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OBSERVATIONS ON THE BEHAVIOUR, PHENOLOGY AND HABITAT PREFERENCES OF MYDAS FLIES IN THE CENTRAL NAMIB DESERT (DIPTERA: MYDIDAE)

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(With one Table)

ABSTRACT

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Of eleven mydid species known from Gobabeb, South West Africa/Namibia, nine are undescribed. Data on adult behaviour, seasonality, and habitat preferences are given for several of these species.

INTRODUCTION

Although half of the known mydid species occur in southern Africa (Hesse, 1969), almost nothing is known of their biology. Prins (Hesse, 1974) witnessed oviposition and recorded activity patterns for a species of the anomalous genus *Namibimydas*. Hesse (1969) gave flower records for several species of *Afroleptomydas* and one species of *Arenomydas*, and also described flight behaviour and habitat preferences. Bowden (1978) and Hesse (1969) discussed distribution patterns of southern African species, and Bequaert (1959) listed collection records for three Kaokoveld species. The most detailed summary of mydid biology is that of Séguy (1928), based largely on the genus *Mydas* (which does not occur in southern Africa). Additional information on extra-limital genera is given by Wilcox and Papavero (1971).

The data presented below contribute to our knowledge of mydas fly distribution patterns in southern Africa, and give additional clues as to why there are more species in arid environments.

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MATERIALS AND METHODS

Mydas flies were collected and observed in the vicinity of the Namib Research Institute, Gobabeb (23° 34'S, 15° 03'E). They were found in four major habitats: seasonally dry Kuiseb River bed; sparsely vegetated, quartz-gravel plains north of the river; vegetated, sandy, interdune valleys south of the river; and large sand dunes bordering the interdune valleys. The paucity of vegetation outside the river bed facilitated collection of phenological data for most species. The following species were collected at Gobabeb from November 1978 through November 1979: Afroleptomydas undescribed species, Agaperemius undescribed species, Eremohaplomydas undescribed species, Halterochis(?) undescribed species I & 2, Namadytes prozeskyi Hesse, 1969, and Nomoneuroides undescribed species I, 2, 3 & 4. Namadytes prozeskyi and Parectyphus namibiensis Hesse, 1972 were the only species previously recorded from Gobabeb. The latter species was not collected during this study. Voucher specimens are deposited in the Natal Museum, Pietermaritzburg, and in the Namib Research Institute reference collection.

Agaperemius sp. and Namadytes prozeskyi oviposited in the laboratory. All other observations were made in the field.

RESULTS AND DISCUSSION

HABITATS

All species were found flying over or sitting on bare soil in direct sunlight. Several species (particularly those in the river bed) were always near bushes. *Agaperemius* sp. was the only mydid found on vegetation or in the shade. It moved into the shade or onto dead stems of *Eragrostis spinosa* on several days in November 1979, after ground surface temperatures rose above 55 °C. Observations on other species took place at surface temperatures below 50 °C, when thermoregulatory behaviour was apparently unnecessary.

Afroleptomydas, Agaperemius, and Namadytes occurred in the river bed. Eremohaplomydas and Nomoneuroides spp. 2 & 4 were found on the gravel plains (Table 1). Halterorchis(?) spp. 1 & 2 and Nomoneuroides sp. 1 occurred on the dunes. Homoneuroides sp. 3 was found in the interdune valleys. Parectyphus namibiensis has been collected on sand dunes (label information), but Hesse (1972) suggests that it is a riverine species. Agaperemius sp. was the only mydid found in more than one habitat during this study (one individual was collected in the dunes). It seems to prefer open sandy patches adjacent heavily vegetated areas.

SEASONAL CYCLES

Central Namib Desert Mydidae are univoltine. Adults are primarily restricted to two seasons. The few available records, however, indicate that the onset of emergence is not fixed from year to year. Afroleptomydas sp. and Agaperemius sp., for example, emerged earlier in 1979 than in 1978. The following species were collected in the spring: Afroleptomydas sp. (October -December), Agaperemius sp. (September-December), Halterorchis(?) sp. 1 (December), Nomoneuroides sp. 1 (December) and sp. 4 (September). Parectyphus namibiensis has been collected in August and September (label information). The remaining species emerged in the fall: Eremohaplomydas sp. (May), Halterorchis(?) sp. 2 (May), N. prozeskyi (April-June), Nomeneuroides spp. 2 & 3 (May). Seasonal activity for all species is summarised in Table 1. Flight activity was observed between 10h00 and 16h00.

