

## Information on the biology and use of *Imbrasia belina*, and other edible moth species

### TAXONOMY

The emperor moths belong to the family Saturniidae, all African species belonging to the subfamily saturniinae. Under present classification the *Imbrasia* falls under the Tribe Bunaeini.

*Imbrasia belina* (Westwood) 1849, Proc. zool. Soc. Lond. 17: 41, pl. 8  
=chevalia Stoneham (1933)  
form ukerewensis Rebel (1906)  
form junodi Oberthur (1910)  
subspecies osiris Druce (1896)

Wingspan: male 100-120mm, female 105-125mm. The ground colour is variable ranging from greyish-green through chocolate-brown, chestnut-brown and orange-brown to pale yellow and greyish. There are two black and white bands on the forewing, one on the hindwing and a large, brown and black hindwing eyespot ringed with white. Eyespot on forewing small, orange, ringed with black and white. Larva up to 80mm long: black but densely speckled with yellow and bluish-grey, some specimens also speckled with red to a varying degree; 6 short, sharp, black spines on each segment. Closest relatives *I. occidentalis* (Rothschild) from West Africa and *I. osiris* (Druce) from East Africa (Oberprieler 1995).

*Imbrasia belina* due to its use as a food has many common names. In Botswana the larvae are referred to as phane, in Northern Zimbabwe as madora (Gardiner and Niemeyer 1998), in South Western Zimbabwe as macimbi, while the English common name of Anomalous Emperor Moth is used for the adult and Mopane worm for the larvae.

### DISTRIBUTION

This species is widespread in Southern Africa (from Northern Province of South Africa northwards), tropical and East Africa. Occurring from semi-desert to thick bush and savannah (Pinhey 1972). The large outbreak populations in Southern Africa mainly follow that of the host plant *Colophospermum mopane*, which occurs in a broad band extending from the Northern parts of South Africa into Zimbabwe and Botswana, and west into Northern Namibia. The main concentration of *I. belina* in Botswana is in the North East (Moruakgomo 1996).

### NATURAL HISTORY

#### Foodplants

*Imbrasia belina* feeds on a number of tree species, including *C. mopane* (Taylor and Moss 1982; van Wyk 1972), *Carissa grandiflora*, *Diospyros* spp., *Ficus* spp., *Rhus lancia*, *Rhus longifolia*, *Sclerocarya birrea*, *Terminalia* spp. and *Trema bracteolata* (Pinhey 1972), *Ozoroa longipes* and *O. crassinervia* in Namibia (Oberprieler 1995), *Pinus radiata* (Oberprieler 1986), and *Terminalia sericea* (Allotey *et al.*, 1996) in South Africa. Laboratory rearing experiments with *Sclerocarya birrea*, *Terminalia sericea* and *C. mopane* found that *C. mopane* was the most suitable of these three hosts in terms of developmental periods, number of emerged adults and nutritional quality (Allotey *et al.*, 1996).

#### Fecundity

Adult moths lay a single cluster of 30 to 355 eggs on the leaves (upper and lower surface), twigs (Ditlhogo 1996b, van den Berg, 1971) or even branches of mopane (Gardiner pers. obs.). Field studies in mixed *C. mopane* and *T. sericea* woodlands indicate that adults moths preferentially oviposit on *C. mopane*, with increasing numbers of egg clusters being laid on larger host plants (Ditlhogo *et al.* 1996). A similar study in Namibia showed that clutch size was independent of *C. mopane* leaf fluctuating asymmetry suggesting that oviposition site choice is not related to leaf nutritional quality within host plant species (Wiggins 1997a).

## Longevity

Under laboratory conditions *I. belina* moths lived for about 5 days with a range of 3-9 days (Ditlhogo 1996b). In the field the adult probably only lives for two to three days, during which time the only function of the imago is to find receptive mates (Oberprieler 1995) and to oviposit (Oberprieler 1995; Wiggins 1997b). The different sexes fly at different times of the night, females early in the evening normally between 20:00 and 22:00 and the males later between 23:00 and 01:00. This is because flying fulfills different functions for the two sexes. The females hatch in the evening, hang and dry and secrete pheromones to attract males. This pheromone is emitted from special glands at the tip of their abdomen (Scoble 1992). The males fly later to locate these females, and are able to detect the pheromone over several kilometers by means of special sensors located on their antennae. The following evening the female, now mated, takes to the wing in order to locate the foodplant and oviposit. Moths are limited to short duration flights which may account for lack of discrimination within host plant species exhibited during subsequent oviposition (Wiggins 1997a; 1997b).

