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Seasonal migration of *Cnaphalocrocis medinalis* (Lepidoptera: Crambidae) over the Bohai Sea in northern China

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Abstract

The rice leaf roller, *Cnaphalocrocis medinalis* (Guenée), is a serious insect pest of rice with a strong migratory ability. Previous studies on the migration of *C. medinalis* were mostly carried out in tropical or subtropical regions, however, and what the pattern of seasonal movements this species exhibits in temperate regions (i.e. Northern China, where they cannot overwinter) remains unknown. Here we present data from an 11-year study of this species made by searchlight trapping on Beihuang Island (BH, 38°24′N; 120°55′E) in the centre of the Bohai Strait, which provides direct evidence that *C. medinalis* regularly migrates across this sea into northeastern agricultural region of China, and to take advantage of the abundant food resources there during the summer season. There was considerable seasonal variation in number of *C. medinalis* trapped on BH, and the migration period during 2003–2013 ranged from 72 to 122 days. Some females trapped in June and July showed a relatively higher proportion of mated and a degree of ovarian development suggesting that the migration of this species is not completely bound by the 'oogenesis-flight syndrome'. These findings revealed a new route for *C. medinalis* movements to and from Northeastern China, which will help us develop more effective management strategies against this pest.

Keywords: *Cnaphalocrocis medinalis*, seasonal migration, searchlight trapping, oversea movements, sexual maturation

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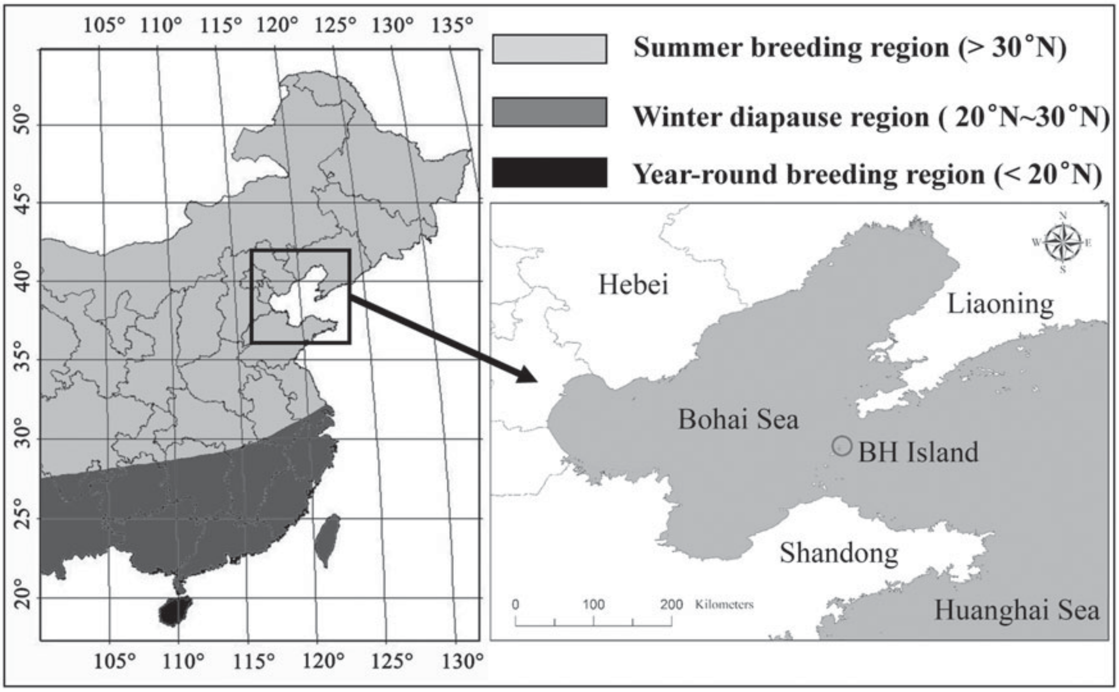

Fig. 1. Maps showing the district distribution of *C. medinalis* in China (left-hand map) and the position of BH Island, the searchlight trap site (right-hand map), relative to the Bohai and Huanghai (Yellow) Sea.

