

Summer activity patterns of the riparian desert beetle *Physadesmia globosa*

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ABSTRACT

The summertime activity pattern of the tenebrionid beetle *Physadesmia globosa* was investigated using focal animal sampling. Beetles have a bimodal activity pattern with activity peaks during the morning and the late afternoon. The morning activity peak is divided into an early bout of foraging, followed by sexual behaviour. There was no clear correlation between ambient temperature and daily levels of inactivity: some of the highest activity levels were recorded during the time period 16h00-17h00, when the ambient temperature was the highest. These data are discussed in the light of evolutionary explanations for beetle activity patterns.

INTRODUCTION

A significant amount of the diversity of the Namib desert fauna comprises Coleoptera (Koch 1962). The tenebrionid tribe Adesminii, including the genera *Onymacris*, *Physadesmia* and others, is prominent among these (Wharton & Seely 1982). *Physadesmia globosa* is often abundant in mixed *Acacia* spp. riparian woodland in river beds such as those of the Kuiseb and Swakop Rivers in the coastal zone of the Namib Desert (Penrith 1979; Wharton & Seely 1982). Although a number of behavioural studies have recently investigated this species (Hamilton & Penrith 1977; Nicolson *et al.* 1984; Rasmussen *et al.* 1985; Osberg & Hanrahan 1986), relatively little is still known about its behaviour.

This paper investigates the diurnal activity of *Physadesmia globosa* in greater detail than as been done before. The concept of 'activity' is ill-defined (Ferguson *et al.* 1988), because a single, quantitative measure corresponding to 'activity' does not exist. For this reason, counts of various tenebrionid beetle species carried out while doing standard transects (Hamilton 1971; 1975; Louw & Hamilton 1972; Hamilton *et al.* 1976; Wharton 1980) bias data towards beetles that are walking and that are in exposed places at the time of the count. The activity of *Physadesmia globosa* has also been recorded in terms of walking behaviour of beetles (Marden 1987) and also leads to biased data since animals can be active even though they do not move about. Feeding and mating are important activities of these beetles and often do not involve their walking about. Focal animal sampling (Altmann 1974) is a method that yields more reliable data, and information on the circadian frequency of all the important behaviour categories can be obtained.

The aim of this paper is to describe the activity patterns of *Physadesmia globosa* in terms of the important behaviour categories of this species. These data form the basis of a more detailed behavioural study in progress.

METHODS

This study was performed during February/March 1987 at Gobabeb in the central Namib Desert, SWA/Namibia. Results reported on here were obtained in an area of about 400 m², containing two large *Acacia erioloba* trees and a *Salvadora persica* thicket in the Kuiseb River bed. Behavioural data on free-ranging beetles were collected through focal animal observations (Altmann 1974). Information

from 211 observation-hours (males: 106 obs-h; females 105 obs-h) was collected, with focal periods of 1 h/individual, covering the diurnal period 08h00 to 19h00. In order to enable identification of the focal animal during the focal period and to avoid duplicating observations on any individual during the study period, each individual was given a distinctive mark by painting a small pattern on its back using white nail polish. The distance over which focal individuals moved during each observation period was measured, as was the behaviour during instantaneous scans every 60 seconds.

Climatic data were measured with a thermohygrograph in a Stevenson screen at the study site, situated on the ground underneath an *Acacia erioloba* tree where it was exposed to the sun after about 11h00. This location was representative of where beetle activity occurred throughout the day.

Because of the nonparametric nature of the information, distance data were transformed through the transformation: $d' = \ln [\text{distance (cm)} + 1]$ (Sokal & Rohlf 1981:419). Proportions of observations comprising each behavioural category during a particular diurnal hour interval (p) were transformed as: $p' = \log_{10} [\arcsin(p)]$ (Sokal & Rohlf 1981:427). Parametric tests were performed on the transformed data.

RESULTS

Five behavioural categories were observed during the study period. These were feeding, walking, chasing, buried and inactive (surface). Table 1 gives the overall proportions of time spent in each behavioural

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TABLE 1: Mean amount of time *Physadesmia globosa* spent in various behavioural categories at Gobabeb during February/March 1987. (Sample size = 211, each measurement representing 1 obs-h.).

Behavioural Category	Mean percentage of time spent in this behaviour	Standard error of mean
Inactive: standing still	17 %	1.4 %
Feeding	6 %	0.6 %
Walking	30 %	1.6 %
Dug in: buried under detritus	28 %	2.3 %
Chasing (Premating & matting)	19 %	1.8 %

category. During the day the greatest amount of time (30 %) was spent walking, while just less than 30 % of the time was spent buried underneath detritus or sand. Beetles were inactive (standing still above ground) for 17 % of the day.