Adults of species from the gravel plains, dunes, and interdune valleys were active for only two weeks during the year. Activity, though a population attribute, closely approximates adult life-span in these species. Adults of species from the Kuiseb River bed and adjacent sandy banks were observed

Species	Number observed in field	Habitat	Season	Mouthparts
A froleptomydas sp.	1	river	October-December	long, functional
Agaperemius sp.	15	river, dunes	September-December	vestigial
Eremohaplomydas sp.	15-20	gravel plains	May	vestigial
Halterorchis(?) sp. 1	2	dunes	December	vestigial
Halterorchis(?) sp. 2	6	dunes	May	vestigial
Namadytes prozeskyi	> 20	river	April–June	vestigial
Nomoneuroides sp. 1	1	dunes	December	vestigial
Nomoneuroides sp. 2	> 20	gravel plains	May	vestigial
Nomoneuroides sp. 3	5-10	interdune valley	May	vestigial
Nomoneuroides sp. 4	³ 3	gravel plains	September	vestigial
Parectyphus namibiensis	õ	dunes	August-September	short, functional

 TABLE 1.

 Habitats, activity periods, and type of mouthparts in two known and nine undescribed species of mydas flies from Gobabeb, South West Africa/Namibia.

over relatively longer periods (at least two months for Agaperemius sp. and N. *prozeskyi*). For these species, adult life-span may be considerably shorter than the activity of the population.

Emergence of most mydid species was correlated with the advent of exceptionally strong winds. Strong east winds are a distinctive feature of the fall season in the Central Namib Desert. In 1979, the first east wind period began in the second week of May. It lasted two weeks, with winds decreasing each day from mid-afternoon through early evening. The first order weather station at Gobabeb recorded a maximum of 48 km/hr (hourly average). *Eremohaplomydas* sp., *Halterorchis*(?) sp. 2, and *Nomoneuroides* spp. 2 & 3 occurred only during this period. Similarly, *Nomoneuroides* spp. 1 & 4 were collected only during short spells of strong west winds in spring. Adults of all these species were absent the rest of the year.

Emergence of many Namib arthropods is correlated with the appearance of strong winds (e.g. Holm and Edney, 1973; Louw and Hamilton, 1972). While the exact emergence cue is unknown, the scouring and shifting of the sandy substrate by the wind could be readily detected by the shallowly buried pupae. A reliable emergence cue of this sort is important to species with brief adult life-spans as it ensures the presence of both sexes at the same time. Concentrating activity for short periods may also decrease predation pressure in habitats with little shelter.

Riverine species are partially sheltered from strong winds by the Acaciadominated forest. Emergence of Afroleptomydas sp. and Agaperemius sp. was not correlated with the presence of such winds. These species may not have discrete emergence cues, and prolonged activity periods might therefore be the result of different adults emerging over a one or two month period. Namadytes prozeskyi appeared during two successive east winds in May and June, but adults could not be found between these periods. It thus has a similar but more prolonged response to wind than species from the gravel plains and dunes.

Feeding

Of the species studied, only Afroleptomydas sp. and Parectyphus namibiensis have well-developed mouthparts. Hesse (1969) records several Afroleptomydas species collected on Mesembryanthemum. Since M. guerichianum was in bloom in the Kuiseb River while Afroleptomydas sp. was active, it may serve as the nectar source for this species.

The remaining species have vestigial mouthparts. With the possible exception of *Agaperemius* sp., all are also short-lived as adults. They most probably do not feed as adults because, in the Namib, few flowers are in bloom outside the river bed, particularly in the fall. Flowering is closely correlated with rainfall (Seely, 1978 and personal observations), whereas mydas fly activity is not. Flowers thus cannot be relied upon as a food source for those mydid species living away from the river. The decrease in adult life-span in a harsh environment is an important factor in the reduction of mouthparts in this group.

MATING

Mating and/or mating attempts were observed for *Halterorchis*(?) sp. 2, *Nomoneuroides* sp. 2, and *Eremohaplomydas* sp. A teneral female *Halterorchis*(?) sp.

2 was found on the sandy surface of a dune base at 13h05 on 16 May. The body was almost completely unpigmented, and the fly was incapable of flight. Thirty seconds later, a low-flying male landed directly on top of her, and the genitalia were quickly coupled without any observable preliminaries. While *in copulo*, the male was situated on top of the female, and the tip of the female's abdomen was twisted around the apex of that of the male—inserted dorsoposteriorly. The wings of both flies were held open. The male's first two pairs of legs grasped the female's wing bases, while the third pair straddled the female's abdomen. They remained in this position for 23 minutes, whereupon the male flew up without noticeable preliminaries to detachment. After hovering for a few seconds he flew away. Ground surface temperatures during this time were 45 ± 2 °C. The female remained on the ground and was now nearly completely pigmented. She was captured one minute later.

Four pairs of Nomoneuroides sp. 2 were observed in copulo on 10 May between 12hoo and 13hoo. All were sitting on the soil surface, but immediately flew off (still in copulo) when approached. One pair was pursued for five minutes without uncoupling. The pair repeatedly flew 5-10 metres distant with each approach. All observed pairs were in the same position i.e. male directly on top of the female, both facing the same direction.

