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Keywords

migration, dispersal, flight, movement ecology, European corn borer, *Ostrinia nubilalis*

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REVIEW

Migratory flight of insect pests within a year-round distribution: European corn borer as a case study

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Abstract

Insect migratory flight differs fundamentally from most other kinds of flight behavior, in that it is non-appetitive. The adult is not searching for anything, and migratory flight is not terminated by encounters with potential resources. Many insect pests of agricultural crops are long-distance migrants, moving from lower latitudes where they overwinter to higher latitudes in the spring to exploit superabundant, but seasonally ephemeral, host crops. The migratory nature of these pests is somewhat easy to recognize because of their sudden appearance in areas where they had been absent only a day or two earlier. Many other serious pests survive hostile winter conditions by diapausing, and therefore do not require migration to move between overwintering and breeding ranges. Yet there is evidence of migratory behavior engaged in by several pest species that inhabit high latitudes year-round. In these cases, the consequences of migratory flight are not immediately noticeable at the population level, because migration takes place for the most part within their larger year-round distribution. Nevertheless, the potential population-level consequences can be quite important in the contexts of pest management and insect resistance management. As a case study, I review the evidence for migratory flight behavior by individual European corn borer adults, and discuss the importance of understanding it. The kind of migratory behavior posited for pest species inhabiting a permanent distribution may be more common than we realize.

Keywords: migration, dispersal, flight, movement ecology, European corn borer, *Ostrinia nubilalis*

1. Introduction

1.1. 'Classic' migration of insect pests

Insect migration is often thought of in its classic sense as

long-distance movement to escape current or pending environmental conditions that will not allow survival or successful breeding. More than simply escaping deteriorating environmental conditions, however, migratory flight behavior is usually directional and designed to move the insect to an area where adequate breeding conditions prevail (Chapman *et al.* 2011). Many pests of field crops are migratory species that fit this description (Magor 1995; Drake and Reynolds 2012). They overwinter in lower latitudes and migrate poleward in the spring to colonize superabundant, but seasonally ephemeral, agricultural host plants. Spring migratory flight is often wind-aided, resulting in rapid transport of hundreds of kilometers in only a few days (Drake and Farrow 1988; Johnson 1995; Chapman *et al.* 2015). After one or more summer generations at

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high latitudes, individuals engage in an autumn “return migration” to low latitudes for overwintering (Johnson 1995; Hu *et al.* 2016). Autumn migration is also wind-aided, but the available winds are generally slower than in the spring, making the return trip correspondingly prolonged.

An example of this classic type of migratory pest is the black cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae), a cosmopolitan species found in all hemispheres. In North America, the black cutworm overwinters along the Gulf Coast or further south in Mexico. It migrates northward in the spring on low-level wind jets, fast moving parcels of air which form several hundred meters above the earth’s surface in advance of approaching cold fronts (Johnson 1995). Spring migration was directly demonstrated by recapture of three marked black cutworm adults 2–4 nights after, and 921–1175 km to the north of their release in May 1987 from east-central Texas. Wind trajectory analyses indicated the moths were flying in fast winds at 300–900 m altitude (Showers *et al.* 1989). Because long-range migration of black cutworm is wind-aided, the timing and specific location of immigrant arrival in the north is impossible to predict. The species is polyphagous, but is mainly a pest of seedling corn. Management relies on pheromone trap monitoring of immigrant adults, subsequent scouting for first generation larval damage, and a foliar rescue treatment if necessary. Two to four generations are produced in the north, and migratory movement seems to be a part of each generation, expanding the northern distribution accordingly through the summer. However, at the same time, the southern overwintering area appears to be largely depopulated by spring emigration, driven by temperatures too hot ($\geq 36^{\circ}\text{C}$) for pupal survival (Showers 1997), shrinking its distribution in the south. The black cutworm cannot survive typical cold winter temperatures north of about 38°N latitude, and the direction of migration during late summer and autumn shifts southward. A marked moth released in the autumn of 1987 from central Iowa was recaptured 1 900 km to the south eight nights later near Brownsville, Texas (Showers *et al.* 1993). Choice of migratory flight direction in any season is through selection of appropriately directed winds, but the mechanism underlying directional preference is unknown. Chang *et al.* (2017) recently characterized expression of *MagR* (magnetoreceptor) and *Cryptochrome* genes in black cutworm, which provide the basis of magnetosensitivity in *Drosophila* (Gegeer *et al.* 2008) and for navigation in migrating birds (Mouritsen and Hore 2012), but their possible role in cutworm migration has yet to be tested.

A number of other noctuid pests of field crops migrate between geographically distinct overwintering and breeding areas. A notable example is the oriental armyworm, *Mythimna separata* (Lepidoptera: Noctuidae), a serious polyphagous pest of small grains in China and other parts

of East Asia. A classic series of mark-recapture experiments by Li *et al.* (1964; reviewed in Jiang *et al.* 2011) revealed the major annual migratory pathways of this species in China. The oriental armyworm overwinters south of about 33°N latitude. In the early spring it migrates northward to reproduce in latitudes between 33° and 36°N . Most adults of the subsequent generation migrate further north. Some migrate westward and others to the southwest, but they do not migrate back to the southern overwintering region where summer temperatures are too hot for reproduction (Jiang *et al.* 2000, 2011). Two more generations are produced in northern areas, and the resultant adults of both migrate southward in anticipation of winter temperatures too cold to allow overwintering. Oriental armyworm migration is wind-aided, and like that of black cutworm, occurs 300–1 000 m up in the atmosphere in the spring, and at lower altitudes in the autumn, a function of weather systems producing winds of optimal or adequate temperature that are moving in the preferred direction (Chen *et al.* 1989; Jiang *et al.* 2011).

The migratory nature of pests such as these is somewhat easy to recognize because of their sudden appearance in areas where they had been absent only a day or two earlier (Drake and Reynolds 2012). A large influx of migratory adult moths may portend an imminent outbreak of their larval offspring, which is the life stage that inflicts damage on the host crop; or in the case of some hemimetabolous species like locusts, an outbreak may directly correspond to the arrival of the migrant adults themselves as they immediately begin feeding and damaging the host crop. Detection of immigration in such species is based on a population-level phenomenon, e.g., the sudden appearance of adults, observed visually or perhaps as a spike in trap captures, or an outbreak in an area where the species was recently absent. For the farmer and applied entomologists, it is this population-level migration event that is of immediate concern, and management tactics likewise target the immigrant pest population. However, population-level migration is an emergent property of individual migratory flight behavior (Dingle 2014; Chapman *et al.* 2015), and understanding the former requires a thorough understanding of the latter.

Migratory flight is a specific kind of individual behavior characterized in insects as persistent, straightened (non-meandering), undistracted flight (Kennedy 1985; Dingle and Drake 2007; Dingle 2014; Chapman *et al.* 2015). Non-migratory kinds of flight behavior are generally appetitive, where the individual is searching for a resource such as food, a mate, an oviposition site, or suitable habitat. Appetitive flight is arrested when the sought after resource is encountered. Escape behavior involving flight can be thought of in the same way, where the ‘resource’ being sought is safety from a predator or parasitoid. Migratory

flight behavior is fundamentally different, because it is non-appetitive (Dingle 2014). It does not reflect active search behavior. Thus, it is not terminated by encounters with potential resources, no matter how eminently suitable they may be. Escape behavior triggered by detection of a predator is a possible exception, but bats feed extensively on the flow of migrating moths in the atmosphere (McCracken *et al.* 2008; Krauel *et al.* 2018). Instead, migratory behavior is terminated in a systematic way based on environmental cues like onset of dusk or dawn, endogenous signals, or perhaps an internal clock (Compton 2002). After termination of migratory flight, appetitive flight behaviors are no longer suppressed and the insect can begin to search in its new environment for needed resources like food and suitable habitat.

Although migratory behavior itself is not a proximate search behavior, at an ultimate, evolutionary level, migration may function as a life-history strategy for escaping a deteriorating environment, or for exploiting an ephemeral resource far removed from its natal habitat (Drake *et al.* 1995; Chapman *et al.* 2012, 2015; Drake and Reynolds 2012). This is the case with the black cutworm and oriental armyworm described above, where escape from a seasonally hostile environment (extreme cold temperatures at high latitudes during winter, extreme hot temperatures at low latitudes in summer), and colonization of abundant annual host plants (high latitudes in spring and summer) are accomplished spatially *via* migration. But not all insect pests escape the rigors of winter by migrating to lower latitudes. Another life-history option, employed by many species, is escape in time by synchronizing a period of dormancy, i.e., diapause, with the winter season (Tauber *et al.* 1986; Drake and Reynolds 2012; Levy *et al.* 2015).