The level of activity before 08h00 was low: beetles were buried or inactive 75 % of the time between 08h00–09h00. None of the focal animals were active before 08h00 and individuals were difficult to find at this time. Likewise, the level of activity was low after 19h00: beetles were inactive or buried for 15 % of the time between 18h00–19h00 and none of the focal animals were active after 19h00. It therefore appears that *Physadesmia globosa* was active mainly between 08h00 and 19h00 during the study period.

The mean amounts of time spent in the five behavioural categories for each hourly interval between 08h00 and 19h00 are shown in Figure 1. A clearly bimodal activity pattern is evident for feeding, walking and chasing. The asterisks in Figure 1, resulting from multiple comparisons using Tukey's studentized range tests (Sokal & Rohlf 1981: 245), indicate mean hourly activity levels differing significantly from some other hourly values ($p < 0.05$). Instead of presenting an 11 × 11 matrix of Tukey's statistics for each graph in Figure 1, the results are summarised on the diagram. Thus, for chasing, data at 17h00 and 13h00 differ significantly from some other data, in this case those at 08h00 and 09h00. The text clarifies some of these differences.

Distance walked: The mean distance that beetles moved over the focal period of 1 h varied from 11.6 cm during 08h00–09h00, to 236 cm during 17h00–18h00. This parameter showed three diurnal peaks: 09h00–10h00, 13h00–14h00, and 16h00–18h00 (Figure 1B). Around 15h00 the beetles walked short distances (80 cm/h): multiple comparisons suggested, however, that distances moved during this period did not differ statistically from that of the late afternoon, but did differ from distances moved during the morning. Data from 08h00 differed significantly from those of most other hourly periods.

Walking: The amount of time spent walking around while not involved in feeding or overt sexual behaviour showed a pattern similar to that of distances moved. An early morning activity peak was, however, more

evident (Figure 1A). An increased amount of time spent walking in the late afternoon did not differ statistically from low levels of walking during midday (Tukey's multiple comparison).

Chasing: This behavioural category comprised sexual behaviour including mate following, mate guarding, mounting and attempted copulation. Like feeding, chasing showed two peaks; from 11h00–13h00 and at 17h00 (Figure 1C). Mating was less common from 14h00–15h00: however, the level of chasing at mid-day did not differ statistically from those at other times of day (Tukey's multiple comparison).

Digging in (buried): Beetles often buried themselves at night, as well as during the day between 12h00–15h00 (Figure 1D). The cover used during this period normally consisted of detritus (dead *Acacia* leaflets) or other vegetation. The amount of time spent buried during midday differed statistically from those during early morning and late afternoon (multiple comparison).

Periods of inactivity: Beetles were inactive (i.e. standing still) early in the morning before 09h00 and in the afternoon, the amount of time spent inactive increasing after 14h00 (Tukey $p < 0.05$; Figure 1D). Levels of inactivity did not resemble those for digging in and showed a small peak during the period of decreased chasing, feeding and walking around 15h00. Levels of inactivity at this time did not differ statistically from those at mid-day (multiple comparison).

Feeding: Feeding was the most commonly recorded activity between 09h00 and 11h00 (Figure 1E). A second, but less important, peak in feeding occurred from 16h00–17h00, with a period of low feeding activity during 13h00–15h00. However, Tukey's multiple comparison suggested that the afternoon peak in feeding did not differ statistically from feeding levels at other times of day.

Ambient temperature: At 08h00 the ambient temperature was about 13 °C, while the hottest part of day was between 15h00 and 18h00, when the mean ambient temperature exceeded 28 °C (Figure 1F).

DISCUSSION

A bimodal activity pattern has been suggested for the Namib tenebrionids *Lepidochora discoidalis* (Louw & Hamilton 1972), *Onymacris plana* (Henwood 1975), *Onymacris rugatipennis* (Hamilton *et al.* 1976), three species of Zophosini (Wharton 1980) and for *Onymacris langi* and *Physadesmia globosa* (Hamilton 1975). Both Hamilton (1975) and Wharton (1980) remarked that the activity of tenebrionids appeared to be unimodal during cool days when exposure to the sun and overheating is reduced. The present observations were made during the hottest time of the year at Gobabeb (Weather Bureau 1985): observations during winter are likely to show trends similar to those observed by these authors.