## Number of generations per season

Across most of its distribution, the species is bivoltine with the first generation emerging from pupation in November to December and the second in February to March; only in more arid areas is it univoltine (Oberprieler 1991; 1995). The first generation population is considerably higher than that of the second (van den Berg 1971). Ditlhogo (1996a) reports that the mean fecundities of first and second generation adults are 231.1 and 156.2 eggs per adult respectively. Klok and Chown (1999) suggest the differences in population sizes may be due to the first generation eggs hatching just after leaf flush while in the second generation there is no new leaf flush, and the caterpillars have to feed on mature leaves, of poor nutritional quality.

## Number of instars and Caterpillar Growth rate

After approximately ten days the larvae emerge and then pass through five instars before pupation (Ditlhogo 1996; Klok and Chown 1999). Instars I to III of the caterpillars are strictly gregarious and they forage together in aggregations of 20 to 200 individuals (Oberprieler 1991; 1995), but do not display complex social and co-operative behaviour to the extent found in other caterpillars (Fitzgerald 1993). Nonetheless, when separated they cease feeding and search continually for the original or other aggregation (Oberprieler 1991; 1995). After moulting into instar IV caterpillars disperse immediately to become solitary. In an effort to account for the maintenance of this aggregation behaviour Klok and Chown (1999) studied both the solitary and gregarious stages of *I. belina* caterpillars in South Africa. Their results suggest that aggregations have considerable advantage to early instars caterpillars because they allow individuals to attain stable and high body temperatures, and to reduce rates of water loss. Such physiological regulation could lead to increased growth rates (see Scriber and Lederhouse 1983; Reynolds and Nottingham 1985), reducing larval developmental times and lessening the time that caterpillars are exposed to natural enemies and adverse biotic conditions. In contrast Frears et al. (1999) showed that there was a poor relationship between foraging activity and temperature when they fed *I. belina* caterpillars on *C. mopane* leaves in the laboratory. This led them to suggest that other factors, such as predation pressure, are the key regulatory factors that influence caterpillar aggregation.

The larval stage lasts approximately 6 weeks during which time the caterpillars undergo a 4000 fold increase in body mass (Gaston *et al.* 1997). The duration of each instar can vary both within the same generation and between generations. The normal length of time for the instars is approximately 8 days for instar I, 7 days for instar II, 8 days for instar III, 9 days for instar IV and 6 days for the final or fifth instar. At the end of the larval stage the fifth instar caterpillars burrow into the soil, where, if they are from the second generation they undergo a period of diapause (Oberprieler 1991). Ecdysis occurs either one or six to seven months after pupation, depending on the generation (van den Berg 1971).

## Mortality factors

Several authors have studied the natural enemy complexes associated with field populations of *I. belina*. These studies have been solely concerned with the egg and larval stages of the moth, there being no data available on adult and pupal predation and parasitism. Adults are likely to be predated upon by mammals such as bats, evidence for bat predation comes from the presence of remains of moths beneath bat roosts and lights (Hill and Smith 1984; Gardiner pers. obs.). Also, there is evidence that bats and moths in general are involved in a coevolutionary response, with moths developing physiological and behavioural means of evading predatory bats, and bats 'responding' to overcome moth defences (Roeder 1965).

Van den Berg (1971) showed there to be four egg parasites in his field study of *I. belina* populations in the Northern Transvaal. *Mesocomys pulchriceps* Cam. was the predominant species. Of the parasites reared from field collected egg masses 90.9 per cent were *M. pulchriceps*, 1.8 per cent *Eupelmus urozonus* (Dal.), 0.2 per cent *Anastatus* spp. (Eupelmidae), and 7.1 per cent *Pediobius* spp. (Eulophidae). Life cycle analysis indicated that population fluctuations of the primary parasitoid, *M. pulchriceps*, are regulated by the egg laying habit of the mopane worm. The inability of this species to suppress *I. belina* numbers being attributed to the emergence of adult parasitoids at a time when no egg hosts are available. Eggs of all stages were shown to be parasitised, mainly at the margins of egg masses, with parasitised eggs even found in the abdomens of dead moths. Parasitism rose to 44.5 per cent between November and December, falling to 30.5 per cent between February and March. Dithlogo (1996a; 1996b) reported Chalcid parasites that attack the larva but emerge from the host pupa. The larvae are also attacked by Ichneumonid and Tachinid parasites in the later instars, similarly these parasites pupate only once the larvae has gone underground (Dithlogo 1996b, Gardiner pers. obs.).

