

EDITORIAL

The migratory behaviour of salt marsh mosquitoes: Revisiting the evidence

In the early 1950s, approximately 1.5 million radiolabelled black salt marsh mosquitoes (Diptera: Culicidae, *Aedes taeniorhynchus* Wiedemann) were released from a point source on Sanibel Island, part of an archipelago of barrier islands and mangrove swamps off the south-west coast of Florida, during one evening in June (Provost, 1957). Carefully synchronising the timing of larval hatch in outdoor tanks filled with water from local marshlands, the research team orchestrated a mass emergence of adults and witnessed that “*wisps of mosquitoes took off spontaneously in puffs*”. After sunset, newly emerged *Ae. taeniorhynchus* adults resting on nearby surfaces gradually departed, and before dawn “*the great mass of mosquitoes had gone*”. In the following days, adults were recaptured using light traps distributed across the archipelago (Figure 1). Recapture rates of females marked with radiolabelled phosphorous-32 (p^{32}) vastly outweighed those of marked males, with the latter concentrated within just a few kilometres. Marked females, however, were found up to 40 km from the release point, mostly downwind, and significant numbers made open-water crossings at least three kilometres in length shortly after release.

This experiment formed part of a series of field trials in Florida investigating the ecology and movement of salt marsh mosquitoes (Haeger, 1960; Provost, 1952; Provost, 1957). For many years, the results from these studies were cited as the primary example that mosquitoes can engage in de facto wind-assisted migration above their flight boundary layer (FBL), where wind speeds exceed that of active flight speed (Taylor, 1974). Among the historical case studies citing long-distance, wind-borne mosquito movement, a disproportionately high number involved mosquitoes adapted to salt marsh habitat, mainly in the *Aedes* genus, and within multiple continents. These include *Ae. taeniorhynchus* (Provost, 1952; Provost, 1957; Vlach et al., 2006) and *Ae. sollicitans* Walker (Crans et al., 1976) in the United States, *Ae. vigilax* Skuse (Chapman et al., 1999; Webb & Russell, 2019) and *Ae. camptorhynchus* Thomson (Jardine et al., 2014) in Australia, and *Ae. detritus* Haliday in France (Rioux, 1958) and the United Kingdom (Clarkson & Enevoldson, 2021) (Table 1).

For some time, the idea that wind-borne mosquitoes are migratory was controversial, and many authors refuted the term migration, insisting that any wind-borne flights are merely accidental or passive and should be considered as simply long-distance dispersal (Service, 1997). Since then, our perspectives on insect migration have changed. Firstly, while a universally accepted definition of migration remains elusive, the synthesis of a broader behavioural definition of

migration (based on ‘persistent and straightened-out movement’ along with ‘temporal inhibition of station keeping resources’ (Chapman et al., 2015; Dingle & Drake, 2007)), permits the categorisation of long-range movements made by mosquitoes as migratory. In a recent review of dipteran migration, the Culicidae family (mosquitoes) meet the four ‘core’ migratory criteria and was ranked among top “migrant families” meeting nine of the 13 criteria (Hawkes et al., 2025). Secondly, we now understand that small dipterans are not passively transported via winds; small, winged insects can control their vertical motions into and above their FBL and, once they have stopped flying, land quickly (Thomas et al., 1977; Wainwright et al., 2017; Wainwright et al., 2020). Finally, based on recent aerial sampling in the Sahel and savannah of West Africa (Bamou et al., 2024; Huestis et al., 2019), and building on earlier observations across different continents (Glick, 1939; Ji-Guang et al., 1993; Reynolds et al., 1996), many more individuals and species of mosquitoes are captured at high altitude on a regular basis than expected. The distinct composition of high-altitude collections compared to those on the ground (at the species, sex and gonotrophic states) corroborates the active control of migration in these mosquitoes (Yaro et al., 2022). At heights between 40 and 290 metres above ground level, females significantly outnumbered males (~6:1) and a high percentage (~90%) were gravid, suggesting some kind of evolutionary strategy based on finding a favourable water body for oviposition (Huestis et al., 2019; Yaro et al., 2022). Given these recent developments, can we consider the historical reports of salt marsh mosquito species, such as those by *Ae. taeniorhynchus* described above, as truly migratory? And if so, what is the nature of this migration and how important is it for pathogen transmission.

