Bulletin of Entomological Research (2002) **92**, 439–443 DOI: 10.1079/BER2002183

SHORT COMMUNICATION

Maize phenology influences field diapause induction of *Sesamia nonagrioides* (Lepidoptera: Noctuidae)

M. Eizaguirre*, C. López and A. Sans

Area de Protecció de Conreus, Centre UdL-IRTA, Universitat de Lleida, Rovira Roure 191, 25198 Lleida, Spain

Introduction

The Mediterranean corn borer *Sesamia nonagrioides* Lefèbvre (Lepidoptera: Noctuidae) is considered to be the most important pest of maize in many countries distributed across southern Europe between the 45°N parallel and north-west Africa (Melamed-Madjar & Tam, 1980; Galichet, 1982). *Sesamia nonagrioides* completes a variable number of generations annually from two in southern France to up to four in Morocco (Anglade, 1972). In the study region of the Ebro Valley in north-east Spain, two complete and one incomplete generations have been recorded (Alfaro, 1972). *Sesamia nonagrioides* overwinters as a fully developed larva in diapause (Galichet, 1982). In the laboratory the two youngest larval instars are the most sensitive to diapause induction. Once diapause is induced, larvae continue to grow and moult without pupating and up to six supernumerary instars have been observed when larvae are maintained in diapausing conditions (Eizaguirre *et al*., 1994). Müller (1965) and Mansingh (1971) proposed the term oligopause to refer to the diapause of those insects in which diapausing larvae continue to feed, moult and grow, as in the case of *S. nonagrioides* (Hilal, 1977; Galichet, 1982). However, other authors (Beck, 1980; Saunders, 1982; Danks, 1987) recognize only two general categories in insect dormancy: quiescence and diapause. Beck (1980) therefore proposed the most widely accepted definition of diapause as 'a genetically determined state of suppressed development, the expression of which may be controlled by environmental factors'. Non-diapausing *S. nonagrioides* larvae pupate after five or six instars (depending on the sex). No criteria such as external morphology or differential behaviour have been identified to distinguish between diapausing and non-diapausing larvae (Eizaguirre *et al*., 1994). López *et al*. (1995) showed the effects of changing the photoperiods from constant darkness 0:24 and 16:8 (L:D) on reversing field diapause induction in larvae of *S. nonagrioides*. Non-diapausing larvae completed their development after the same length of time under both photoperiods. However, diapausing larvae exposed to 0:24 (L:D) showed an extreme prolongation of their development, with supernumerary moults before they pupated or died, whereas those kept at 16:8 (L:D) overcame the diapause and pupated quickly. This different response of diapausing larvae to these photoperiods may be the only way of distinguishing diapausing from non-diapausing young larvae when they are collected in the field.

Eizaguirre & Albajes (1992) and Fantinou *et al*. (1995) confirmed that the photoperiod is the most important factor in diapause determination in this species, but the influence of temperature is also important when the photoperiod is close to the critical value. The critical photoperiod in the laboratory for studied populations of *S. nonagrioides* originating from north-east Spain occurs in the region from August 15 to 30 (Eizaguirre & Albajes, 1992).

Diapause allows insect survival under adverse conditions and synchronizes the life cycles of the individual insects within a population as well as with their food supply (Danks, 1987). Food has been shown to be a major factor regulating diapause in a few species of insects, particularly those that undergo aestival rather than hibernal diapause (Tauber *et al*., 1986). However, it is probably more usual for food quality to interact with photoperiodic and temperature responses to influence diapause (Hunter & MacNeil, 1997). For herbivorous insects, the host plant is the primary interface between individuals and their environment (Juniper & Southwood, 1986) and nutritional features of the host plant that result in variable growth rates may also result in variable diapause induction (Beck, 1980).

In north-east Spain it is common to sow grain maize *Zea mays* L. (Poaceae) from March to June and forage maize, which is harvested green, from June to late July after wheat or barley. As a consequence of this cultural practice, in late August, the time of critical photoperiod for diapause induction in *S. nonagrioides*, grain-senescent maize and green maize can be found growing simultaneously in the field. Eizaguirre & Albajes (1992) obtained data which suggested

*Fax: +34 973 238301
E-mail: Matilde.Eizaguirre@irta.es

that green maize could delay diapause induction under critical photoperiods, as occurs in other lepidopterous larvae (Steinberg *et al.*, 1988; Goto, 1985). This could influence winter survival of this species.