Introduction

The rice leaf roller, *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Crambidae), one of the most important pests of rice, is distributed widely in the humid tropical and temperate regions of Asia, Oceania and Africa between 48°N and 24°S latitude (Pathak & Khan, 1994; Kawazu *et al.*, 2001). *C. medinalis* has a broad host range, including rice, corn, sugarcane, wheat and sorghum, as well as some graminaceous weed species (Luo, 2010); rice is the most preferred host plant (Yadava *et al.*, 1972). The larvae damage the rice plant by folding leaves and scraping green leaf tissues within the fold during the tillering to heading stage, causing great yield losses by reducing photosynthetic activity (Wang *et al.*, 2011).

'Migration' is a movement which involves the temporary suppression of an animal's station-keeping responses – responses which would otherwise retain the animal within its current habitat patch – thus allowing displacements of much longer duration and typically over much greater distances than those arising from normal foraging activities (Dingle & Drake, 2007). Long-distance migration plays a key role in the life-history of *C. medinalis* by enhancing its opportunities to use favourable resources across huge areas; this, in turn, leads to severe area-wide damage to crops. In recent decades, a series of major outbreaks of *C. medinalis* has been reported in Asian paddy fields, and severe infestations commonly reduce yields by 30–80% (Yang *et al.*, 2004; Nathan *et al.*, 2005; Nathan, 2006; Zhai & Cheng, 2006; Padmavathi *et al.*, 2012). In China, *C. medinalis* has 1–11 generations from north to south each year, and the species' range can be divided into three zones: the 'year-round breeding region', 'winter diapause region' and 'summer breeding region' (fig. 1) (Zhang *et al.*, 1981; Zhang & Tang, 1984; Luo, 2010). Evidence from capture–mark–recapture studies and from light-traps on ships in the East China Sea suggest that *C. medinalis* moths make long-distance migration from the tropics towards the north-east in a series of five northward mass migrations from March to August, and possibly three southward 'return' migrations from September to November each year in the eastern part of China (Chang *et al.*, 1980; Zhang *et al.*, 1981). The Chinese populations of *C. medinalis* are also able to migrate over water, reaching Japan every year in the East Asian rainy season (June to July) (Mochida, 1974; Miyahara *et al.*, 1981; National Coordinated Research Team on Rice Leafroller, 1981; Oya & Hirao, 1982; Liu *et al.*, 1983; Kisimoto, 1984; Geng *et al.*, 1990), and such movements are similar to those of the rice planthoppers, *Sogatella furcifera* (Horváth) and *Nilaparvata lugens* (Stål) (Otuka *et al.*, 2005*a*, *b*, 2006, 2008, 2012; Syobu & Otuka, 2012).

Previous studies on the migration of *C. medinalis* have been mostly carried out in tropical or subtropical rice planting regions. However, whether the migration of *C. medinalis* in Northern China, where they cannot overwinter (National Coordinated Research Team on Rice Leafroller, 1981; Zhang *et al.*, 1981; Riley *et al.*, 1995; Luo, 2010), is a regular ecological event remains unknown. Considering the poleward expansion of many insect species under current global warming scenarios (Wilson *et al.*, 2005; Pöyry *et al.*, 2009; Robertson *et al.*, 2009; Pateman *et al.*, 2012), and the increasing areas of rice planting in Northeastern China (China Agricultural Yearbook Editing Committee, 2012), it is critical to enhance our understanding of the migration patterns of this species in such regions. In the present study, long-term (11 years) observations on the seasonal migration of *C. medinalis* over the Bohai Sea were carried out by means of searchlight trapping on a small island located in the centre of the Bohai Strait.

Although it cannot illuminate the backgrounds and evolution process of the population fluctuations of *C. medinalis* on the mainland, this study provides direct evidence that this species regularly migrates across the sea into northeastern agricultural region of China, and to take advantage of the abundant food resources there during the summer season. These findings will improve our knowledge of the migration pattern and outbreaks of *C. medinalis* in Eastern Asia, and will help us develop more effective management strategies against this pest.