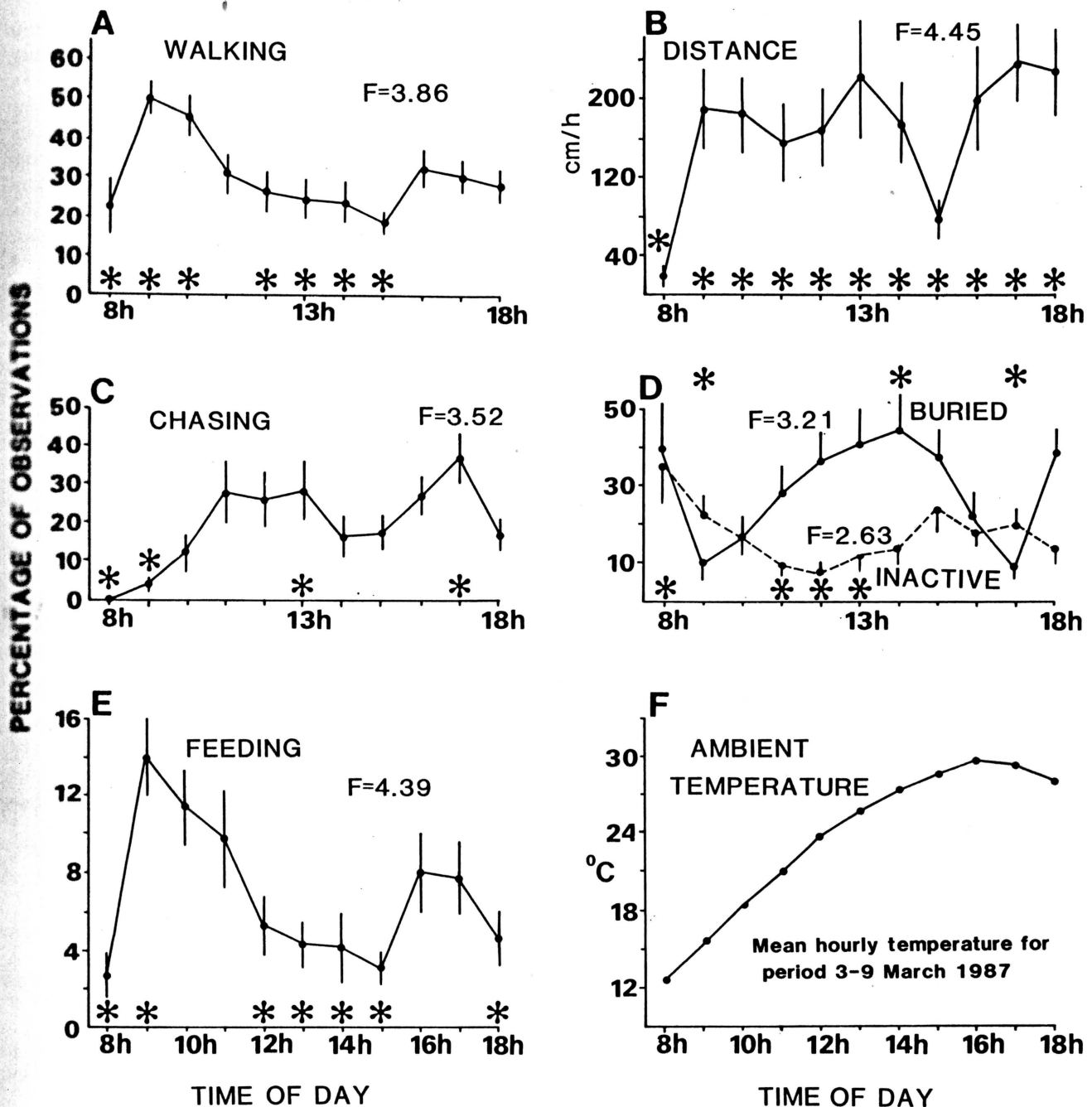


FIGURE 1. Mean percentages of time that *Physadesmia globosa* spent in various behavioural categories at different times of the day during February and March 1987. Tick marks indicate hourly periods starting with the indicated time, e.g. 18 h represents the hour 18h00–19h00. F-values (d.f. = 10, 189) resulting from a single classification ANOVA on transformed data indicate the significance ($p < 0.005$ in all cases) of diurnal variations in behavioural patterns over the 11 hourly periods. Asterisks indicate mean hourly activity levels differing significantly from other hourly values of the same behavioural category (Tukey's studentised range test, $p < 0.05$). Vertical bars indicate SEM. Figure 1D indicates variations in amount of time inactive aboveground (broken line; bottom F-value and asterisks) and time buried (solid line; top F-value and asterisks).

