
CALLING BEHAVIOR: CAN IT BE USED TO IDENTIFY MIGRATORY SPECIES OF MOTHS?

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SYNOPSIS
There is considerable debate concerning the fate of populations of noctuid moths, founded during the summer, by migrants moving considerable distances northward of areas where permanent populations persist. This paper compares the female calling behavior of moth species that maintain permanent populations in Canada with those that are known immigrants. Residents initiate calling soon after emergence, regardless of climatic conditions, while the mean age of calling for immigrant species is variable, even under favorable conditions. Furthermore the onset of calling by immigrants is

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strongly influenced by prevailing temperature and photoperiodic conditions during adult life. These differences may only be of importance for the northward spring dispersal, but as fall conditions induce a delay in the onset of calling of known immigrants it is proposed that this could potentially permit a southerly, upper air migration to suitable overwintering sites.

INTRODUCTION

A number of noctuid moths of major economic importance in North America (see Rabb and Kennedy 1979) are known to be highly mobile and, during the summer months, expand their geographic distribution into northerly areas where they are unable to establish permanent populations. These temporary populations have often been considered as dead end ones that are killed off at the onset of adverse weather conditions in the fall. Rabb and Stinner (1978) referred to this type of movement as the “Pied Piper” phenomenon, suggesting that man’s agricultural practices temporarily increase suitable and available habitats and that “this [the Pied Piper effect] seems to “pervert” the survival strategies of the species involved . . .” . However, Walker (1980) proposed that if there is a genetic basis for this repeated seasonal dispersal, the demise of individuals exploiting these temporarily available habitats would create an evolutionary dilemma as such suicidal dispersal would be strongly selected against. Stinner et al. (1982) provided a counter argument on this point, but agreed that the testable predictions proposed by Walker (1980) would help elucidate whether or not noctuids have a return fall migration.

There is considerable concrete evidence that some butterfly species have unidirectional spring and fall migrations, generally occurring within the boundary layer (Walker 1980; Baker 1984 and references therein). On the other hand there is little data for night flying moths, one obvious reason being the difficulty with which direct observations can be made. Two well documented cases for noctuids do exist: the bogong moth in Australia (Common 1954) and the army cutworm in North America (Pruess 1967; Kendall 1981) migrate, as adults in reproductive diapause, to the mountains for the summer before returning in the fall to the plains where they reproduce. Dingac (1982) pointed out that migration associated with adult reproductive diapause is quite common, and the derived advantages of such a system are evident for Lepidoptera that migrate to aestivation (the army cutworm) or overwintering sites (the monarch) and return before the onset of reproduction. However, temperate species that expand their range into temporarily available habitats during the summer months, if capable of a return fall migration, would benefit from pre-reproductive strategies permitting the optimal utilisation of both summer and winter resources. Based on data pertaining to the calling behavior of several temperate species of Lepidoptera, I propose that certain insects undertaking long distance, upper air, northward migrations (i) possess pre-reproductive traits that differ considerably from resident species and (ii) that these traits, which fit within the context of the diapause syndrome (Tauber et al. 1984), would facilitate a return southward migration to suitable overwintering sites in the fall.

