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Mass windborne migrations extend the range of the migratory locust in East China

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Abstract

1 Migratory insect pests pose a substantial challenge to global food security. These issues are particularly acute when pest incursions occur considerably beyond the expected range, through natural migration or human-aided transport, because the lack of species-specific control strategies and a potential absence of species-specific natural enemies in the newly-invaded area may lead to rapid establishment of a new pest.

2 One such threat is posed by the Oriental migratory locust *Locusta migratoria manilensis* in China, which, historically, has been restricted to eastern China from the Bohai Gulf southwards, and now threatens to expand its range into the agriculturally important region of northeast China.

3 We analyzed data from a recent outbreak of migratory locusts in Heilongjiang Province (extreme northeast China), > 700 km north of its current known range, and identified the source region, timing of arrival and probable migratory routes of this incursion.

4 We further show that warming temperatures in this region will likely allow subsequent invasions to establish permanent populations in northeast China, and thus authorities in this important crop-producing region of East Asia should be vigilant to the threat posed by this species.

Keywords Atmospheric trajectory simulation, China, locust outbreak, *Locusta migratoria manilensis*, oriental migratory locust.

Introduction

Migratory insect pests constitute serious threats to food security because their shared traits of great fecundity, high mobility and broad host plant range (Chapman *et al.*, 2015) make them prone to outbreaks that are difficult to predict. Thus, it is necessary to understand their annual migration patterns to develop effective management strategies (Wu *et al.*, 2018; Hu *et al.*, 2019). These challenges are exacerbated when migratory pests appear in new areas, either through natural expansion beyond historical ranges in response to climate change (Bebber *et al.*, 2013) or through incursions (often human aided) into completely new and distant regions (Tay *et al.*, 2013, 2017; Jones *et al.*, 2019). The increased threat partly stems from migrant populations benefiting from colonization of ‘enemy-free space’, where the colonists experience reduced rates of predation, parasitism and pathogen infection compared with their historical range (Altizer *et al.*, 2011; Chapman *et al.*, 2015). In addition, arrival in regions where they remain undetected for a considerable period, or where pest managers are unprepared for the emerging threat, can allow pest populations to establish. This threat was emphasized recently by the emergence and subsequent spread of the Old World cotton bollworm moth *Helicoverpa armigera* throughout the Americas (Kriticos *et al.*, 2015; Jones *et al.*, 2019) and the New World fall armyworm moth *Spodoptera frugiperda* throughout Africa and southern Asia, in both cases after accidental importation (Goergen *et al.*, 2016; Sharanabasappa *et al.*, 2018), as well as the emergence of new pests such as the mirid bug *Apolygus lucorum* within their native range (Fu *et al.*, 2014b). It is important to remain vigilant to the threat of emerging pests and thus the rapid determination of new incursions is imperative if adequate crop protection measures are to be implemented (Tay *et al.*, 2013).

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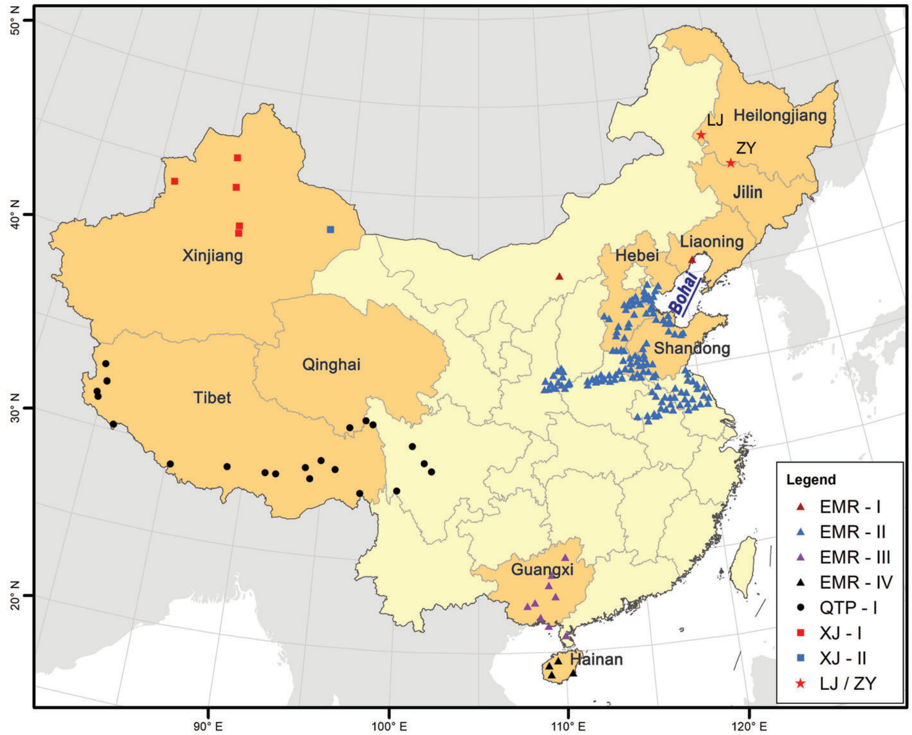

Figure 1 Distribution of *Locusta migratoria* in China. Red stars indicate locations of the 2009 outbreaks. Triangles: Geographical distribution of *Locusta migratoria manilensis* in the eastern monsoon region (EMR); circles: Geographical distribution of *Locusta migratoria tibetensis* in the Qinghai-Tibet plateau (QTP); squares: Locations of *Locusta migratoria migratoria* in western China (Xinjiang, XJ). Roman numerals refer to the number of generations per year at each locality. Provinces mentioned in the text are labelled and coloured in orange, and the location of searchlight trapping site (Bohai Gulf) is labelled. LJ, Longjiang County; ZY, Zhaoyuan County. [Colour figure can be viewed at wileyonlinelibrary.com].