Materials and methods

Light-trapping and field observation

The searchlight trapping studies were carried out from 2003 to 2013 at Beihuang (BH, 38°24′N, 120°55′E), the northernmost island of Changdao county in Shandong province (fig. 1). This small (~ 2.5 km^2) island is located in the centre of the Bohai Strait at a distance of ~ 40 km from the mainland to the north and ~ 60 km to the south. A vertical-pointing searchlight trap (model DK.Z.J1000B/t, 65.2 cm in diameter, 70.6 cm in height and ~30° in spread angle; Shanghai Yaming Lighting Co. Ltd, Shanghai, China) (Feng & Wu, 2010) was placed on a platform ~8 m above sea level, and used to attract and capture high-altitude migrants (up to ~500 m above ground level) (Feng *et al.*, 2009). The trap was equipped with a 1000-W metal halide lamp (model JLZ1000BT; Shanghai Yaming Lighting Co. Ltd, Shanghai, China), which produces a vertical beam of light with a luminous flux of 105,000 lm, a colour temperature of 4000 K; and a colour rendering index of 65.

The searchlight trap was turned on at sunset and turned off at sunrise on all nights from April to October during 2003–2013. Incomplete data sets that resulted from power cuts or heavy rains were excluded from the analysis. Trapped insects were collected with a nylon net bag (60 mesh) beneath the trap, which was changed manually every 2 h each night. The trapped insects were kept in a freezer at −20°C for 4 h before being identified and the female *C. medinalis* dissected.

There are some pine trees and graminaceous weeds on BH, but no arable lands and host crops of *C. medinalis*. To investigate whether any *C. medinalis* moths were produced on BH itself, visual observations were carried out daily to detect larvae of this species on any potential wild hosts from spring through autumn during 2003–2013.

Ovarian dissection

From 2010 to 2013, a subsample of 20 females (or all individuals if the total capture of females was <20) was randomly taken from adults trapped each night, and dissected under a stereomicroscope (model JNOEC-Jsz4; Motic China Group Co. Ltd, Xiamen, China). The level of ovarian development was estimated according to the criteria described in table 1 (Zhang *et al.*, 1979). Females with ovarian development level 1–2 were regarded as 'sexually immature individuals' and others with level 3–5 were regarded as 'sexually mature individuals' (Zhang *et al.*, 1979; Zhu *et al.*, 2009). These data were used to generate an average monthly level of ovarian development (i.e. the sum of individual levels of ovarian development divided by the number of females dissected). Mating rate and mating frequency of *C. medinalis* were determined by the number of spermatophores in the female spermatheca.

Table 1. Criteria of ovarian development level of *C. medinalis* moths.

Development level	Characteristics of ovary
1	Transparent and light milky white ovarioles with length of about 5.5–8 mm
2	Developing eggs appeared in milky white ovarioles with length of about 8–10 mm
3	Well-developed yellowish green ovarioles with length of about 11–13 mm and five to ten fully chorionated eggs stored in the egg calyx
4	Approximately 15 mature eggs stored in the egg calyx, with the ovarioles length > 13 mm
5	The ovary has atrophied and contains almost no mature eggs, with the ovarioles about 9 mm long

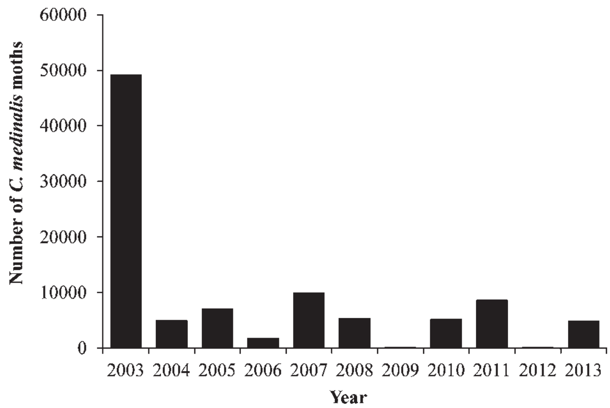

Fig. 2. Annual catch of *C. medinalis* in the searchlight trap on BH from 2003 to 2013.

Data analysis

All data obtained from these studies are presented as means ± SEM. Population size of *C. medinalis* captured in the searchlight trap varied in different years and months, so the inter-year and inter-month variations in the number of trapped *C. medinalis*, and the proportion of females, mated females and sexually mature females were analysed by two-way analysis of variance (ANOVA) with month and year as the variables (Zhao *et al.*, 2009). If the ANOVA indicated a significant difference, Tukey's Honestly Significant Difference (HSD) tests were followed to separate the means. All the proportion data were arcsine transformed before ANOVA to meet the assumptions of normality. Differences of the sex ratio (females:males) in each month were analysed by chi-squared test. All statistical analyses were carried out with SAS software (SAS Institute, 1990).

