology on 28th June 2007 (at the Linnean Society).

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Biosketch

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Left to right: Michael Boppré, Karen Oberhauser, Lincoln Brower, Dick Vane-Wright and inset: Andy Brower



Figure 1. (left) Clusters of Monarchs at a Mexican overwintering site. Figure 2 (top right). A heterosexual Monarch pair struggling on the ground, just after aerial “take down.” Figure 3 (bottom right). Female Monarchs adopt a variety of positions that make it difficult for males to couple with them. (Photos by R.I. Vane-Wright, Mexico, March 2006)

Introduction

Milkweed butterflies are a distinctive group of about 170 mostly tropical species of Lepidoptera that typically exhibit complex courtship behaviour mediated by chemical communication. A striking exception, however, is the very well-known North American Monarch (*Danaus plexippus plexippus* Linnaeus), once famously dubbed by Miriam Rothschild as “nature’s prime example of the male chauvinistic pig” (Rothschild, 1978). She noted how “The other members of this genus bemuse and subdue their females by means of a sophisticated aphrodisiac — a love dust ... shaken over her like a golden snow flurry during courtship. The male Monarch on the other hand, dispenses with these refinements and, more often than not, knocks down his female ... and

takes her by force ... He is simply a thug.”

Mass migration and forced copulation

Danaus plexippus plexippus is extreme in another behavioural characteristic: the annual mass migration cycle and formation of huge overwintering colonies, notably in California and Mexico (Figure 1). At the Mexican sites hundreds of millions of Monarchs spend November through February huddled in dense groups (Brower *et al.*, 2004). In March they prepare to fly north again and, if you sit quietly under the trees full of these massed butterflies, you will soon become aware of pairs, two males or a male and female, falling to the ground in a tight embrace. This is a so-called “take-down” (Van Hook, 1993), which is followed by an

attempt at forced mating on the ground (Figure 2). Heterosexual struggles end in one of three ways: either the male is successful, and achieves coitus; the male releases the female; or the female breaks free and flies away.

At the overwintering sites, about one third of these attempts end in a successful mating (Oberhauser & Frey, 1999). One gets the distinct but possibly anthropomorphic impression that the male’s attentions are unwanted. Even those that are eventually successful seem to be resisted, although previously-mated females are more likely to evade mating (Frey, 1999). The female fends off the male by adopting a variety of positions that make it difficult for him to bring his genitalia into contact with hers (Figure 3). The most effective position is the

abdominal curl: the female folds her abdomen ventrally towards the thorax, and grasps it with her legs. So far as we are aware, nobody has ever observed a successful mating after a female has assumed this posture. The duration of observed struggles in one study ranged from a few seconds to 30 minutes. Rather surprisingly, Oberhauser & Frey (1999) found that the difference in duration between homosexual and heterosexual attempts was statistically indistinguishable!

Oberhauser & Frey (1999) tentatively proposed that these extreme behavioural peculiarities — mass migration and copulation by force — are connected. By late in the wintering season many Monarchs have used most of their lipid reserves (Alonso-Mejía *et al.*, 1997), and have little chance to re-migrate and reproduce subsequently. For such males it seems their best strategy is to attempt to mate at the overwintering sites, even though most females are still in diapause and resistant. In addition to female resistance, pheromones may be ineffective in dense congregations.

While the gain in fitness from winter mating is probably low (due to sperm precedence and the likelihood of female re-mating: Oberhauser, unpublished), the males' poor condition means that the net benefit of mating at this time, relative to just dying without mating, will be high. Sperm survive for several weeks within the female (Oberhauser, 1997), so some sperm from early matings may be used to fertilize eggs when the females become reproductive. Once coercion evolved, it may have become a mating strategy that was used in both overwintering and summer generations, and much of the dependence on chemical cues may have been lost. Thus, the evolution of mass overwintering may have predisposed the Monarch's dramatic shift in mating behaviour.

If, as has been suggested (Vane-Wright, 1993), the evolution of mass migration in the North American Monarch is a recent phenomenon, is mating by force a newly evolved "wrong," an act of male violence

