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Food and Habitat Use by Three Tenebrionid Beetles (Coleoptera) in a Riparian Desert Environment

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Use of food and habitat by three species of diurnal adesmine tenebrionid beetles was assessed by crop analyses and pit trapping. *Physadesmia globosa* (Haag), *Onymacris rugatipennis rugatipennis* (Haag) and *Stenocara gracilipes* Solier were chosen for this study as they are the three most common conspicuous macrodetritivores living in the riparian woodland of the usually dry Kuiseb River in the central Namib Desert. The types of food consumed overlapped extensively among species and months of the year, whereas the overlap of habitat use among species and months was less.

### INTRODUCTION

Desert environments generally have abundant detritus with relatively slow or variable rates of decomposition (Crawford and Gosz, 1982). As decomposition by bacteria and fungi is limited by the pervading aridity, macrodetritivores are relatively important to nutrient and energy cycling (Crawford and Taylor, 1984). Endogenous enzymes (Marcuzzi and Lafisca, 1977) and symbiotic gut fauna (Crawford and Taylor, 1984) enable macrodetritivores to use detritus effectively.

One group of purported macrodetritivores, tenebrionid beetles, are a numerically important component of the biota of the Namib Desert (Koch, 1962). Within the riparian woodland of the Kuiseb River, three species of adesmine tenebrionid beetles are among the most common and conspicuous components of the diurnal epigeaic fauna (Wharton and Seely, 1982): *Stenocara gracilipes* Solier, *Physadesmia globosa* (Haag) (Penrith, 1979) and *Onymacris rugatipennis rugatipennis* (Haag) (Penrith, 1975).

Distinctive activity patterns with temporal and spatial differences have been documented for the more common species of tenebrionid beetles living in the lower Kuiseb River and adjacent gravel plains (Wharton and Seely, 1982). Despite the apparent importance of food in determining the density and the habitats used by these species, little work has been directed toward examining the types of food consumed. Holm and Scholtz (1980) stated that 'virtually all desert animals are euhiphagous opportunists' whereas Wharton and Seely (1982) described desert tenebrionids as 'opportunistic omnivores' and stated that 'most of the adesmines ... were observed to feed on animal remains and faeces while foraging for plant material'. A number of authors have observed the three species under consideration, as well as other tenebrionids, foraging near or under particular riverine plant species and have assumed that the beetles were feeding on locally derived detritus (Holm and Edney, 1973; Penrith, 1975; Hamilton, Buskirk and Buskirk, 1976; Hamilton and Penrith, 1977; Roer, 1977; Penrith, 1979; Wharton and Seely, 1982).

This paper investigates the diet of the three most common tenebrionid species in the Kuiseb riverine environment by: 1) examining crop contents to directly determine what food was eaten, a method not often used by workers in this field; 2) using pit-fall traps to establish any possible relationships between selected food and habitat in this environment.

### MATERIALS AND METHODS

The study area was located in the Kuiseb River course near the Namib Research Institute (23° 34' S, 15° 03' E). *Cladoraphis spinosa* (L. fili.) S. M. Phillips is the dominant grass of the river-bed. The perennial woody vegetation of the floodplain is dominated by *Acacia albida* Del. and *A. erioloba* E. Meyer (Seely, Buskirk, Hamilton and Dixon, 1981). Because of the lack of pronounced seasonal change in climate and water availability, trees and grasses growing in the river course produce leaves, flowers and fruit throughout most of the year, contributing substantially to surface litter. This plant material, together with other organic debris, constitutes the detritus that accumulates in the environment.

To examine food consumed by the three tenebrionid species, ten individuals of each species were collected by hand in the field in September and December 1983 and March and June 1984. Beetles were immediately placed on ice in the field and crops were removed within three hours. Crops were fixed in Pamplie's fluid and stored in 70 % alcohol.

Reference slides were made by dissecting fresh and dry plant material from species likely to be present in detritus. Samples were processed in a Waring blender and mounted in Hertwig and Hoyer's solution (Bear and Hansen, 1966).

To analyse the food consumed, crops were severed at the base of the osophagus and at the cardiac valve. Total crop contents were washed into 5 ml of water and spread evenly in a Petri dish (53 mm diameter) containing a grid of 2 x 2 mm units. Presence or absence of animal material, plant material,
sand or unidentifiable fragments were recorded for 100 2 × 2 mm units across 5 rows of the grid.

To determine relative availability of the four major crop components in detritus found under three major plant species, three samples of surface detritus (0–5 mm) from beneath each plant species were spread in a thin layer in a Petri dish and the percentage occurrence in four quadrats was estimated (Crawford, Hanrahan and Seely, this volume).

To examine habitat use by the three tenebrionid species, twenty pit traps (150 mm diameter, 240 mm deep) were set out: five placed in a region dominated by *A. albida*, ten placed in areas dominated by *A. erioloba* (5 north and 5 south of the river course); five placed near clumps of *C. spinosa* where *Nicotiana glauca* R. Graham also occurred. Trap distribution was in proportion to the occurrence of vegetation types. Traps were emptied at two or three day intervals, the identity and numbers of beetles noted, and the beetles released.

Statistical analyses followed procedures outlined in Sokal and Rohlf (1981) and Siegel (1956). A symmetrical overlap index (Pianka, 1973), which ranges from 0 (no overlap) to 1 (complete overlap), was used to evaluate overlap of food and habitat use within and between species.

**RESULTS**

Detritus samples taken from beneath individual plants were found to be derived predominantly from plants in that immediate vicinity and did not consist of a random admixture of detritus from all plant species growing in the riverine habitat. All plant material in the detritus had wind-blown dust and sand adhering to its surface. Proportions of flowers, leaves, sand and unknown material were estimated from samples taken beneath *Acacia albida*, *Acacia erioloba* and *Cladoraphis spinosa* (Fig. 1). Small animals and animal fragments, mainly insect material, represented such a small proportion of the surface detritus that they were not represented in Fig. 1, although closer inspection revealed small insects associated with *Acacia* flowers.

