

Natural enemies of the maize cob borer, *Mussidia nigrivenella* (Lepidoptera: Pyralidae) in Benin, West Africa

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Abstract

Mussidia nigrivenella Ragonot is a pest of maize cobs in West Africa. It significantly reduces maize yields and grain quality, with quantitative losses of 2–25% at harvest, and up to 10–15% indirect losses due to an increase in storage pest infestation levels. Infestation by *M. nigrivenella* also significantly increased the susceptibility of maize to *Aspergillus flavus* infection and subsequent aflatoxin contamination. Surveys conducted in different agro-ecological zones of Benin on cultivated and wild host plants during 1994–1997 revealed one egg parasitoid, three larval parasitoids and one pupal parasitoid attacking *M. nigrivenella*. Egg parasitism was scarce on all host plants sampled and in all four agro-ecological zones. Parasitism by larval and pupal parasitoids was usually less than 10%, and varied with host plant species. Both larval and pupal parasitoids were rare or absent in cultivated maize fields. The solitary chalcidid pupal parasitoid, *Antrocephalus crassipes* Masi, was the predominant species, contributing approximately 53% of the observed mortality. Logistic regression analysis indicated that this parasitoid was more prevalent on fruits of *Gardenia* spp. (Rubiaceae) than on the other host plant species including maize used by *M. nigrivenella*, and was most abundant between February and September. The differences in parasitoid diversity and parasitism between Benin and other regions suggest that there are opportunities for biological control through introduction of exotic parasitoids or using the ‘new association’ approach, which uses natural enemies of closely related host species that occupy similar ecological niches to the target pest.

Introduction

In West Africa, *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) is a pest of cotton bolls (Stäubli, 1977; Silvie, 1990) and maize cobs (Moyal, 1988; Bosque-Pérez & Mareck, 1990;

Moyal & Tran, 1991; Gounou *et al.*, 1994; Ndemah *et al.*, 2001). Although more than half of the cobs in the field are usually infested, reported yield losses varied from 5 to 25% (Whitney, 1970; Moyal & Tran, 1991; Sétamou *et al.*, 2000a). *Mussidia nigrivenella* continues to feed on maize grains in storage leading to an additional 5% in yield loss (Sétamou, 1996). However, more importantly, its damage also predisposes maize to pre- and post-harvest infestations by storage beetles, infection by *Aspergillus flavus* Link (Hyphomycetes) and

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subsequent aflatoxin contamination (Sétamou *et al.*, 1998). Increases of up to 15% of yield loss due to storage beetles were reported in the presence of *M. nigrivenella* damage (Sétamou, 1996).

Though described from East, southern and Central Africa from wild hosts (Sorauer, 1925; Janse, 1941; LePelley, 1959; Bouyckx, 1962; Entwistle, 1972; Waiyaki, 1973), *M. nigrivenella* has never been reported as a pest of annual crops outside western Africa (i.e. West Africa and Cameroon, in this study). Either eastern (i.e. East and southern) African populations do not recognize these plants as hosts and/or *M. nigrivenella* is under biological control in its wild habitats, thereby preventing it from moving into crop fields. This would open up opportunities for expanding the geographical range of natural enemy species to areas where they do not exist yet, or for using the 'new association' approach to biological control. The first approach has been proposed by several authors as a solution to lepidopterous pest problems on maize and sugarcane in Africa and has been variously termed 'redistribution' or 'classical biological control' (Rao, 1965; Mohyuddin & Greathead, 1970; Conlong, 1997; Schulthess *et al.*, 1997). For example, a coastal strain of the larval parasitoid *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae) from Kenya was released and established on *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) in southern Benin (Schulthess *et al.*, 1997); the larval parasitoid *Sturmiopsis parasitica* Curran (Diptera: Tachinidae) was introduced from western into South Africa, where it does not occur, and released against *Eldana saccharina* Walker (Lepidoptera: Pyralidae) on sugarcane (D. Conlong, South African Sugar Experimental Station, Durban, South Africa, personal communication). Similarly, it is planned to introduce the western African egg parasitoid species *Telenomus isis* Polaszek (Hymenoptera: Scelionidae) into eastern Africa for control of *Busseola fusca* Fuller (Lepidoptera: Noctuidae). Success in the longer run thus depends largely on the permanent establishment of an exotic biological control agent in a new area.