The index of occurrence (*O*) was calculated by the formula: $O = (p/n) \times 100\%$, where p is the number of nights in which *C. medinalis* were trapped in a month and n is the number of nights in which all insect species were trapped in a month (Zanuncio *et al.*, 1998). Occurrence status of *C. medinalis* captured in the searchlight trap was divided by the following criteria (Serafim *et al.*, 2003): as an accidental species with

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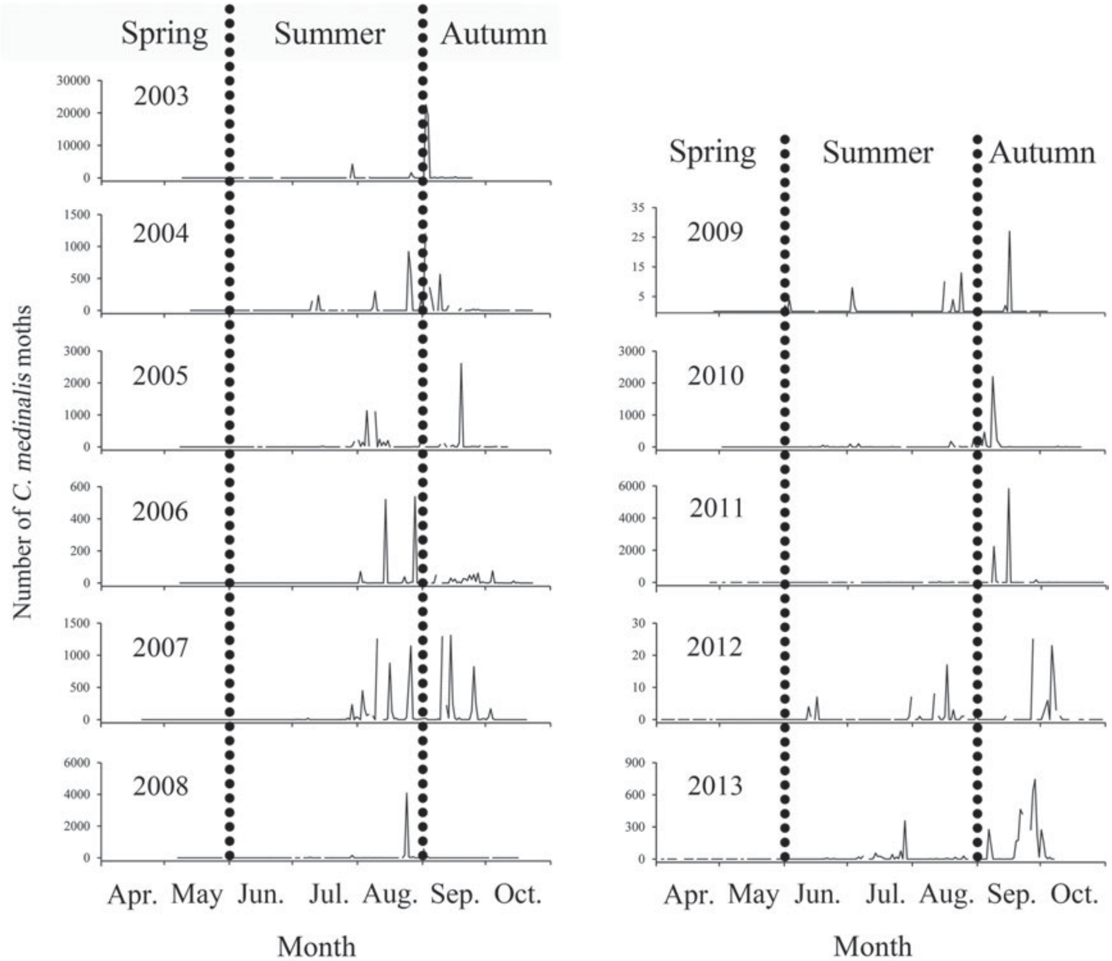

Fig. 3. Nightly catch of *C. medinalis* in the searchlight trap on BH from April to October.