1.2. Migratory behavior within a permanent distribution

Research during my career has focused mainly on the movement ecology of several serious agricultural pests. Except for the black cutworm, the others are not classic migratory species. These include the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), boll weevil, *Anthonomus grandis grandis* (Coleoptera: Curculionidae), and western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae). The boll weevil attacks cotton, and the other two are primary pests of corn. Although all three are invasive species, each has occupied a permanent range in North America for many decades. They do not escape the hostile conditions of winter in space through migration, but instead escape in time through an overwintering diapause. Or, another way to put it, they do not gain access to superabundant

summer resources in areas where they cannot overwinter by migrating, but by permanently inhabiting those areas through the winter *via* diapause. Because of this, and because of my early immersion in the study of the long-range seasonal migration of black cutworm, I had no serious suspicion that any of these diapausing species might be migratory when I and co-workers began studying them. However, certain puzzling experimental results, as well as numerous observations in the literature, compelled me to entertain the idea.

There is in fact evidence of migratory behavior at the individual level for European corn borer (reviewed in this paper), boll weevil (e.g., Spurgeon *et al.* 1997; Kim *et al.* 2006, 2010; Westbrook *et al.* 2011), and western corn rootworm (e.g., Isard *et al.* 2004; Kim and Sappington 2005; Gray *et al.* 2009; Meinke *et al.* 2009; Flagel *et al.* 2014), as well as a number of other insects that inhabit a year-round range. Population-level consequences of migratory flight are not immediately visible, however, because obvious displacement of populations between overwintering and breeding ranges does not occur. In other words, if migratory behavior occurs in these species, it takes place for the most part within their larger year-round distribution.

My task in this paper is to present the case that much long-distance dispersal of European corn borer results from migratory behavior, not simply ranging behavior. To set the stage, I briefly review the importance of this pest to agriculture and why understanding its movement ecology (Nathan *et al.* 2008) matters. Then I review the station-keeping, or short range daily movement behaviors of European corn borer adults that include a somewhat strange phenomenon called commuting. These well-studied daily flight behaviors are fascinating, and are important to understand before examining long-distance dispersal behavior. This is because the paradigm that emerged from them about European corn borer adult movement ecology shaped interpretation of evidence for other kinds of movement for several decades. Next, I review experimental results and field observations that support the reality of long-distance movement by adults of this species. Finally, I present evidence that much of this long-distance displacement is a consequence of migratory behavior, and not simply of extended foraging (ranging).

2. European corn borer: Pest status and local dispersal behavior

2.1. Background

The European corn borer (*Ostrinia nubilalis*) was introduced at least three times into the eastern U.S. from Europe in the early 20th century (Caffrey and Worthley 1927a; Dopman *et al.* 2010) and then spread westward across the Corn Belt,

reaching Iowa in the 1940s and the Rocky Mountains by the late 1970s (Showers 1979, 1993). It is a chronic and major pest of corn (*Zea mays*) in the eastern two-thirds of North America (Mason *et al.* 1996) and much of Europe. Moths lay their eggs on leaves, and half-grown larvae bore into the stalk causing physiological and mechanical damage to the plant (Lynch 1980; Bode and Calvin 1990). After 1–5 generations, depending on latitude and voltinism rate (Showers *et al.* 1993; Levy *et al.* 2015), the insect overwinters inside stalk debris as diapausing 5th (last) instars, which pupate and emerge as adults the following spring (Caffrey and Worthley 1927a; Mason *et al.* 1996).

It is a difficult pest to manage by conventional chemicals, biological agents, host-plant resistance, and cultural measures, despite enormous research efforts to improve management options (Lewis *et al.* 2001; Ma and Subedi 2005). Until the introduction of commercial transgenic corn containing the Cry1Ab toxin gene from *Bacillus thuringiensis* (hereafter, Bt corn) in 1996 (Rice and Pilcher 1998), this insect was responsible for over 1 billion USD in yield and control costs annually in the U.S. (Mason *et al.* 1996). The near 100% efficacy of Bt corn against European corn borer larvae (Graeber *et al.* 1999; Archer *et al.* 2000; Ma and Subedi 2005) led to rapid and wide adoption in the U.S. (Hutchison *et al.* 2010; James 2010).

Given the widespread planting of Bt corn by producers and its attendant heavy selection pressure on European corn borer populations, the threat of resistance development to the Bt toxin has long been recognized, and is an ongoing concern (Andow *et al.* 1998; Tabashnik *et al.* 2009, 2013; Siegfried *et al.* 2014; Oyediran *et al.* 2016; Thieme *et al.* 2018). The extensive use of Bt corn in many parts of the U.S. has led to a substantial areawide suppression of European corn borer populations (Hutchison *et al.* 2010; Dively *et al.* 2018). While rightly celebrated, such regional suppression substantially increases the risk of resistance evolution (Caprio 2001; Ives *et al.* 2011). To slow development of resistance in natural European corn borer populations, the U.S. Environmental Protection Agency (EPA) mandates implementation of insect resistance management (IRM) strategies (Bourguet *et al.* 2005; Sivasupramaniam *et al.* 2007). Currently, preventive IRM tactics are implemented at the local scale, and are based on the high-dose/refuge strategy (Gould 1998; Andow and Ives 2002; Bourguet *et al.* 2005; Tabashnik 2008; Tabashnik *et al.* 2009; Miller and Sappington 2017). There are two basic components to this strategy: 1) the use of a high dose of Bt toxin to render heterozygous resistant individuals functionally susceptible, and 2) the provision of non Bt corn refuges as blocks within 800 m of Bt corn, or as Bt/non Bt seed mixtures (Onstad *et al.* 2011) to serve as nurseries for production of homozygous susceptible moths to mate with survivors of nearby Bt plants.

Together, these tactics are expected to delay the production of homozygous resistant individuals and the subsequent increase in resistance allele frequency (Ives and Andow 2002; Tabashnik *et al.* 2009; Carrière *et al.* 2010).

EPA must make its regulatory decisions regarding IRM strategies for current and new transgenic crops based on the best scientific data available (Sappington *et al.* 2010). Data inevitably include those generated by modeling resistance evolution under different refuge and resistance scenarios. While necessary and valuable, all models incorporate assumptions and abstractions to make them tractable, and assumptions about insect dispersal resulting in gene flow are among the most important (Qiao *et al.* 2008). Dispersal and gene flow in European corn borer is complicated, and incorporating the results into the assumptions for associated model parameters is critical to ensuring robust output from IRM models. It is in this context that many studies designed to clarify European corn borer movement ecology have been conducted during the last two decades.

Individual European corn borer adults engage in many categories of movement over a lifetime (Dorhout *et al.* 2008; Dingle 2014), much of it local in nature. Station-keeping activities involve seeking mates, free water, and oviposition sites (Schurr and Holdaway 1966; Showers *et al.* 1974; DeRozari *et al.* 1977; Pilcher and Rice 2001), as well as daily commuting between grassy aggregation sites and cornfields (Showers *et al.* 1976; DeRozari *et al.* 1977; Sappington and Showers 1983; Sappington 2005; Bailey *et al.* 2007). Such behaviors by themselves may generate low net displacement. Facultative ranging behavior in search of, for example, suitable oviposition and aggregation sites that are not available in the local vicinity may result in greater net displacement, permanently moving the insect out of its previous home range.

2.2. The daily commute: Adult movement between cornfields and weedy aggregation sites

European corn borer adults are commonly found aggregated during the daytime in the weedy vegetation surrounding the borders of cornfields; locations of adult clusters are called action sites or aggregation sites (Showers *et al.* 1976, 1980; DeRozari *et al.* 1977). In these studies, sampling of adults at different times of the day and night by combinations of light trap, pheromone trap, drop net, flush bar, and visual observation demonstrated a daily flux of adults between the field border vegetation (comprised of various grassy and broad-leaf weeds) and nearby cornfields. The summary of European corn borer adult movement synthesized from these studies presented by Showers *et al.* (1980) became the general paradigm: Adults evacuate the aggregation sites at dusk, with both sexes searching for free water in the form

of dew which forms first over short grass as the temperature drops after sunset. After imbibing free water, unmated females return to the same or a different aggregation site and begin pheromone “calling” for males, with peak mating activity occurring around midnight. Mated females enter cornfields to oviposit, and return to the border vegetation by morning. In the case of males, after finding and imbibing water (usually dew) sometime after sundown, males spend the rest of the night flying low over border vegetation searching for female pheromone plumes. By dawn, males have settled in the aggregation sites along with unmated or newly mated females to spend the day resting.