SUBJECT SPECIES

The true armyworm, Pseudaletia unipuncta is a noctuid that is found annually throughout much of eastern Canada but does not establish permanent populations due to the inability to overwinter in these areas (Ayre 1985; Fields and McNeil 1984). The closely synchronized appearance of adults over a wide area, having very different local climatic conditions, strongly supports the hypothesis that moths immigrate on prevail-
ing weather fronts, as suggested for other Lepidoptera (Arthur and Bauer 1981; Domino et al. 1983). Studies investigating the nocturnal calling behavior of true armyworm virgin females has shown that even under favorable summer conditions (25°C, 16L:8D) individuals initiate calling for the first time from 2 to 12 days following emergence; the mean age for the onset of calling varying from 4 to 6 days (Turgeon and McNeil 1982; Delisle and McNeil 1986). The mean calling age of *P. unipuncta* is also significantly influenced by ambient temperature conditions during adult life (Turgeon and McNeil 1983); the lower the temperature, the older females are when they start calling, e.g. at 10°C the mean age of calling is 17.9 days. Furthermore there is a photoperiodic effect, with females at 25°C calling significantly later under 12L:12D (X = 7.9 days) than at 16L:8D (X = 6.0 days) (Delisle and McNeil 1986). The combined effect of 10°C, 12L:12D, during adult life resulted in a mean calling age of approximately 21 days, and when females were transferred to 25°C, 16L:8D, at 5, 10, or 15 days following emergence, calling was initiated within six days (Delisle and McNeil, unpublished). The observed delays in the onset of calling fit the “oogenesis-flight syndrome” (Johnson 1969), being initiated by short days and low temperatures, conditions responsible for the initiation of diapause of many temperate species (Beck 1980). I believe the responses observed in the true armyworm reflect one extreme within the spectrum of adult reproductive diapause associated with the migration of Lepidoptera as (i) ovarian development does occur, albeit slowly, under short day/low temperature conditions and, (ii) females initiate calling rapidly when transferred to long day/high temperature conditions. As previously stated this strategy would benefit species that reproduce in both the summer and winter limits of the distribution. This contrasts with the other extreme reported in other noctuids, such as the army cutworm and the bagon moth (Common 1954; Pruess 1967), where reproductive diapause persists for several months. In these cases, little or no reproductive activity occurs before the adults that immigrated to the mountains initiate their return migration.

A markedly different situation is seen with the Bertha armyworm, *Mamestra configurata*, a species that does overwinter in Canada. For this moth temperature and photoperiodic conditions have very little effect on the age at which calling starts. At 25°C, 16L:8D, all females initiated calling by the fourth night following emergence, with a mean age of first calling of 2.2 days (Howlander 1985; J. Haley, unpublished data), while at 10°C, 16L:8D, it is 5.2 days (Howlander 1985). In addition, 100% of all females held at 25°C, 12L:12D, were calling by the second night following emergence (Howlander 1985).

While the data base relative to calling behavior under different abiotic conditions is less substantial, there is evidence that differences similar to those observed between the true armyworm and the Bertha armyworm may exist for other resident and immigrant noctuids. Greater than 83% of virgin females of the potato stem borer, *Hydropotes inermis*, an introduced European species that is now an established resident in Canada, called the first night following emergence at 25°C, 14L:10D, in the laboratory, while 100% did so under field conditions (West et al. 1984). On the other hand Swier et al. (1976) reported that at 24-27°C under 16L:8D, the black cutworm, *Agrotis ipsilon*, a suspected spring immigrant (Domino et al. 1983; Kaster and Showers 1982), had an average precopulatory period of 4.4 days, and that it took at least three nights following emergence for more than 33% of the virgin females to initiate calling under a 18L:6D photoperiod at 24°C (Swier et al. 1977). A high incidence of unmated females in full light trap catches, together with low male catches in pheromone traps, was interpreted as evidence of a reproductive diapause that might facilitate a return fall migration of the black cutworm (Kaster and Showers 1982). Similar results have been collected since 1979 for the true armyworm in our Quebec trapping program (McNeil, unpublished), and the delay in the onset of reproductive activity has been proposed as potentially
facilitating a return migration of this species to suitable overwintering sites (McNeil 1986). Consequently, I suggest that the black cutworm responds to fall conditions in the same way as the true armyworm, with only a short delay in the onset of reproduction. Examination of the calling behavior of *A. ipsilon* under a range of different climatic conditions would test this hypothesis.