A study by Styles (1995b), at two sites in the Alldays area of the Northern Transvaal Province of South Africa, documented 34 different species of birds attacking the mopane worm during its larval phase. There was only a moderate variation in the numbers of species feeding on each of the five instars. However, the species composition changed markedly, such that more widely separated instars were eaten by less similar assemblages. Furthermore the body masses of bird species feeding on successive instars were strongly positive correlated with the masses of those instars (Gaston *et al.*, 1997). Temporal turnover in specific identities of the predators consuming different instars was considerable, resulting in a potentially strong temporal dynamic in the selection pressures faced by mopane worms. The caterpillars are also attacked by invertebrate predators such as spiders, ants and reduviid bugs in the early instars, and mantids in the later instars (Gardiner, Knell, pers. obs., Styles and Skinner 1996). Styles and Skinner (1996) speculated that *I. belina* was excluded from the Northern Tuli Game Reserve in Botswana by high levels of ant predation.

The larvae of *I. belina* are known to suffer from two viruses: an iridovirus and a currently undescribed non-occluded virus. In a recent study the viral mortality of *I. belina* larvae populations was measured in the Hans Merensky Game Reserve, Northern Province, South Africa (Knell, unpublished). Only the non-occluded virus was found in field collected larvae, with a 3.7% overall infection rate recorded in late instar, first generation, caterpillar populations.

## EFFECTS ON HOST PLANT

There has been little work conducted on the impact that *I. belina* have on their host plants. A field study in Botswana by Dithlogo *et al.* (1996) found that only 14 percent of *I. belina* defoliated *C. mopane* trees produced seeds compared with 84% of undefoliated trees (Dithlogo *et al.*, 1996). They also found a relationship between tree size and seed production following defoliation with larger trees able to withstand the impacts of caterpillar grazing compared with smaller trees. However, this was a limited study and further work is needed to fully quantify the influence that *I. belina* has on its hosts.

## POPULATION DYNAMICS

There are no reliable data available on the population dynamics of *I. belina*, but there is considerable anecdotal evidence to suggest that it displays outbreak dynamics similar to those known from many species of Northern Hemisphere woodland Lepidoptera. Hilton (1995) described the life-history characteristics most commonly associated with outbreak dynamics, and it is notable that *I. belina* conforms to her picture

of the 'typical' outbreak lepidopteran closely: eggs in masses, gregarious, large, brightly coloured larvae which begin feeding early in the season and which are reasonably polyphagous.

Typical outbreak lepidoptera show population cycles of 3-4 years of increasing densities, followed by 1-3 years at the peak density, which is often 3-4 orders of magnitude greater than the population density at the minimum point in the cycle, and then 1-3 years during which the population declines (Myers 1988). These cycles are sometimes synchronized across areas of hundreds of kilometers and may involve more than one species fluctuating together. Recent work has shown that this synchrony may be an example of a 'Moran effect' whereby populations that are fluctuating because of an endogenous effect are brought into phase by external environmental phenomena (Myers 1998).

The cause of these population cycles has been the matter of much debate, and a variety of hypotheses have been proposed, including maternal effects, induced plant defenses, parasitoids and disease (Myers 1988). Recent attention has focused on the role of disease (Anderson and May 1981, Dwyer *et al.* 2000) and parasitoids (Berryman 1996, Maron and Harrison 1997) as being important in the population dynamics of these species. Alternatively, a recent theory to explain outbreaks of Gypsy moth, *Lymantria dispar*, in North America has suggested that outbreaks are linked to masting by the oak tree hosts, which influences *L. dispar* populations indirectly via populations of small mammals which feed on acorns (produced during masting) and also on *L. dispar* larvae (Liebhold *et al.* 2000).

Given the apparent convergence between *I. belina* and these Northern Hemisphere woodland lepidoptera it is likely that similar processes are controlling outbreaks of *I. belina*. As discussed in the section on natural enemies, *I. belina* is known to suffer from high mortality from parasitoids and also from disease, so we might predict that these should have an important role in the population dynamics of the moth. Of particular interest is the recent work on Western Tussock Moth (*Orgyia vetusta*) and its parasitoids (Maron and Harrison 1997, Wilson *et al.* 1999) in coastal California. This has shown that host-parasitoid interactions lead to pattern formation in this species causing abundant localized outbreaks of the moth in otherwise very low density populations, despite the host plant being common and widespread. This is a similar situation to that which can be observed with *I. belina*, with localized outbreaks causing defoliation but surrounded by otherwise untouched mopane trees. This will remain as speculation however until quantitative data on where, when and why outbreaks occur and particularly high quality data on the spatial and temporal population biology of the moth have been collected. A final consideration that must be remembered is that *I. belina* can suffer high mortality from harvesting, and this is likely also to have important effects on the population dynamics of the moth.