O = 0–25%, as an accessory species with *O* = 25–50% and as a constant species with *O* = 50–100%.

Results

Annual and seasonal pattern of migration

No *C. medinalis* larvae were found on BH by daily field investigations although some graminaceous weeds were available as potential wild hosts. However, *C. medinalis* were regularly captured in the searchlight trap during the period from 2003 to 2013 (fig. 2). This means *C. medinalis* moths migrated at least 40–60 km (and probably much greater distances) across the Bohai Strait waters. The strength of this oversea migration varied annually. Mass migrations took place in 2003, 2005, 2007 and 2011, with the annual total catches reaching 49,187, 7032, 9918 and 8560 individuals, respectively. Very weak migrations took place in 2009 and 2012, with the annual total catches falling to 72 and 133 individuals, respectively. In other years, the annual total catches of *C. medinalis* ranged between 1000 and 5000 individuals (fig. 2).

The number of *C. medinalis* captured in the searchlight trap varied monthly ($F = 2.63$, df = 4, $P = 0.048$) during 2003–2013. The 53.9 ± 9.3 and 46.1 ± 9.3% of *C. medinalis* were trapped in autumn (September to October) and summer (June to August), respectively, while none were trapped in spring (April to May) (fig. 3). During 2003–2013, *C. medinalis* were captured frequently in the searchlight trap and considered as a constant species in September. In July, August and October, *C. medinalis* were captured occasionally and considered as an accessory species, while in other months this species occurred as an accidental species. The migration period of *C. medinalis* over the Bohai Strait during 2003–2013 ranged from 72 to 122 days, with the earliest and latest trapping on 1 June 2009 and 20 October 2006, respectively (table 2).

Sex ratio, mating rate, mating frequency and ovarian development

From June to October during 2010–2013, the vast majority of trapped *C. medinalis* were females. Chi-squared tests showed that the sex ratio (females:males) was significantly greater than 1:1 in all months, except in June 2010 ($\chi^2 = 0.39$; df = 1; $P = 0.528$) and June 2013 ($\chi^2 = 0.89$; df = 1; $P = 0.346$) (fig. 4A). There were no significant inter-month differences in the proportion of females, which ranged from 61.4 ± 3.1% (June) to 70.2 ± 5.6% (October) (linear model, $y = 0.01x + 0.55$,

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Table 2. Duration and occurrence status of *C. medinalis* captured in the searchlight trap on BH Island from April to October during 2003–2013.

Year	Occurrence status[1]							Date of first capture[2]	Date of final capture[2]	Duration (day)
	April	May	June	July	August	September	October			
2003								7 June (1)	21 September (1)	106
2004								10 July (143)	18 October (3)	100
2005								14 July (8)	8 October (2)	86
2006								26 June (1)	20 October (1)	116
2007								2 July (1)	4 October (17)	94
2008								19 June (2)	30 August (56)	72
2009								1 June (2)	16 September (27)	107
2010								13 June (12)	13 October (7)	122
2011								26 June (8)	8 October (6)	104
2012								12 June (4)	10 October (1)	120
2013								19 June (1)	5 October (16)	108

[1] ■ Occurrence index between 50 and 100%, ■ occurrence index between 25 and 50%, and ■ occurrence index between 0 and 25%.
[2] The numbers of *C. medinalis* captured are given in parentheses next to name of the months.