From an evolutionary perspective, obligate migration for salt marsh mosquitoes seems maladaptive unless a favourable combination of topography, landscape, and wind fields allow migrating females to land in suitable habitat and locate resources while avoiding being carried out to their death in the sea. Indeed, under some circumstances, small dipterans are at risk of perishing at sea due to coastal circulations (Sauvageot & Despau, 1996). At the individual level, the success of any migratory strategy is only realised if the female can eventually oviposit in suitable salt marsh. To do this, either (i) the wind directions must align with the distribution of the coastal salt marsh, (ii) the salt marsh must be large enough to support intra-habitat movement regardless of wind direction, or (iii) if the winds transport mosquitoes inland, the females must return to salt marsh habitat suitable

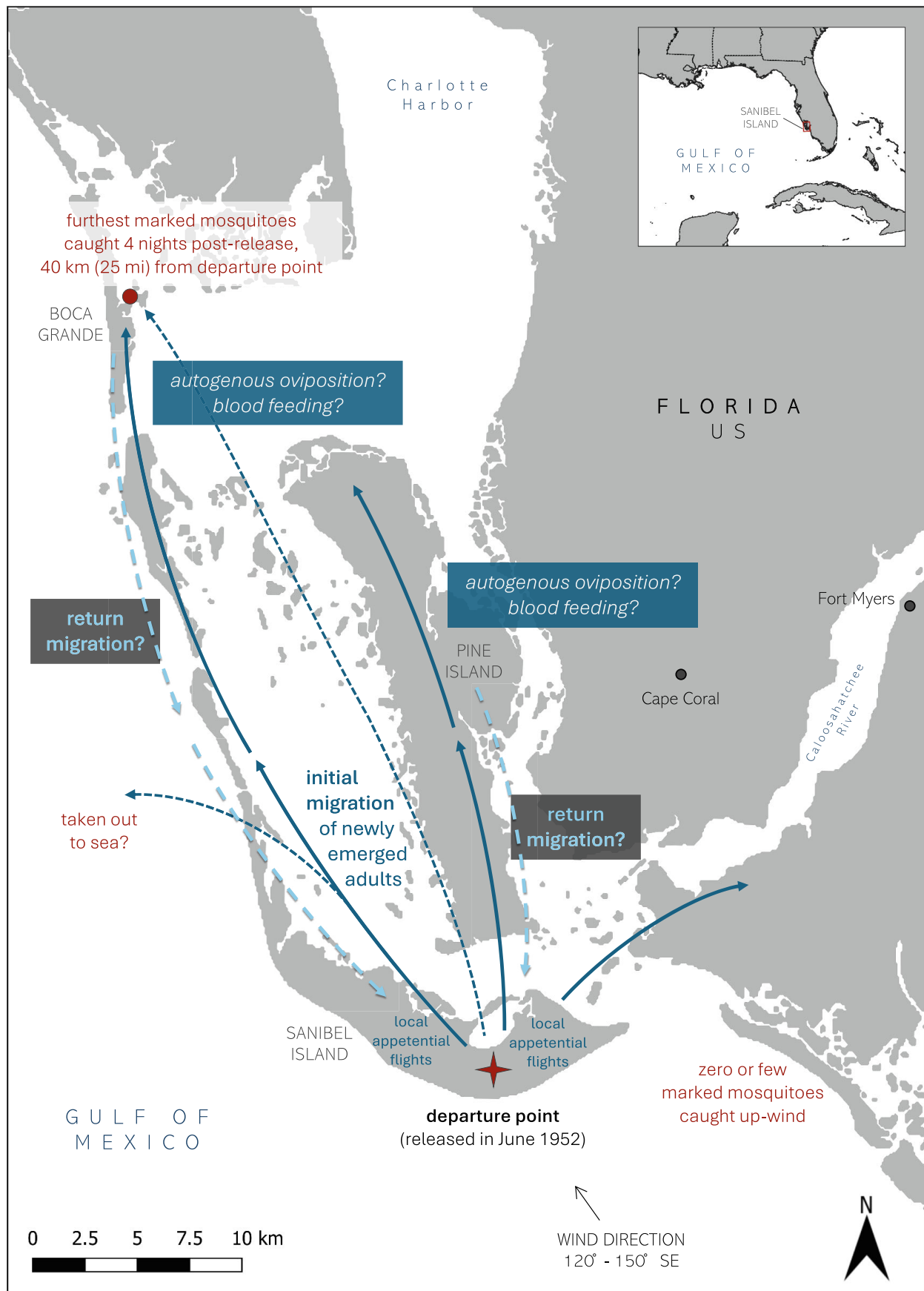


FIGURE 1 Legend on next page.

TABLE 1 Summary of reports describing long-distance salt marsh mosquito movements, including approximate distances recorded, geographic regions, and key references.

Mosquito species and common name	Distance recorded in kilometres (and miles) ^a	Study region, country	Reference(s)
<i>Ae. taeniorhynchus</i> , black salt marsh mosquito	Up to 51 km (32 mi)	Florida, United States	Provost (1952), Provost (1957), Vlach et al. (2006)
<i>Ae. sollicitans</i> , eastern salt marsh mosquito	Up to 285 km (177 mi)	Atlantic coast (New Jersey), United States	Crans et al. (1976)
<i>Ae. vigilax</i> , Australian salt marsh mosquito	Up to 50 km (31 mi)	Queensland and New South Wales, Australia	Chapman et al. (1999), Webb and Russell (2019)
<i>Ae. camptorhynchus</i> , southern salt marsh mosquito	Up to 3 km (1.9 mi)	Victoria and Tasmania, Australia	Jardine et al. (2014)
<i>Ae. detritus</i> , coastal floodwater mosquito	Up to 8 km (5 mi)	Coastal North-West England, United Kingdom	Clarkson and Enevoldson (2021)
