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Movement Ecology of Pest *Helicoverpa*: Implications for Ongoing Spread

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Abstract

The recent introduction and spread of *Helicoverpa armigera* throughout South America highlight the invasiveness and adaptability of moths in the *Helicoverpa* genus. Long-range movement in three key members, *H. armigera*, *H. zea*, and *H. punctigera*, occurs by migration and international trade. These movements facilitate high population admixture and genetic diversity, with important economic, biosecurity, and control implications in today's agricultural landscape. This is particularly true for the spread of resistance alleles to transgenic crops expressing *Bacillus thuringiensis* (Bt) toxins that are planted over vast areas to suppress *Helicoverpa* spp. The ability to track long-distance movement through radar technology,

population genetic markers, and/or long-distance dispersal modeling has advanced in recent years, yet we still know relatively little about the population trajectories or migratory routes in *Helicoverpa* spp. Here, we consider how experimental and theoretical approaches can be integrated to fill key knowledge gaps and assist management practices.

INTRODUCTION

Since its introduction into the New World (122), the cotton bollworm moth, *Helicoverpa armigera* (Lepidoptera: Noctuidae), has expanded its range throughout South and Central America (79), highlighting the invasiveness and natural dispersal ability of this major agricultural pest (47, 123). The invasion of the Americas by *H. armigera* has alerted the global community to the consequences of future incursions of pest *Helicoverpa* into areas previously not infested. Here, we synthesize our current understanding of long-range movement/migration across the global range of the most economically damaging *Helicoverpa* species: *H. armigera*, *H. zea*, and *H. punctigera*. The genus includes some of the most injurious and highly polyphagous lepidopteran pests of agriculture worldwide (30, 79, 113).

Each of these three pests is a major threat to agricultural systems, and they particularly threaten high value crops such as cotton, soybean, maize, and tomato and various horticultural hosts (30, 80). *Helicoverpa armigera* is the most globally widespread species of *Helicoverpa* (native to Africa, Asia, Europe, and Australasia). A major factor contributing to the pest status of this genus is the ability to spread via long-range migration (47, 49–52, 65, 97–100) and international trade (123). The costs due to lost production and control from *H. armigera* alone in the Old World were estimated at US\$5 billion (111), while damage to Brazilian agriculture from *Helicoverpa* spp. between 2012 and 2014 following the invasion was approximated at US\$0.8–2 billion (113).

Helicoverpa moths can move over multiple spatial scales within and between host crops (~1–10 km) as well as over entire regions (~10–500 km) (37, 49, 50, 53, 65). A common feature of noctuid pests such as *Helicoverpa* is the capacity to nocturnally migrate at high altitude (typically 400–800 m) where they are assisted by tailwinds (20, 40, 49–52). This adaptation facilitates high population admixture and the spread of adaptive genes (e.g., insecticide-resistant alleles) and allows populations to flourish in ephemeral agricultural ecosystems (33).

An understanding of the movement ecology of *Helicoverpa* is crucial for successful integrated pest management practices (33). Quantifying moth immigration/emigration rates, dispersal potential, and spatial structure of populations can help identify spatial units of management (106), assess biosecurity threats and identify range margins (79, 123), provide regional forecasts (102), and predict the spread of resistance genes (14). In practice, however, determining the frequency, scale, and trajectory of long-distance movement is extremely challenging owing to the spatiotemporal variation in migratory behavior both within and between populations, ill-defined environmental triggers for migration, coexistence of morphologically near-identical species in a similar ecological niche (e.g., *H. armigera*/*H. zea* in the Americas) (82, 114), and the difficulty of nocturnal observation (101).

It has been nearly three decades since the movement ecology of pest *Helicoverpa* (previously classified in *Heliobthis*) was last reviewed (47, 53). Since then, the field of insect movement ecology has benefited from advances in simulation models (48, 93), experimental methods of aerial detection (e.g., optical and radar remote sensing) (18, 40), and, particularly, population genetics (3, 6, 103,

120, 129). Here, we consider how contemporary experimental and theoretical approaches can be integrated to fill key knowledge gaps and assist management practices. Other recent reviews have covered *Helicoverpa/Heliobis* pest biology such as polyphagy (30), insecticide/transgenic *Bacillus thuringiensis* (Bt) resistance (35), and area-wide pest management and ecology (33). These topics are not discussed here unless relevant to movement ecology.