This type of regular round-trip movement of insects between local habitats offering different resources is termed ‘commuting’, and constitutes a type of station-keeping behavior (Dingle and Drake 2007; Dingle 2014). The ‘station’ in this sense refers to the home-range of an individual insect, within which its normal daily maintenance activities take place, including foraging for resources like food, oviposition sites, mates, sheltering habitat, and so forth (Kennedy 1985; Dingle 2014). Commuting is equivalent to Tschamtko and Brandl’s (2004) depiction of a ‘multihabitat population’, where individuals move daily between patches of different habitat. Round-trip commuting behavior differs from round-trip (albeit often multi-generation) migratory behavior in that the latter is non-appetitive and results in displacement out of the home range (Dingle 2014).

The details of Showers *et al.*’s (1980) general paradigm of European corn borer daily flight activity were refined and elaborated in important ways in subsequent studies (e.g., Sappington and Showers 1983; Derrick and Showers 1990, 1991; Sappington 2005; Dalecky *et al.* 2006; Bailey *et al.* 2007), but it is broadly correct. Its robustness is demonstrated by the ability to predict and suppress larval populations in a cornfield by monitoring and controlling the adults in adjacent aggregation sites (Showers *et al.* 1980; Derrick and Showers 1990, 1991; Hellmich *et al.* 1998). Thus, the paradigm nicely describes the movement ecology of European corn borer through most of its adult lifespan. However, it has a couple of weaknesses. The first is that the foundational experiments were conducted in the rain-fed central Corn Belt, where weedy field margins suitable for adult aggregation are ubiquitous. But irrigation is used to grow corn in most of the arid Great Plains, making the cornfield itself potentially more attractive to European corn borer adults than the field borders, which often are too dry to support weedy aggregation sites. Hunt *et al.* (2001) and Qureshi *et al.* (2005) conducted experiments to address this issue, anticipating that the paradigm for European corn borer flight behavior would need to be adjusted for areas of irrigated corn. Their results were unexpected, as described later (see Section 4.2), and derived largely from the second,

more serious weakness: The experiments underlying the paradigm did not address the movement of newly emerged moths. Instead, the assumption was that newly emerged moths aggregated in weedy sites just outside the natal field, presumably in the first suitable aggregation habitat they encountered. Certainly a high proportion of young unmated females were found in aggregation sites. But their natal origin was undetermined.

3. Evidence of long-distance dispersal by European corn borer adults

In this section, I present evidence that European corn borer is capable of, and engages in, long-distance dispersal. This is important to establish, because it is easy to become preoccupied with local station-keeping behaviors when incorporating this species’ movement ecology into understandings of its population ecology and dynamics. Even if we dimly recall reading about long-distance movement during the North American range expansion or a mark-release-recapture experiment, and thus know at some level it must occur, we may assume such cases are exceptional or involve only a minor part of the population and can be ignored. As we will see, a variety of evidence, both observational and experimental, shows long-distance dispersal by European corn borer during part of its adult lifespan is the norm, not the exception. After making the case in Section 3 that it occurs and is common, I then present evidence in Section 4 that this long-distance dispersal is accomplished *via* migratory (non-appetitive) behavior. While several experimental methodologies, strategies, and specific studies overlap between the two sections, it is beneficial to revisit them in Section 4 with fresh eyes. We must look at the results of those studies in a different way to see what they reveal about the generally overlooked question of the underlying behavior driving long-distance dispersal.

3.1. Range expansion and captures outside of the species distribution

Annual changes in the European corn borer’s distribution as it expanded its range after multiple introductions to the U.S. and Canada provide indications of per generation dispersal distances by at least some individuals. Caffrey and Worthley (1927a) suggested the most likely scenario for the source of new infestations on the southern shore of Lake Erie in 1921 was wind-aided flight of moths from large populations on the north shore in Ontario, a distance of roughly 45–80 km over water. Rate of spread of this univoltine race out of the Great Lakes region in the 1930s was only about 19 km/generation. However, the westward expansion of the bivoltine race through the U.S. Corn Belt in the 1940s

was three-times faster, at about 57 km/generation (Palmer *et al.* 1985). The initial invasion of Minnesota by the bivoltine race began in the southeast corner of the state in 1943. Advancement westward into northern Minnesota by 1950, as well as into the fifth tier of counties in South Dakota by 1948, averaged about 46–48 km/generation (Chiang 1961, 1972).

In Europe, the univoltine race of the European corn borer has been expanding its range northward in Germany and Poland since the 1980s (Langenbruch 2007). Rate of spread from a focal infestation appears to be on the same order as that seen in the U.S. for the univoltine race: 10–15 km/generation in different parts of Germany (Gathmann and Rothmeier 2005; Heidel 2007), and 3–5 km/generation suggested in Poland (Bereś and Konefał 2010). However, judging from the map of range expansion in northeastern Germany (Heidel 2007), a pattern of stratified dispersal by founder populations is apparent ahead of established populations (Liebhold and Tobin 2008) at a rate of at least 40 km/generation. In Poland, the rate of spread may be limited more by rate of northward expansion of corn production than by the insect's dispersal capacity (Bereś and Konefał 2010).

Captures of European corn borer in the British Isles on several occasions indicated long-distance dispersal across water from mainland Europe (Bretherton and Chalmers-Hunt 1989; Colnutt 1995; Langmaid and Young 2006). Similarly, Mikkola (1986) reported that European corn borers were collected in light traps in Finland in 5 of 10 years of surveys, presumably originating from somewhere in northern Europe and crossing the Gulf of Finland. Pedgley and Yathom (1993) described the collection of a single European corn borer in a light trap in Eilat, Israel. The moth was captured in a desert area where it could not have originated closer than "at least several hundred" kilometers away.

3.2. Mark-release-recapture studies

Evidence for long-distance dispersal capacity of European corn borer adults includes data from mark-release-recapture (MRR) experiments (Table 1). Recapture of a marked insect constitutes direct proof that the insect flew at least the distance between the release and recapture sites. One must be careful in interpreting MRR recapture rates and distances, however, because of the rapid reduction in density, or dilution effect, of released moths with increasing distance from the release site. As Reynolds *et al.* (2006) points out, such dilution generally makes a MRR strategy for examining dispersal effective over only tens of meters or a few kilometers. This means that lack of recapture beyond a few kilometers from the release site cannot be taken as evidence that none of the released insects flew that distance. In addition, a host of factors associated with

experimental design can potentially affect behavior of the released insects. Among others, these include the source of the insects (e.g., feral or lab-reared); the type of mark and the handling involved in its application; where, when, and how the release is made; and abiotic conditions at the time of release (e.g., temperature, wind). Unanticipated, perhaps unique, circumstances can compromise a particular test. I watched in fascinated dismay one early evening in southern Texas as scores of hand-marked boll weevil adults ascending into the atmosphere were snapped up eagerly by nighthawks (*Chordeilinae*; *Chordeiles* sp.) that rapidly assembled above their release site for an unexpected feast. Although many weevils undoubtedly escaped predation by these birds, the total number "released" (meaning those that left the release area) was no longer known.

A clear example of both the limitations and strengths of the MRR strategy is an early study of European corn borer by Caffrey and Worthley (1927a). The authors recaptured a marked moth across Cape Cod Bay, 32 km from the release site on the Massachusetts mainland (Table 1). These and other releases were made during daylight from broad sandy beaches devoid of vegetation, so they do not reflect normal dispersal behavior of this nocturnal insect from agricultural habitat, but they do indicate adults are capable of traversing at least 32 km. Upon release, the authors observed the moths ascending to about 15 m and flying in the direction of a strong offshore wind, which clearly aided transport of the moths eastward. The low recapture rate (1 of >60 000 released) across the bay suggests many traveled even farther, beyond the small spit of land in their path and out to sea.