The aim of this work was to confirm the laboratory results of diapause induction and critical photoperiod under conditions in the field, and to study the influence of maize phenology on diapausing induction using the method described by López *et al.* (1995).

Materials and methods

General procedure

The study was carried out in 1994, 1995, 1997 and 1999. In each year larvae were collected every week, from mid-August until late September in two commercial fields: one sown in April (normal sown) and the other in June–July (late sown). The two fields were chosen each year by their growth stage: at the first sampling, in mid-August, the stage of normal sown maize was between 9.1 (cob full size; kernels in blister stage) and 9.2 (kernels in soft dough stage) and that of late sown maize was 6 (vegetative, late whorl stage) (Hanway, 1966). At the last sampling the stage of the normal sown maize was 9.5 (grain mature and drying) and the stage of late sown maize was 7 to 8 (between tips of tassel visible and pollen shedding). The two fields had similar FAO 700 cycle varieties (approximately 130–135 days needed to complete their life cycle), which are the most common in the region.

Larvae collected in each field were divided into two groups with the same number of larvae of the same age in each group. Field-collected larvae were transferred and held at either 16:8 (L:D) or 0:24 (L:D) in an environmentally-controlled climatic chamber (FredControl, Spain) at 25 ± 1°C. Larvae were placed in small transparent plastic cages (3.2 cm high × 5.5 cm in diameter) provided with a semi-artificial diet (Eizaguirre & Albajes, 1992) and observed individually until pupation or death. Larvae held in complete darkness were observed under a red light (4 lux). Larvae were in the second or third instar in all samples, except for some first instars collected in the first samples of 1994.

The number of larvae was determined by availability and is specified for each treatment or collection day. Sample cages differed among weeks and among years due to the difficulty of finding sufficient larvae, with endophytical behaviour, of the same age on the same day. Generally, the last samples in September were bigger than the first samples in August because the population was larger in September. The number of larvae collected ranged from 20 (10 larvae per treatment) in all samples in 1994 to 60 (30 per treatment) in almost all samples in 1999.

Data analysis

Duration of larval development

Data comparing the duration of development (days) of larvae exposed to 16:8 and 0:24 (L:D) photoperiods at each sowing date and sampling date were analysed statistically using Student's T-test ($P > 0.05$). Duration of larval development was calculated as the number of days elapsed up to pupation plus the number of days needed to reach the collected instar, according to López *et al.* (2001). Thus, if a field-collected larva was in the third instar, 7.2 days were added; if the larva was in the second instar, 4.2 days were added.

Assessment of percentage of diapause

In 1994 it was observed that when diapausing larvae were exposed to 0:24 (L:D), after several supernumerary moults some of them died before reaching the pupal stage. For this reason they were not included in the calculation of the duration of larval development (but they were considered as diapausing larvae), and in some cases the number of larvae that reached pupation was very low. For this reason, in the following years the percentage of diapausing larvae was also calculated as the percentage of individuals that remained as larvae when 150% of the duration of development under 16:8 (L:D) h (control conditions) had elapsed. In this study both duration of larval development and percentage of diapause forms are presented because they were considered complementary. The means of differences between percentage of diapause in normal and late sown fields were compared using a t-test on all sampling dates in 1995, 1997 and 1999 to contrast diapause induction.

Results and Discussion

The current study conducted over four years confirmed the suitability of the criteria described by López *et al.* (1995) for identifying diapause induction in young larvae of *S. nonagrioides* in the field, which until now had not been possible with other methods. Young larvae from normal sown maize in north-east Spain entered diapause after the second fortnight in August, depending on the year, while young larvae from late sown maize entered diapause one week (1995, 1999) or more later (1994, 1997) (fig. 1). In the first samples, collected before the critical photoperiod established from August 15 to 30 by Eizaguirre & Albajes (1992), there were no diapausing larvae. However, in the last samples, corresponding to larvae developed under clearly inducing photoperiod and temperature, there were some non-diapausing larvae mainly in green maize. The occurrence of non-diapausing larvae with a poor chance of survival at this time can be stated as a cost related to maintaining genetic variation (Tauber *et al.*, 1986).