GLOBAL DISTRIBUTION OF *HELICOVERPA*

Historical Native Range of *Helicoverpa*

The major *Helicoverpa* pest species (*H. punctigera*, *H. armigera*, *H. zea*) are distributed throughout the tropical and warm-temperate regions of the world (24, 67, 134). In the first comprehensive taxonomic separation of the morphologically homogeneous *Heliobis armigera* complex, Hardwick (67) considered *H. armigera* a widespread cosmopolitan Old World species that included the subspecies *H. armigera armigera* (Africa, Europe, and Asia), *H. armigera conferta* (endemic to Australasia), and *H. armigera commoni* (limited to Canton Island, central Pacific) (for current distribution of *H. a. armigera* and *H. a. conferta*, see **Figure 1**). In the North and South American continents, *H. zea* is the dominant *Helicoverpa* pest species; it arrived around 1.5 Mya as a result of a founder event (10, 85, 95), and it remains restricted to the Americas (46). In evolutionary terms, *H. punctigera* is regarded as basal to *H. armigera/H. zea* as shown by multigene (21) and genome-wide analyses (3, 95) and is restricted to mainland Australia, although adult migrants have reached Tasmania and New Zealand (47).

Potential and Inferred Climatic Range of *Helicoverpa armigera*

The potential spatial extent across which a species could establish can be determined by distribution models. They can help identify areas at risk of the pest establishing, should it arrive. At the global scale, bioclimatic models are currently available only for *H. armigera* but have previously predicted the potential suitability of regions in South America (in which we now find *H. armigera*), before the species became established there (135). This modeling also predicted that regions to the north of Brazil could form a continuously suitable bridge into North America, including via the Caribbean islands. A refined version of this model (79) confirms the suitability throughout this region and thus the risk of spread in North America; to date, the species has reached Puerto Rico and Cocos Island (**Figure 1**).

In Europe, *H. armigera* has probably reached the northern boundary of its natural year-round distribution (40–45°N) owing to limitations of survival by overwintering pupae (80). Catches of *H. armigera* north of this range are common in the summer months in countries such as the United Kingdom, The Netherlands, and Sweden, but the chances of permanent populations establishing outdoors are highly unlikely unless global warming assists future spread north.

Recent Incursions of *Helicoverpa armigera* into New Regions

Progress in genetic analyses now allows us to rapidly determine whether a suspected incursion is a new arrival and to infer likely origins. In Brazil, during the cropping season of 2012–13, crop damage patterns, caterpillar feeding behavior, and insecticide resistance profiles were reported to be significantly different from that traditionally observed for *H. zea*. An examination of adult genitalia indicated the presence of Old World *H. armigera* attacking soybean and cotton in three central Brazilian states (Goiás, Bahia, and Mato Grosso) (31), which was confirmed by molecular