The maximum radius of sampling arenas for most MRR studies of European corn borer have been less than 250 m (Table 1). However, sampling at much greater distances from the release site was attempted in a few studies. In addition to the over-water flight of 32 km described above, Caffrey and Worthley (1927a) recovered marked individuals up to 8 km from a release site on Cape Cod after overland flight. Showers *et al.* (2001) analyzed data collected from MRR experiments conducted in the late 1980s. Recapture of internally marked moths targeted newly-emerged males by pheromone traps placed in square rings at intervals from 200 m to 49 km from the release site. A few marked females were recaptured fortuitously, including one that apparently blundered into a pheromone trap at 49.1 km from the release site, and two (plus one male) that hit the windshield of a vehicle as a group of about 10 or 11 moths crossed a road 100 min after release 14 km away. Additional males were captured in traps at 26.5, 40.2 and 40.3 km from the release site. In MRR studies of the closely related Asian corn borer (*Ostrinia furnicalis* Guenée) by Wang *et al.* (1994) in China, two males were captured in pheromone traps 45.5 km from the release site, and a few were recaptured at distances up to 30 km.

Table 1 Summary of results of mark-release-recapture experiments on European corn borer, indicating rates and distances of recapture

Reference	Release habitat	No. of trials	Total released	Age of released adults	Recapture method ¹⁾	Mean no. or % recaptured per release ²⁾	Range of % recaptured	Max. distance sampled	Max. recapture distance	Comments
Caffrey and Worthley (1927a)	Ocean beach	1	60988	Unknown (feral)	SN	1 M		32 km	32 km	Daytime release on mainland, offshore wind, recapture across Cape Cod Bay.
	Ocean beach	1	8650	Unknown (feral)	SN	4 F, 3 M		8 km	8 km	Daytime release on Cape Cod, recapture along Cape.
Showers <i>et al.</i> (2001)	Open field	6 sets (of 3–5 each)	639892	<24 h	PT	0.25% (per set)	0.12–0.33% (across sets)	67 km	49.1 km (female in male PT)	Square rings of traps, transect distances varied over 3 years of study.
Hunt <i>et al.</i> (2001)	Irrigated corn	2	10578	24–72 h	LT	40 F, 43 M	0.7–0.8%	207 m	207 m	
	Non-irrigated corn	2	10578	24–72 h	LT	6 F, 14 M	0.1–0.3%	207 m	163 m	
Qureshi <i>et al.</i> (2005)	Irrigated corn	7	43019	Newly emerged	PT+LT	1.05% F, 2.93% M	0.08–7.6%	1 133 m	823 m	Continuous emergence from pupae in field; daily sampling meant those present after even 1 night would be detectable in principle.
Reardon <i>et al.</i> (2006)	Non-irrigated corn	12	215900	Newly emerged	SN	13 F, 90 M (0.05%)	154 to 1580-fold fewer than expected	211 m	Between 137–211 m	Continuous emergence from pupae in field; daily sampling meant those present after even 1 night would be detectable in principle.
Dalecky <i>et al.</i> (2006)	Non-irrigated corn	17	8788	<24 h	SN	4.3%	0.2–26.9%	31 m		Recaptures were exhaustive in 100 m strip of border vegetation parallel to release site, which was 7 m into cornfield.
Bailey <i>et al.</i> (2007)	Border weeds	2	437	Unknown (feral)	SN	1.3%	0–2.6%	0		Recaptures were exhaustive in same 50-m strip of border vegetation where releases were made; dusk releases only, next to corn only.
Reardon and Sappington (2007)	Border weeds	6	2093	Unknown (feral)	SN	7.7%	1.4–18.9%	50 m	Between 0–50 m	Recaptures were exhaustive in 110-m strip of border vegetation where releases were made (in center 10 m); dusk releases only, next to corn only.
	Small grain aggregation plots	8	59445	Mixed ages, 0–10 days old	SN	0.80%	0–4.4%	0		Recaptures from same plot of release.

¹⁾ SN, sweep net; PT, pheromone trap; LT, light trap.

²⁾ F, female; M, male.

Table 2 Median performance of unmated and mated European corn borer adults of different ages on laboratory flight mills during 8 h of darkness

Mating status	Age	Sample size		Distance of longest flight (m)		Speed of longest flight (m s ⁻¹)	
		Female	Male	Female	Male	Female	Male
Unmated	1	42	47	3 143 a	456 [*] a	0.52 a	0.26 [*] a
	2	42	34	1 845 ab	1 386 [*] a	0.49 a	0.32 [*] a
	3	49	45	2 428 ab	1 153 [*] a	0.57 a	0.23 [*] a
	5	45	36	742 b	1 351 a	0.44 a	0.33 a
Mated ¹⁾	2	41	46	1 071 a	1 249 a	0.43 a	0.34 [*] a
	3	45	–	1 481 a	–	0.39 a	–
	5	32	54	605 a	1 163 a	0.36 a	0.32 a

¹⁾ Individuals were flown the first full night after mating.

There were no significant differences ($\alpha=0.05$) between mated vs. unmated within any age and sex categories (modified from Dorhout *et al.* 2008). ^{*} indicates a significant difference between males and females within a given age and mating status. Values within a column and of the same mating status followed by the same letter are not significantly different ($\alpha=0.05$) (Kruskal-Wallis test).

3.3. Flight mill studies

The median longest flight by young unmated European corn borer females on flight mills ranged from 1.8–3.1 km (max. 5.1 km); those of males ranged from 0.46–1.4 km (max. 20.5 km) (Table 2) (Dorhout *et al.* 2008). Flight mill experiments generally provide an indication of minimum (rather than typical) flight distances, because friction at the pivot and weight of the flight arm inevitably slow the insect. Nevertheless, flight mill experiments are good for relative comparisons of treatment groups or categorical variables like sex and age, and provide estimates of flight capacity, circadian rhythmicity of flight activity, and means of probing aspects of flight physiology (e.g., Sappington *et al.* 1995; Dorhout *et al.* 2008, 2011; Dingle 2014; Sappington and Burks 2014; Rovnyak *et al.* 2018).

After accounting for wind speed and direction, the free-flight speed of the mixed-sex group of marked European corn borer sampled “by windshield” described above (Showers *et al.* 2001) was estimated as 1.47 m s⁻¹. Median flight speeds of 1-d-old females (0.52 m s⁻¹) and males (0.26 m s⁻¹) on the flight mills (Table 2) (Dorhout *et al.* 2008), suggest that the distances measured on the mills were underestimated compared to free-flight by about 2.8-fold for females and 5.6-fold for males. This illustrates in part why directly translating flight mill distances to net displacement in the field is generally inadvisable. Translation is also hindered by the effects of wind speed and direction relative to flight direction of a moth in nature, and because the pathway of station-keeping flight activities is often meandering. On the other hand, Wang *et al.* (2017) demonstrated how combining forward trajectory analyses on field data for rice leafroller (or rice leafroller), *Cnaphalocrocis medinalis*, populations in China with flight mill and reproductive development data (Zhang *et al.* 2015) could elucidate the probable number of nights this insect engages in migratory flight and how far they travel. Such an approach holds promise for other classic

migrant species perhaps more than for European corn borer, but should inspire exploring novel ways to combine field, modeling, and flight mill data to answer difficult questions about migratory flight.

3.4. Gene flow and population genetics

Population genetics analyses are useful for inferring patterns of dispersal over geographic scales far beyond the normal effectiveness of MRR strategies (e.g., Kim *et al.* 2006; Jiang *et al.* 2007, 2010; Nagoshi *et al.* 2009; Fligel *et al.* 2014). Allele frequencies of selectively neutral genetic loci change in a population over time by genetic drift. However, the rate of change at such loci is affected in part by the rate of gene flow from other populations, so that gene flow is fundamentally tied to dispersal (Kim and Sappington 2013). Thus, pairwise genetic differentiation between populations, usually measured as F_{ST} (Wier and Cockerham 1984), can be used to make a rough estimate of the number of migrants exchanged per generation (migration as used in population genetics sense may or may not involve migratory behavior; it simply denotes movement, by any mode, of individuals into or out of a population). Thus, low differentiation indicates high gene flow, and *vice versa*, as long as the populations are in migration-drift equilibrium (Slatkin 1987; Hutchison and Templeton 1999). This is an important assumption. A population in a recently invaded area may show little genetic differentiation from other populations, even when exchange of migrants is low or nonexistent, because allele frequencies (similar after an invasion or expansion caused by founder effects) have not had time to drift apart. Rate of dispersal can also be estimated by analyzing changes in allele frequencies over time at a given location (Wang and Whitlock 2003), a method less sensitive to the assumption of migration-drift equilibrium.