In an effort to determine whether the proposed differences between resident and migrant species have any wider application within the Lepidoptera my students and I have recently started comparative work on the calling behavior of pyralids, because members of this family, like noctuids, are capable of upper air migration (Drake 1985). The sunflower moth, *Homoeosoma electellum*, which migrates annually into Canada (Arthur and Bauer 1981), was chosen as the migrant species as it has a number of biological attributes that differ considerably from the true armyworm. The sunflower moth calls during the photophase (Arthur 1978) rather than the scotophase, even though for most other activities this species is nocturnal, and has the ability to enter diapause as a last instar larva (Chippendale and Kikukawa 1983; Kikukawa and Chippendale 1988; Teetes et al. 1969). However, in Canada non-diapausing larvae leave the host in August and give rise to adults in September. At this time climatic conditions do not permit the completion of another generation, making it highly unlikely that *H. electellum* successfully overwinters this far north (Arthur 1978). If this is the case then these adults, like those of the true armyworm, would have to migrate southward if their offspring are to survive. The resident species chosen for this study was the European corn borer, *Ostrinia nubilalis*, which like the sunflower moth overwinters as a last instar larva. While studies have only recently been initiated, the data obtained to date support the hypothesis that the pre-reproductive behavior of migrant and resident temperate Lepidoptera vary considerably. Females of both univoltine and bivoltine races of the European corn borer call within two days of emergence at 25°C, 16:8D (L. Royer and McNeil, unpublished), while under the same conditions sunflower moth females have a mean age of calling of 0.7 days (McNeil and Delisle, unpublished). The longevity of our *H. electellum* adults, established from immigrants collected in Saskatchewan, while similar to that of the Missouri strain (Kikukawa and Chippendale 1988), was considerably longer than the 8.5 days reported for adults from Texas (Randolph et al. 1972). Temperature and photoperiodic conditions were similar in the laboratory rearings, although other aspects such as relative humidity, available food, and adult densities could explain the observed differences in adult longevity. However, an alternate explanation that merits further investigation within the context of the migration of this species is the possible existence of polymorphism in the population, where life statistics of migrants exploiting temporarily available habitats differ from those that remain in the area of permanent occupation.

**Discussion**

The evidence presented above strongly supports the hypothesis that pre-reproductive strategies of resident and migrant moth species differ markedly. Indigenous species mate soon after emergence, which would permit rapid exploitation of the resources available in the immediate habitat. On the other hand, species that have significant northward expansions in their summer distribution show considerable variability in the time required for the onset of reproduction, even under optimal summer conditions. At least in the case of the true armyworm, and most probably in the case of the black cutworm, fall conditions induce a further delay in reproductive activity. This could provide the time necessary for a southerly migration to favorable overwintering sites if dispersal occurred in upper air masses, where it has been shown that moths may be carried for at least 90 km in 24 h (Rose et al. 1985). Furthermore, the rapidity with which sexual activity is resumed when females are transferred to favorable conditions
would permit successful emigrants to maximize their reproductive potential upon arrival in acceptable overwintering habitats. However, whether or not seasonal variability in pre-reproductive behavior is uniquely associated with emigration from sites where permanent populations occur or, as suggested by McNeil (1986), is a life history trait permitting a return migration remains to be elucidated. There is one encouraging point for those of us who believe that the answer to Walker's question, "are butterflies better than moths?" (Walker 1980), is no. The oriental armyworm, *P. separata*, the only noctuid species where clear evidence for both north and south migration has been obtained by means of a massive adult mark-recapture program (Li et al. 1964, reference from Baker 1978), has at least a 3 day delay in the onset of calling after emergence at 25°C, 16L:8D (Hirai 1984), similar to *P. unipuncta*.

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PREZYGOTIC MALE REPRODUCTIVE EFFORT IN INSECTS: WHY DO MALES PROVIDE MORE THAN SPERM?

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SYNOPSIS

Males' incentives for providing benefits to females and/or their offspring are ambiguous during the period prior to zygote formation. The benefits may function to increase the number of available eggs fertilized by a male and/or enhance the production and survival of his offspring. In some cases, male prezygotic investment may be an adaptation to secure fertilizations despite the fact that it incidentally benefits the female or her offspring. More often, the benefits to offspring production and survival are not simply incidental and probably account, in part, for the magnitude of the male investment. Regardless of the adaptive significance of male provided benefits, they typically reduce the females' costs of producing surviving offspring while raising the males' costs. The extent to which provision of benefits increases males' costs and decreases females' costs will affect the degree to which females limit male reproduction (or vice versa). If male-provided benefits (prezygotic or otherwise) are more costly than female costs of offspring production, reproductively-ready males will act as resources limiting female reproduction. From an evolutionary perspective it is important to consider the effect of male-provided benefits. The primary function of the investment (e.g., to maximize sperm transfer) is irrelevant in terms of the degree to which one sex limits the other's reproduction.

"Women and men move back and forth in between effect and cause. Just beyond the range of normal sight, this glittering joker was dancing in the dragon's jaws"

(B. Cockburn)

During the past two decades there has been considerable interest in Darwin's (1871)

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