## HUMAN CONSUMPTION

The eating of mopane worms by humans has been widely published (DeFoliart 1995; van Huis 1996; Pinhey 1972; Oberprieler 1995; Frears 1995; Sekhwela 1988; Weaving 1973; Gashe & Mpuchane 1996; Chavanduka 1975; Roberts 1998). When available they are nearly always harvested, but because of major population fluctuations from year to year they are not a reliable food source (Ditlhogo 1996b). It also seems some areas have high populations and others very little (Roberts 1998). The impacts of wild harvesting are also not known, some authors (Marais 1996) suggest wild harvesting will have little effect on the populations while others feel it may have a major impact (Roberts 1998).

The larvae are collected, gutted, roasted or cooked with a little salt and dried (Bartlett 1966; Gardiner pers. obs.). Approximately 43 hours are required for the product to be sufficiently dry for storage (DeFoliart 1995). The caterpillars are either eaten on their own or served with a relish for a main meal (Gardiner and Niemeyer 1998)

Harvests are usually large; for instance in the Kasungu National Park in Malawi they average about 15 kg per Ha (Munthali and Mughogho 1992), and Quin (1959) mentions that in South Africa a good picker can average 18 kg per ha. In Zimbabwe DeFoliart (1995) mentions that a local company in Harare packages the caterpillars and when he visited them they had 90 tons to hand. According to Dreyer and Wehmeyer (1982) in South Africa 1600 tons per annum enters reported channels of commerce (this figure does not include those privately collected and consumed or sold). In Botswana Moruakgomo (1996) found that over a four year period an average of 1113 tons per annum of dried phane were exported from Botswana.

## OTHER EDIBLE EMPEROR MOTHS

There are many species of emperor moth eaten in Africa (Table 1.). Probably the most widely eaten lepidopteran caterpillar in Africa is the emperor moth *Cirina forda*. The methods of collecting, preparation, storage and the way they are eaten are similar for all the species.

Table 1. List of edible Saturnid species known to the authors and the countries they are known to be eaten in (sources of Material; Malaisse & Parent 1980; Pinhey 1972; Oberprieler 1995; Chavanduka 1975; van Huis 1996; Marais 1996).

Saturnid species	Country eaten
<i>Athletes gigas</i> Sonthonnax	C.A.R (Zaire)
<i>Athletes semialba</i> Sonthonnax	C.A.R (Zaire)
<i>Bunea alcinoe</i> (Stoll)	Southern Africa
<i>Bunaea caffraria</i> Stoll	Tanzania
<i>Bunaeopsis aurantiaca</i> Rothschild	C.A.R (Zaire)
<i>Cirina butyrospermi</i> Vuillot	Burkina-Faso
<i>Cirina forda</i> Westwood	from northern Namibia across the northern province of South Africa to Mozambique and northwards to tropical and West Africa
<i>Cynabra hyperbius</i> (Westwood)	C.A.R (Zaire)
<i>Goodia kuntzei</i> (Dewitz)	C.A.R (Zaire)
<i>Gynanisa maja</i> (Klug)	South-Central Africa
<i>Heniocha apollonia</i> (Cramer)	Namibia
<i>Heniocha dyops</i> Maassen & Weymer	Namibia
<i>Imbrasia dione</i> Fabricius	C.A.R (Zaire)
<i>Imbrasia epimethia</i> (Drury)	C.A.R. (Zaire)
<i>Imbrasia ertli</i> Rebel	South-Central Africa
<i>Imbrasia hecate</i> (Rougeot)	C.A.R (Zaire)
<i>Imbrasia macrothyris</i> Rothschild	C.A.R (Zaire)
<i>Imbrasia richelmanni</i> (Weymer)	C.A.R (Zaire)
<i>Imbrasia rubra</i> Bouvier	C.A.R (Zaire)
<i>Imbrasia truncata</i> Aurivillius	C.A.R. (Zaire)
<i>Imbrasia tyrrhea</i> Cramer	Namibia
<i>Imbrasia zambesina</i> (Walker)	C.A.R (Zaire)
<i>Lobobunaea saturnus</i> Fabricius	C.A.R (Zaire)
<i>Melanocera parva</i> Rothschild	C.A.R (Zaire)
<i>Microgone cana</i> Aurivillius	C.A.R (Zaire)
<i>Pseudobunaea irius</i> (Fabricius)	Namibia
<i>Rohaniella pygmaea</i> (Maassen & Weymer)	Namibia
<i>Tagoropsis flavinata</i> Walker	C.A.R (Zaire)
<i>Urota sinope</i> Westwood	Southern Africa
<i>Usta wallengrenni</i> Felder	Namibia

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