Using AFLP markers, Krumm *et al.* (2008) found evidence of high gene flow between widely separated regions from

north to south in the western part of the species range in the U.S., but there was some evidence of differentiation. Kim *et al.* (2009), using microsatellite markers, found no significant differentiation between sample sites along north-south and east-west 720-km transects intersecting in central Iowa. Because of its relatively recent history of range expansion in the U.S., it was possible the lack of differentiation was caused by lack of migration-drift equilibrium. However, temporal analyses of gene flow between four locations on the transects suggested high migration rates were preventing differentiation. Kim *et al.* (2011) extended the geographic dimensions of sampling across >1 200 km from New York to Colorado, and found significant differentiation at 29% of pairwise comparisons, over half of which involved the New York and Pennsylvania populations. Analyses of allozyme data from European corn borer sampled at 29 locations throughout France, where migration-drift equilibrium is a safe assumption, suggested extensive gene flow between most regions (Bourguet *et al.* 2000). Malausa *et al.* (2007) found some pairwise differentiation across France using microsatellite markers, but in general the evidence indicated high gene flow.

In a continuous distribution, as is essentially the case for European corn borer in the U.S. Corn Belt, one would expect the level of differentiation between locations to depend on distance alone. In other words, populations closer together should be more similar than those farther apart. Such isolation by distance (IBD) relationships are detected as a positive regression of genetic distance on geographic distance (Wright 1943; Slatkin 1987; Guillot *et al.* 2009; Aguillon *et al.* 2017). Coates *et al.* (2004) examined mtDNA RFLP haplotypes from cytochrome oxidase I and II and found them to vary little among 14 populations collected from Maine to Kansas, and IBD was not detected. A lack of IBD among European corn borer populations has been consistently reported across France based on allozymes (Bourguet *et al.* 2000; Martel *et al.* 2003; Leniaud *et al.* 2006) and microsatellite markers (Malausa *et al.* 2007). Similarly, Kim *et al.* (2009) did not detect IBD along two 720-km long transects in the central U.S. Corn Belt. However, a significant IBD was detected by Kim *et al.* (2011) along the 1 200+ km transect running from the northeastern U.S. to the Great Plains. The slope was shallow suggesting high gene flow across long distances.

Using this estimate of IBD and adult population density calculated from flush sample data reported by Sappington (2005), Kim *et al.* (2011) calculated Wright's genetic neighborhood area for European corn borer. In a species with a continuous distribution, the genetic neighborhood is the space (conceptually a circle) within which individuals constitute a random mating, or panmictic, population (Wright 1946; Slatkin and Barton 1989; Roussett 1997;

Allendorf and Luikart 2007; Shirk and Cushman 2014). The radius of the neighborhood is roughly the lifetime effective dispersal distance of about 87% of individuals. For European corn borer, the genetic neighborhood radius was estimated as approx. 12 km/generation. This routine lifetime dispersal distance of an adult is compatible with data on the disappearance of moths from the vicinity of the natal field (see Section 4.2). The reciprocal implication is that 13% of individuals disperse further than 12 km, which could account for various observations of longer distance flights described in the above sections.

4. Nature of European corn borer long-distance dispersal behavior: Evidence it is migratory

The idea that European corn borer are capable of dispersing long distances had been noted for many years, but the possibility that such movement is a normal part of their life history strategy was seldom entertained until recently. Results from the relatively recent burst of experimentation on this species' dispersal behavior, in response to IRM imperatives, have repeatedly revealed that long-distance flight is common. It was simultaneously clear that we know disturbingly little about it. A major question concerns the nature of the behavior underlying long-distance dispersal. Both ranging and migratory behavior can result in spatial displacement of an individual out of its home range (Reynolds *et al.* 2006; Dingle 2014). Distinguishing between them depends on evidence for non-appetitive flight, which defines migratory behavior, as opposed to appetitive flight, which, by definition, characterizes ranging behavior. Direct demonstration of non-appetitive flight behavior is not easy, but the accumulated weight of indirect evidence, as described below, strongly supports engagement in true migratory behavior by European corn borer adults. The consequences of migratory flight to population dynamics and evolutionary response of populations to selection (such as imposed by agricultural control tactics) are non-trivial. Migratory flight within a permanent distribution implies consistent mixing of individuals originating across a relatively large and consistent spatial scale. In contrast, the spatial scale of mixing of individuals generated solely by ranging behavior will vary across locations within and between years, and may not occur at all when local resources are adequate.

4.1. Sudden appearance: Guilt by association with known migrants and winds

The arrival of known migratory insect species in an area are often characterized by a sudden appearance or increase in numbers during or immediately after passage of a weather

system that generates winds for transport from source areas (Krauel *et al.* 2015). In contrast, a sudden appearance of immigrant European corn borer adults would be difficult to detect inside the permanent range of the species where other individuals are already present and common (Chiang 1972). However, Chiang *et al.* (1965) monitored European corn borer adults during two summers with light traps along an approximate 240-km east–west transect near the southern border of Minnesota. Peaks in European corn borers captured per trap were positively associated with nights of southerly winds, and the authors hypothesized that many of the moths were migrating into Minnesota from somewhere to the south in Iowa.

Pedgley and Yathom (1993) noted that an insect captured in the company of known migrants in a location where it cannot breed, especially accompanied by a change in wind direction favorable for transport from a potential source area, is likely to be a migrant itself. This was the case for a single European corn borer adult captured along with a small peak in numbers of the well-known migrant *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) in an isolated desert location in southern Israel (Pedgley and Yathom 1993). The nearest likely sources were the Nile Delta about 300 km to the west or from irrigated highlands in central or northern Israel 150 km or more to the north. Migratory insects >10 mg usually take advantage of tailwinds to move in a preferred direction (Chapman *et al.* 2010, 2015; Drake and Reynolds 2012; Hu *et al.* 2016). Vast numbers of many species of insects migrate into the United Kingdom on southerly winds from Europe in the spring, and from the U.K. to Europe on northerly winds in the fall (Hu *et al.* 2016). Captures of European corn borer in the British Isles were often associated with the arrival of other migratory insects from Europe on southerly winds (Bretherton and Chalmers-Hunt 1989; Colnutt 1995; Langmaid and Young 2006), as were European corn borer immigrants to Finland across the Gulf of Finland (Mikkola 1986).

4.2. Sudden disappearance: Puzzling MRR results and inference from sampling data

Just as the sudden appearance of adult insects in an area of previous absence suggests an influx of migrants, a sudden disappearance of adults usually indicates mass emigration (Drake and Reynolds 2012). An occasion when such a disappearance is particularly noticeable is during a MRR study. As mentioned earlier, the dilution effect inherent to MRR studies (Reynolds *et al.* 2006) means a lack of recapture at long distances from the release site does not constitute evidence of lack of flight to that distance. Importantly, however, very low recapture near the release site does constitute good evidence that the released moths

dispersed beyond the local sampling arena, especially if the released numbers were large, sampling effort was relatively intensive, and results are replicated over time and space. A series of independent MRR studies with European corn borer found just that: often very low recapture rates in the vicinity of release sites, despite the presence of favorable adult habitat (Table 1).

In the MRR study of Showers *et al.* (2001), daytime sampling indicated that while some marked adults settled in nearby aggregation sites on the night of release, few remained after the following night. The authors concluded that when adults disperse from an aggregation site, “they may move a considerable distance before resettling” and found it surprising that dispersing adults were bypassing seemingly good aggregation habitat. The authors concluded that European corn borer adults were capable of long-distance dispersal, but they were left wondering what proportion of adults engaged in long flights, and what their underlying motivation might be.

A MRR study by Hunt *et al.* (2001) in Nebraska compared dispersal of newly emerged European corn borer moths from release sites in irrigated and non-irrigated fields (Table 1). The difference in dispersal between irrigated and non-irrigated fields was statistically significant, but this finding is relevant only to the small percentage of adults that remained in the 207-m sampling arena. The most important take-home finding was that almost all marked moths dispersed beyond 207 m within 24 h of adult eclosion.

