Clutch size and oviposition site characteristics of a nocturnal African silk moth *Imbrasia belina* (Lepidoptera: Saturniidae)

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Oviposition site characters, clutch size, and hatching success were studied in a population of nocturnal silk moths (*Imbrasia belina* Westwood) in arid northwestern Namibia. There was little evidence of oviposition site choice based on host-tree (*Colophospermum mopane*) characteristics, although trees with eggs were closer to neighboring conspecific trees and small (< 1 m) trees rarely received clutches. Clutch size and hatching success were positively correlated, but neither was influenced by any of the measured tree characteristics. Similarly, neither clutch size nor hatching success was related to oviposition orientation on the leaf surface (i.e., inner or outer leaf surface). The apparent lack of host discrimination in this species may be due to a series of ecological constraints, including limited nocturnal flight periods and an unusually short adult lifespan.

1. Introduction

When choosing host plants, ovipositing Lepidoptera may use a variety of cues to discriminate among plants differing in age, size, defensive chemical composition, and nutritional quality (see reviews in Jones 1991, Thompson & Pellmyr 1991, Renwick & Chew 1994). Host discrimination may also vary with the spatial distribution of potential host plants (Brussard & Ehrlich 1970, Singer 1972, Kareiva 1982, Stanton 1983) and with the distribution of predators and parasites (Lawton & McNeill 1979, Price *et al.* 1980). Ovipositing females may discriminate within plants, and oviposit on sites with optimal microclimates and suitable leaf surfaces (Reavey & Gaston 1991). Typically (though not always: see Thompson & Pellmyr 1991) ovipositing Lepidoptera show some level of host discrimination and this discrimination is usually related to differential offspring performance (measured as growth and/ or survival; Thompson & Pellmyr 1991) on different host species or individuals. However, despite the clear benefits to discrimination among hosts, some Lepidoptera show little host discrimination (e.g., Courtney 1986, Robertson 1987, Underwood 1994). A lack of discrimination can occur for a variety of reasons including physiological and environmental constraints (e.g., Robertson 1987), as well as tight time and energy budgets (Karban & Courtney 1987, Underwood 1994).

Both empirical and theoretical studies of oviposition in Lepidoptera have focussed on diurnal taxa, with less consideration for the constraints

faced by nocturnal ovipositors (Thompson & Pellmyr 1991; but see Ramaswamy 1988, Renwick & Chew 1994). In this study I describe the oviposition-site characteristics, clutch size, and hatching success within a population of silk moths (*Imbrasia belina* Westwood) breeding in an arid mopane (*Colophospermum mopane*) woodland in southern Africa. As is in all Saturniid moths (Janzen 1984, Scoble 1992), *I. belina* adults lack functional mouthparts, are active only during a short period each night, and the entire adult lifespan, covering 2–5 days, consists of searching for mates (males) and ovipositing (females; see also Oberprieler 1995). The aim of this study was to quantify oviposition ecology within such a life-history, and to compare it with patterns typical of diurnal Lepidoptera.

2. Methods

Data on oviposition site characteristics were collected from 14–18 March 1996 along a 300-m stretch of the Huab River (19°55´S, 14°46´E) in arid, northwestern Namibia. In this area, *C. mopane* is the most common tree, comprising approximately 90% of the tree community. Although large *Acacia* spp. form a well-structured canopy along the Huab river, this study was conducted approximately 200 m from the river floodplain, in an area where *C. mopane* cover approximately 20% of the available habitat.

In northwestern Namibia, eclosion of *I. belina* pupae takes place after sufficient rains have fallen, typically between December and March (pers. obs.). Adults live less than a week, during which mating and oviposition occur (Oberprieler 1995). Eggs typically hatch after 3 weeks, and larvae spend the next 4–6 weeks foraging on the host trees (typically *C. mopane*). Although bivoltine in other areas of southern Africa (Oberprieler 1995, C. Styles, pers. comm.), *I. belina* is univoltine in northwestern Namibia, an arid area with low and erratic yearly rainfall.

I systematically searched only those trees under 3.5 m in height, as adequate searches of taller trees (which were

uncommon in the study area) was not possible. In addition, small (< 1 m) saplings rarely contained moth clutches and, consequently, were not included in the sampling. Clutches of eggs were usually clearly visible even from a distance of several meters. I measured the height (m above ground) of each clutch, as well as its orientation on the leaf surface (i.e., inner or outer surface). Eggs were counted and classified as hatched (eggshell open) or unhatched (eggshell not broken).

The following characteristics were recorded for each tree: height (to the nearest 0.1 m), diameter (cm) at 0.5 m above ground level, distance (to the nearest 0.1 m) to the nearest conspecific neighbor tree, and total number of conspecific trees within a 10-m radius of the tree. Oviposition in relation to fluctuating asymmetry in leaf length is reported elsewhere (Wiggins 1997).