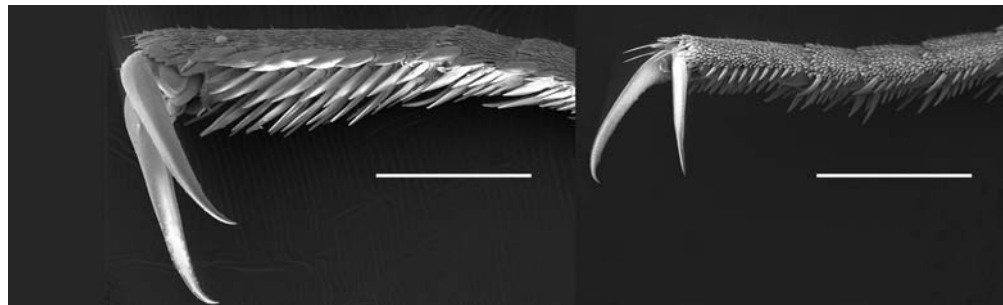
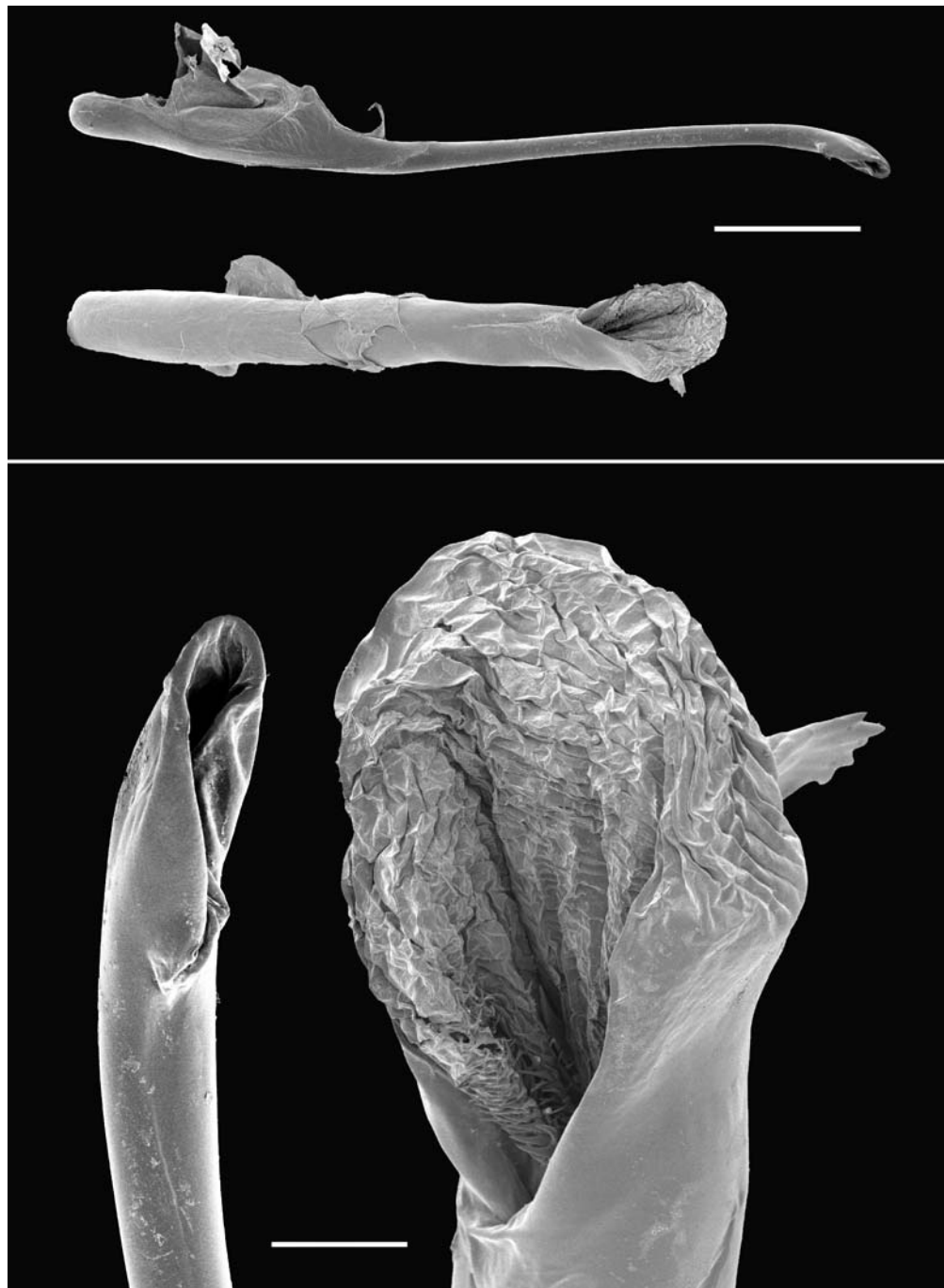


Figure 4. Tarsal segments: left, 5th of *D. plexippus*; right, 2nd–5th of *D. chrysippus*. Scale bars: 1 mm. (SEMs by O. Fischer & M. Boppré)

Figure 5. Aedeagi: upper and left (tip), of *D. plexippus*; lower and right (tip), of *D. chrysippus*. Scale bars: 1 mm (whole aedeagi, upper) and 200 μ m (details, lower). (SEMs by O. Fischer & M. Boppré)



driven by a situation in which chemical courtship may not be effective? Alternatively, are these phenomena long-established (Brower, 1995), ancient “rites”, a way of mating integral to the whole Monarch lineage, with both male and female co-adapted to this different strategy?