	Up to 20 km (12 mi)	Southern France	Rioux (1958)

^aDistances are shown in kilometres, with approximate mile equivalents in parentheses for international readability and clarity.

for breeding. While migration would offer some population benefits under the first two scenarios, for the latter, given the distances that wind-borne salt marsh mosquitoes are carried, it is unlikely (although not impossible) that all females can return using self-powered flight alone, especially if this return is against the direction of prevailing winds that displaced them in the first place.

Migratory mosquitoes caught at high altitude in the Sahel are mostly gravid females, with more recent data showing a considerable prevalence of thoracic *Plasmodia* and viral infection (Bamou et al., 2024), indicating an age structure commensurate with at least one or two gonotrophic cycles. By contrast, historic field and behavioural observations of salt marsh species support a younger migratory population (Haeger, 1960; Provost, 1957). While an initial migration could maximise the chance of locating a blood meal, many intertidal hematophagous Diptera are autogenous – produce eggs on a blood-free diet – including multiple salt marsh mosquito species, including *Culex salinarius* Coquillett (Tveten & Meola, 1988), *Ae. taeniorhynchus* (O'Meara & Edman, 1975), *Ae. detritus* (Ben Ayed et al., 2019), and *Ae. vigilax* (Hugo et al., 2003). The expression of autogeny would allow emerging adult females to lay their eggs upon landing post-migration. Autogeny is not, however, fixed within a species or a population and is subject to genetic and environmental control (Ariani et al., 2015), with clinal variation observed in *Ae. taeniorhynchus* (O'Meara & Evans, 1973). The role of autogeny and its co-expression with migration requires further evaluation but offers a potentially intriguing strategy adopted by salt marsh species to cope with the stresses of their environment.