3. Results

3.1. Oviposition-site characteristics

Moth clutches were laid on 33 of the 65 sampled trees. Trees where oviposition occurred were significantly closer to neighboring conspecifics than were trees without clutches (Table 1). However, mean leaf length, tree height, trunk diameter, and the number of trees within 10 m were not significantly different between the two groups of trees (Table 1). Moths showed no preference for ovipositing on either the inner (27 clutches) or outer (35 clutches) surface of the leaf (Chi-square = 0.52, $df = 1$, $P > 0.47$).

3.2. Clutch size and hatching success

Eggs were laid in batches and clutch size averaged 50 eggs ($S.E. = 5$, range 2–130, $N = 63$ clutches). Clutch size (mean for trees with more

Table 1. Differences in mean leaf length (mm), tree height (m), diameter at 0.5 m above ground (mm), density (number of trees within 10 m), and distance (m) to nearest conspecific neighbor for trees that did ($n = 33$) and did not ($n = 32$) hold moth clutches.

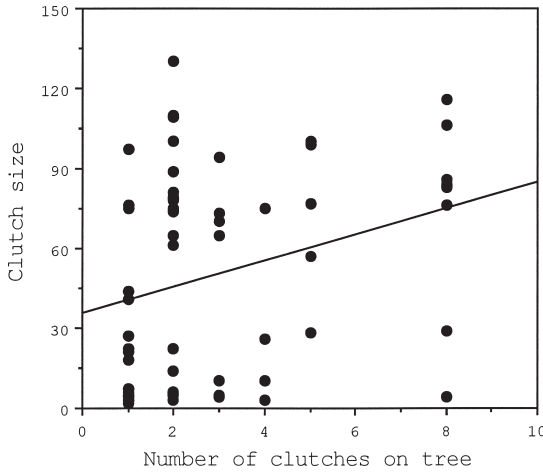| | Trees with eggs | | Trees without eggs | | | |
	Mean	*S.E.*	Mean	*S.E.*	*t*	*P*
Leaf length	62.0	1.6	60.9	1.4	0.49	0.62
Tree height	2.5	0.1	2.6	0.1	0.22	0.83
Tree diameter	72	7	74	10	0.17	0.87
Tree density	6.2	0.5	5.5	0.5	0.91	0.37
Nearest neighbor	2.0	0.3	3.1	0.3	2.74	0.008

Fig. 1. Clutch size in relation to the number of clutches on the tree (linear regression line for illustrative purposes only; Spearman Rank Correlation, $r_s = 0.50$, $N = 33$ trees, 63 clutches, $P < 0.01$).
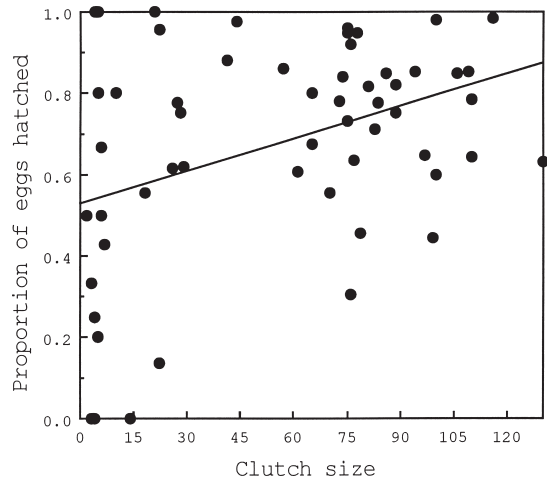

Fig. 2. Proportion of eggs hatched in relation to clutch size (linear regression line for illustrative purposes only; Spearman Rank Correlation, $r_s = 0.30$, $N = 63$, $P = 0.019$).

than one clutch) did not vary with the overall height ($r_s = -0.10$, $N = 33$, $P > 0.59$) or trunk diameter ($r_s = -0.09$, $N = 33$, $P > 0.63$) of the tree, but there was a weak negative relationship between clutch size and height above ground level ($r_s = -0.25$, $N = 62$, $P = 0.044$). There was a positive correlation between clutch size (mean for trees with more than one clutch) and the number of clutches in the tree (Fig. 1). Hatching success of individual clutches ranged from 0 to 100% (mean = 0.66 larvae hatched per egg laid, S.E. = 0.04, $N = 63$ clutches) and there was a significant, positive relationship between hatching success and clutch size (Fig. 2). The orientation (inner or outer leaf surface) of the leaf had no effect on clutch size or on hatching success (Table 2).

4. Discussion

Studies of oviposition in diurnal Lepidoptera have typically shown that females exhibit a strong hierarchy in oviposition site preference (see references in Thompson & Pellmyr 1991). However, despite the extensive theoretical and empirical work on insect oviposition, relatively few studies have addressed oviposition behavior and site choice in nocturnal Lepidoptera (Ramaswamy 1988, Renwick & Chew 1994). Nocturnality likely imposes a different suite of constraints on ovipositing insects. For example, chemical and tactile cues probably play a much larger role, relative to visual cues, for ovipositing females (Renwick & Chew 1994).

Table 2. Differences in hatching success and clutch size between clutches of eggs laid on the inner and outer leaf surfaces. As leaves typically hung in a vertical position, the inner (lower) leaf surface typically faced in towards the trunk, whereas the outer surface faced away from the trunk. Proportion hatched data were arc-sin transformed prior to analysis.