The influence of maize phenology is evident in all the years studied. In the normal sown maize fields 50% diapause was achieved one week after critical photoperiod and in the late sown maize 50% diapause occurred in some years a week later (1995, 1999) and in 1997 this percentage was never attained (fig. 2). Similar results have been obtained by several authors who have studied the effect of nutrient factors in diapause induction in stem borers. Usua (1970) found diapausing larvae of *Busseola fusca* Fuller (Lepidoptera: Noctuidae), an African maize borer, in dry tissues of maize and non-diapausing larvae in young maize tissues. El-Gamil *et al.* (1978) and Morris (1967) considered nutrition to be one of the most important factors influencing diapause induction of some phytophagous insects. Hunter & McNeil (1997) indicated that in insects with diapause induction in a specific life instar, nutritional features of host plants result in variable growth rates that may also result in variable diapause induction.

The effect of temperature on diapause induction in the field is difficult to assess. The temperature modifies

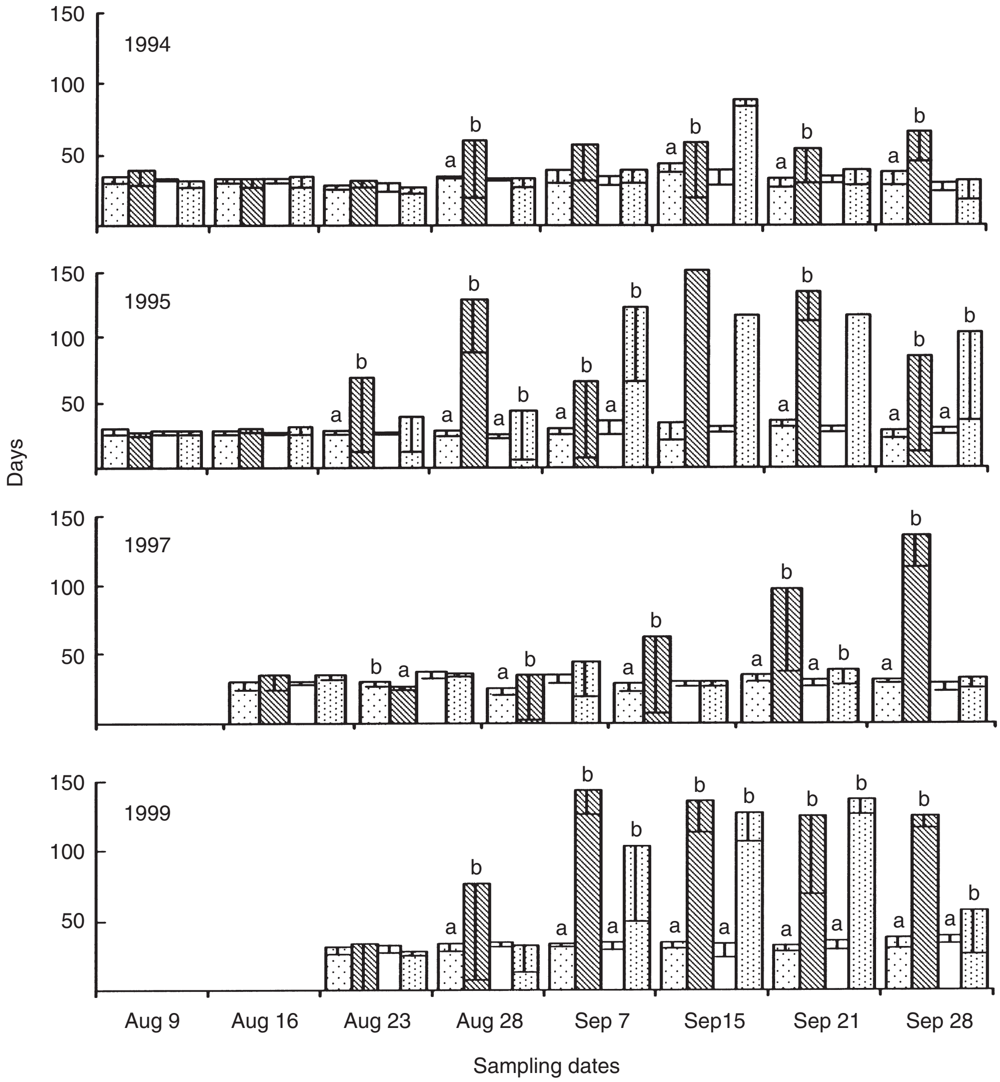

Fig. 1. Duration of larval development (in days) of *Sesamia nonagrioides* larvae collected in 1994, 1995, 1997 and 1999 in fields of normal sown maize exposed to 16:8 L:D photoperiod (□) and 0:24 L:D photoperiod (▧) and late sown maize exposed to 16:8 L:D (□) and 0:24 L:D (⊡) at 25°C. Bars with different letters indicate a significant difference in the duration of development of larvae from the same field exposed to 16:8 L:D and 0:24 L:D and thus indicate diapause. The line inside each column represents the standard error.