The 'new association' approach to biological control uses natural enemies of closely related host species occupying similar ecological niches, that do not share a common evolutionary relationship with the target pest (Hokkanen & Pimentel, 1989). Thus, in our case, species of primary interest would be other *Mussidia* species and their parasitoids occurring in eastern Africa that attack the same wild host plant species that *M. nigrivenella* feeds on in western Africa.

Janse (1941) described eight *Mussidia* spp., five from the African mainland, two from Madagascar and Réunion, and one from Asia. However, with the exception of *M. nigrivenella*, which was the only species identified by the author in West Africa so far, no information is available about the biology and ecology of other *Mussidia* spp. The first steps when considering either of the two biological control approaches is the establishment and comparison of a list of host plants and associated natural enemies of *Mussidia* spp. in the different African regions. Moyal (1988) compiled a list of host plants published by various authors but a detailed list is available only for the Republic of Benin (Sétamou *et al.*, 2000b). The results of several country-wide surveys have revealed that *M. nigrivenella* feeds on at least 20 plant species from 11 different families, most of them trees and bushes. However, less information exists on the natural enemies attacking *M. nigrivenella*. Surveys conducted on maize in Ghana (Gounou *et al.*, 1994) and Benin (Shanower *et al.*, 1991) yielded no larval or pupal parasitoids. Likewise, Moyal (1988) working on maize in Côte d'Ivoire found only a few unidentified trichogrammatid and scelionid egg parasitoids, whereas in Cameroon, five parasitoid species were obtained that emerged from parasitized larva and pupae (Nonveiller, 1984; Ndemah *et al.*, 2001). However, all these collections were restricted to maize, which owing to its ephemeral nature is a rather unstable habitat for both borers and their natural enemies, and nothing is known about the natural enemy complex attacking *M. nigrivenella* on wild and especially annual host plants. Parasitoids often show a clear preference for particular food plants when foraging for polyphagous insect hosts (Taylor, 1932; Vinson, 1981; Benerey *et al.*, 1997), and maize and cotton, the principal hosts, may not be preferred host plants. Also, as maize is highly susceptible to borer attack and subsequent *A. flavus* infection and aflatoxin contamination, and damaged plants cannot be sold as green maize, reduction of pest populations is best achieved on the wild hosts.

In this study an attempt was made to catalogue the natural enemies of *M. nigrivenella* occurring on cultivated and wild hosts in different agro-ecological zones of Benin. A detailed study of the abundance of both *M. nigrivenella* and its natural enemies on selected host plants was undertaken over a two year period. Similar attempts to identify the host plant range and natural enemies' complexes of *Mussidia* spp. are underway in East Africa.

Materials and methods

A preliminary 10 day survey of pod and fruit-bearing herbaceous plants and shrubs, considered potential host plants of *M. nigrivenella* (sampled in a random manner) was carried out in all four agro-ecological zones of Benin during autumn 1991. The zones were, from south to north, the Forest Savanna Mosaic, the Southern Guinea Savanna, the Northern Guinea Savanna, and the Sudan Savanna with highest annual rainfall of 1400 mm in the Forest Savanna Mosaic and lowest rainfall of 900 mm in the Sudan Savanna. Further country-wide surveys conducted from July 1993 to December 1995 at three-monthly intervals, and monthly from January 1996 to December 1997 concentrated on tree species (see Sétamou *et al.*, 2000b). Data from maize fields sampled throughout the country or from on-station experiments were also included (Sétamou & Schulthess, 1995; Sétamou *et al.*, 1995, 1998, 1999, 2000a,b). Maize and all encountered wild plant species with fruiting structures, including known host plants, were sampled. Whenever possible, a sample of 20 fruits was taken. All collected fruits were first visually examined for eggs or first instar larvae, and then dissected for borers. Because the immature stages are difficult to identify, eggs, larvae and/or pupae collected from the different hosts were brought back to the laboratory for examination. The eggs were incubated at $26 \pm 2^\circ\text{C}$ and $65 \pm 5\%$ rh, on moistened tissue paper until larval or parasitoid emergence. The emerged larvae as well as the field-collected larvae were reared on jackbean pods, *Canavalia ensiformis* (L.) DC. (Fabaceae), following the protocol developed by Sétamou *et al.* (1999), until pupation or parasitoid emergence. Pupae were kept individually in 30 ml transparent plastic capsules, until moth or parasitoid emergence. Parasitoid species were identified at the insect museum of the International Institute of Tropical Agriculture (IITA), Calavi, Republic of Benin, and *Mussidia* spp. using the key prepared by Moyal (1988).