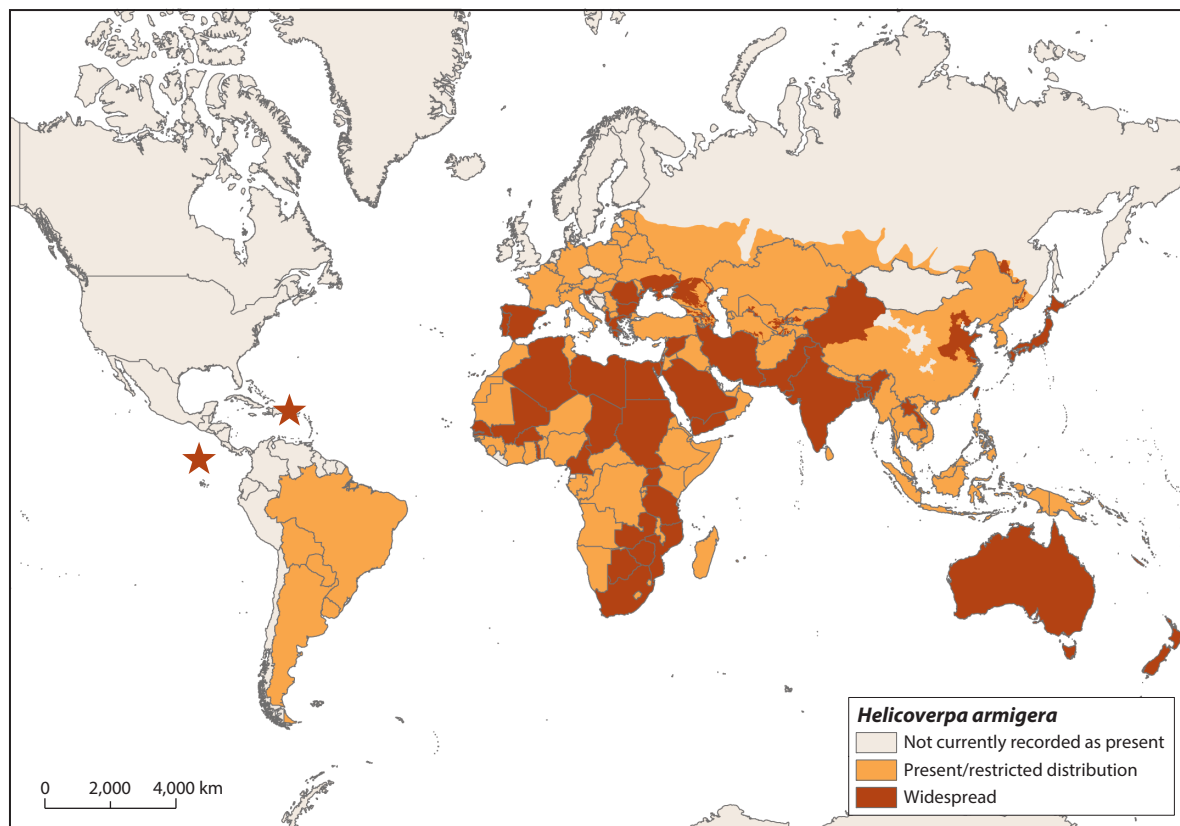


Figure 1

Regions where *Helicoverpa armigera* is known to be absent, present/restricted in distribution, or widespread (established populations). Stars represent presence in Puerto Rico and Cocos Island. The majority of data for the map originate from Reference 46. The map includes country-/region-specific data for Russia (22); Uganda, Burkina Faso, Cameroon, Chad, Senegal, Mali, and Togo (124); Sudan (66, 77); Guinea-Bissau (16); Djibouti (68); Zimbabwe, Zambia, Mozambique, and Tanzania (96); Botswana (104, 105); Bolivia (79); Oman (44); and Pakistan (10). We have mapped *H. armigera* as present/restricted in distribution throughout Brazil rather than by subregion, as it has spread rapidly in recent years and cannot reliably be mapped at a finer scale. The apparent absence in the African countries of Liberia and Equatorial Guinea is due to a lack of studies and not likely a real absence, given the often widespread presence of the pest throughout this continent.

barcoding of the mitochondrial cytochrome I (mtDNA *COI*) and cytochrome b (*Cyt b*) regions (114, 122). This incursion arose from multiple maternal founders [e.g., at least four in Mato Grosso (122)], with similar founder diversity confirmed elsewhere in Brazil (82, 86). Following the high-profile report of *H. armigera* in Brazil, this Old World pest was confirmed in neighboring countries [Argentina (89), Bolivia (79), and Paraguay and Uruguay (6)] on the basis of either genitalia or the partial mtDNA *COI* gene.

Although the precise arrival time line of *H. armigera* to the South American continent is unknown, an analysis of a 2006 population of *Helicoverpa* moths from the state of Mato Grosso (10) did not detect the presence of *H. armigera*, suggesting that arrival of this species in Brazil may have occurred after 2006 (122). Sosa-Gómez et al. (113) examined samples of *Helicoverpa* moths from Brazil collected between 2008 and 2014 using restriction fragment length polymorphism methods (9) and reported the detection of one *H. armigera* larva collected during October 2008 from Rolândia,

Paraná (southern Brazil), while patterns of *H. armigera* detection in the state of Rio Grande do Sul (also in southern Brazil), Paraguay, and Uruguay suggested an arrival time line of pre-2013 (6).

The confirmation of *H. armigera* in central Brazil and subsequent spread in the southern Brazilian states and neighboring countries of Argentina, Paraguay, and Uruguay would indicate Brazil as the probable origin of the New World population. Haplotype analyses have detected a total of 25 mtDNA *COI* haplotypes in the South American continent, of which six were detected only in Argentina, Paraguay, and Uruguay (5, 6, 82, 86). An analysis of the partial mtDNA *COI* and *Cyt b* genes similarly identified 22 haplotypes in Brazil, with 5 shared uniquely with a region/country in the Old World (123). Unique New World haplotypes found exclusively in Brazil further support the potentially diverse Old World origins of introduced *H. armigera*. Natural colonization from the African continent is highly unlikely despite the long-range migration ability of *H. armigera*. Moths have reached Ascension Island in the mid-Atlantic, 1,600 km from the African coast (13), but east-to-west insect migrations across the Atlantic are extremely rare. It is far more likely that the high haplotype diversity of New World *H. armigera* is associated with increased importation of agricultural and horticultural commodities in recent years into Brazil (123). Remarkably similar invasions are currently ongoing with two other major noctuid pests, previously indigenous throughout the Americas, the fall armyworm (*Spodoptera frugiperda*) and the southern armyworm (*Spodoptera eridania*). The two main host strains of *S. frugiperda*, now considered closely related species (41, 42, 60), were first recorded in West and Central Africa in early 2016 (58) and have rapidly spread to East Africa (23, 91). Similarly, *S. eridania* was first detected in Nigeria in December 2016 and subsequently in Cameroon, Gabon, and Benin (17, 57), although it has yet to spread across the African continent. The origins and time line of the invasion and mechanism of spread in the African continent remain unknown. The detection of *S. frugiperda* on maize fields in South India in May 2018 (70) is a further alarming development and major concern for both the Indian subcontinent and the rest of Asia, with seemingly few barriers to its rapid ongoing spread. It is too early to speculate the extent to which natural dispersal will contribute to the spread of *H. armigera* and the New World *Spodoptera* species in the Americas and Africa/India, respectively, but given these noctuids perform similar high-altitude nocturnal migrations and their host-range overlap (e.g., maize, cotton, soybean), it will be fascinating to see how, or indeed whether, parallel migration strategies evolve. Multidisciplinary approaches to studying migration in field populations offer ways to follow these developments.