the diapause induction in *S. nonagrioides*. Moreover, thermoperiods reinforce the inductor effect of photoperiod (Eizaguirre *et al.*, 1994). Temperature also affects maize development and therefore the quality of the host plant. Furthermore, thermoperiods in the field vary daily and different thermoperiods can produce the same mean daily temperature. Temperature during the critical period explains the differences in diapause induction in three of the four years studied (1994, 1995 and 1997). However, though 1999 was the year with the highest heat accumulation during the critical period, the percentage of diapausing larvae was higher than expected.

The low percentages of diapausing larvae of *S. nonagrioides* collected in September from green maize may explain the high number of adults of the third generation in late September–early October recorded in the region in some years.

The fact that late sown maize was still green in September could be considered as an advantage to populations of *S. nonagrioides* because non-diapausing larvae use resources more efficiently than diapausing larvae. This is probably true in southern Spain and North Africa (the region of origin of the species), where these larvae reach pupation and give rise to a the third generation of adults whose offspring then enter diapause. In these regions early crop harvesting has been proposed as a possible measure to reduce winter populations of the pest, as Crowder *et al.* (1975) proposed for the pink bollworm *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae). However, in the region of this study this could be an additional mortality factor as late maize is harvested green for forage and resident larvae will be destroyed; in addition, non-diapausing larvae could be more easily affected by the first frosts in autumn. On this