A sample consisted of all immature stages of *M. nigrivenella* (i.e. eggs, larvae, or pupae) collected in a given field for crops or on a given wild host plant species during each survey or field study, respectively. Only hosts with emerging parasitoids were considered as being 'parasitized', thus leading to an underestimation of the impact of natural enemies since hosts killed by parasitoids but not yielding any parasitoid were not considered as dying from parasitoid-related mortality. Percentage parasitism, calculated separately for each of the three immature stages and per host plant species, was expressed as the number of 'parasitized hosts' (hosts yielding parasitoids) compared to the total number of *M. nigrivenella* in the respective developmental stage.

For the 1996/97 survey data on wild hosts, backward stepwise logistic regression models (Hosmer & Lemeshow, 1989) were used to evaluate the effects of sampling year and month and the different host plants as predictors of the level of parasitism of the different developmental stages of *M. nigrivenella*. All predictor variables were coded as dummy variables, i.e. 0 for absence and 1 for presence. Hence, for months 11 dummy variables were used, and three dummy variables for host plants, corresponding to the four host plants from which larval and/or pupal parasitoids were obtained during the surveys. Analyses were conducted using the PROC LOGISTIC of SAS (SAS institute, 1996), and the fit of the models was determined using the χ^2 values (Hosmer & Lemeshow, 1989).

Results

Species composition and distribution of parasitoids

Only five parasitoid species were found on immature stages of *M. nigrivenella*. With a few exceptions they were all obtained from *M. nigrivenella* collected from tree species which are common in the savannahs, and especially the Southern Guinea Savannah but are rare in the Forest Savannah Mosaic in the south (table 1). The *Telenomus* sp.

(Hymenoptera: Scelionidae) was the only egg parasitoid and emerged mainly from samples collected from fruits of *Parkia biglobosa* (Jacq.) Benth. (Mimosaceae). No egg parasitoids were recorded from maize cobs. The larval parasitoids *Bracon sesamiae* Cameron and *Apanteles* sp. (both Hymenoptera: Braconidae) were obtained from maize and some tree species. About 65% of the larval parasitism was due to *B. sesamiae*, but from maize only seven specimens were collected during all surveys. A few individuals of a *Perilampus* sp. (Hymenoptera: Perilampidae) also emerged from *M. nigrivenella* larvae.

Only one parasitoid species, *Antrocephalus crassipes* Masi (Hymenoptera: Chalcididae) was obtained from pupae (table 1). This solitary parasitoid emerged mainly from pupae collected from fruits of wild host plant species with one specimen only from maize in the Northern Guinea Savannah. *Antrocephalus crassipes* emerged from pupae collected in the Southern Guinea Savannah, Northern Guinea Savannah, and the Sudan Savannah, but not from samples collected in the Forest Savannah Mosaic in the south (table 1). Across all host plant species, *A. crassipes* was the predominant parasitoid species, accounting for approximately 53% of all emerged parasitoids (fig. 1).

No parasitoids were recorded from other herbaceous plants such as the cover crops, jackbean, *C. ensiformis* and velvetbean, *Mucuna pruriens* DC. (Fabaceae).

Incidence and levels of parasitism

Egg parasitism was in general extremely low (< 0.1%) and thus not included in the subsequent analyses. Mean larval and pupal parasitism, and total parasitism across all sampling occasions on the different host plant species are presented in fig. 1. Larval parasitism ranged from < 0.5% on *Ximenia americana* L. (Olacaceae) and the baobab tree *Adansonia digitata* L. (Bombacaceae) to 4–5% on *Parkia biglobosa* and *Gardenia* spp. (Rubiaceae). A similar trend was observed for pupal parasitism, with a highest

Table 1. Summary of parasitoid species recovered from *Mussidia nigrivenella* collected on various host plants in different agro-ecological zones in Benin, 1994–1997.