MIGRATORY MOVEMENT

Biological Propensity to Initiate Migration

An early review ranked *Helicoverpa* species in decreasing order of migratory activity as *H. punctigera* > *H. zea* > *H. armigera* (47). In the context of Australian populations, there is some truth in this characterization for *H. punctigera* and *H. armigera*, yet the latter is tremendously variable in the distances it can migrate, depending upon region and season.

Helicoverpa punctigera appears to be an obligate migrant (i.e., all individuals of a given generation migrate) owing to its winter breeding on ephemeral native host plants in the semiarid inland of Australia—these annual hosts die off in late winter/spring and so the sites cannot support more than one generation (55, 65, 134, 136). By contrast, the cosmopolitan *H. armigera* is a facultative migrant par excellence with highly variable distances traveled under different circumstances. Careful censusing by multiple complementary techniques of the number of *H. armigera* adults emerging from local crops, taking to the air, and in flight at different heights above ground has

shown that mass ascent to altitude does not occur under some circumstances (37, 53, 101) and that most movement takes place within a few meters above the crop canopy. For example, in post-rainy season central India (101), and in the Gezira area of Sudan (77), only 5% of the populations ascended to altitudes above the flight boundary layer where wind-dominated movement would occur (101). This is not to say that migration is absent; short prereproductive migration has been recorded at dusk on the night after emergence (101), but this resulted in low-altitude movements. In addition, nonmigratory foraging movements such as flights in search of nectar or oviposition sites can easily take individual moths over distances of several kilometers or more if there is any delay in finding the sought-after resource (53, 77, 101). Highly attractive blocks of host plants can restrict movement owing to moths turning back into the block when they reach an edge (37, 54).

In other circumstances, a substantial proportion of the emerging *H. armigera* appears to ascend to altitude and embark on long-distance migration (49, 50), although most of the observational evidence comes from studies of migration-in-progress or of immigration events (28, 49–52, 63, 64, 66, 97, 98), rather than detailed observations of mass ascent, such as those available for *H. zea* in the United States (131). Where it occurs, high-altitude windborne migrations are very likely to be prereproductive in *Helicoverpa* spp. (see the section titled Physiological Basis of Migration below). For example, the vast majority of *H. armigera* and *H. punctigera* females caught 40–50 m above ground were unmated and immature (28).

Long-range migration in *H. zea* is also facultative (53), and the major radar-based research program in Texas (99, 130, 131) showed that, generally, a high proportion of adults emerging from fruiting-stage maize emigrated. The moths showed very high climb rates immediately after takeoff, which is an adaption for high-altitude flight.

The evolution of migration as a strategy for *Helicoverpa* spp. is a response to the heterogeneous nature of the environment in both space and time, which varies strongly in agricultural landscapes. Like many other insects, migration systems of *Helicoverpa* moths are primarily driven by seasonal changes in temperature, resulting in movement to higher latitudes in spring and the reverse in the fall or, in semiarid regions, are primarily a response to variable rainfall (32, 40). For a given population of *Helicoverpa* spp. during a favorable migratory window, it is unclear, however, what proportion of individuals migrate at high altitude (i.e., emigration takes them above their flight boundary layer) under different environmental conditions. The recent decline in empirical field observations on migratory behavior, except for entomological radar studies in China (49–52), has severely hindered this area of research. Nevertheless, it seems clear that spatiotemporal seasonal variation in the local habitat will influence the extent of migration, with consecutive seasons of poor habitat quality selecting for a higher proportion of migratory individuals (32).

Environmental Factors Initiating Migration

The environmental factors that initiate migration within a given population or season are relatively unknown (32). Owing to the variation in *Helicoverpa* migratory behavior and difficulty in observing migration events, these mechanisms have still not been clearly defined. Suggestions regarding the nature of the so-called switch (from nonmigratory to migratory) include meteorological factors, host-plant availability, and responses to abiotic cues such as photoperiod and temperature.

Responses to weather systems. Mass arrivals of migrant *Helicoverpa* spp. are frequently associated with the passage of disturbed weather systems, such as depressions, troughs, and cold fronts, and so it is frequently assumed that these weather systems promote emigration from source areas (8, 47, 53, 66, 78). However, it is not clear whether the passage of such weather systems stimulates moths to initiate migratory flights, and this topic warrants further study.

Responses to host availability. Migration is unlikely if food sources are promptly encountered by postteneral adults (usually flowers to provide nectar); there is some evidence that the lack of food in 1–2-day-old female *H. armigera* moths delays maturation and promotes longer flights (66). If the young adults find food, they stay and mate after which there will be no long-range movements (24, 47, 53, 101); however, there still might be dispersive movements up to tens of kilometers. The exact behavior of emigrating moths in relation to whether an attempt is made to assess the favorability of the local habitat before departing en masse is not clear.