It therefore appears that the crude activity measures used on *P. globosa* by Hamilton (1975) and Marden (1987) do in fact reflect the walking, feeding and mating behaviour of this species.

This study revealed that the morning activity peak is clearly divided into two components: feeding takes place mostly before 11h00 (Figure 1E) while chasing behaviour is performed mostly after 11h00 (Figure 1C). These two peaks are reflected in Figure 1B which depicts the activity as measured in terms of distance

walked per hourly observation period. One would expect that two factors, the relatively cool temperatures of the morning before 11h00 (Figure 1F) and the fact that feeding behaviour does not require walking over large distances would predispose beetles towards shorter distances moved before 11h00. Figure 1A, however, indicates that *P. globosa* individuals move over large distances soon after becoming active after 09h00. In addition, beetles spent a significantly greater amount of time (Tukey multiple comparison $p < 0.05$; Figure 1A) walking during the early feeding

peak (around 09h00) than during the late morning (around 12h00) when chasing behaviour was more prevalent. Although not statistically different, *P. globosa* appears to spend more time feeding during the morning than during the afternoon: the morning peak is 3 h long and higher than the 2 h long feeding peak around 17h00. This phenomenon is not surprising as one would expect these small animals to be in need of food immediately after a period of inactivity lasting about 12 h overnight.

Mean relative humidity often came close to the saturation point in the early mornings between 06h00 and 08h00. This would cause the moisture content of the detritus upon which the beetles feed to be greater before 10h00 than at other times of the day and could be an important source of moisture in a desert environment. If this were the case, early morning feeding would be advantageous.

Chasing behaviour included mate following, mate guarding, mounting and attempted copulation: all these components of mating behaviour showed a bimodal pattern broadly resembling the behavioural categories discussed above. The spurt of chasing activity in the late afternoon (around 17h00) was the highest of the day (Figure 1C).

P. globosa individuals often dig themselves into detritus or sand of the Kuiseb River bed in a similar way to other *Adesmiini*, e.g. *Onymacris unguicularis* in the sand dunes (Louw *et al.* 1986). *P. globosa* individuals spent the least amount of time buried beneath sand during the early morning feeding period (around 09h00) and during the late afternoon (around 17h00). Digging could, however not be directly correlated with the daily temperature (Figure 1F) or humidity profiles at the study site: the highest temperatures and the lowest humidities normally occurred after 15h00, when the amount of time spent beneath the sand was decreasing rapidly (Figure 1D).

Above-ground inactivity was the most prevalent during the early morning and during the afternoon from 14h00–17h00, when chasing, feeding and walking were at low levels. This behavioural category invariably occurred in the dappled shade of *Acacia erioloba* trees or *Salvadora persica* thickets. The early morning period of inactivity was associated with the emergence of beetles from their nocturnal sleeping places. It therefore appears that surface inactivity is not directly connected with digging behaviour.

From an evolutionary point of view, a bimodal activity pattern need not be an evolved adaptation in response to an environmental constraint, but could be a fortuitous effect. As far as feeding is concerned, one would expect a high feeding level immediately after an animal has become active. If a large part of the animal's food requirements were met by early feeding, a later drop in feeding would be the fortuitous effect of sufficient food intake. In the case of *P. globosa*, however, all the behavioural categories show a bimo-

dal pattern, including chasing and time buried. As the latter two behavioural patterns are probably not governed by the same motivational factors as feeding, it is unusual to find a bimodal activity pattern in all these behavioural categories. This is not easily explainable as an effect and one should therefore consider the possibility that the bimodal activity pattern is an evolved adaptation. However, this paper does not offer data providing the adaptiveness of a bimodal activity pattern. In the literature, much discussion has surrounded this type of activity pattern of Namib tenebrionid beetles: Hamilton (1975) used bimodal data in support of his maxithermy hypothesis while Henwood (1975) and Wharton (1980) emphasised that this activity pattern is advantageous because of heat stress avoidance. Hamilton, however, subsumes the latter explanation in his hypothesis. The heat stress hypothesis is relatively easily and directly testable and because of its simplicity, should have preference over higher-level hypotheses like the maxithermy hypothesis.

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