The migratory locust *Locusta migratoria* is the most widely distributed orthopteran in the world and poses a potentially serious threat to agricultural crops throughout Africa, Eurasia and Australasia as a result of its propensity to outbreak in massive swarms and to migrate long distances (Ma *et al.*, 2012; Ma & Kang, 2013). Historically, it has been one of the most serious threats to food production in China, with numerous plagues during the last 1000 years originating from the floodplains of the Yangtze and Yellow Rivers in east China (Guo *et al.*, 1991; Chen, 1999; Zhang & Li, 1999; Zhu, 1999; Chen, 2007; Stige *et al.*, 2007; Feng & Lv, 2010). Subsequent to the 1950s, management of these wetland areas to reduce the breeding grounds, as well as the intensive use of insecticides to prevent swarms from forming, has largely proved successful at keeping locust populations in check (Zhang & Li, 1999; Stige *et al.*, 2007), reducing the area to be treated each year (Zhang & Hunter, 2017). However, *L. migratoria* is once again becoming a serious threat in China (Zhang & Li, 1999; Stige *et al.*, 2007) and there have been recent outbreaks further to the north around the Bohai Gulf region (Feng & Lv, 2010) (Fig. 1).

Based on morphological characterization, three subspecies of *Locusta migratoria* are traditionally recognized in China (Ma, 1958; Guo *et al.*, 1991), with distinct geographical distributions (Fig. 1): the Oriental migratory locust *Locusta migratoria manilensis* occurs in the eastern monsoon region (EMR; east China as far north as the Bohai Gulf); *Locusta migratoria migratoria* is found in Xinjiang Uygur Autonomous Region (XJ) of west China; and *Locusta migratoria tibetensis* is present on the Qinghai-Tibet Plateau (QTP) (Fig. 1) (Zhu, 1999; Chen, 2007). More recent genetic studies only recognize two subspecies, namely *L. m. migratoria* of northern Eurasia, and *Locusta migratoria migratorioides* of Africa, Australasia, the Middle East and southern Asia; these classifications synonomize *L. m. manilensis* and *Locusta migratoria tibetensis* as geographical populations of a more widespread *L. m. migratorioides* than is recognized traditionally (Ma *et al.*, 2012; Ma & Kang, 2013). However, to keep in line with the traditional taxonomy familiar in the Chinese locust literature, we use the traditional three subspecies in the present study. *Locusta m. manilensis* poses the greatest threat to food security because its range is centred on the major cropping regions and the most densely populated area of China. The northern limit to the outbreak area in China is generally considered to be around 42°N (Guo *et al.*, 1991), on the northern shore of the Bohai Gulf in Hebei and Liaoning Provinces of northeast China (Fig. 1), although locusts are occasionally reported north of this area. This northern range margin is determined by the thermal requirements of *L. m. manilensis*, which requires a specified number of degree-days (DD) above the developmental threshold temperature of 14.2 °C (Tu *et al.*, 2012, 2014). However, given that many mobile insects are shifting their geographical distributions to higher latitudes in response to warming climates (Chen *et al.*, 2011; Bebber *et al.*, 2013), *L. m. manilensis* may now pose a significant threat beyond its historical range.

This potential was starkly illustrated by the occurrence of a severe migratory locust outbreak in 2009 in Heilongjiang (HLJ) Province in extreme northeast China (Fig. 1), which is more than 700 km north of the currently accepted northern limit for major outbreaks (Feng & Lv, 2010). The locust outbreaks were discovered in July 2009 in two distinct regions approximately 300 km apart [Longjiang County (LJ): 46°13′ to 47°40′ N, 122°24′ to 123°37′ E; and Zhaoyuan County (ZY): 45°23′ to 45°59′ N, 123°47′ to 125°45′ E] (Fig. 1) and, in total, occurred over an area of approximately 20 000 ha. When discovered, the outbreaks comprised gregarious-phase fifth-instar nymphs (indicating that locusts had produced at least one generation at both sites) and field densities were very high in the core areas. In the LJ region, the locust outbreak was discovered on 15 July 2009 in reeds (*Phragmites australis*) at Halahaixiang, at the junction of Longjiang, Gannan and Meilis Counties, Qiqihar City, in the far west of HLJ Province bordering Inner Mongolia (Fig. 1). In this region, the locusts damaged an area of approximately 8000 ha of reeds, and were estimated to occur at a density of 4000–5000 individuals/m^2 in the worst affected area (approximately 1% of the total area, i.e. 80 ha or 800 000 m^2) (Feng & Lv, 2010). In the ZY region, a smaller high-density locust outbreak was discovered on 18 July 2009 in reeds in the Weitang wetland area, at the junction of Zhaoyuan and Zhaozhou Counties, Daqing City, in the south of HLJ Province bordering Jilin (Fig. 1). Here, locusts damaged an area comprising approximately 500 ha of reeds, and were estimated to occur at a density of 1000–2000 individuals/m^2 in the worst affected area (Feng & Lv, 2010). Because the locust outbreaks were gregarious fifth-instar nymphs and only 2 weeks from being flight-active adults, the Ministry of Agriculture took urgent action upon the discovery, and the outbreaks were controlled with insecticide sprays on 22 July 2009.