Qureshi *et al.* (2005) conducted a MRR in western Kansas in an area dominated by pivot irrigation, and with only a few cornfields in the vicinity of the releases. Median recapture rates were low (males 1.97%; females 0.33%) in traps out to 823 m from the release point, supplemented by a few traps up to 1133 m distant placed in or near neighboring fields. Decay curves based on recapture data indicated a very sharp drop in recaptures beyond the release site itself, with long flat tails stretching through the rest of the field and beyond. Unfortunately, the paper’s abstract states that >90% of marked adults were recaptured within 300 m of the release site, and that this suggests dispersal was limited. These are errors, apparently left uncorrected as an oversight during manuscript preparation, that were not repeated in the body of the text. Instead, of the small percentage of marked moths recaptured, >90% were recaptured within 300 m of the release point. In the paper itself, the authors make what I think is the correct interpretation of their results: “The low recapture rate for marked European corn borer in this study could indicate that many of the marked insects were not staying in the study field and were not available for capture in the traps we installed. The relatively uniform distribution of marked adults across the release field suggests that corn borers have the potential to disperse extensively”.

Furthermore, captures of feral European corn borer during the Qureshi *et al.* (2005) study were high. The pattern of feral captures among traps was linear and indicated entry of the cornfields from all directions. These data suggested to the authors that the feral moths were immigrants and that production of insects from neighboring fields must be high, even though the nearest possible source fields were 587–1 387 m distant.

If a hotspot of European corn borer resistance to Bt-corn is detected, mitigation measures will be necessary to contain it spatially and to possibly return the population to susceptibility (Miller and Sappington 2017). A potential mitigation strategy discussed for a few years involved inundating a resistance hotspot with large numbers of Bt-susceptible adults mass-reared in the laboratory to mate with Bt-resistant adults emerging from the field. A precondition of that strategy's success is that the Bt-susceptible adults remain near their release site long enough to mate. Reardon *et al.* (2006) conducted MRR experiments to demonstrate proof of principle. Internally marked moths were allowed to emerge from pupae placed in the center of 0.8-ha corn plots under the assumption they would settle in nearby aggregation plots. The aggregation plots were provided as plantings of small grains (wheat, oats, or foxtail millet) at different densities, some of which were spiked with pheromone lures to potentially enhance adult density. Hellmich *et al.* (1998) had found that feral European corn borer adults colonized such small grain habitats planted as potential aggregation sites. The aggregation plots were likewise colonized by feral adults in the Reardon *et al.* (2006) study, but the recapture rate of marked adults was very low (Table 1). It was clear that newly emerged adults were not colonizing suitable aggregation sites encountered within at least 372 m of the natal site. The authors suggested European corn borer has an obligatory dispersal phase expressed soon after emergence. Reardon and Sappington (2007) followed up with an MRR of adults of different ages and mating status released directly in the aggregation sites. While significantly more 4–6 day old adults were recovered than younger or older age groups, the overall recapture rate was still very low (<1%) (Table 1).

In France, Dalecky *et al.* (2006) released marked European corn borer adults within 8 m of the cornfield border. Recapture by exhaustive sweep net sampling of bordering aggregation habitat 36 hours (2 nights) after release was somewhat higher than in the North American studies, but still averaged only 4.3% (Table 1). Bailey *et al.* (2007) conducted MRR experiments in which feral adults were captured in the field, marked in the laboratory, released within 24 h into aggregation habitat cleared of feral moths, and recaptured by exhaustive sampling of aggregation habitat. In this study, recapture rates were

highly variable, but on the whole greater than in the other MRR studies described above (Table 1). This is likely related in part to the experimental design in which age of released moths (captured from local wild populations) could not be controlled. Even so, based on spatial patterns of recapture, the authors suggested that those not recovered probably engaged in long-range dispersal out of the area.

4.3. Intergenerational independence of population densities in a cornfield

Population densities of European corn borer are essentially unrelated from one generation to the next in a single field of non-rotated corn (Chiang and Hodson 1959a, b; Chiang 1972; Showers *et al.* 1978). These authors presented evidence that larval mortality caused by weather might explain the observed lack of correlation, but Chiang (1972) suggested immigration of adults also could be involved. Lack of intergenerational correlation of population densities in a particular field makes cultural practices, such as destruction of crop residue to kill overwintering larvae, or crop rotation to prevent population buildup, generally ineffective in protecting a field from economic loss (Pilcher and Rice 1998; Hyde *et al.* 1999). The same conclusion was reached for the closely related Asian corn borer in Japan, where infestation of a field in the previous generation was not predictive of infestation level in the next generation (Saito and Oku 1985; Shirai 1998). Wang *et al.* (1995) also noted the erratic correspondence of infestation levels between generations in China. They mentioned a flood event in Hebei Province in summer 1963 that engulfed all crops and thus prevented reproduction by Asian corn borers, yet the population level was quite high in that area the following spring. The implication was that the flooded region must have been recolonized by immigrants from unflooded areas where the larvae had successfully overwintered.

It has been known for almost a century (e.g., Crawford and Spencer 1922; Caffrey and Worthley 1927b; Umeozor *et al.* 1985) that burial or destruction of corn stubble in the fall causes high mortality of European corn borer larvae overwintering in the stalks. However, it has been known for just as long that destroying larvae in this way in a particular field has little or no effect on the level of infestation in that same field the next year (Crawford and Spencer 1922; Umeozor *et al.* 1985). Felt (1922) reported contemporary speculation that “moths drifting from another badly infested area” could be the reason, although he cautioned readers that this possibility had not yet been proven.

Crop rotation can provide some benefit in reducing European corn borer damage in a field. In small plot experiments in North Carolina, Brust and King (1994) found less European corn borer damage in corn after two years of

planting to other crops. Importantly, this effect was caused by increased predator populations (and thus increased larval mortality) in the rotated plots, not to intergenerational buildup of pest populations in non-rotated corn plots. Examining scouting records for commercial fields in Ohio, Willson and Easley (1992) found that 2-crop (1-year) rotations of corn with another crop (including soybean, the most common rotation in the Corn Belt) reduced incidence of infestations by offspring of the overwintering generation of European corn borer compared to fields planted continuously to corn. They attributed this finding to, “presumably” the emergence of adults from stalks from the previous season in the non-rotated cornfield. This was a reasonable presumption, but it also could have been caused by increased natural enemies in the rotated fields (e.g., Brust and King 1994), or to differential attractiveness of rotated and non-rotated corn to ovipositing females, perhaps through differential effects on soil (e.g., Phelan *et al.* 1995). Regardless, the potential positive effects of crop rotation in reducing European corn borer damage are not great enough or consistent enough to warrant routine recommendation as a management tactic for this pest. In other words, crop rotation is not considered a relevant factor in practical guides to European corn borer pest management at the farm level (e.g., Tollefson and Calvin 1994; Mason *et al.* 1996). Even the nearly complete absence of infestation in one year, say because the field was planted to soybean, does not provide adequate protection from infestation the following year when that field is returned to corn. Rotated corn must be scouted for possible European corn borer infestation to the same extent as non-rotated corn when determining if a foliar insecticide rescue treatment is needed to protect yield. Similarly, a high infestation suffered by a cornfield in one generation does not portend a high level of infestation in the next generation (Chiang and Hodson 1959; Chiang 1972; Showers *et al.* 1978).

Tollefson and Calvin (1994) discuss the importance of a landscape sampling approach to obtain data on first generation larval demography needed for initiating a European corn borer phenology model; the model is used to properly time scouting and implementation of tactics to control second generation larvae. Sampling from multiple fields is necessary because the pest’s demographic structure varies across the landscape based on temporal variation in attractiveness of corn plants at different developmental stages to first-flight females. Second-flight females that oviposit in any particular field will have been drawn from across that landscape, and sampling from the target field will not represent the more relevant population occupying the larger neighborhood.