Parasitoid species	Families	Host plants	Agro-ecological zones ³
Egg parasitoid <i>Telenomus</i> sp.	Scelionidae	<i>Parkia biglobosa</i> (Jacq.) Benth. (Mimosaceae)	SGS, NGS
Larval parasitoids <i>Bracon sesamiae</i> Cameron	Braconidae	<i>Adansonia digitata</i> L. (Bombacaceae) <i>Gardenia</i> spp. (Rubiaceae) <i>Parkia biglobosa</i> (Jacq.) Benth. (Mimosaceae) <i>Ximenia americana</i> L. (Olacaceae)	SGS SGS, NGS, SS SGS, NGS NGS
<i>Apanteles</i> sp.	Braconidae	<i>Zea mays</i> L. (Poaceae) <i>Gardenia</i> spp. (Rubiaceae) <i>Parkia biglobosa</i> (Jacq.) Benth. (Mimosaceae)	FSM, SGS NGS, SS SGS, NGS, SS
<i>Perilampus</i> sp. ¹	Perilampidae	<i>Zea mays</i> L. (Poaceae) <i>Parkia biglobosa</i> (Jacq.) Benth. (Mimosaceae) <i>Zea mays</i> L. (Poaceae)	SGS, NGS SGS SGS
Pupal parasitoid <i>Antrocephalus crassipes</i> Masi	Chalcididae	<i>Gardenia</i> spp. (Rubiaceae) <i>Parkia biglobosa</i> (Jacq.) Benth. (Mimosaceae) <i>Ximenia americana</i> L. (Olacaceae) <i>Zea mays</i> L. (Poaceae) ²	NGS, SS SGS, NGS, SS NGS, SS NGS

¹ Parasitoid of, or hyperparasitoid on many lepidopterous larvae.

² Collected on one occasion in late harvested maize fields.

³ FMS, Forest Savannah Mosaic; SGS, Southern Guinea Savannah; NGS, Northern Guinea Savannah; SS, Sudan Savannah.

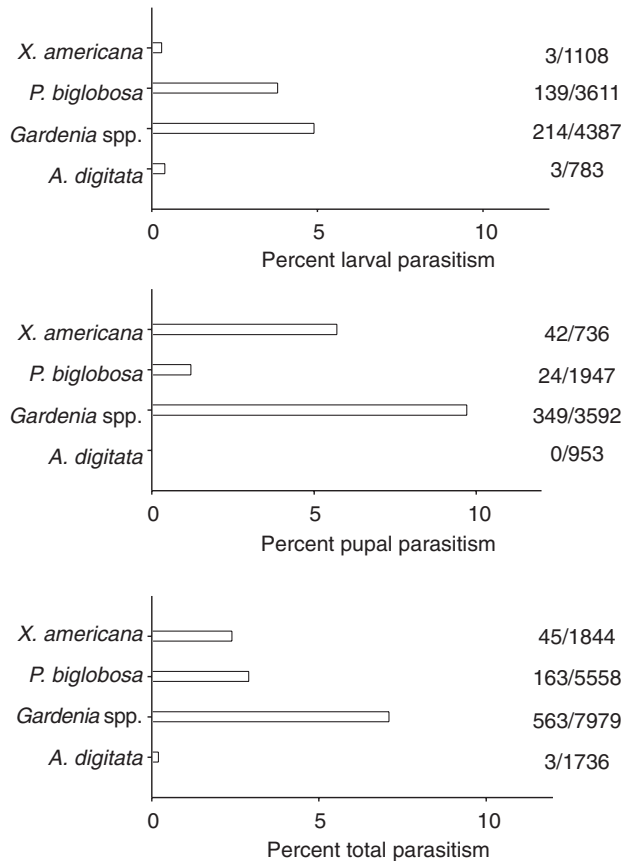


Fig. 1. Mean larval and pupal parasitism, and total parasitism of *Mussidia nigrivenella* across all sampling occasions on four host plant species (Benin, January 1996 to December 1997).

mean level of about 10% on *Gardenia* spp., but no specimens were recovered from *A. digitata*. Total parasitism ranged from 0.2% on *A. digitata* to 7.1% on *Gardenia* spp.; on maize it was < 0.1%. The incidence of larval and pupal parasitism varied with host plant species and time, thus reflecting the phenology of fruit setting of individual host plant species, and the pattern was similar in both years (figs 2 and 3). On *X. americana*, larval parasitoids were recorded only in September, and the pupal parasitoid *Antrocephalus crassipes* was found in November and December (figs 2 and 3). Levels of pupal parasitism were also low on *P. biglobosa*, but larval parasitism was recorded throughout the whole fruiting period, with higher values towards the end (figs 2 and 3). On *Gardenia* spp., both parasitized larvae and pupae were found throughout the whole year, but levels of parasitism varied with time (figs 2 and 3).