Even though locust distribution has been continuously recorded in China for the past 3000 years, these were the first records of *L. migratoria* outbreaks in HLJ Province (Table 1) and, consequently, they represented a substantial northward expansion. The origins of this locust plague were a mystery, and so, in the present study, we identify the likely source region and migratory routes. We also analyze recent temperature trends for the LJ and ZY region of HLJ to investigate the potential of *L. m. manilensis* populations from east China to expand northwards and permanently colonize northeast China. At these latitudes, migratory locust populations will be univoltine if they permanently colonize this region (Fig. 1).

Materials and methods

Temperature suitability for locust development and population growth rate

Hourly temperature data for the period 2003–2016 at the two outbreak sites in HLJ (LJ and ZY) were obtained via: http://www.escience.gov.cn/metdata/page/index.html. Accordingly, the DD for each developmental stage was calculated to determine whether *L. migratoria manilensis* could complete a full generation. This was based on growth and development data from locusts collected in Hebei because this region was identified as a likely source region (see Results). Degree-day calculations (Fig. 2) were based on the DD model developed by Tu *et al.* (2012, 2014).

Table 1 Migratory locust plagues in Northeast China

Location	Frequency	Years
Jilin	5	Song Dynasty (960–1279), 2001, 2002, 2009, 2017*
Liaoning	6	Tang Dynasty (618–907), Song Dynasty (960–1279), Yuan Dynasty (1271–1368), Ming Dynasty (1368–1644), Qing Dynasty (1644–1912) and 1912–1949
Heilongjiang	1	2009

All data collected from Zhang (2004) and Feng and Lv (2010). *Field observations conducted in Jilin, 2017 by the lead author (XT).

Wind fields and trajectory analysis: evidence that the EMR is the source area

To assess the probability that locusts could have achieved windborne migration to the outbreak areas in HLJ during the most likely period of arrival (late-July to mid-August) (Table 2) in the years 2006–2008, we produced plots of mean nocturnal wind speeds and direction at 800 m a.s.l. during these periods (Fig. 3). Average values of nocturnal wind speed and direction were produced from two time points each night (06.00 and 12.00 h UT) and vector addition of the U (i.e. zonal velocity) and V (i.e. meridional velocity) components of the wind were used. National Centers for Environmental Prediction (NCEP) Final Analysis Data (FNL) provided the wind data for the model input. FNL is a six-hourly, global, 1° grid meteorological dataset. The model forecast time is 72 h with data outputs, at 1-h intervals, for horizontal and vertical wind speeds, temperature and precipitation.

We estimated take-off regions (i.e. potential source areas) for *L. migratoria* that may have reached the outbreak areas (ZY and LJ) by constructing backward flight trajectories for every date during the most likely arrival period (20 July to 10 August) of 2006, 2007 and 2008 (Fig. 4). Our trajectory analyses incorporated a number of assumptions, which we based on radar studies of a range of nocturnal insect migrants because these factors have not been quantified in *L. migratoria manilensis*. First, we assumed that locusts fly downwind with a self-powered air speed of 3 m/s because this is typical flight behaviour not only of locusts (Guo *et al.*, 1991), but also of many nocturnal migrants (Drake & Reynolds, 2012; Chapman *et al.*, 2015). Second, we assumed that locusts were capable of flight for 9 h, from sunset (about 20.00 h local time, UTC + 8) until sunrise (about 05.00 h local time) because night-long flight durations have been observed, for part of the population at least, in Australian plague locusts *Chortoicetes terminifera* (Walker) (Drake & Farrow, 1983) and many other nocturnal pest insects (Drake & Reynolds, 2012). Third, we assumed that locusts will typically migrate at a range of heights between 500–1500 m above the ground, depending on the precise meteorological conditions at altitude, because this has been observed in Australian plague locusts (Drake & Farrow, 1983); thus, our trajectories were calculated at five different flight

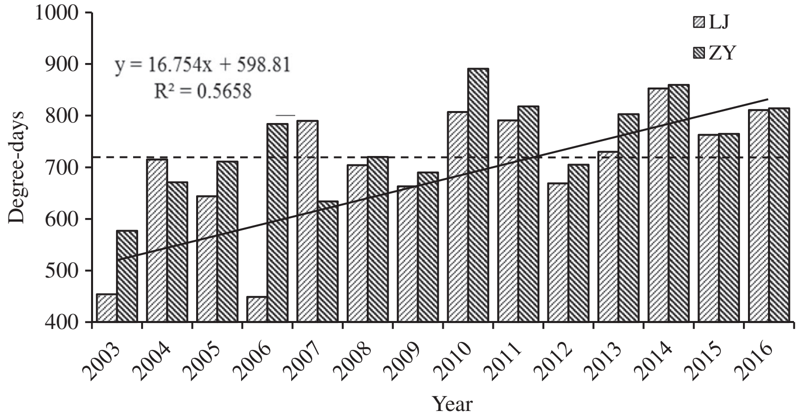

Figure 2 Number of degree-days (DD) available for locust development in the outbreak sites [Longjiang County (LJ) and Zhaoyuan County (ZY)] during 2003–2016. Developmental threshold temperature: 14.2 °C. dashed line: Minimum number of DD required for *Locusta migratoria* to complete a full generation. Solid line: linear regression of DD values against time, for the combined LJ and ZY data.