Although stochasticity of larval mortality caused by weather may certainly contribute (Chiang 1972; Showers

et al. 1978), high mobility of adults seems the main driver of independence of European corn borer population densities between generations within a field. Sappington (2005) used flush sampling in long segments of roadside vegetation in central Iowa to examine the spatial distribution of first-flight (overwintered generation) European corn borer adults in relation to larger landscape features such as current and previous years’ crops. The hypotheses I tested were formulated under the assumption that newly emerged moths colonize nearby aggregation habitat, followed by possible redistribution across the landscape over time based on the location of their favored oviposition host, corn. This pattern was borne out by the data (Fig. 1-A). However, the number of adults in aggregation habitat was not substantially influenced by the previous year’s crop in the adjacent field (Fig. 1-B). Furthermore, proximity to minimum tillage fields of corn stubble from the previous year, in which overwintering survival of larvae is greater than in conventionally tilled fields (Umeozor *et al.* 1985), had only a weak effect on adult density in adjacent aggregation sites. The conclusion was that there is little or no effect of the previous year’s crop on the current year’s spatial distribution of adults, and that if

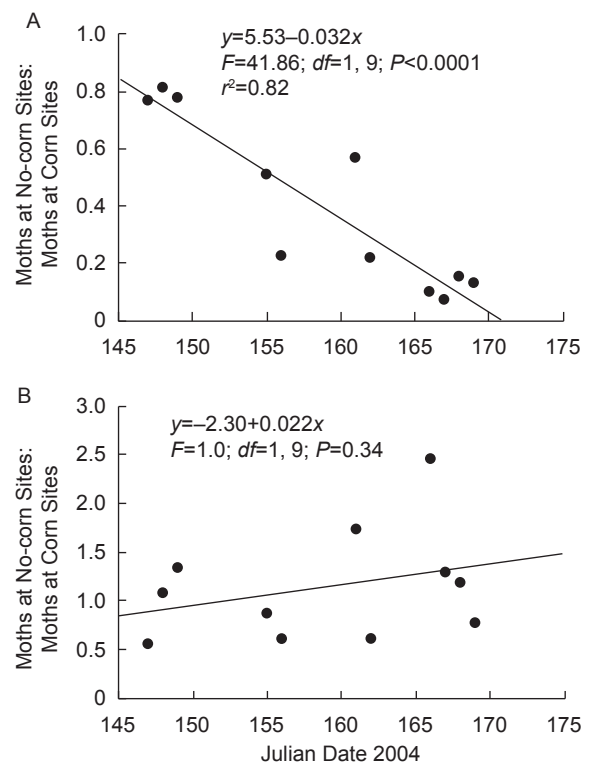


Fig. 1 Linear regression of the ratio of the number of European corn borer moths flushed from grassy ditches with no corn on either side of the road to those with corn on at least one side vs. time (sample date, 2004). Regressions are based on the cropping pattern of corn of the current year (A), and corn of the previous year (B) (adapted from Sappington 2005).

some newly emerged adults colonize vegetation near their natal field, they do not remain there long.

These considerations along with several other lines of evidence, including the rapid disappearance of marked moths in the MRR studies described above (Section 4.2; Table 1), support the following scenario: Most of the adults emerging from a cornfield disperse away from that field and its local neighborhood up to at least several hundred meters to oviposit elsewhere. Reciprocally, the great majority of eggs laid in that same field are from immigrant adults that emerged elsewhere. A consistently high rate of dispersal of newly-emerged European corn borer adults away from the natal field may underlie the recognition that tillage of infested corn stubble and crop rotation must be implemented on an areawide scale to be effective management strategies (Crawford and Spencer 1922; Umeozor *et al.* 1985; Mason *et al.* 1996; Pilcher and Rice 1998). Such emigration, even from a field of suitable habitat, is evidence of migratory behavior, because it suggests the dispersal is pre-programmed, i.e., non-appetitive.

4.4. Typical migratory behaviors: High altitude flight, wind-aided transport

Most long-distance seasonal migrants use strong winds high in the atmosphere to facilitate fast displacement (Drake and Reynolds 2012). While migration does not require high-altitude flight (Chapman *et al.* 2015), the presence of an insect at high-altitude and oriented with the wind is a strong indication that it is indeed engaged in migratory flight behavior. To my knowledge, there is no direct evidence of European corn borer flight at high altitude. However, Asian corn borers were caught by aerial netting in east-central China at 250 m above ground level in the company of two pyralid migrants, the beet webworm, *Loxostege sticticalis* L., and rice leafroller, *Cnaphalocrocis medinalis* Guenée (Riley *et al.* 1995). In addition, large numbers of Asian corn borer were captured over a number of nights in the company of the migratory *L. sticticalis* in northern China by a searchlight trap designed to sample migrating insects simultaneously detected by radar (Feng *et al.* 2004). On most nights, the migrating insects were flying in fast winds at altitudes from 300–500 m.

There is some evidence for use of surface winds for dispersal by European corn borer. Showers *et al.* (1995) monitored dispersal of bivoltine European corn borer that emerged from large artificial larval infestations at a corn breeding nursery in North Dakota into the native univoltine population surrounding the site. By measuring differences in voltinism of F_2 offspring of larvae collected at different distances and directions from the nursery, the authors detected infiltration of the bivoltine trait out to the maximum

sample distance of 32 km. The inferred dispersal was predominantly in the most frequent directions of surface winds of ≤ 8 km h⁻¹ during the predicted period of adult activity. Recaptures of moths suggested that surface wind direction affected direction of dispersal. In the MRR study by Showers *et al.* (2001), the active interception of a 'swarm' of marked moths by a vehicle 14 km from the release site within 100 min is direct evidence of surface flight in the direction of the surface breeze over a significant distance.

4.5. Coordination of long flights with age and reproductive development

Migratory flight can sometimes be distinguished from appetitive or 'trivial' flight on flight mills. For example, black cutworms on flight mills flew about twice as fast during long flights (≥ 1 h) than during short flights (Sappington and Showers 1992). In addition, some aspects of long-duration flight behavior were age-dependent, including nightly periodicity, duration, and propensity. Together, these characteristics suggested that the long-duration flights on the flight mills reflected migratory behavior. In the case of European corn borer (Dorhout *et al.* 2008), speed of long flights on flight mills did not differ from that of short flights. However, the moths did exhibit age-dependent flight behavior, which differed between the sexes. The longest uninterrupted flight of females occurred on the first night after emergence, then decreased but remained relatively high through 3 days of age before dropping substantially by 5 days (Fig. 2). In contrast, duration of the longest uninterrupted flight of males was lowest on the first night after emergence, about one-fourth that of 1-d-old females (Dorhout *et al.* 2008). Based on their MRR experiments and those of others (see Section 4.2), Reardon *et al.* (2006) suggested an obligate dispersal phase for newly emerged adults. The age-dependent flight behavior on the flight mills (Dorhout *et al.* 2008) supports the idea that dispersal of young females is pre-programmed and thus non-appetitive.

Many migratory insects exhibit the oogenesis flight syndrome, in which reproductive development of the female is delayed until after the termination of migratory flight (Johnson 1969). Not all migratory species display the syndrome, however (Sappington and Showers 1992; Zhao *et al.* 2009), so lack of a substantial preoviposition period does not indicate the lack of migratory behavior. Conversely, correspondence of the ages at which a species engages in its longest uninterrupted flight behavior with a preoviposition period does lend support (though not definitive) to those flights being migratory. European corn borer females have a 3–5 day preoviposition period (Kuang *et al.* 2004), so the ages of greatest long-flight activity on flight mills falls during that developmental time window. However,

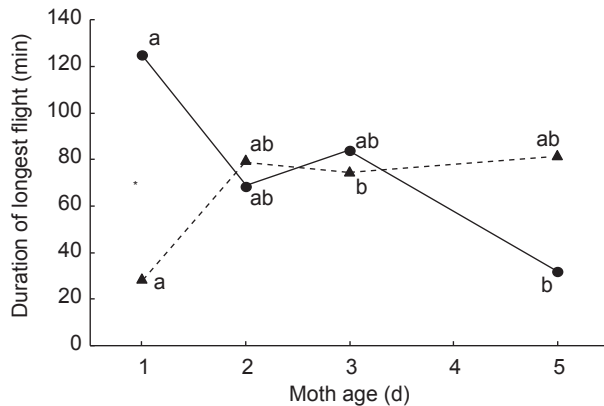


Fig. 2 Median duration of the longest continuous flight of unmated female (circles and solid line) and male (triangles and dashed line) European corn borers of different ages during 8 h of darkness on laboratory flight mills. Sample sizes are the same as those in Table 2. Values within sex followed by the same letter are not significantly different ($\alpha=0.05$) (Kruskal-Wallis test). *, significant difference between males and females at indicated age ($\alpha=0.05$) (Wilcoxon Rank Sum Test) (adapted from Dorhout *et al.* 2008).

the ovaries undergo development (oogenesis) during the preoviposition period in the laboratory (Kuang *et al.* 2004), so the oogenesis flight syndrome may not be characteristic of this species. The possible suppression of reproductive development in individuals displaying different propensities for long-duration flight on flight mills should be examined directly before a conclusion is drawn.