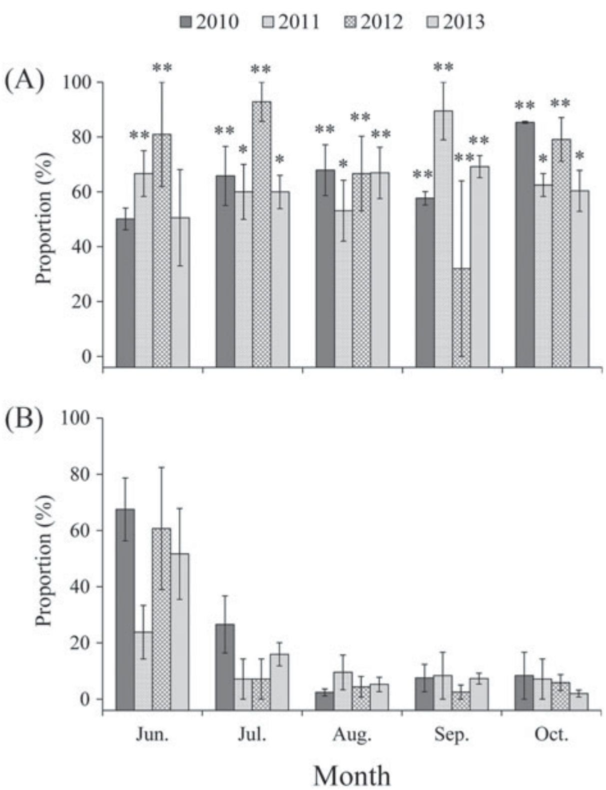

Fig. 4. Proportion of *C. medinalis* females (A) and mated females (B) captured in the searchlight trap on BH during 2010–2013. The histogram indicates mean proportion that were combined by averaging the daily proportions in each month, and the bar represents standard error between different days in that month. Single asterisk (*) or double asterisks (**) above a bar indicates the proportion of females was significantly greater than that of males in that month at the 5 or 1% level as determined by a chi-squared test.

$R^2 = 0.35$, $n = 5$, $F = 1.58$, $P = 0.298$) (fig. 6A). Most of the trapped females were virgins (fig. 4B), and there were significant inter-month differences in the proportion of mated females (mating rate), which ranged from 6.0 ± 1.0% (September) to 43.2 ± 8.0% (June) (fig. 6B). The seasonal variation in the proportion of mated females showed a weak downward trend from June to October (linear model, $y = -0.09x + 0.87$, $R^2 = 0.75$, $n = 5$, $F = 9.06$, $P = 0.057$) (fig. 6B). There was a significant difference in the mating frequency among the mated females, the vast majority (82.6 ± 6.9%) had mated once, the 17.4 ± 6.9% had mated twice, and no individuals mated ≥3 times.

In all years, no *C. medinalis* females with ovarian development level 5 were found on BH (fig. 5). The vast majority of the early-summer migrants (June) had a certain degree of ovarian development, and the proportion of sexually mature females reached 65.4 ± 4.3%, which was significantly higher ($\chi^2 = 11.00$; df = 1; $P = 0.001$) than the proportion of sexually immature females (figs 5 and 6C). However, there was no significant difference ($\chi^2 = 2.47$; df = 1; $P = 0.116$) between the proportion of sexually mature females and immature females in mid-summer migrants (July) (fig. 6C). In other months, the proportion of sexually mature females was significantly lower than that of sexually immature females (fig. 5). Overall, the seasonal variation in the proportion of sexually mature females showed a significant downward trend from June to October (linear model, $y = -0.15x + 1.46$, $R^2 = 0.86$, $n = 5$, $F = 17.81$, $P = 0.024$) (fig. 6C).

Discussion

The long-term (11 years) searchlight trapping study on BH Island provided direct evidence that both male and female *C. medinalis* moths regularly migrate across the sea into Northeastern China, because no host crops or larvae of this species were found on this small island. The long-range movements of *C. medinalis* observed in this study were similar to previous observations of other insects in the orders Lepidoptera, Odonata and Coleoptera migrating over the Bohai Sea (Feng *et al.*, 2005, 2006, 2009).

In June and July, *C. medinalis* mainly migrate from the northern part of their winter diapause region (25°N–30°N) (fig. 1) into Northern China (Zhang *et al.*, 1981). Our data clearly show that the mating rate and the index of ovarian development of *C. medinalis* females during this period are significantly higher than in other months. This may be due to these moths emigrating from sites far from the trapping site