Table 2 Number of generations and occurrence of mature adult locusts capable of migratory flight at different locations in China (based on field observations at the locations in 2008)

Location	Voltinism (generations per year)		Duration of mature adults
Huludao (Liaoning)	One	I	10 July to 11 August
Cangzhou (Hebei)	Two	I	25 June to 5 August
		II	10 August to 13 September
Nanning (Guangxi)	Three	I	20 May to 13 June
		II	3 August to 31 August
		III	10 October to 31 October
Dongfang (Hainan)	Four	I	1 April to 19 April
		II	11 June to 30 June
		III	6 July to 23 July
		IV	20 October to 9 November

altitudes (500, 750, 1000, 1250 and 1500 m a.s.l.) to ensure we captured the most likely flight height on each night. Finally, backward trajectories were calculated for up to five consecutive nights because migration durations of 3–5 nights are typical for a range of migratory insects (Drake & Reynolds, 2012; Chapman *et al.*, 2015; Minter *et al.*, 2018).

Thus, trajectories were terminated at LJ or ZY at dawn (about 05.00 h local time) on the fifth migration night, the displacement speed of migrating locusts was assumed to be the local wind speed plus the self-powered flight speed (3 m/s) and they were terminated after 9 h. Locusts were presumed to migrate for five nights. On the second migration night, and each subsequent migration, trajectory analysis continued from the location where the previous night's trajectory terminated, with the same take-off time and altitude, using an established methodology (Hu *et al.*, 2013; Wang *et al.*, 2017; Li *et al.*, 2019). Trajectories were continued at each of the five flight altitudes only if the terrain remained below the height (m a.s.l.) values used. Trajectories that followed the low-lying coastal plain from HLJ towards the Bohai Gulf could be continued for five nights, although those that headed towards the Mongolian Plateau (where the land rises above 1000 m a.s.l.) typically ended in fewer than five nights. The wind-field data used in the trajectory calculations was obtained from the Weather Research and Forecasting (WRF) Model; this is a next-generation mesoscale numerical weather prediction system (Skamarock *et al.*, 2008). The model was used to produce a high resolution atmospheric background for the trajectory analysis carried out in the present study. The dimensions of the model domain were 99 × 84 grid points in a resolution of 30 km. Twenty-nine vertical layers were available and the model ceiling was 100 hPa. The scheme selection and parameters used for the WRF in the present study are in accordance with those reported in Wang *et al.* (2017).

Searchlight trapping: evidence for high-altitude migration

We assumed that the 2009 outbreak in HLJ must have arisen from long-range migration of locusts from further south sometime in the few years preceding the discovery because there is no possibility that large populations could have existed for many years previously in HLJ without detection. There is no record of an outbreak in the EMR during 2005–2008 and so it must have been migration of solitarious individuals, migrating at night (Lecoq, 1995; Lecoq & Sukirno, 1999), which gave rise to the 2009 outbreak in HLJ. Thus, to gather evidence for long-range migratory flights of solitarious locusts, catch data from a searchlight trap on an island along the proposed migratory route, although some distance from the nearest land, was examined. Searchlight trapping was carried out every night from May to October 2003–2015 on Beihuang Island (BHI) (38°24′ N, 120°55′ E), the northernmost island of Changdao county, Shandong Province. BHI (with a surface area of approximately 2.5 km^2) is located in the centre of the Bohai Strait, approximately 40 km from the mainland to the north and approximately 60 km to the south (Fig. 1). There are some pine trees and graminaceous weeds on BHI but no