The costs of forced copulation

Miriam Rothschild also observed that, in the greenhouse, sexually active male Monarchs will try to force themselves on male or female *Danaus chrysippus* (Linnaeus) — the Plain Tiger or African Queen butterfly — which can sustain serious injury in the process. Totally different butterflies may also be attacked: according to Carol Boggs (quoted by Rothschild, 1978), male *plexippus* can kill *Heliconius* in captivity. By what means could male Monarchs inflict injury and even death on other butterflies?

In some cases, forced copulation can be extremely costly. Monarch females can receive so much spermatophore material that their bursa copulatrix ruptures, leading to internal damage, no subsequent oviposition, and an early death — both in captivity (Oberhauser, 1989), and at overwintering sites (Oberhauser, unpublished).

Monarchs have two morphological specialisations that are probably responsible for other forms of damage. First, in both sexes, the fifth tarsal segments of the middle and hind-legs are relatively longer than those of related species such as *D. chrysippus*, and are armed with stronger spines (Figure 4). Males apparently use these to grasp females in the air and, once on the ground, in their mating struggles. Both sexes of the Monarch also have much tougher wings than *D. chrysippus* or *Heliconius*, and so female Monarchs, although often battered, survive relatively unscathed: they rarely suffer wing tearing, and lose few scales (Oberhauser unpublished; Dennis Frey pers. comm.). But this is not so if other butterflies are mistakenly engaged: they can literally

have their wings crushed or torn in the process. These same specialisations may also be important in other contexts: tougher wings for facilitating long migration, and more spiny tarsi for clinging to trees and other Monarchs in overwintering clusters — and for the abdominal curl.

The second specialisation is the potentially lethal factor for other butterflies: the Monarch’s penis. The aedeagus of most milkweed butterflies comprises a relatively broad tube with a blunt end. But the Monarch’s aedeagus is longer, much narrower and more strongly sclerotised, ending in a sharp point, like a syringe (Figure 5). This lance-like instrument, if misdirected, is capable of piercing the abdomen of less robust species, and of disrupting their genitalia even if correctly located.

Although this must be a very rare event, it is perhaps comparable to the phenomenon of *traumatic insemination* in bed bugs (Carayon, 1959) and certain other Hemiptera. Female bedbugs and their relatives have a specialised area of the abdomen — the spermalege — recently demonstrated to be an adaptation to traumatic insemination. If a male bedbug penetrates the female abdomen elsewhere, this results in significant reduction of female lifespan and fecundity (Morrow & Arnqvist, 2003; Reinhardt *et al.*, 2003).

Why aren’t female Monarchs mutilated? Because the ostium bursae forms a toughened funnel leading into the correspondingly elongated and sclerotised ductus bursae (Ackery & Vane-Wright, 1984: fig. 185). So long as the male thrusts in more or



Figure 6 (above). Abdominal hairpencils of male *Euploea* (Danainae). (Macrophoto by M. Boppré)

Figure 7 (below). Male Monarch hairpencilling on ground while attempting to mate. (Photo by George Lepp, Natural Bridges State Park, Santa Cruz, California; with permission)



less the right place, the specially formed orifice of the female Monarch will safely accept him — but this is not so in other species.

Monarchs and chemical communication

Except the Monarch, all milkweed butterflies whose courtship behaviour has been studied, indulge in complex behaviour, involving prolonged hovering and the use of at least one, and probably several pheromones, including those derived from pyrrolizidine alkaloids gathered from plants (Boppré, 1993). In many species pheromones are passed to the females on transfer particles, variously produced but invariably stuck to the female antennae during courtship by means of the male’s eversible hairpencils (Figure 6). The hairpencils are also often involved in male pre-courtship activity, interacting with specialised alar organs that variously produce transfer particles (e.g. in *Tirumala*: Boppré & Vane-Wright, 1989), specific enzymes necessary for pheromone synthesis (e.g. in *Danaus*:

Boppré, 1993), or (possibly) actual pheromones.