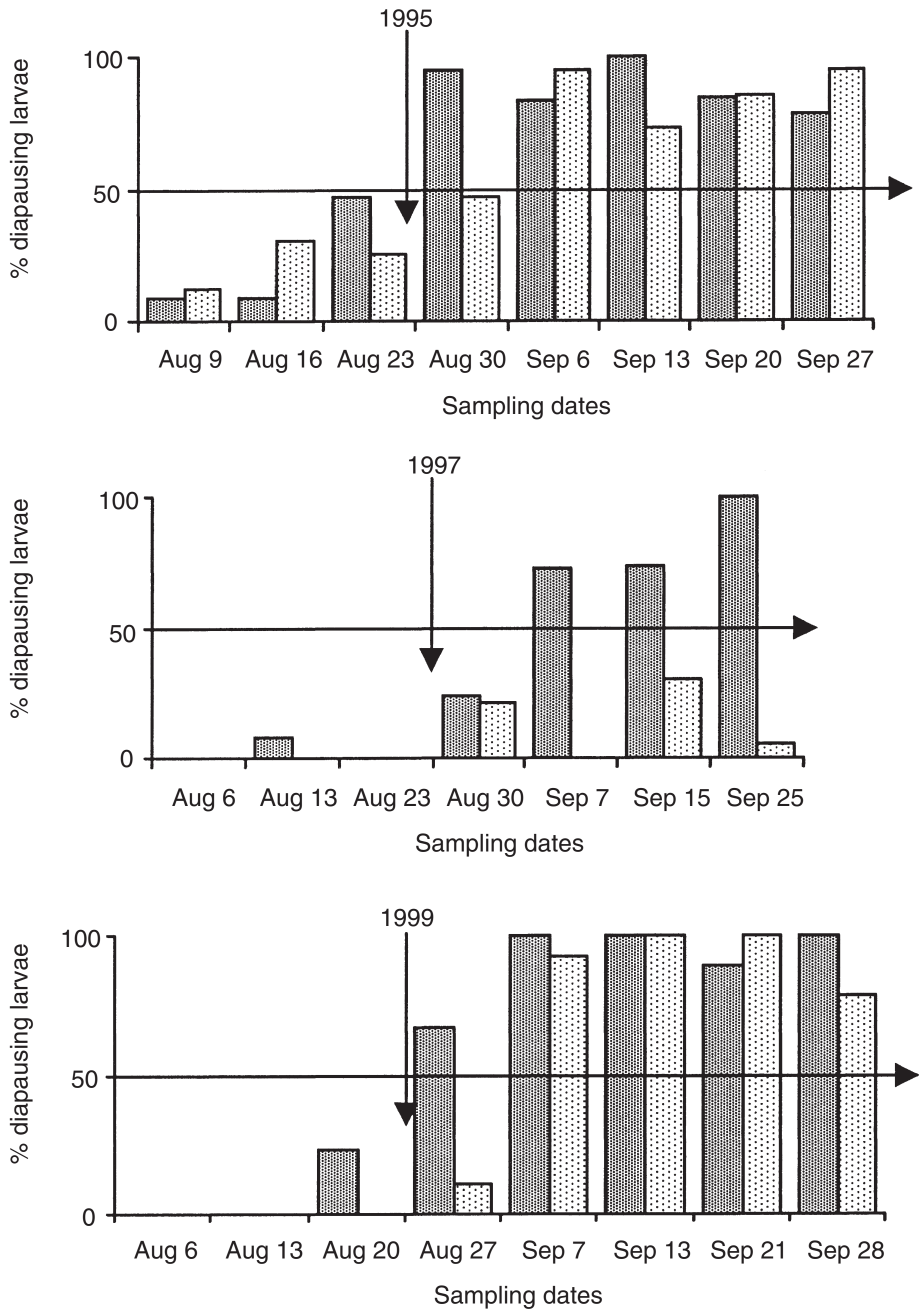

Fig. 2. Percentage of diapausing larvae of *Sesamia nonagrioides* in normal sown (▩) and late sown maize (⬚) fields in 1995, 1997 and 1999. Horizontal arrows show 50% of diapause and vertical arrows the date of theoretical critical photoperiod.

point, Tauber *et al*. (1986) stated that is clearly disadvantageous for multivoltine species to produce incomplete generations at the end of the growing seasons because individuals that do not reach the diapause stage almost invariably succumb.

To the north of the study region, in the south of France the great majority of second generation larvae will enter diapause due to environmental conditions of short photoperiod and low temperature, and due to French populations of *S. nonagrioides* having a longer critical photoperiod and longer duration developmental time than Spanish populations (Bues *et al.*, 1996).

Acknowledgements

The authors wish to thank Dr Ramon Albajes for his critical reading of the manuscript. The study was carried out with financial support from the Spanish Agency Comisión Interministerial de Ciencia y Tecnologia (CICYT), project AGF92-0298.

References

Alfaro, A. (1972) Notas sobre *Ostrinia nubilalis* (Hub.) y *Sesamia nonagriodes* (Lef.). *Anales INIA Serie Protección Vegetal* **2**, 145–170.

Anglade, P. (1972) Les Sesamie. pp. 1389–1401 *in* Balachowski, A.S. (*Ed.*) *Entomologie apliquée à l'agriculture, Tome II. Lépidoptères*. Paris, Masson et Cie.

Beck, S.D. (1980) *Insect photoperiodism*. 2nd edn. New York, Academic Press.

Bues, R., Eizaguirre, M., Toubon, J.F. & Albajes, R. (1996) Population genetic structure and ecological differences among nine populations of *Sesamia nonagrioides* (Lepidoptera: Noctuidae) from the western Mediterranean Basin. *Canadian Entomologist* **128**, 849–859.

Crowder, L.A., Watson, T.F. & Langston, D.T. (1975) Diapause of the pink bollworm as related to crop maturity. *Journal of Economic Entomology* **68**, 110–112.

Danks, H. (1987) *Insect dormancy: an ecological perspective*. Biological survey of Canada Monograph series No. 1. Ottawa.

Eizaguirre, M. & Albajes, R. (1992) Diapause induction in the stem corn borer, *Sesamia nonagrioides* (Lepidoptera: Noctuidae). *Entomologia Generalis* **17**, 277–283.

Eizaguirre, M., López, C., Asín, L. & Albajes, R. (1994) Thermoperiodism, photoperiodism and sensitive stage in the diapause induction of *Sesamia nonagrioides* (Lepidoptera: Noctuidae). *Journal of Insect Physiology* **40**, 113–119.

El-Gamil, F.M., Gaaboub, I.A. & El-Sawaf, S.K. (1978) Biology of the codling moth *Cydia* (*Carpocapsa* = *Laspeyresia*) *pomonella* L. (Olethreutidae, Lepidoptera) and effect of fruit age on its diapause induction. *Journal of Agricultural Science* **90**, 233–236.

Fantinou, A.A., Karandinos, M.G. & Tsitsipis, J.A. (1995) Diapause induction in the *Sesamia nonagrioides* (Lepidoptera: Noctuidae). Effect of photoperiod and temperature. *Environmental Entomology* **24**, 1458–1466.

Galichet, P.F. (1982) Hibernation d'une population de *Sesamia nonagrioides* Lef. (Lep., Noctuidae) en France Méridional. *Agronomie* **2**, 561–566.