5. Conclusion and remaining mysteries

In general, the various lines of evidence presented above suggest that typical European corn borer adult lifetime dispersal distances are probably greater than 1.5 km and less than 12 km, but that dispersal to distances up to 80 km are not rare. The occasional individual captured far outside of its breeding range (Pedgley and Yathom 1993; Langmaid and Young 2006), and population genetics data (Kim *et al.* 2009, 2011) suggest that a small proportion of individuals per generation may disperse several hundred kilometers. About 17% of 1-d-old unmated females flew continuously for at least 7 h on flight mills (Dorhout *et al.* 2008), and if such long flights in nature were wind-aided, flight distances much greater than 100 km would not be implausible. The most compelling evidence that European corn borer engages in migratory flight is the quick disappearance of both native and marked moths from the natal field and its surroundings out to at least several hundred meters, because it implies pre-programmed non-appetitive behavior. In conjunction with the other lines of evidence presented above, the case for migratory flight in this species is strong, despite the

distances seeming short, perhaps even trivial, compared to the immense distances covered by many classic seasonal migrants.

There are a number of unanswered questions though. Most pressing from an applied viewpoint is whether European corn borer mating occurs before or after dispersal from the natal field, or both. It is especially important to understand this for modeling resistance evolution, spread, and mitigation (Hunt *et al.* 2001; Dalecky *et al.* 2006). The evidence is somewhat difficult to interpret. The fast disappearance of adults from the natal field in MRR and other studies suggests little time for mating before dispersal. On the other hand, of the 4.3% of marked adults recaptured near their release site in the MRR studies by Dalecky *et al.* (2006), 97% of females were mated. In companion experiments, Dalecky *et al.* (2006) placed newly emerged females on corn stalks and visually tracked their movements within 50 m. An average of 18.1% of those released mated locally. At the same time, we know that most females mate in weedy aggregation sites (Showers *et al.* 1976, 1980), and that very few released females are recaptured in nearby weedy sites (Section 4.2). Mating did not affect the flight behavior of either sex on flight mills (Dorhout *et al.* 2008).

It is curious that cohorts of both males and females of different ages and mating status did not colonize aggregation sites they were released in (Reardon and Sappington 2007). This does not sit easily with the proposed narrative of migration out of the natal field by newly emerged adults. On the other hand, the sampling arena in that study was only the plot of release, and local commuting behavior could have emptied the plots of older non-migratory adults on the first night after release if they redistributed themselves to abundant natural aggregation habitat nearby. Furthermore, it is unclear whether males and females both engage in migratory flight. Patterns of age-dependent behavior on flight mills suggested to Dorhout *et al.* (2008) that only 1-day-old females are migratory and that flight by 1-day-old males is appetitive. But males disappeared as rapidly as females from the natal field in MRR studies, and this cannot be due to ranging in search of dispersed females, because the local aggregation sites harbored unmated feral females.

A typical characteristic of insect migration is that flight is directional (Chapman *et al.* 2010, 2011; Hu *et al.* 2016; Reynolds *et al.* 2016). Long-distance seasonal migrants are adapted to fly in a preferred direction, which differs depending on the time of year. In the case of a migratory pest, the abundant, widely distributed host crop it seeks may be hard to miss as long as it travels in the appropriate general direction (Reynolds *et al.* 2016). But in the case of insects that are not tracking seasonal habitats across different latitudes, such as European corn borer and others that occupy a permanent range through the seasons,

there may not be a reason to migrate in a compass-biased orientation. In cases such as these where the individual is surrounded by suitable habitat in all directions, simple downwind orientation may be the most adaptive strategy (Reynolds *et al.* 2016). Even in long-distance seasonal migrants, migratory flight is randomly directed during the summer (Hu *et al.* 2016), a period when individuals are also surrounded by suitable habitat; only in spring and fall do they have a preferred direction for migration and select appropriate tailwinds accordingly.

As reviewed above, there is some evidence that dispersing European corn borer may orient downwind. Though not a random heading strictly speaking, an orientation strategy based only on maintaining a downwind heading will be random to the extent that wind direction is random during the developmental window of migratory flight activity. In other words, a downwind orientation strategy is functionally similar to a random orientation strategy in that no destination is targeted. Random headings by night-flying migrants are uncommon, but may serve to increase population dispersal (Chapman *et al.* 2015). A downwind orientation strategy could serve a similar purpose of ensuring dispersal from the natal field at the level of different cohorts of insects migrating on nights of different wind direction.

The distances traversed by European corn borer in putative migratory flight are not very impressive compared with those of classic seasonal migrants, for which 2 000 km is not unusual (e.g., Chapman *et al.* 2010). However, displacement over long distances is presumably unnecessary for insects migrating within a permanent distribution and surrounded by abundant breeding habitat, for the same reasons that compass-biased orientation is irrelevant in such circumstances. It may even be disadvantageous to engage in flight that covers too much ground, because it would increase risk of displacement beyond the area where the moth can find (by ranging behavior) breeding habitat after terminating migratory flight. Limiting the distance traveled would also limit expenditure of energy reserves which could otherwise be allocated to egg production. Adaptive advantages of engaging in migratory movement unrelated to tracking of seasonal resources potentially include reduced inbreeding, reduced crowding in the host crop, or escape from pathogens or natural enemies by entering temporarily 'enemy-free space'. Enjoying such benefits is about leaving the vicinity of the natal field, and the displacement distances necessary to accomplish that goal usually will be far less than for seasonal migrants tracking spatial changes in breeding habitat over large latitudinal distances.

I have presented evidence that European corn borer exhibits migratory behavior, but I do not mean to imply that all adults in a population migrate. Despite an evidently high rate of dispersal from release sites in MRR studies, there

are always at least a few that remain nearby. Likewise, some individuals in flight mill studies engage in only short-duration flights. As is the case with many other migratory animals, including vertebrates (Dingle 2014), it is likely that European corn borer exhibits "partial migration", where part of a population migrates and part remains resident in or near the natal habitat. Qureshi *et al.* (2005) suggested this same idea based on results of dispersal models built to explain spatial patterns of captured marked and feral European corn borer. Remaining to reproduce in the natal field as a resident can potentially be less risky than dispersing, depending on conditions, and if genetically controlled, the two life-history strategies could be maintained through balancing selection. The strategy an individual adopts could be a strictly controlled "obligate" trait, or could involve a facultative decision based on environmental cues experienced during the larval or adult stage. In principal, candidate gene(s) controlling either an obligate or facultative mechanism could be identified by comparing the transcriptomes of residents and dispersers. These are challenging questions, but promise to be fruitful areas of future research employing MRR or flight mill methodologies to behaviorally identify residents and migrants for genetic comparison. For example, Jones *et al.* (2015) used flight mills to phenotype individuals of the migratory crop pest *Helicoverpa armigera* (Lepidoptera: Noctuidae) from different populations as short- or long-distance fliers, then used RNA-seq to compare transcription profiles. A number of differentially expressed genes were identified that may underlie facultative migratory behavior and physiology in this insect.

The potential population-level consequences of individual migratory behavior within a larger permanent species distribution can be quite important in the contexts of pest management and IRM (Miller and Sappington 2017). In this paper, I have reviewed in some detail the evidence for migratory flight behavior by individual European corn borer adults. It is an instructive story, not least because it illustrates how the assumption that this is not a migratory insect can affect the experimental questions, design, and interpretation of results in field, laboratory, and modeling studies of dispersal behavior. This assumption was particularly tenacious in the case of the European corn borer, at least as I experienced it. When my graduate student confronted me with the data from his MRR study (Reardon *et al.* 2006) showing that the released adults had nearly unanimously spurned his laboriously prepared small grain plots as places to aggregate, it pulled me up short. Like any good graduate student, his first impulse was to go over in his mind the set-up, protocols, and other aspects of methodology trying to identify what he had done wrong. But he had not done anything wrong. The insects were telling us something. The situation reminded me of advice a mentor

had given me as a graduate student. In most cases, when the results of an experiment do not turn out as expected, it does not mean that we have failed, but rather that we have discovered something. Our job as scientists is to figure out what we have just discovered. In this case, Dr. Reardon had discovered something very interesting about European corn borer behavior. The results took us by complete surprise, despite the explanation being in plain sight and trying to get our attention for a long time. But the evidence was scattered, and I was so blinded by an assumption (i.e., European corn borers do not migrate) so reasonable, widespread, and obviously true that I had never thought to examine it. I suspect that as this assumption is tested in other insect species that occupy a permanent range, we will find that migratory behavior, unspectacular though it may be in terms of population density pulses and distances traveled, is more common than we realize.

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