Plant material identified in beetle crops consisted of flowers of *A. albida*, *A. erioloba* and *C. spinosa*, and leaves of *Acacia* species. Anthers and stamens of the flowers were most commonly eaten and leaf material was rarely consumed. The animal material in beetle crops consisted almost exclusively of insect fragments, mainly unrecognizable except as parts of insect cuticle. Ant and dipteran and lepidopteran larvae remains were occasionally identifiable to order. The few whole insects consumed were probably inadvertently eaten because of their association with flower matter. Sand was also found in the crops, but it is not known if it was consumed inadvertently or is involved in digestion. All three tenebrionid species had mixed diets containing all food items listed. In three of the four
months in which we examined diet, there was an overwhelming preference for flower material (Fig. 2).

Using a symmetrical overlap index (Pianka, 1973) we found a high degree of overlap between the species of food types consumed in all months (Table 1). We also found high overlap values for a single species among seasons (Table 2). The high overlap values for crop contents among species and months confirm that the beetles feed upon similar types of food most of the time, agreeing with the casual observations of Robinson and Seely (1980). Moreover, all four items found in the beetle crops also occurred in detritus under A. albida, A. erioloba and C. spinosa (Fig. 1), although the proportions differed from those found in the beetle crops.

Individuals of the three tenebrionid species were captured in every pit trap during every month of the year (Fig. 3). Total numbers captured were 18,228 P. globosa, 2,346 O. rugatipennis, and 555 S. gracilipes. For all three species the distribution throughout the year was non-uniform (P. globosa = 930.29; O. rugatipennis = 713.91; S. gracilipes = 120.73; chi-square, all species df = 11, P < 0.001) although the Kendall coefficient of rank correlation indicated that values for the species varied independently (P. globosa vs O. rugatipennis = 0.424, P = 0.055; P. globosa vs S. gracilipes = 0.182, P = 0.412; O. rugatipennis vs S. gracilipes = 0.242, P = 0.271). A degree of seasonality was suggested for O. rugatipennis, which was trapped most frequently in the winter months of June and July. The percentage trapped in those two months (36%) is more than twice that which would be expected from uniform monthly captures. In contrast, numbers of S. gracilipes declined throughout most of the year; this trend reversed the following year. No pattern of monthly capture was apparent for P. globosa.

For comparison with the food analyses, the percentage occurrence of the beetles within each habitat type has been depicted for September, December, March and June (Fig. 4)
and symmetrical overlap indices calculated. When habitat use between species was compared for the four months, mean overlap values (Table 1) indicated greater variation between species in habitat use than in food type consumed. When habitats occupied by a single species were compared on a monthly basis, the mean overlap values (Table 2) indicated that P. globosa and O. rugatipennis were trapped fairly consistently in the same sites; S. gracilipes showed slightly greater variability in its use of habitat.

Inspection of Figs 1 and 4 shows that there may be a positive relationship between relative amount of time spent near C. spinosa, as indicated by pit-fall trap captures, and amount of insect material consumed. The Spearman’s rank correlation coefficient was, however, not significant, falling between 0.10 > P > 0.05.

**DISCUSSION**

Analyses of crop contents of the three Kuiseb species show that these tenebrionid beetles are definitely detritivores, as has been suggested previously by a number of authors. They are not, however, indiscriminate omnivores as they consistently selected specific food types from detritus irrespective of species of plant under which the detritus occurred. Leaves are the major food type available in detritus (Fig. 1), whereas flowers and fruits formed a conspicuous part of the crop contents (Fig. 2). Those materials consumed appeared to be the more nutrient-rich components of the detritus.

Although the Kuiseb tenebrionids were found to be entirely detritivores, characteristics of their diet do not differ widely from those of the more herbivorous tenebrionids of North American deserts and grasslands. Based on field observations, dissection of digestive tracts and literature citations, Rust (1986) found four detritivores and one herbivore among the tenebrionids of a sand dune insect community in the Great Basin. Staminate conifer cones represented an average of 51% of the diet of six beetle species in Arizona, as determined by feeding observations (Doyen and Tschinkel, 1974). The remainder of the diet consisted of living or dry vegetation. Fifty-two plant species were ingested as living, dead or litter material by 13 beetle species in a community in western Washington, although flower material was not particularly mentioned (Rogers, Woodley, Sheldon and Uresk, 1978). In the latter study, arthropod remains ranged from < 1% to 19% of the contents of the digestive tract of the various species. In the latter two studies, there was a high degree of overlap in diets among species examined, similar to that found in the Kuiseb detritivores.

Our results from the Kuiseb agree with previous descriptions of food and habitat use derived from a number of shorter term studies in the same area (Hamilton and Penrith, 1977; Penrith, 1979; Wharton and Seely, 1982). Although previous authors did not always differentiate between habitat and food use, they generally provided anecdotal observations of selected foraging areas (e.g., Penrith, 1975; Hamilton et al., 1976; Hamilton and Penrith, 1977; Roer, 1977; Wharton and Seely, 1982). Our analyses expand on these observations and provide direct evidence as to the types of food eaten.

The above results do not provide any evidence for exclusive habitat use by any of the three species of tenebrionid beetles investigated. They also leave unanswered the further question as to whether beetles occur randomly within their environment according to microhabitat or according to differences in availability or relative attractiveness of particular food types. Crawford et al. (this volume) provide a detailed evaluation of the question with respect to Physadesmia globosa.

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