The logistic regression models yielded a clear association between both larval and pupal parasitism and host plants (tables 2 and 3). Likewise, time of the year had a significant impact on the levels of parasitism. No significant effect of year of sampling was observed for both larval and pupal parasitism. The fit of both models was good ($\chi^2 = 3.41$, DF = 4, $P = 0.49$ and $\chi^2 = 4.90$, DF = 7, $P = 0.67$ for larval and pupal parasitism, respectively). Larval parasitism was most likely

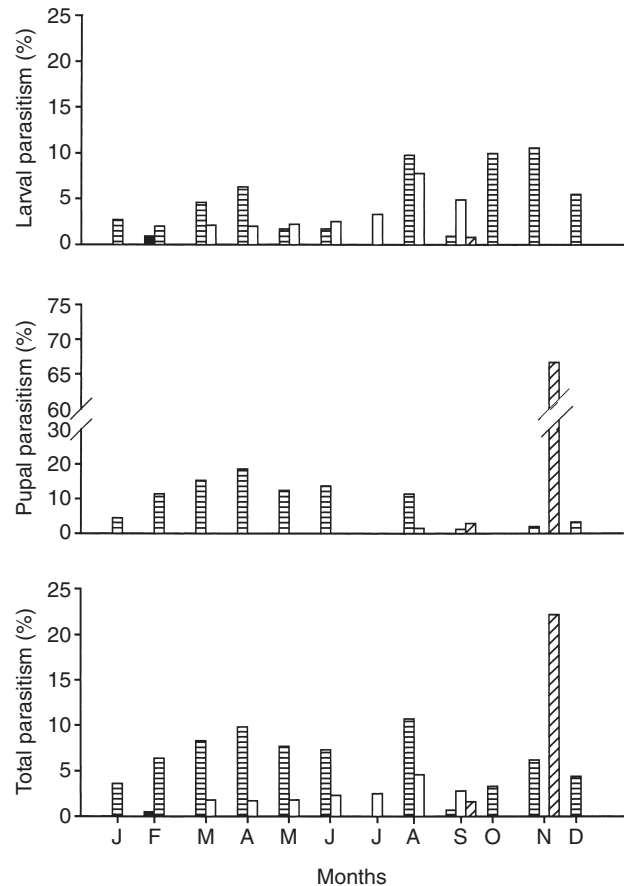


Fig. 2. Parasitism of *Mussidia nigrivenella* by larval and pupal parasitoids and total parasitism on fruits of four host plant species (Benin, January to December 1996). ■, *Adansonia digitata*; ▨, *Gardenia* spp.; □, *Parkia biglobosa*; ▩, *Ximenia americana*.

to occur when larvae were collected from *P. biglobosa* and *Gardenia* spp., whereas the other host plant species made no significant contribution (table 2, fig. 1). The high odds ratios for *Gardenia* spp. and *P. biglobosa* (22.9 and 16.7, respectively) indicated a preference of the larval parasitoids for larvae on these host plant species (table 2). Larval parasitism was significantly higher between August and November than during the other months of the year (table 2, figs 2 and 3).

The likelihood of parasitism of *Mussidia nigrivenella* pupae by *A. crassipes* was significantly higher on *Gardenia* spp. than on other host plant species (table 3). The high odds ratio for *Gardenia* spp. (9.7) indicated that pupae on this host plant species were about ten times more likely to be parasitized by *A. crassipes* as those on the other host plant species. Likewise, the occurrence of *A. crassipes* was significantly higher between February and September, with the likelihood of parasitism being three to four times higher during this period than between October and January.