Goto, M. (1985) Ecological study on a barnyard grass stem borer, *Emmalocera sp*. IV. Effects of day-length and host plant on the onset of larval diapause. *Japanese Journal of Applied Entomology and Zoology* **29**, 298–303.

Hanway, J.J. (1966) *Growth stages of maize corn*. US Department of Agriculture Technical Bulletin 976.

Hilal, A. (1977) Mise en evidence d'un etat de diapause vraie chez *Sesamia nonagrioides* Lef. (Lepidoptera: Noctuidae). *Comptes Rendus de l'Académie des Sciences Series III, Paris* **286**, 365–367.

Hunter, M.D. & McNeil, J.N. (1997) Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. *Ecology* **78**, 977–986.

Juniper, B.E. & Southwood, S.R. (1986) *Insects and the plant surface*. London, Edward Arnold.

López, C., Eizaguirre, M. & Albajes, R. (1995) Diapause detection and monitoring in the Mediterranean corn stalk borer. *Physiological Entomology* **20**, 330–336.

López, C., Sans, A., Asin, L. & Eizaguirre, M. (2001) Phenological model for *Sesamia nonagrioides* (Lepidoptera: Noctuidae). *Environmental Entomology* **30**, 23–30.

Mansingh, A. (1971) Physiological classification of dormancies in insects. *Canadian Entomologist* **103**, 983–1009.

Melamed-Madjar, V. & Tam, S. (1980) A field survey of changes in the composition of corn borer population in Israel. *Phytoparasitica* **8**, 201–204.

Morris, R.F. (1967) Factors inducing diapause in *Hyphantria cunea*. *Canadian Entomologist* **99**, 522–528.

Müller, J.J. (1965) Problem der insektendiapause. *Zoologischer Anzeiger* **29** (suppl.), 192–222.

Saunders, D.S. (1982) *Insect clocks*. 2nd edn. Oxford, Pergamon Press.

Steinberg, S., Podoler, H. & Applebaum, S. (1988) Diapause induction in field populations of the codling moth, *Cydia pomonella*, in northern Israel. *Phytoparasitica* **16**, 3–13.

Tauber, M.J., Tauber, C.A. & Masaki, S. (1986) *Seasonal adaptations of insects*. New York, Oxford University Press.

Usua, E.J. (1970) Diapause in maize stemborer. *Journal of Economic Entomology* **63**, 1605–1610.

(Accepted 5 June 2002)

Insect Movement: Mechanisms and Consequences

Edited by **I P Woiwod**, *IACR-Rothamsted*, **D R Reynolds**, *NRI*, *University of Greenwich*, and **C D Thomas**, *University of Leeds*, *UK*

April 2001 **464 pages** **Hardback**
ISBN 0 85199 456 3
£70.00 (US$130.00)

Readership: Entomology, animal physiology, behaviour and ecology.

Knowledge of insect movement, particularly of flight, is crucial to our understanding of the great ecological and evolutionary success of insects. The last 20 years have seen many advances in this subject area. New fields have arisen, such as metapopulation theory, and dramatic developments have taken place in methods of studying movement, as a result of new techniques in molecular biology and radar monitoring. There have also been advances in our knowledge of flight-related physiology and behaviour. This book, which is based on the main papers presented at the Royal Entomological Society's 20th Symposium held in September 1999, brings us up to date with these developments.

It contains chapters on:
- flight mechanisms
- foraging movements
- migration
- the evolution of movement strategies
- the interactions between dispersal rates, population structure and gene flow
- the effects of climate change on geographical distribution

It is essential reading for entomologists, and of interest to those researching animal behaviour, physiology, ecology and genetics.

Contents

CABI Publishing, CAB International,
Wallingford, Oxon, OX10 8DE, UK
Tel:+44(0)1491 832111 Fax:+44(0)1491 829292
Email: orders@cabi.org
CABI Publishing, CAB International,
10 East 40th Street, Suite 3203, New York, NY 10016, USA
Tel:+1 212 481 7018 Fax:+1 212 686 7993
Email: cabi-nao@cabi.org

For further information or to order please contact CABI *Publishing*, UK or an exclusive CABI *Publishing* distributor in your area. For pre-paid orders in the UK, please add £2.75 for the 1st book and 60p for each additional book ordered (up to max. of 10). For pre-paid orders elsewhere, please add £4.00 for the 1st book and £1.00 for each additional book. For orders not pre-paid, postage and packing will be charged according to the weight of the book.