Plasticity in response to environmental cues. A third possible explanation for the initiation of migration is phenotypic plasticity (112) in which the environmental conditions experienced in the larval/pupal stage lead to the emergence of adult migrants. This has been suggested as a migratory mechanism in other insects, including density-dependent processes in *Spodoptera* spp. (20, 133). Triggers include overcrowding, declining food quality, and changing photoperiod and are likely to be mediated by genotype–environment interactions (112). The nutritional factors influencing the larvae and adults are probably not independent; a nutritious larval diet could offset the effects of deficient adult nutrition (and vice versa) on the duration of the migratory window—specifically, the duration of the female precalling period, the period before release of sex pheromones (15). Switches in the larval/pupal stage may be controlled by stable predictors of seasonal change such as day length; for example, temperature and photoperiod conditions during larval and pupal development affect adult reproductive physiology (via juvenile hormone synthesis) in populations of *H. armigera* (139). Delays in female sexual maturation can extend the prereproductive migratory window (138) (see the next section).

Physiological Basis of Migration

The difficulty of observing *Helicoverpa* embarking on, or engaged in, high-altitude nocturnal flight and capturing long-distance migrants means that alternative proxies for understanding the physiological basis of migratory behavior that are readily measurable are sought. Two interlinked traits commonly used to identify migratory individuals are delayed reproduction (24, 75) and increased flight activity. Typically, noctuid moth species perform long-range migration prior to reaching sexual maturity (87). This prereproduction period (PRP) in *Helicoverpa* can last between 2 and 5 days (25, 27) and can be used to estimate the potential number of nights in which migratory flight can occur. In reality, the PRP is not a binary measure and is influenced by local environmental conditions, particularly temperature (26, 139). Nevertheless, flight activity measurements using tethered flight have shown a positive relationship between the length of the PRP and peak flight activity in immature female *H. armigera* (4, 24–26), with individuals capable of maintaining flight for up to 13 h during a single night (76). There are limitations in using tethered flight data to characterize migration owing to the artificial environment in which the insects are flown; however, relative flight performance can be quantified in insects reared and flown under similar conditions. Using this approach, Jones et al. (76) detected interpopulation differences in *H. armigera* from China and Greece and identified over 200 genes differentially expressed between short- and long-distance fliers. These expressed genes showed clear associations with flight activity, including lipid metabolism, flight muscle structure, and hormonal control. Migration genomics remains an understudied area of research (84, 103) but could yield DNA-based markers for migratory behavior that would be of practical use for detecting migrant individuals in populations of unknown migratory potential.

POPULATION TRAJECTORIES

Population trajectories [i.e., the spatiotemporal population demographics produced by migration (39)] of various *Helicoverpa* spp. have been investigated through several major multidisciplinary research programs, utilizing remote sensing (radar and optical), ground surveys and aerial sampling, mark and recapture, and atmospheric transport modeling (40). The studies include research on *H. punctigera* and *H. armigera* in Australia (36, 37, 63, 64, 65, 102), *H. armigera* in India and China (49–52, 98, 101), and *H. zea* in Texas (130, 131).

The flexible migration strategy of *Helicoverpa* spp. allows them to exploit both temperate and semiarid regions and, when local conditions are unsuitable for reproduction, to undertake long-range migrations; some of these movements require all-night flight for more than one consecutive night to account for the distances moved (48). In temperate areas, such as those in North America and East Asia, migrations appear to be poleward in spring or early summer (up to ca. 50° latitude), with an equatorward return migration in the fall (8, 51, 52, 61, 78, 130). These return movements may require selection of favorable wind transport opportunities—for example, flight associated with the passage of cold fronts (8, 78, 92). In apparent contrast, in semiarid areas such as those encountered in Australia, downwind displacement toward wind convergence zones may be a better strategy to track seasonal rainfall. In these cases, movements will be erratic and in various directions, but some of these will eventually lead to seasonal reinvasion of the original source areas (e.g., the far inland of Australia) (36, 65, 126). The variability in the propensity to emigrate in *H. armigera* results in variable migratory behavior for this species, and thus there is no clear picture on the overall population trajectories, as they are largely dependent on the environmental context at any given time.

Studies in Australia make it clear that the closely related *H. punctigera* and *H. armigera* do not necessarily follow similar migration trajectories (37, 55). This implies that it may be difficult to predict the speed at which *Helicoverpa* spp. invading completely new regions (e.g., Brazil) will evolve migratory routes, but it seems judicious to assume that this will happen rather quickly.

For the obligate migrant *H. punctigera*, the most obvious migratory movements are flights on northwesterly winds ahead of cold fronts in spring, resulting in early-season invasions of the cropping areas of southeastern Australia (36, 126). Examples of multigenerational autumn–winter return migration from the continental periphery back to the far inland have been observed (36, 65, 126), and backcasting of wind trajectories demonstrate that it is possible for *H. punctigera* to cover the 400 km between far inland and eastern cropping areas over 2–3 nights of flight (62, 65).