Two male *Eremohaplomydas* sp. attempted to mate with a single female on the ground at 13hoo on 12 May. Ground surface temperatures were 45 ± 1 °C. After several minutes, copulation still had not been achieved due to interference by the competing males. The three individuals were then collected. Attempts to induce mating in the laboratory were unsuccessful.

Hesse (1969) described mydid flight as a characteristic rapid gliding, and this seems particularly applicable to the low-flying males. Females of *Eremohaplomydas* sp., *Namadytes prozeskyi*, and *Nomoneuroides* spp. have shorter, more hop-like flights. The male flight pattern is well-suited to the detection of females as soon as they have emerged, and is similar to myzinine tiphiids in this respect. Mating with teneral or very young females is an important adaptation for short-lived species.

OVIPOSITION

Oviposition was recorded for Namadytes prozeskyi, Nomoneuroides sp. 2, and Agaperemius sp. N. prozeskyi usually oviposited in shallow depressions (e.g. hoof prints) in the sandy river bed. Five females were observed. Four oviposited several times in succession before being captured or frightened off. The fifth attempted several times to oviposit (with abdomen inserted part-way into the substrate), but was apparently unsuccessful (no eggs were found). For the first four females, the oviposition sequence (Irwin, 1976) was as follows: approach was direct, without noticeable searching or sensing movements. Stance was upright, with abdomen straight. A greater angle into the substrate was achieved by positioning at the lip of a depression. Insertion was achieved with the female moving backwards a few paces and pushing the tip of the abdomen into the sand. This continued with the entire abdomen, and usually most of the thorax, entering the sand. Wings were always held out perpendicular to the body. Insertion required $q \pm 1$ seconds (n = 8). Females remained buried in this position for 6 ± 1 seconds. Withdrawal of the abdomen occurred immediately afterwards. Females then flew off and the oviposition sequence resumed a few metres away. Not all starts were successful. In several cases the

female backed into the sand only to pull out again 1-2 seconds later and shift position for another attempt. Thus the type of soil (possibly compactness or purity of the sand) apparently has some importance.

Captured females readily oviposited in the above fashion in pill vials (25 mm diameter), laying up to 24 eggs in two hours. The orange, hyaline, pear-shaped eggs were unsculptured with a simple micropyle at the narrower end. Eggs measured 2×1 mm (length and maximum width), and were laid in a loose cluster in the vial. Eggs dissected from *Halterorchis*(?) sp. 2 were pale orange, but otherwise not distinctly different.

Nomoneuroides sp. 2 oviposited in the open gravel plains. The approach and stance were similar to that of N. prozeskyi, but Nomoneuroides sp. 2 did not oviposit in depressions. The abdomen was also pushed into the ground in a similar manner, but was never inserted more than half-way into the soil (n = 3 females, 5 ovipositions). The wings were folded over the abdomen during oviposition. Timing of the sequence, as well as withdrawal and immediate resumption, were as in N. prozeskyi. Differences between Namadytes and Nomoneuroides are thus limited to the depth at which the eggs are laid; the more shallow depth being correlated with a rockier substrate. Based solely on this criterion, oviposition behaviour of Namibimydas (Hesse, 1974) is more closely related to Namadytes than Nomoneuroides—again suggesting the influence of a sandy substrate.

Hesse (1969) suggested that acanthophorites at the apex of the female abdomen are used for digging in sandy or loose soils. This is verified by the oviposition behaviour of Agaperemius sp. A single female of this species was placed in a cage. No activity occurred and after several hours it was removed by hand. During handling the acanthophorite-bearing segment began rotating, producing a high-speed, egg-beater like motion for 2-3 seconds. Immediately afterwards a small white egg was extruded. The egg was $1,5 \times 0,7$ mm, and narrower basally than in *N. Prozeskyi*. The speed and timing of acanthophorite twirling indicate usage in construction of a small oviposition chamber beneath the surface. It is doubtful that such high-speed twirling would be possible in anything other than loose, sandy soils.

BRIEF ACTIVITY PERIODS AND SPECIES DIVERSITY

A brief activity period is an adaptation to an extreme environment. In the Central Namib Desert precipitation and strong winds serve as emergence cues for many species with such activity patterns (Holm and Edney, 1973; Louw and Hamilton, 1972; personal observations). The response to winds by some mydid species is seasonal, however, and thus differs from reports of other species (mainly tenebrionid beetles) which respond to such cues throughout the year.

Bowden (1978) attributes the high diversity of southern African Mydidae to limited dispersal abilities in persistent habitats. For species living in the dunes and gravel plains, the short adult life-span and relatively poor flight capabilities (sustained flight was never observed) restrict gene flow between populations. If emergence is governed by local weather conditions, interchanges between populations may be further reduced. In contrast, riverine species may not necessarily be longer-lived, but the populations are active for longer periods. This increases dispersal ability and probably results in a greater geographic range for these species.

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