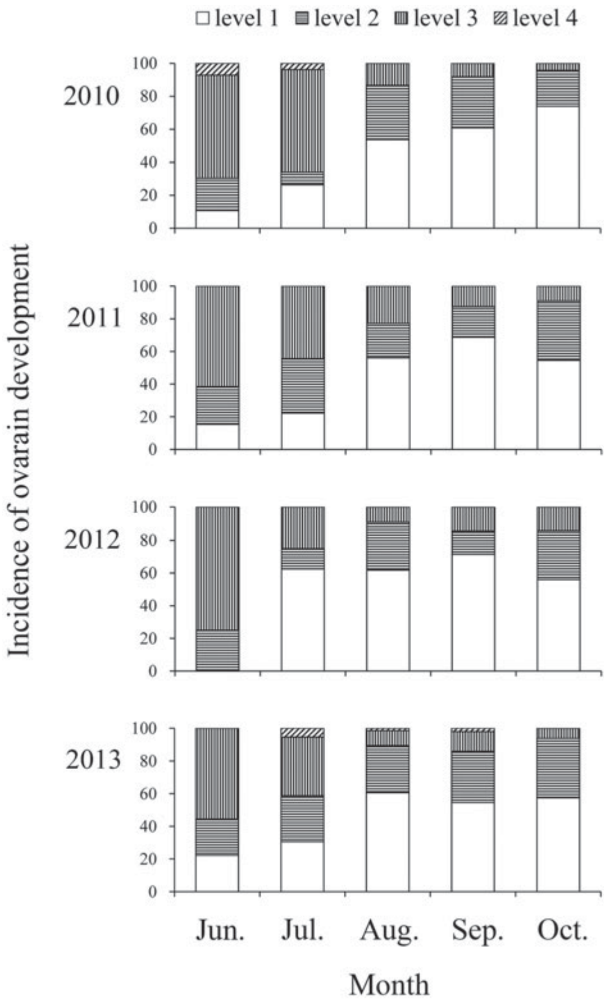

Fig. 5. Incidence of ovarian development in *C. medinalis* females captured in the searchlight trap on BH during 2010–2013.

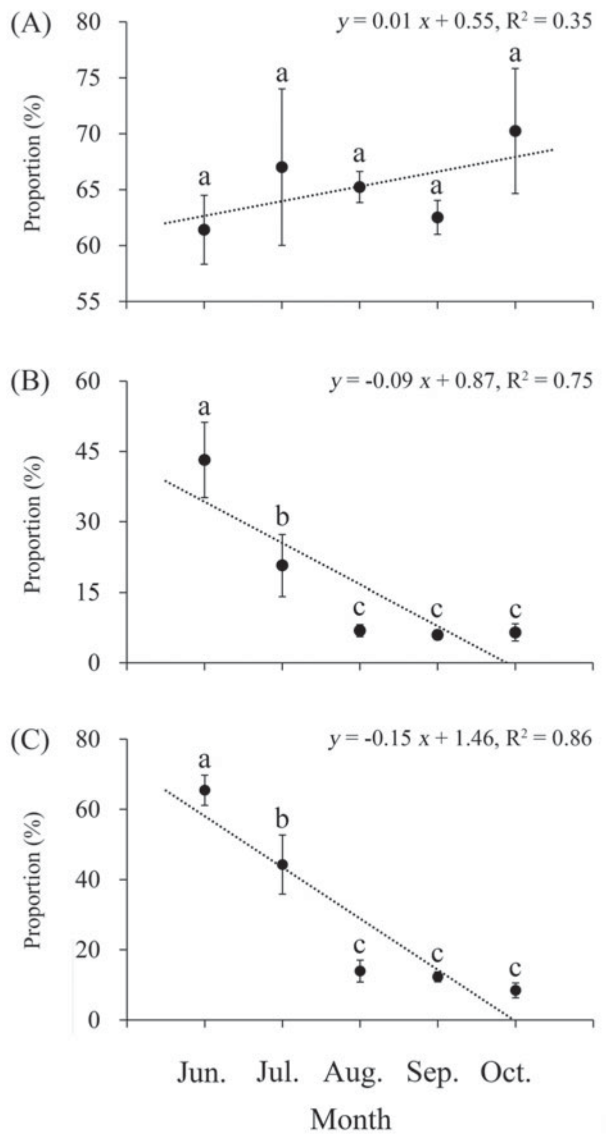

Fig. 6. Seasonal variation of the proportion of *C. medinalis* females (A), mated females (B) and sexually mature females (C) captured in the searchlight trap on BH during 2010–2013. The dot indicates mean proportion that were combined by averaging the yearly numbers in each month and the bar represents standard error between different years in that month. Dots sharing the same letter mean that there were no significant inter-month differences at the 5% level by Tukey's HSD tests.