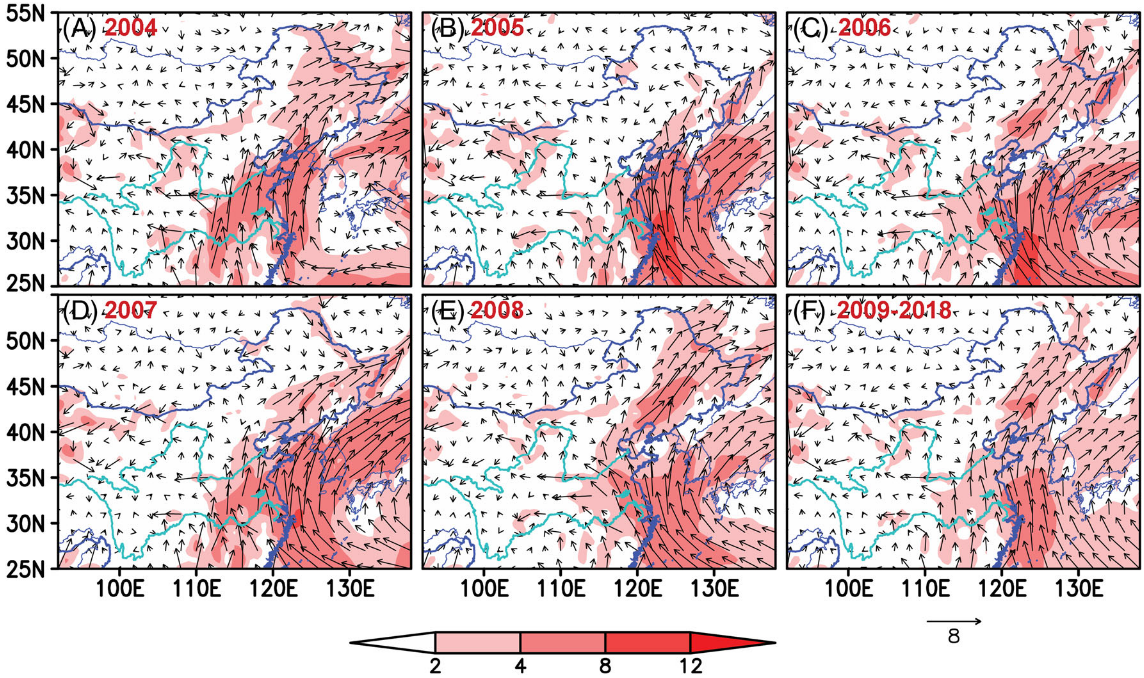

Figure 3 Mean nocturnal wind speeds and directions at 800 m a.s.l. from 20 July to 10 August over East China. Arrow direction indicates the wind direction, and the length of the arrow indicates the wind speed. Colour scale bar indicates wind speed (ms^{-1}). [Colour figure can be viewed at wileyonlinelibrary.com].

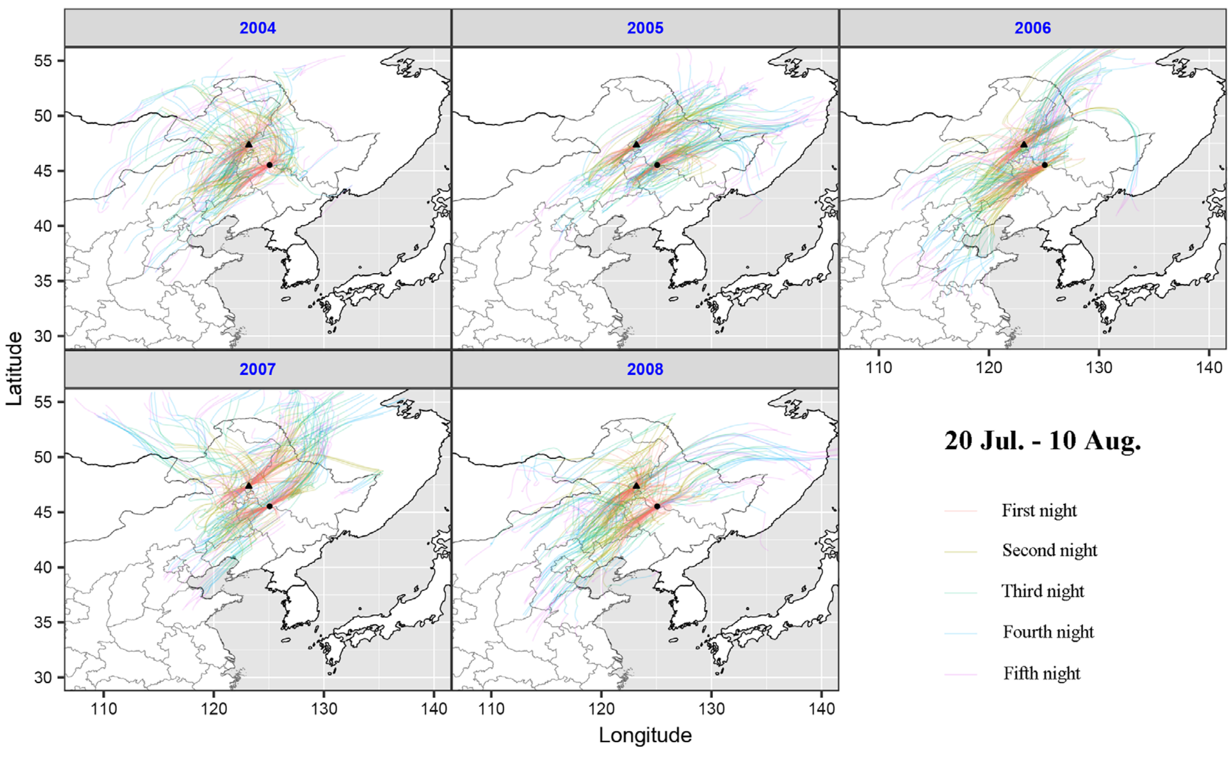

Figure 4 Simulated backward trajectories for identifying potential source areas of *Locusta migratoria* immigrating to Heilongjiang Province. There are 5-day simulated backwards trajectories for different heights (500, 750, 1000, 1250 and 1500 m above mean sea level) for each night. Trajectories were calculated for each night from 20 July to 10 August from Longjiang County (black star) and Zhaoyuan County (white star), and were extended back through up to four previous nights. Each coloured line is the trajectory for a single night, flying from sunset (dusk) until sunrise (dawn). The different colours of the lines represent up to five successive nights of migration, and the sea is coloured in grey. [Colour figure can be viewed at wileyonlinelibrary.com].