Salt marshes are constantly in flux, subject to rising and falling tides, as well as the often variable but strong coastal winds. Native salt marsh invertebrates are therefore subject to constant shifts in

biotic (nutrients, predators) and abiotic (salinity, water depth) factors to which they must adapt. In herbivorous planthoppers, for example, the temporal nature of food availability leads to the evolution of dispersive winged morphs (Denno et al., 1996). Many migratory insects are facultative, migrating as adults in response to environmental cues experienced at the larval stage, an example of phenotypic plasticity (Menz et al., 2019). One such cue that may lead to migration in salt marsh mosquitoes is a high density of immature stages. Salt marsh mosquitoes lay eggs on dry or damp soil substrates with eggs remaining viable for long periods until repeated tidal inundation (Service, 1968). Depending on the season, topography, and tidal patterns, this can lead to brackish pools containing several thousand larvae and pupae (Rochlin & Morris, 2017). A density-dependent migratory state has been demonstrated for adult *Ae. taeniorhynchus* under laboratory conditions (Nayar & Sauermaier Jr., 1969). Host scarcity and the harsh coastal conditions may also select for migration, as has been suggested for the evolution of autogeny (O'Meara & Edman, 1975; O'Meara & Evans, 1973). Whatever the ecological driver, and during times of favourable winds, it is possible that newly emerged mosquitoes fly steeply above their FBL to 'escape' this pressure as part of an environmental response.

One of the difficulties of inferring population estimates and dispersal rates using mark-release-recapture (MRR) data is that trapping effort is rarely proportional to the size of the area under study. This is particularly true at the outer limits of the trapping design where only a few (or zero) marked individuals might be captured and, without accounting for trapping effort, interpretations of flight distances can be misleading. As a case in point, a reanalysis of the disaggregated data in the MRR studies conducted in southwest Florida (Provost, 1952; Provost, 1957) shows that the original estimates of

FIGURE 1 The *Aedes taeniorhynchus* mark-recapture experiments of the early 1950s. Solid blue arrows depict the possible routes and hypothesised biological drivers of adult female dispersal/migration following the emergence of radiolabelled adults. The departure point on Sanibel Island, the wind direction and furthest recaptures during the 1952 experiment (Provost, 1957) are highlighted.

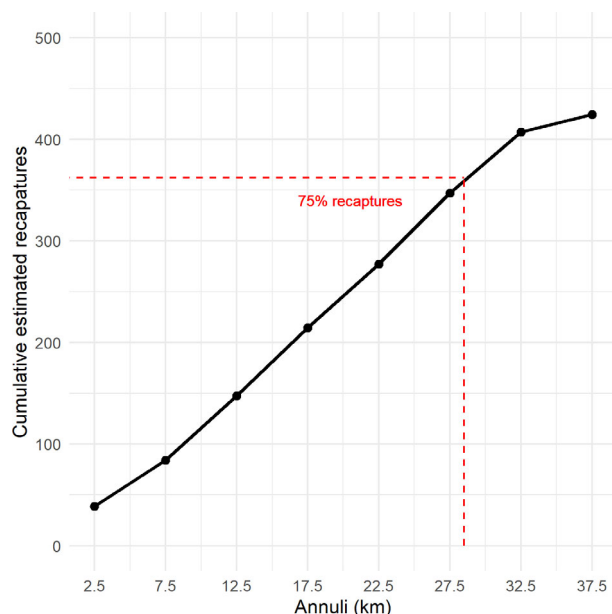


FIGURE 2 Cumulative estimated recapture rates from a reanalysis of mark-release-recapture *Aedes taeniorhynchus* data from the 1952 study described in Provost (1957). Disaggregated mark-recapture data were grouped into eight annuli (5 km radii) based on the distance of light traps from the release point given in tab. 2 of Provost (1957). Mosquitoes caught up to nine nights post release are included. Recapture rates were estimated by accounting for trapping effort across the study area based on the method in Morris et al. (1991).