Discussion

Only five out of the 20 host plants known to be attacked by *M. nigrivenella* (Moyal, 1988; Sétamou et al., 1999) yielded parasitoids. The differences in both parasitoid diversity and

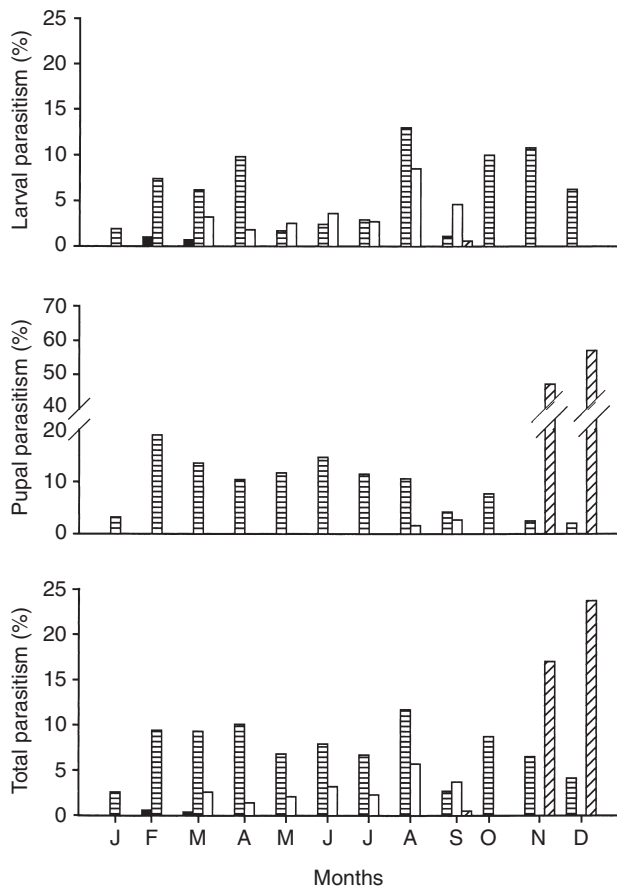


Fig. 3. Parasitism of *Mussidia nigrivenella* by larval and pupal parasitoids and total parasitism on fruits of four host plant species (Benin, January to December 1997). ■, *Adansonia digitata*; ▨, *Gardenia* spp.; □, *Parkia biglobosa*; ▩, *Ximenia americana*.

abundance between annual herbaceous plants and trees, as well as between the different tree species were striking. However, some of the most suitable and preferred annual host plants such as maize, jackbean and velvetbean are exotic to Africa and may not produce the necessary chemical and physical clues needed by natural enemies to detect their insect hosts (see Smith *et al.*, 1993; Janz & Nylin, 1997). A similar situation is found among the natural enemy complex of the maize pest *E. saccharina* on sugarcane in South Africa. On its most common natural host plant, the sedge *Cyperus*

papyrus L. (Cyperaceae), the natural enemy fauna is quite diverse and rates of parasitism range between 10 and 40% (Conlong, 1990, 1994). However, these parasitoid species rarely attack *E. saccharina* on sugarcane in adjacent fields. Direct accessibility of the host very likely also plays a major role. *Mussidia nigrivenella* spends most of its life cycle inside cobs, seed pods or fruit, and most of the plant species show no external feeding damage until shortly before pupation, when the borer produces an exit hole. As a result, larval parasitism is generally considerably lower than pupal parasitism, and *B. sesamiae*, the most common parasitoid attacking larvae, belongs to the drill-and-sting guild (Smith *et al.*, 1993).

In our study *M. nigrivenella* larvae were also occasionally parasitized by a *Perilampus* sp., but species of this genus can be either primary or hyperparasitoids (Subbiah, 1987), and are thus of limited use for biological control. The duration of fruit formation and the availability of fruits may also affect the population dynamics of both the pest and natural enemies. In contrast to maize, many wild hosts have a non-determinant growth pattern. They produce new fruits during an extended period, which are mostly not harvested and remain on the plants until they drop. Thus, they allow several generations of *M. nigrivenella* to develop per year (Sétamou *et al.*, 2000b), and thereby increase the likelihood of parasitism. In this respect, wild woody host plants represent a far more stable habitat than rather ephemeral maize plants. This, however, does not explain the differences in parasitism between tree species, and the fact that on most species, parasitoids are absent. According to Hare & Luck (1991), and Karowe & Schoonhoven (1992) these differences may also reflect the suitability of herbivorous hosts for the developing parasitoid, which may vary with the host plant fed upon.