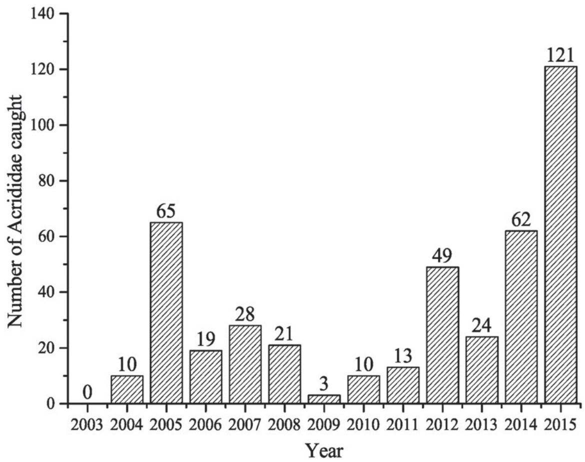

Figure 5 Annual totals of grasshoppers and locusts caught during July and august in the searchlight trap on Beihuang Island in the Bohai Gulf.

arable land or suitable host plants for *L. migratoria* development. A vertical-pointing searchlight trap (model DK.Z.J1000B/*t*; Shanghai Yaming Lighting Co. Ltd, China) (Feng & Wu, 2010) was placed on a platform approximately 8 m a.s.l. and used to trap high-altitude migrants flying overhead up to approximately 500 m above ground level (Feng *et al.*, 2009; Fu *et al.*, 2014a, 2014b, 2015). From 2003 to 2014, the number of 'grasshoppers and locusts' (Orthoptera: Acrididae) was recorded (Fig. 5) but, in 2015, the proportion of these acridids that were *L. migratoria* was determined. To demonstrate that it is feasible that acridids (presumably including migratory locusts) migrating over BHI can reach HLJ, we ran forward trajectories using the same parameters described above, for five successive nights, starting on each date at dusk that acridids were caught in the searchlight trap on BHI. We then plotted the number of trajectories landing in each 100 × 100 km grid cell in the surrounding region after five nights of flying (Fig. 6) and calculated how frequently the reached HLJ.

Results and Discussion

Temperature suitability for locust development and population growth rate

Between 2004 and 2009, DD values at both LJ and ZY typically hovered around the limit required for the complete development of a generation of *L. migratoria* (Fig. 2), although they were sometimes well below the limit (e.g. 2006 at LJ) and occasionally exceeded it (e.g. 2007 at LJ). However, the DD model does not take into account microclimatic variation in temperature, nor the fact that locusts may behaviourally thermoregulate by basking, and so it is quite likely that the DD model slightly underestimates the likelihood of completing a generation. We therefore interpret Fig. 2 as evidence for continuous locust survival, as well as completion of a full generation from overwintering eggs in each year, being marginal but probably feasible during 2004 to 2009 in at least one of the sites, although not in 2003 when the value was well below the required limit (Fig. 2). A plausible hypothesis would therefore appear to be that locusts first arrived sometime during 2004 to 2006 and then built up the population gradually over subsequent years, before reaching outbreak levels in 2009 when they were discovered. It appears highly unlikely that the outbreaks in 2009 could have arisen from an immigration of reproductive adults in the spring of 2009 because this would have had to have occurred in early-spring 2009 for any eggs that they might lay to reach fifth instar by the time of discovery. In early spring, the only adults present are to be found in southernmost China (Fig. 1 and Table 2), approximately 3500 km away, an implausible distance to have been traversed by natural migration; furthermore, the immigration would have had to have been implausibly large to produce the numbers observed in the summer of 2009 (see below).

The core region of the largest outbreak site (LJ) had a density of up to 5000 locust nymphs/m^2 distributed over an area of approximately 800 000 m^2 (Feng & Lv, 2010) when discovered in July 2009, equating to a total of approximately 4 billion individuals. If we assume that locusts in this region will be univoltine (Figs 1 and 2 and Table 2), we calculate that at least three or four annual generations subsequent to the initial immigration would be required to produce these numbers, as follows. Each female produces one to three egg pods in each generation (Ma, 1958), and each egg pod contains 60–180 eggs (Tu *et al.*, 2011), and so we assume an average fecundity of approximately 150 eggs per female. Given that there is much suitable habitat and, during the early stages of the population establishment the impact of specialist predators, pathogens and parasites is likely to be low, we assume that survival of eggs to adulthood will be high (estimated to be in the region of 100 eggs per female). Thus, we assume that the population grew by a factor of 50 (i.e. 100 eggs per female, with females assumed to make up 50% of the immigrants) after the initial arrival, and in each subsequent annual generation. The 2009 population of 4 billion locusts could therefore have been produced after three generations of breeding if the initial immigration to the LJ region had comprised approximately 32 000 adult locusts arriving in 2006, or after four generations if the initial immigration had been approximately 640 locusts in 2005. This indicates that the initial immigration must have occurred in 2006 at the latest (because the initial immigration would have had to be enormous in subsequent years; e.g. 1.6 million locusts at LJ in 2007 and 80 million in 2008), and perhaps even more likely before 2006, although there may have been reinforcement from further immigration in later years.