Clutch laid on:		Proportion of eggs hatched				Clutch size			
	N	Mean	S.E.	t	P	Mean	S.E.	t	P
Inner surface	27	0.62	0.06			45	8		
				0.90	0.37			0.92	0.36
Outer surface	35	0.69	0.05			55	7		

Studies of neotropical Saturniidae (e.g., Janzen 1984) suggest that the short life span of adult moths leaves little opportunity for extensive sampling of potential host plants. In addition, ovipositing female Saturniids are typically active for only a short period (2–4 hours) each night, further restricting their opportunities to sample potential hosts (Janzen 1984, Oberprieler 1995). While the results of this study also suggest little sampling by ovipositing moths, the impacts of nocturnality on host discrimination remain unknown.

As there were no indications of egg predation by birds, ants or other potential egg predators, I assume that the observed pattern of egg depositions accurately reflects those sites chosen by females. There were no physical (e.g., height, trunk width, leaf length) differences between trees chosen as oviposition sites, and those not chosen. The lack of association between tree height and oviposition, however, likely arose due to the bias in tree sampling. Young trees less than 1 m in height were not sampled as they rarely contained eggs. Thus, a complete sampling protocol of the local tree population would likely have revealed a positive (threshold) correlation between tree height and oviposition. The only significant physical factor related to oviposition site choice was the proximity of the nearest conspecific tree. Proximity to neighboring trees may be important for larval survival (Rausher 1981, Thompson & Pellmyr 1991), as larvae often strip their host tree and then move on to nearby trees (pers. obs.). Unfortunately, there are no available data on the frequency of between-tree movements by *I. belina* larvae.

The lack of any preference for oviposition on the inner (lower) or outer (upper) leaf surface is surprising given that studies on the British microlepidoptera showed that 73% typically oviposited on the inner surface of the leaf and only 6% of the 227 species surveyed showed no apparent preference for either the inner or outer surface (Reavey & Gaston 1991). For many species, oviposition on the inner leaf surface may reduce egg predation and parasitism (Reavey & Gaston 1991, but see Gold *et al.* 1989), reduce exposure to inclement weather, and may allow for a more stable microclimate for developing eggs (Willmer 1982, 1986). The leaf surface structure of *C. mopane* is similar on the inner and outer surfaces, likely reducing any differences in microclimatic effects

(Reavey & Gaston 1991). Accordingly, I found no difference in hatching success between eggs laid on the inner and outer surfaces. However, a clearer test of the microclimate hypothesis would be to compare development times of eggs laid simultaneously on the inner and outer surfaces of the same leaf.

Clutch size varied greatly in this population. Unfortunately, the laying patterns of individual females are not known, although there are suggestions that females lay only a single clutch (e.g., Oberprieler 1995, C. Styles pers. comm.). The wide range of clutch sizes, however, suggests that females may deposit their eggs in several batches, as is common among neotropical Saturniids (Janzen 1984). Interestingly, clutch size tended to be larger on trees with multiple clutches, suggesting that females are not reducing clutch size when conspecific egg masses are present (see also Damman 1991). Hatching success correlated positively with clutch size, largely due to poor hatching success among some of the smaller clutches. The reasons for poor hatching success among small clutches are unknown. However, among many Lepidopterans several measures of fecundity are known to decrease with increasing female age (e.g., Gossard & Jones 1977, Begon & Parker 1986, Wiklund *et al.* 1987), suggesting that poor hatching success within small clutches may be the result of female senescence.

The results of this study suggest that ovipositing *I. belina* females utilize few of the potential indicators of host-tree quality (see also Wiggins 1997). Rather, oviposition may simply relate to tree "apparency" (Courtney 1982) and to the proximity of surrounding conspecific trees. There may be little benefit for extensive host selection by ovipositing females, given that *I. belina* larvae frequently move between trees during their development. However, several aspects of *I. belina* natural history (e.g., host tree rejection behavior by females, incidence of multiple clutches by individual females) that may affect oviposition behavior remain unknown. Due to a widespread population crash (for unknown reasons, at the first larval instar stage) in the area, I was unable to follow the performance of caterpillars on different trees — such data would help to clarify the potential benefits of host-plant discrimination among females.

While my results suggest that host-plant discrimination may not be under strong selection in this population of *I. belina*, direct observations of female oviposition behavior as well as a more detailed analysis of variation in host quality (e.g., leaf chemistry) are clearly needed for a better understanding of the factors influencing oviposition-site choice in this short-lived species. Although it is tempting to ascribe the apparent lack of strong oviposition-site preference to the nocturnal behavior of *I. belina*, such a conclusion would be premature given that a short adult lifespan and the high degree of larval mobility may also contribute to a lack of strong oviposition preference among Saturniids. The degree to which nocturnality affects oviposition-site selection should rather be studied in nocturnal taxa (e.g., Lepidoptera: Sphingidae) whose life-history traits are more similar to those of well-studied diurnal Lepidoptera.

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