While male Monarchs have both hairpencils and alar organs, these are much reduced in size in comparison to other *Danaus* species (Boppré, 1993), and milkweed butterflies in general. Their small hairpencils are not deployed consistently in courtship, although when struggling with females on the ground, in as many as 50% of cases observed, males do extrude them (Figure 7) (L.P. Brower, unpublished). But, unlike *D. chrysippus*, male Monarchs have never been observed to insert their hairpencils into the alar organs.

Miriam Rothschild (1978) suggested that the Monarch has dispensed with chemical communication. While not proven, its hairpencils and alar organs are reduced in size, no pheromone-transfer-particles are produced, and no pyrrolizidine-alkaloid-derived pheromones are detectable (Boppré, 1993). In addition, Monarchs can mate successfully with their hairpencils removed (Pliske & Eisner, 1969). More work is needed to establish the possible extent and significance of chemical communication in the Monarch. But whatever the details, at least four structural modifications reflect a shift from persuasion to force: specialised tarsi that can be used for grappling, a lance-like penis for rapid penetration, a vagina that is lengthened and toughened to receive the otherwise potentially damaging penis, and a reduction of the pheromone system.

Which male Monarchs are successful?

Mating at overwintering colonies is not random. The males that mate tend to be smaller and more worn than would be expected if mating were indiscriminate, and the females tend to be larger, and possibly fresher (Van Hook, 1993; Oberhauser & Frey, 1999; Frey, 1999). As indicated already, by mating with large females in good condition, males in poor condition give themselves the best possibility of reproductive fitness. On the other hand, large males in good

condition are able to make the return journey, and can afford to wait to mate at or near oviposition sites, where they are likely to be far more successful.

Is loss of female choice a disadvantage?

Given evidence for the generally widespread occurrence of mate choice by female butterflies, it is tempting to assume that the loss of choice by female Monarchs must represent some form of disadvantage, at least for females. However, the genes that are carried by the males will also be found in the females' sons, and if this strategy represents enough of an advantage for males and a low enough cost for females (albeit still a cost), it is likely to evolve (Oberhauser & Frey, 1999). Moreover, the morphological changes described above, affecting both sexes, suggest that the Monarch has made an adaptive shift, from persuasion to forced copulation.

The Monarch is not the only butterfly in which female mate choice appears largely precluded. Several butterflies engage in pupal mating, including a number of passionvine butterflies (*Heliconius*: Brown, 1981; Deinert, 2003), and some lycaenids such as the Imperial Blue (*Jalmenus evagoras* (Donovan): Pierce & Nash, 1999). Males search host plants for pupae, and mating occurs before the females have completely eclosed. Pupal-mating has evolved independently in several insect orders (Thornhill & Alcock, 1993), suggestive that, in particular circumstances, a switch from female-choice to male-demand can be favoured.

What do phylogenetic considerations suggest?

In a recent comprehensive catalogue of Latin American butterflies, six subspecies of the Monarch are recognised. However, mitochondrial DNA sequences suggest that few if any of these supposed races are genetically distinct — including *plexippus nigrippus*, the name that correctly applies to the Monarchs found in the northern half of South

America (Lamas, 2004). Four of the supposed races are confined to the Antilles. The sixth subspecies, *plexippus tobagi*, occurs in northern Brazil, the Guianas, Trinidad, and Tobago. The molecular comparison, published in the same year as the catalogue, was based on samples collected from eastern and western populations of the North American Monarch (*plexippus plexippus*), six South American sites occupied by *plexippus nigrippus*, and two sites occupied by *plexippus tobagi*. In the molecular analysis, no geographical clustering was evident at all, suggestive that these putative races are, at most, very weakly differentiated (Brower & Jeansonne, 2004).

Whatever their status, these Latin American Monarch populations do not, as far as we know, undertake mass migrations or form large colonies. Observations on their mating behaviour are essentially wanting — but they all share the same morphological modifications to the legs, genitalia and pheromone system seen in *plexippus plexippus*.

Generally it has been assumed that the migratory behaviour of the North American Monarch, essentially a tropical butterfly, has evolved to take advantage of the extensive subtropical and temperate milkweed flora of North America (Brower, 1995). Due to the butterfly's frost intolerance, this required the evolution of autumn migrations to the California coast and central Mexico (and perhaps Florida and Cuba) to avoid the otherwise harsh North American winter. Were the change in mating strategy related to the evolution of this migratory behaviour, the likely occurrence of the same mating strategy in non-migratory tropical populations suggests that, contrary to the normal assumption, the Latin American populations should be derived from the North American — or, alternatively, from a common migratory ancestor.