Wind fields and trajectory analysis: evidence that the EMR is the source area

The most likely scenario for the arrival of locusts in HLJ is that they migrated from the large populations that occur in wetlands in the EMR and, being the closest, the populations around the Bohai Gulf (e.g. from Hebei and Liaoning) are the most likely sources (Fig. 1). Locusts from these regions are adult and flight-capable mostly in the late-summer and early-autumn (peaking in mid-July to mid-August) (Table 2) and so we speculated that this would be the most likely time for locusts to arrive in HLJ because, at this time, winds are generally favourable and there is sufficient time for them to oviposit before temperatures drop too low. We therefore analyzed wind-field patterns for the period 20 July to 10 August during the potential

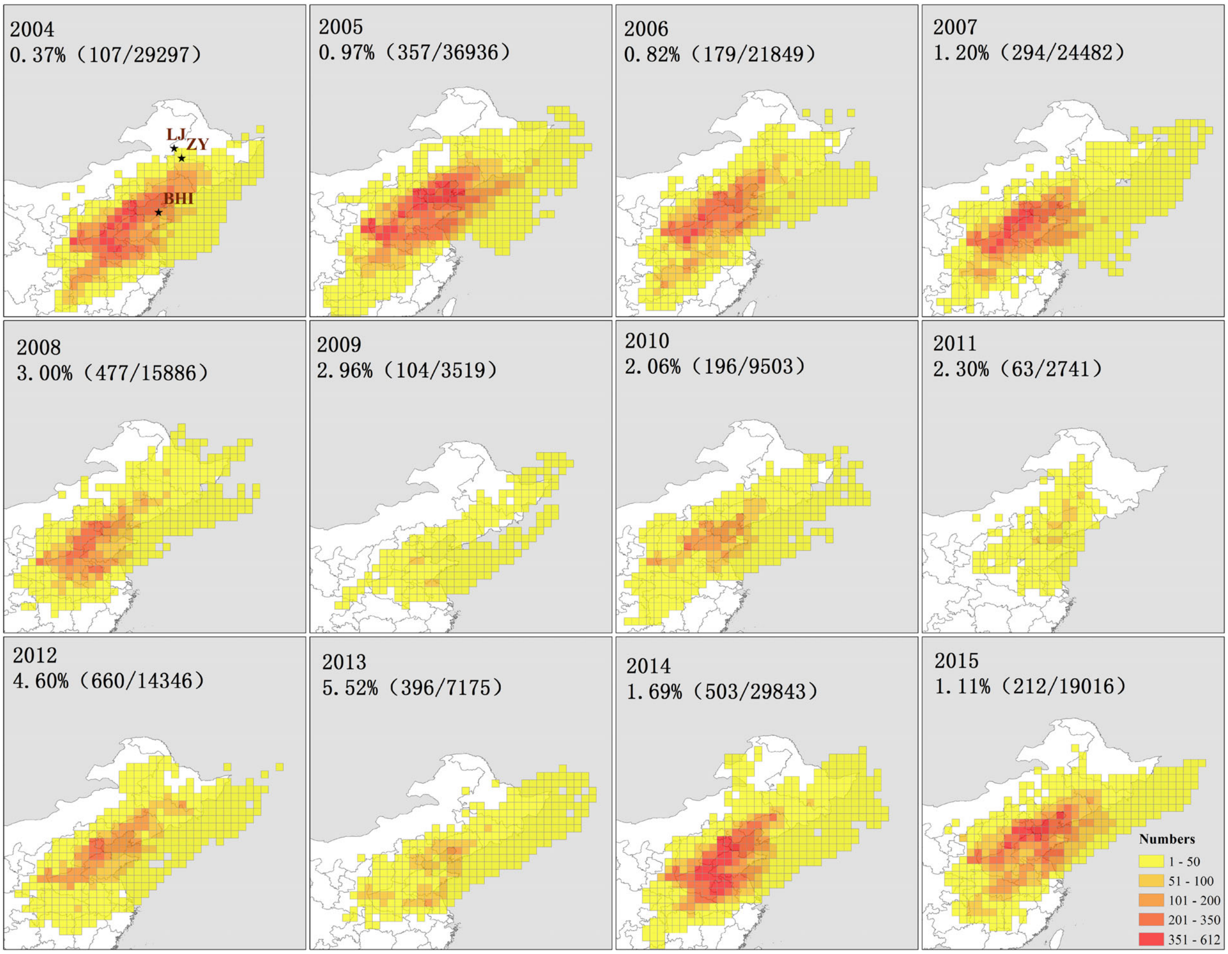

Figure 6 The distribution of the endpoints of five-night forward trajectories over east and northeast China, starting from Beihuang Island in the Bohai Gulf on nights when acridids were caught in a searchlight trap there, ending in each 100 × 100 km grid cell of the surrounding regions. The text in each panel shows the percentage of the total trajectories that ended in Heilongjiang Province. [Colour figure can be viewed at wileyonlinelibrary.com].

invasion years (2004–2008) in more detail. Wind patterns in this time period were highly favourable for long-range transport from the Bohai Gulf region in the northern part of the EMR to HLJ in all years (Fig. 3). The mean nocturnal wind pattern was often > 8 m/s, and directed towards the northeast. It is also clear that windborne transport from any of the other possible source areas, such as the southern EMR, western China, QTP, Mongolia or south-east Russia, is extremely unlikely (Fig. 3). Analysis of the mean patterns from 2009 to 2018 (Fig. 3) indicates that there would have been many opportunities for further arrivals if source populations produced sufficient migrants, highlighting the necessity of adequate monitoring and control of populations in the EMR.