In Texas, *H. zea* emigrants typically undertake hours of long-distance movement up to several hundred kilometers northward. Later generations of *H. zea* invade vast swathes of the corn belt of the midwestern United States (130). Southward return migrations occur in the fall (61), with rapid movements on strong northerly winds just behind advancing cold fronts (8, 78). Notwithstanding this, there are situations where alternative hosts are available in the vicinity and *H. zea* adults engage only in local movements (29, 53, 99).

Seasonal migration distances and directions have been shown to be driven not just by environmental factors (i.e., wind speed, direction, and temperature) but also by seasonal behavior of noctuid moths themselves, which can be studied using a combined radar and trajectory modeling approach (19, 52). The complex interaction between the moth's biology and the environment (wind, temperatures) affects not only the migration pathway but also the overall flight duration and propensity to land. Thus, estimates of realistic flight duration required to calculate population trajectories should take account of multiple factors and are rarely well estimated from tethered-flight studies. Parry et al. (93) summarize these factors as the following:

- the individual's physiological state and age (4, 24, 27, 87)
- genetics that affect flight activity such as flight time and longest flight (24, 25)
- energetics (i.e., body fat and weight affecting flight capacity) (87)
- physiological stress experienced before or during flight (24, 87)
- host-mediated visual and olfactory responses—for example, stimuli regulating long-range crop–crop movement, causing a switch from migratory behavior to landing (53)
- local weather conditions (e.g., precipitation, wind, temperature, and updrafts) (53, 78)

This poses challenges in estimating long-distance migration pathways, backcasting to determine the origin of a pest, and predicting movements of more than a day or two, as over several days, the uncertainty in estimates will be amplified (36).

POPULATION STRUCTURE OF *HELICOVERPA*

Population structures of species within *Helicoverpa* are best characterized for *H. armigera* owing to its historical importance; studies have been carried out in Africa (124), Europe (90, 140), Australia (45, 107, 108), India (7, 11), Brazil (82, 86, 122), and Paraguay, Argentina, and Uruguay (6). On a global scale, these studies have been largely based on the partial mtDNA *COI* gene sequence (10) and genome-wide single nucleotide polymorphism (SNP) markers (3), including those investigating gene flow between *H. zea* and *H. armigera* in the New World (3, 83, 110). Gene flow patterns and the availability of genome resources (95) have provided the genomic signatures of hybridization (2) between the latter, thereby confirming the potential occurrences of *H. armigera*/*H. zea* hybrids under natural conditions (2, 67, 81).

Nuclear DNA and mtDNA markers [e.g., allozyme markers, microsatellite DNA, mtDNA *COI*, RAPD (random amplified polymorphic DNA) markers, genome-wide SNPs] have generally shown high gene flow in *H. armigera*, consistent with (a) extensive spread in global commerce and (b) capacity for long-range adult movement. For example, a lack of population substructure in *H. armigera* populations has been reported (90, 124, 140), with high gene flow patterns between distant populations being attributed to high migratory capacity. Global population analysis of *H. armigera* using mtDNA markers (10, 122) and subsequent analyses of invasive populations in Brazil (6, 82, 86) also concluded high gene flow.

However, a spatial analysis and simulation model of haplotype distribution patterns in *H. armigera* from Paraguay, Argentina, and Uruguay, and to a lesser extent from southern Brazil, demonstrate extensive genetic substructure when compared to *H. armigera* populations from central and northern Brazil (5). The general lack of gene flow barriers between the Old World (Asia, Europe, Africa) and northern/central Brazil was also reported on the basis of genome-wide SNP markers (3) and corroborated the high levels of gene flow inferred from mtDNA *COI* diversity across global populations from the Old World, including Australia (10). Overall, the findings from these diverse population genetic approaches (3, 6, 10, 123) lend support to multiple independent *H. armigera* introduction events that have led to the current heterogeneous spatial mtDNA *COI* haplotype patterns in South America. The origins of unique mtDNA *COI* haplotypes (6) in South America are unknown and likely represent as yet unidentified Old World *H. armigera* populations.

There is now strong genomic support based on genome-wide SNP markers (3, 95) for two subspecies of *H. armigera*: *H. a. armigera* (Eurasia, Africa) and *H. a. conferta* (Australia), as first proposed by Hardwick (67). Contrary to the general conclusion of global panmixis within these subspecies, population substructures have been reported in Australian populations of *H. a. conferta* on the basis of microsatellite DNA markers (107–109), although subsequent reanalyses have argued that inconsistencies with microsatellite allele calling could have led to an overestimation

of genetic structure in this case (45, 129). The presence of multiple allelic bands in selected microsatellite DNA markers in *H. zea* and *H. armigera* was subsequently associated with mobile elements (59, 119), the consequences of which can lead to the interpretation of hemizygotes as homozygotes and an overinterpretation of population substructure due to increased fixation index estimates.