The Southern Monarch, *Danaus erippus* (Cramer) (Figure 8), is found in the southern half of South America. Recent molecular work,



Figure 8. Southern Monarch, *Danaus erippus*. The only obvious difference from *D. plexippus* is the orange instead of black posterior forewing margin. *D. erippus* has same modifications to tarsi, genitalia and male scent organs as *plexippus*.

although not extensive, supports the currently accepted status of *erippus* as the Monarch's sister-species (Brower & Jeansonne, 2004). *D. erippus* shows the same suite of morphological changes as the Monarch. If mating strategy and migratory behaviour go together, then *erippus* should also have evolved from a migratory ancestor. There is some evidence of mass migration in *D. erippus* within southern South America, and at least one record of the butterfly reaching the Falkland Islands (Islas Malvinas), 600 km off the Argentine coast (Ackery & Vane-Wright, 1984).

Has mass migration been lost once — or even twice?

Such a scenario would be consistent with the migratory behaviour of the Monarch being a very old phenomenon (Brower, 1995). However, this conclusion is potentially challenged by *Danaus cleophile* (Godart), the last remaining member of the subgenus *Danaus*, and currently accepted as the sister of *plexippus* + *erippus*. *D. cleophile* is only known from Jamaica and Hispaniola, and it too shows exactly the same morphological changes. There is nothing to suggest that *cleophile* undergoes mass migrations or forms mass colonies — it is a much smaller, rare species, included on the IUCN Red Data List. The morphological characters indicating that *cleophile* groups with *plexippus* and *erippus* are compelling (Ackery & Vane-Wright,

1984), but for inferring that *cleophile* forms the sister group to *plexippus* + *erippus*, rather than one or the other, they are very weak. Were molecular data forthcoming that unequivocally placed *cleophile* as sister to *plexippus*, with *erippus* sister to these two combined, then the argument for an ancient and possibly necessary link between a shift in mating strategy and migration could be proposed with more confidence.

Such a scenario would imply that mass migration has been lost at least twice. We do know that it is a labile trait: Hawaiian, New Zealand, New Guinea and Australian *plexippus* populations are believed to have originated from accidental

introductions of North American Monarchs in the mid to late 19th century (Zalucki and Clarke, 2004), suggestive that loss of mass migration can be rapid. Indeed, populations of several species of Danainae seem to switch between clustering and migrating, or not doing so, dependent on local conditions.

Alternatively, if *D. cleophile* is confirmed to be the sister group of *erippus* + *plexippus*, it could also have evolved from a migratory ancestor — but there is then nothing to support such a contention. While there is no doubt that further molecular investigations are highly desirable, they will not lead to a clearer solution to this question without, in addition,



Figure 9. Mating Monarchs. As with all Danainae (and unlike e.g. Papilionidae), once coupled, the female hangs from the male's abdomen. (Photo by R.I. Vane-Wright, Mexico, March 2006)

good information regarding the mating and migratory strategies of all the species involved, and their major populations. The authors would be delighted to hear from anyone willing to make and share behavioural observations on Latin American *Danaus* — and collect (legitimate) samples for molecular work — and on clustering and mating behaviour in Old World Danainae that make large migrations (e.g. *Euploea* and *Parantica* species).

Is the Monarch a Male Chauvinist Pig?

For whatever reason (fun, or genuine or feigned feminist outrage?), Miriam Rothschild (1978) chose to draw attention to the shift in mating strategy of the Monarch by the use of

emotive terms. According to her account, the males take the females “by force”; other males may be “irresistibly drawn” to such a “lustful scene”; the female is the subject of a “brutal onslaught”; after coupling the male can be seen “nonchalantly feeding on flowers”, while she “hangs unconscious from the end of his body” (Figure 9). In a greenhouse, she notes, the “ungovernable lust” of a male Monarch “drives him to rape”. He is simply a “thug” she concludes, a “male chauvinist pig.”

Psychologists have often seen rape as dysfunctional in human males, more an act of violence than a reproductive strategy. In the case of the Monarch, and its two most closely related species, this behaviour has apparently evolved and persisted

over tens of thousands, perhaps even a million years. In order to make sense of this phenomenon, while it is arresting to think of it as “rape”, it may not be helpful to do so if we are to understand the biological significance of this unusual and paradoxical shift in mating behaviour. It may not be an accident that the less emotionally charged term “forced copulation” was introduced soon after Rothschild’s paper (Thornhill 1979) to describe aspects of the evolved behavioural repertoires of males that are widespread within a taxon, and are not abnormal or aberrant. We conclude, tentatively, that we are dealing with ancient rites in these butterflies — and not with wrongs, ancient or modern.

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