The backward trajectory analyses demonstrate that there were frequent opportunities for successful migration from the potential source area (the northern EMR) to the outbreak areas during late-summer of 2004–2008 (Fig. 4). The trajectories identified the Bohai Gulf region (Liaoning, Hebei, Tianjin municipality and Shandong) as potential source regions for the immigrants (Fig. 4). These are regions where migratory adult locusts of the first generation would have been present at that time (Fig. 1 and Table 2). Many of the backward trajectories reached potential source areas around the Bohai Gulf in just 2–3 nights of migratory flight (Fig. 4). Notably, relatively few of the trajectories crossed the Bohai Gulf itself, and none passed over the region where the searchlight trap was situated on BHI (Figs 1 and 4).

Searchlight trapping: evidence for high-altitude migration

To produce an outbreak of the scale witnessed in 2009, a comparatively large number of locusts must have engaged in high-altitude windborne migration away from the breeding areas further to the south in the EMR. To provide evidence for this, we looked at data collected by the long-term searchlight trapping undertaken on BHI in the centre of the Bohai Gulf (Fig. 1). It is not possible to say how many *L. migratoria* were caught during 2003 to 2014; however, in 2015, they comprised 43% of the sample, consisting of 121 Acrididae in total (Fig. 5) and it appears reasonable to assume that they would have been represented in the catch in at least some of the previous years. The searchlight catches of acridids on BHI were not especially large (Fig. 5), although there are two reasons to expect that migration intensities to the west of the trap site may have been considerably bigger. First, our backward trajectories from the outbreak locations typically had a more westward route than the Bohai Gulf, and none of them passed as far east as BHI (Fig. 4), and so it appears that the searchlight is located on the eastern periphery of the migration route. Second, it is likely that migratory locusts will avoid flying over extensive areas of water when possible because it has been shown previously that desert locusts (*Schistocerca gregaria*) detect reflected polarized light to avoid sea crossings (Shashar *et al.*, 2005), thus further reducing the migration traffic of locusts crossing BHI. Thus, the 2015 searchlight catches confirm that *L. migratoria* does indeed engage in long-range migration through northern China during at least some years, and we suspect that migration intensity may have been considerably greater further to the west, taking an overland route that avoids crossing the Bohai Gulf. Studies of the species elsewhere (Lecoq, 1995; Lecoq & Sukirno, 1999) have shown that long-range migration of solitarious individuals is a common phenomenon that can lead to outbreaks. Also, forward trajectories from BHI, started on all dates when acridids were caught in the searchlight trap there, demonstrate that migratory locusts flying over the Bohai Gulf are capable of reaching HLJ after five nights of flight in every year (Fig. 6). Only a minority of the total of 214 593 trajectories reached HLJ in any year (3548 in total, with an annual mean of 296 endpoints in HLJ (1.7%), ranging from 0.4% in 2004 to 5.5% in 2013) (Fig. 6). The majority of trajectories either ended in provinces bordering the Bohai Gulf (e.g. Shandong, Hebei, Liaoning), or in the sea (Fig. 6), although these data indicate that it is feasible for locusts migrating over this region to reach HLJ (albeit rather infrequently) in every year.

Could L. migratoria *colonize HLJ permanently in the future?*

The DD values for 2009 indicate that at LJ and ZY there would probably not have been sufficent DD to go through a full developmental cycle in that year (Fig. 2) and so the locust population would likely have become locally extinct by 2010 even if it had not been controlled by the authorities. However, temperatures in this region are rising (linear regression: $y = 16.754x + 598.81$; $n = 28$, $r^2 = 0.566$, $P = 0.0019$) (Fig. 2) and the majority of years from 2010 onwards have been sufficiently warm for locusts to have completed a full developmental cycle if they had continued to be present at the HLJ outbreak sites (Fig. 2). Therefore, if *L. m. manilensis* migrates into this area in large numbers again, permanent colonization of HLJ (constituting a northward range expansion of approximately 700 km) would become a realistic possibility. The locust control services in China clearly need to remain vigilant for major migrations into north-east China from the EMR, and to be ready to act against any populations arising there before they become established.

Conclusions

In the present study, we have combined DD and meteorological data to identify the most likely origins, migration routes and arrival period of the 2009 locust outbreak in HLJ. The results obtained strongly suggest that the outbreak was derived from an immigrant population, probably arriving in the late-summer of either 2004, 2005 or 2006, and that the source was most likely the Bohai Gulf region (Liaoning, Hebei, Tianjin and Shandong) (Figs 1 and 4). The adult locusts that migrated into HLJ sometime in 2004–2006, perhaps as a single founder event or perhaps in multiple immigration events spread across 2 or 3 years, would have encountered suitable climate conditions and an abundance of the principal larval host plant (common reed), promoting breeding and oviposition. The ensuing population would have grown over the next 3–4 years, perhaps supplemented by further immigration in 2007 and/or 2008, until densities reached a sufficiently high level to cause the switch to the gregarious phase and an outbreak to form. At this point, the locust population was noticed and swiftly controlled. As a result of the presence of large areas of potential breeding habitat in northeast China, and the fact that temperatures are becoming more amenable for the permanent colonization of this region, it is important to remain vigilant to prevent future outbreaks. Given that the provinces of northeast China (HLJ, Jilin and Liaoning) are the major producers of cereal crops and maize in China, potential range expansion of migratory locusts represents a major threat to food security in East Asia.

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