PRACTICAL IMPLICATIONS OF *HELICOVERPA* MOVEMENT AND PROSPECTS FOR MANAGEMENT

Biosecurity

Between 1984 and 2013, a total of 1,017 *H. armigera* were intercepted by the US Department of Agriculture/Animal and Plant Health Inspection Service at the US national ports on agricultural commodities such as vegetables, ornamentals, and fruits (79), although the total may be higher, since morphological similarity between *Helicoverpa* species makes accurate species identification challenging. In addition to the 1,017 *H. armigera* identified, an additional 7,203 individuals were further intercepted that were identified only as *Helicoverpa* spp. On the basis of these US interception records, there is a clear increasing trend for the detection of putative *H. armigera* individuals (79). Interception records of Old World *Helicoverpa* spp. in South America are scarce and, despite the incursion into the New World, data are not available for Brazil, Paraguay, Argentina, Uruguay, and many Caribbean nations. The establishment of *H. armigera* in the New World and the threat to the United States have led to a push for simple and sensitive DNA-based assays for discriminating *H. armigera* and *H. zea*. So far, assays have been developed on the basis of internal-transcribed spacer region genes (*ITS1* and *ITS2*), using real-time quantitative polymerase chain reaction (qPCR) for discriminating individual specimens (56) and droplet digital PCR for identification of *H. armigera* from bulk samples of *H. zea* (reportedly sensitive enough to detect one *H. armigera* among 999 *H. zea*) (141). These assays negate the need for post-PCR processing, potentially offering rapid diagnostic solutions for early detection but with unknown sensitivity to the detection of *H. zea*/*H. armigera* hybrids that are known to be present in Brazil (2, 3).

Why has *H. armigera* established in South America and *H. punctigera* has not? There is considerable overlap in the host range of both *H. armigera* and *H. punctigera* at the family and species level (30), so a similar adaptation by *H. punctigera* to New World host plants is feasible. The lack of agricultural and horticultural trade between Australia and Brazil in the years preceding the *H. armigera* invasion (79), however, suggests this incursion route is limited.

Resistance Management

The multiple introductions of *H. armigera* into South America from the Old World present a problem for resistance management, as *H. armigera* is resistant to many classes of insecticide as well as the Bt toxins Cry1Ab, Cry1Ac, and Cry2Ab (34, 35, 118, 137) and Vip3A toxin (127). Bt soybean, cotton, and maize are grown widely in Brazil, Paraguay, Argentina, and Uruguay. Population-wide molecular characterization and monitoring of known genes affecting Cry1Ac and Cry2Ab resistance [e.g., mutations within the *ABCA2* gene (121)] and resistance to conventional insecticides [e.g., the P450 CYP337B3 (128)] will be required as a baseline for future long-term resistance allele frequency monitoring to prolong Bt crop technologies.

Migration of *Helicoverpa* spp. must be considered in the context of resistance management strategies (35). Long-distance movement can introduce new resistance alleles into a locale, and incursions can be monitored by genetics (as discussed above), but the extent of localized dispersal

is key for Bt resistance management. A central tactic for delaying the evolution of resistance to Bt is the planting of non-Bt host refuges (that do not produce Bt toxins) in proximity to or within the target Bt crop (117). When resistance is recessively inherited, this facilitates the admixture of rare resistant insects with susceptible ones from the refuges producing heterozygote offspring that are killed by the high doses of Bt toxin. The benefits of refuges are well established (35, 74, 116, 117), but the optimal spatial design for planting is not known and will vary across spatial scales and heterogeneous landscapes (72). Parry et al. (94) recently developed a spatially explicit individual-based model to address this. By modeling individual movement behavior of *H. armigera* and *H. punctigera* in Australian Bt cotton landscapes and validating with independent field data, the model links movement with oviposition in the context of the landscape and can be applied to different settings. So long as the resistance alleles are recessive (e.g., Cry1Ac and Cry2Ab), optimal spatial strategies for refuges can be designed with such a model for reducing selection of resistance. Further empirical and indirect estimates (e.g., population genomics) of *Helicoverpa* spp. movement could improve such models.

Forecasting and Monitoring Movement for Better Pest Control

Environmental niche models tell us the potential extent of an invasion, but what is needed is a better understanding of the potential migration routes into novel regions, how soon this may occur, and what the pest pressure is likely to be when it does occur. A combination of field surveys, global meteorological data, and a Lagrangian dispersion model has estimated fungal spore transmission across continents (88). A similar approach applied to *Helicoverpa* movement risks would allow for the identification of zones of connectivity, including where and when key stepping stones may facilitate movement from potential source locations into new regions (132). This would also allow for estimation of where surveillance and management efforts may have the greatest impact to slow spread.