The pupal parasitoid *A. crassipes* was the main parasitoid species and was found only on wild host plants. It occurred only in the three northern agro-ecological zones, which reflects the diversity and abundance of wild host plants in these zones (Sétamou *et al.*, 2000b). High levels of parasitism were recorded between February and September, i.e. before and during cob formation in maize. Thus in those regions, biological control activity on wild host plants may have an impact on pest infestations on crops such as maize and cotton. By contrast, in the south, the most common host is maize and to a lesser extent jackbean and velvetbean (Sétamou *et al.*, 2000b) on which parasitoids were scarce although both jackbean and velvetbean are highly suitable for growth and development of *M. nigrivenella* (Sétamou *et al.*, 1999). In Cameroon, the natural enemy fauna on maize is much more diverse than in West Africa. Nonveiller (1984) reported *Hemimetopius anguilarsis* Benoit and *Syzeuctus* sp.

Table 2. Logistic regression analysis of the effect of sampling months and host plant species on larval parasitism levels of *Mussidia nigrivenella*.

Variable	DF	Parameter estimate	SE	Wald χ^2	P-value	Odds ratio
Intercept	1	-6.05	0.42	212.33	< 0.01	-
January	1	-0.81	0.25	10.95	< 0.01	0.44
May	1	-0.69	0.23	8.97	< 0.01	0.50
August	1	0.77	0.16	23.03	< 0.01	2.17
October	1	0.72	0.30	5.60	0.02	2.05
November	1	0.78	0.36	4.66	0.03	2.18
<i>Gardenia</i> spp.	1	3.13	0.42	55.70	< 0.01	22.92
<i>Parkia biglobosa</i>	1	2.81	0.42	45.07	< 0.01	16.67

Table 3. Logistic regression analysis of the effect of sampling months and host plant species on levels of parasitism of *Mussidia nigriovenella* pupae by *Antrocephalus crassipes*.

Variable	DF	Parameter estimate	SE	Wald χ^2	P-value	Odds ratio
Intercept	1	-5.44	0.31	307.27	< 0.01	–
February	1	1.32	0.19	48.60	< 0.01	3.75
March	1	1.40	0.18	61.90	< 0.01	4.06
April	1	1.43	0.19	57.06	< 0.01	4.18
May	1	1.14	0.21	30.60	< 0.01	3.14
June	1	1.30	0.34	14.79	< 0.01	3.67
August	1	1.13	0.27	18.05	< 0.01	3.10
September	1	1.06	0.34	9.90	< 0.01	2.89
<i>Gardenia</i> spp.	1	2.27	0.28	65.13	< 0.01	9.72

(both Hymenoptera: Ichneumonidae), and Ndemah *et al.* (2001) obtained *A. crassipes*, *B. sesamiae* and species of the *Tetrastacus atriclavus* Waverston complex (Hymenoptera: Eulophidae), which are both primary parasitoids and hyperparasitoids, from larvae and/or pupae of *M. nigriovenella*. The latter were the most common but rates of parasitism were generally below 10%. According to Polaszek (1998) the complex includes six species. As the use of facultative hyperparasitoids in biological control is highly controversial (Ehler, 1979; Weseloh *et al.*, 1979), further studies are required to clarify the taxonomy and biology of these species before any conclusions about their status as candidates for biological control can be drawn. In the present study, egg parasitism was in general < 0.1%, and was zero on maize, whereas in the savannahs of Côte d'Ivoire, Moyal (1988) found up to 20% parasitism of *M. nigriovenella* eggs on maize.

The difference in parasitoid diversity between West Africa and Cameroon suggests that there are local opportunities for biological control. If in Cameroon the trends follow the same as in Benin, an even higher parasitoid species diversity can be expected on wild hosts than annual crops. Furthermore, in a recent survey in the coastal region and Lake Victoria area of Kenya, *Mussidia* spp. were commonly found on some wild host plant species (F. Schulthess, unpublished data). Further surveys in the different regions of Africa are planned with the aim of identifying the natural enemy complexes on various wild host plant species. Because of the exceedingly cryptic larval feeding behaviour of *Mussidia* spp., emphasis will be given to finding egg and pupal parasitoids. Promising candidates will be taken to West Africa for evaluation in the laboratory before release into the wild, in areas with a high diversity and density of alternative host plants.

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Insect Movement: Mechanisms and Consequences

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- 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.

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