the percentage of marked *Ae. taeniorhynchus* females recaptured are grossly underestimated (Figure 2). By applying a correction factor for trapping effort (Morris et al., 1991) and plotting the adjusted estimated recapture rates of individuals caught up to 9 days post release, 25% of marked adults flew over 27.5 km downwind, with a mean distance travelled (MDT) of 19.6 km. Similar flight ranges are estimated for the 1951 study (MDT = 15.6 km) (Provost, 1952). In the case of *Ae. taeniorhynchus*, the magnitude of mass salt marsh mosquito movement is probably much greater than previously thought, and although the calculations above are based on a single pair of MRR experiments, the commonality of long-distance movements across different salt marsh mosquito species reported from similar studies (Chapman et al., 1999; Jardine et al., 2014) and ‘accidental’ captures out at sea (Asahina, 1970; Curry, 1939; Sparks et al., 1986) suggest a wider behavioural phenomenon.

In summary, we postulate that the long-distance wind-assisted movements of salt marsh mosquitoes can be categorised as migratory (Hawkes et al., 2025) and are in response to one or more environmental triggers (e.g. overcrowding at the larval stage). Emerging migrant mosquitoes ascend above their FBL and use local winds to maximise the chances of either finding a host, or in the case of an autogenous population, locating an oviposition site. This is a risky strategy but may be beneficial if the topography of the coastal landscape permits and most mosquitoes can descend within favourable salt marsh. That said, if the winds take individuals inland then some may not return to

the marsh for egg-laying, or indeed they may be carried out to sea. These individuals do not contribute to the next generation, but their loss is unlikely to harm the overall stability of the population due to high reproductive rates, overwintering and/or autogeny. This is not a definitive account of salt marsh mosquito migration and much more empirical evidence is needed to interpret population dynamics in relation to seasonal winds, as well as the physiological status and age of mosquitoes, but it is a starting hypothesis that warrants further investigation. An important point to note is that the restricted larval habitat and the synchronicity of population abundances make it much easier to detect and infer migratory behaviour from salt marsh species, and this may bias migratory observations over freshwater species. Nevertheless, their unique ecology within the Culicidae makes salt marsh mosquitoes an excellent model in which to address knowledge gaps in dipteran migration compared to more charismatic migratory species (Hawkes et al., 2025). A similar re-evaluation of historic MRR experiments (Dickinson, 2014) has led to the discovery of surprising navigational adaptations underpinning straightened-out, long-distance movements in *Drosophilidae* (Giraldo et al., 2018; Warren et al., 2019).

Ultimately, the spread of any mosquito-borne infection is determined by the maximum distance in which an infectious host or mosquito can travel and infect a new host or mosquito at their destination. Furthermore, given the introduction of a pathogen or virus in a new environment, the likelihood of onward transmission is determined by the conditions occurring at the point of introduction and over just a few kilometres. These conditions arise from contributions of multiple, seasonally dynamic, mosquito and host species. Many of the salt marsh species described here are putative viral vectors (e.g. West Nile virus (Blagrove et al., 2016) and Ross River virus (Jardine et al., 2014)). Newly emerged salt marsh mosquitoes that engage in wind-assisted movements will not, of course, be infectious upon their migratory ascent, but any subsequent successes in finding suitable hosts, and/or laying eggs (in the case of vertical transovarial viral transmission) will increase the geographic range of transmission. Most salt marsh populations breed in coastal wetlands, coexisting with potentially viraemic migratory bird species, and the migration of salt marsh mosquitoes adds an additional dynamic to these epizootic mosquito-borne disease life cycles.

AUTHOR CONTRIBUTIONS

Christopher M. Jones: Conceptualization; writing – original draft; funding acquisition; writing – review and editing; visualization. **Don R. Reynolds:** Writing – review and editing. **Nadja C. Wipf:** Writing – review and editing; visualization. **Jason W. Chapman:** Funding acquisition; writing – review and editing. **Tovi Lehmann:** Writing – review and editing.

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