and therefore having several successive nights of migratory flight. It is clear from flight-mill studies (Wang *et al.*, 2010) that both male and female *C. medinalis* have a strong remigration capacity and more than 50% of the tested moths could fly for four to five successive nights. Active flight results in a significant increase in body temperature (Heinrich, 1993) and juvenile hormone (JH) biosynthesis (Bühler *et al.*, 1983; Cusson *et al.*, 1990); for example, when *C. medinalis* females were transferred from 10 to 15°C there was a significant increase in JH biosynthesis within 24 h, which significantly accelerated female's reproduction by shortened the period of first egg-laying, and increased mating rate, mating frequency and the total fecundity (Sun *et al.*, 2013). Thus, just considering these points alone it is to be expected that some degree of sexual maturation would occur within several days of initiating migration, and this onset of maturation would be advantageous for immigrant females, allowing them to mate and initiate oviposition as soon as possible after finding a suitable habitat (Wada *et al.*, 1988). The relatively higher mating rate and more advanced ovarian development in this period suggests that the migratory behaviour in this species is not inhibited by the onset of ovarian development and/or mating, as might be expected from the oogenesis-flight syndrome (Kennedy, 1961; Johnson, 1963).

However, it is clear that *C. medinalis* females undertaking the northward migration in August (mainly migrating from 30° to 35°N; fig. 1; Zhang *et al.*, 1981) and the return migration in early autumn (mainly migrating from 40 to 45°N; fig. 1; Zhang *et al.*, 1981) have little or no ovarian development, supporting the idea that the onset of migration is initiated mainly by sexually immature individuals. These findings are consistent with the autumn migration of *C. medinalis* in Eastern China studied by Riley *et al.* (1995) between 1988 and 1991. In this study, more than 90% of female moths caught by hand-net

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near the radar site at Dongxiang county (28°N, 121°E) in Northern Jiangxi province in late October 1991, were in stage I or early stage II. At the same time and place, females caught by aerial netting during the actual process of high-altitude southwards migration were also immature. The sexual immaturity of the moths caught later in the season at BH may be accentuated because individuals are emigrating from sites not too far from the trapping site (Fu *et al*., unpublished data).

The relationship between long-duration flight and the state of oogenesis appears to be similar to that of *Agrotis ipsilon* (Rottemberg) (the black cutworm) in North America (Showers, 1997). Here the northward-moving spring migrants developed reproductively, and it was suggested (Showers, 1997) that there was no need to shut down reproductive development because the movement takes place rapidly, aided by the low-level jet stream. The southward movement in late summer and autumn is generally much slower (8–15 nights) due to the lighter winds, and in this case the moths did enter reproductive diapause. Cases such as these where there is a partial or limited suppression of reproductive development/behaviour until late in the migration period are distinct from those where the oogenesis-flight syndrome clearly does not apply, such as the tortricid *Choristoneura fumiferana* (Clem.) (the spruce budworm), the females of which typically lay about 50% of their eggs around their natal site, before they ascend above the forest canopy and engage in windborne migration (Greenbank *et al*., 1980; Rhainds & Kettela, 2013).

Migratory insect pests have been studied for many years because of their economic and ecological importance, and a good understanding of the migratory behaviour is essential for the development of forecasting systems and Integrated Pest Management (IPM) strategies for management of such pest species (Irwin, 1999; Wu & Guo, 2005; Wu *et al*., 2006). For example, real-time prediction systems have been developed for migratory rice planthoppers, *S. furcifera* and *N. lugens*, in recent years based on a comprehensive knowledge of their flight parameters (Tang *et al*., 1994; Otuka *et al*., 2005*b*, 2012). The current study provides direct evidence that *C. medinalis* make regular long-distance migrations across the Bohai Strait, in order to exploit the abundant but transient resources that develop over vast areas of Northeast Asia during spring and summer. The fact that many of the moths were flying at high altitude before their capture, as well as other evidences (e.g. the radar studies of Riley *et al*., 1995) strongly suggest that the flights are windborne and occur over a broad front. Nonetheless, further studies are needed to better understand the migration trajectories and high-altitude flying characteristics of this species.

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