Application of atmospheric trajectory modeling approaches could help identify likely sources of pests that pose risks to crops within a season. This could enable early pest detection and inform management actions before pests arrive into crops at a much broader scale (69). A pest management trajectory model (PMTRAJ) for *H. punctigera* and *H. armigera* in Australia was developed 20 years ago (102) but was not put into practice for *Helicoverpa* (although was subsequently applied by the Australian Plague Locust Commission for locust management). Changes in meteorological data formatting in recent years would require modifications to the data import tools for it to be applied in the future. In the meantime, there have been more general developments in trajectory modeling along with complementary technologies that may be adopted to forecast *Helicoverpa* pest arrival. One such development in Australia is TAPPAS (Tool for Assessing Pest and Pathogen Aerial Spread) (43). This allows users to access and run trajectory models such as HYSPLIT (Hybrid Single-Particle Lagrangian Integrated Trajectory) (115) from a simple online graphical user interface, considering some basic biological factors such as flight capacity and time of flight initiation, as well as to simulate releases or arrivals from a source area rather than a point. Although designed as a stand-alone tool rather than for integration with species distribution or pest outbreak models, this promises to be a useful means to assess pest risk using real-time data, particularly if combined with knowledge generated by other tools, such as radar and genetic studies. In the past, atmospheric trajectory research for *Helicoverpa* and other noctuids has been most successful when observational and simulation tools are combined (19, 40), and novel tools such as TAPPAS now present possibilities to rapidly explore potential movement trajectories without requiring a high level of technical expertise.

CONCLUSIONS

The recent arrival of *H. armigera* in South America and the Caribbean, followed closely by the introduction of both corn and rice strains of *S. frugiperda* as well as *S. eridania* into Africa, have highlighted important global biosecurity concerns surrounding polyphagous lepidopteran pests.

Now that *H. armigera* has been introduced into the continent, and given the migratory propensity of *Helicoverpa* spp., preventing the likely poleward spread (either north or south) until the species reaches its overwintering limit, which is currently about the 40–45° parallels of latitude (80), will be extremely difficult. Agricultural sectors of countries previously not exposed to *H. armigera* damage will be seriously challenged through crop losses and an increased cost of control. Risk assessments (79, 125) found that *H. armigera* is likely to colonize continental North America. *Helicoverpa armigera* is already present in Puerto Rico, and while the prevailing wind trajectories in the summer from the Caribbean are likely to take invading moths westward to Central America (rather than directly northward), any infestation established in, say, Mexico, would quickly spread north into the United States (99). Moreover, under tropical cyclone conditions, invading moths could move straight to the United States from the Caribbean islands or even from coastal countries of northern South America (71).

A potentially worrying scenario is that New World species (either *H. zea* or hybrids of *H. zea*/*H. armigera*), or New World *H. armigera* with novel fitness traits and/or with enhanced adaptation to novel ecoclimatic environments, will (re)invade the Old World. A precedent for this is currently being observed with the fall armyworm (*S. frugiperda*), a native of the tropics and subtropics of America, which has recently invaded Africa and has spread across much of the continent in only a few years (1, 23, 58), with subsequent spread to the Indian subcontinent (70). Extraordinary parallels between the two invasions exist. For example, it is not known how the formerly allopatric species *H. armigera* and *H. zea* will compete for maize in South America (12) or how the rice and corn strains of *S. frugiperda* will interact with host plants in Africa/India. Furthermore, there is evidence that natural *H. armigera*/*H. zea* hybridization is occurring in South America, which could produce locally adapted and resistant ecotypes (2, 3). There is currently no evidence for *S. frugiperda* hybrid races, but the strains appear to be spreading across the African continent together and hybridization events should not be ruled out (1). Taking advantage of the newly published genomes for both species (60, 95) and using genome-wide signatures will permit the identification of new and potentially damaging hybrid ecotypes (2).

Once an incursion has occurred and the population has established, preventing the subsequent spread of members from the *Helicoverpa* genus is virtually impossible. Sophisticated programs of area-wide pest management—for example, those used against *H. armigera* and *H. punctigera* in cotton growing regions of Australia (33)—can, however, be effective in mitigating damage. The challenge will be to extend these programs to newly invaded agricultural systems with multiple existing Bt crops and to develop risk management strategies, which could be informed by spatiotemporal resistance models (94). This is particularly difficult in the context of new resistance alleles appearing in the population, especially of the dominant forms as reported for Cry1Ac in *H. armigera* (35, 73). In this regard, priority should be given to understanding how newly developed population genomic markers can inform movement patterns at different landscape scales.

The recent incursion and subsequent spread of *H. armigera* in the Americas and *S. frugiperda* in Africa/India, plus the potential emergence of new hybrid species, clearly present a significant threat to global food security, due in part to the highly adaptive and flexible movement ecology of these pests. However, these large-scale and replicated natural experiments in invasion biology, occurring at the same time as the publication of their genomes, provide tremendous opportunities for migration ecologists and molecular biologists to significantly advance this field.

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