Dunefield detritus: its potential for limiting population size in *Lepidochora discoidalis* (Gebein) (Coleoptera: Tenebrionidae) in the Namib Desert

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Lepidochora discoidalis (Gebein) in the central Namib Desert dunefield feeds mainly on small, wind-transported grass detritus. We assessed the limiting influence of this food on an ephemeral beetle population of 1000 individuals (mark-recapture estimate) inhabiting a 70-m long dune crest and its associated slip face. We evaluated two sources of detritus: (1) accumulated material at the slip face base, most of which was progressively buried; and (2) fine, rapidly moving particles blown regularly over the dune crest. In 18- to 19-d feeding tests, beetles ate more detritus containing fine diameter grass awns than they did detritus consisting of large ("coarse") or abraded ("fine") grass leaves. Beetles eating the awn-containing detritus had significantly more fat body and larger eggs. However, published values for daily detritus requirements indicate that this *L. discoidalis* population could not have captured enough of the windblown detritus to maintain its existing density. Thus, accumulated detritus at the slip face base is essential for its continuous occupation of the habitat. Because the presence of accumulated detritus fluctuates greatly, we conclude that food availability may limit the population size of this detritivore.

Les détritus des champs de dunes : leur potentiel à limiter les populations de Lepidochora discoidalis *(Coleoptera: Tenebrionidae) dans le désert du Namib.* - Le coléoptère *Lepidochora discoidalis*, qui vit au centre du Désert Namib dans les champs de dunes, se nourrit principalement de débris organiques apportés par le vent (les détritus). Nous avons mesuré par capture-marquage-recapture dans quelle mesure cette nourriture a influencé et limité une population éphémère de coléoptères de 1000 individus qui habitaient la crête et le versant d'une dune de 70 mètres. Nous avons étudié deux sources de détritus: 1) les débris partiellement enterrés au pied du versant; et 2) les particules miniscules balayées régulièrement au dessus de la crête de la dune. Dans les analyses réalisées aux jours 18 et 19, les coléoptères ont mangé plus de détritus composés de barbes de petit diamètre que du détritus qui contenaient les grosses ou de petites feuilles d'herbe. Les coléoptères qui se nourrissaient de barbes fines avaient plus de corps gras et pondaient des oeufs plus gros. Néanmoins, selon des études publiées, la quantité de détritus nécessaire pour nourrir un coléoptère par jour indique que la population de *Lepidochora discoidalis* ne pouvaient capturer suffisamment de détritus fins pour maintenir le nombre d'individus observés. Donc, les détritus partiellement enterrés sont très importants pour une occupation continuelle des dunes par ce coléoptère. Puisque la quantité de détritus amassés au pied des versants de la dune varie considérablement, nous concluons que la quantité de nourriture disponible peut limiter la population de ce détritivore.

Key words: dunefield habitat, detritus availability, food limitation, habitat occupation, *Lepidochora discoidalis*, Namib Desert.

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INTRODUCTION

Selection and use of living plants by herbivorous arthropods is well documented and known to be strongly influenced by the chemical and physical traits of those plants (e.g., Rosenthal & Janzen, 1979; Slansky & Rodriguez, 1987). Whether similar characteristics of dead vegetation affect its selection and use by terrestrial detritivorous arthropods has received little attention. However, Horner *et al.* (1988) point out that the secondary metabolites in plant litter can be expected to influence the population dynamics of such organisms. As to the physical traits of plant litter, Vincent (1982) indicates that the tissue organization of grass leaves makes it difficult for insects to break them into units suitable for ingestion. Presumably this type of constraint applies to arthropods that eat dead as well as living plant food.

Land dwelling macroarthropods known to select certain types of dead organic material include species of isopods and millipedes in mesic regions (Neuhauser & Hartenstein, 1978; Hassal & Rushton, 1984) and tenebrionid beetles in deserts (Crawford *et al.*, 1990). Here we reason that in deserts, where detritus is comparatively labile, patchy in distribution and restricted in diversity, this material should be more limiting to detritivores than it is in environments where it is relatively stationary, often more uniform in distribution and more diverse. If so, deserts should be useful environments for testing whether detritus quality and quantity can limit populations of terrestrial detritivores.

Dunefields in the hyper-arid Namib Desert of southern Africa support sparse assemblages of surface-active arthropods (Crawford & Seely, 1987). Apparently, the main consumers in these assemblages are detritus-feeding *Psammotermes allocerus* Silvestri termites (Crawford & Seely, 1994) and a diverse assemblage of tenebrionid beetles (Seely, 1978, 1983). The subterranean termites move less rapidly than the surface-active tenebrionids, which should therefore be more capable of using transient and irregularly distributed patches of wind-blown grass detritus. In this paper we assess the influence of such detritus on the density of an ephemeral population of *Lepidochora discoidalis* (Gebein), a species restricted to dune slip faces.

MATERIALS AND METHODS

Site description: detritus and beetle populations

Field studies were conducted on the slopes of a vegetationless north-south dune ridge, ± 70 m in length, located in the Station Dune system ± 1 km south of Gobabeb in the central Namib dunefield. The ridge's east slope descends ±40 m to a sandy plain; its steeper (30-33 °) west slope (the slipface) meets 3-5 m below the ridge crest with a more gradual (5-10°) and much longer slope. The Station Dune system, one of a large series of linear dune systems, begins at and runs roughly south from the usually dry Kuiseb River bed. To the east of the Kuiseb an extensive gravel plain supports a sparse cover of mainly *Stipagrostis* grasses which grow rapidly after infrequent rains. Most of the time these grasses take the form of standing dead detritus, which is progressively abraded by blowing sand and transported by seasonal winds (Robinson & Seely, 1980).

Allochthonous detritus, consisting mainly of wind-imported *Stipagrostis* particles from the plains and local interdunes, was examined at the slip face base and the ridge crest. Using a sieve, on 17 June 1989 we collected as much buried and exposed detritus as possible from the slip face base. Most consisted of leaves of the large dune inhabiting

S. sabulicola (Pitger) de Winter and awns of the widespread *S. ciliata* (Desf.) de Winter. The freshly collected material (405 g) was mixed thoroughly with "neon red" Daglo fluorescent powder in a plastic bag and redistributed in its original pattern.

Detritus flowing over the crest was measured with stiff fiberglass nets (1-mm mesh, which catches almost all detritus, but not sand). Net openings (5 cm high x 28 cm wide) were framed with thin wire, allowing entering detritus to settle in the flat trailing bag, 28 cm in length. (Initial trials showed that particles were seldom trapped higher than 5 cm above the crest.) A heavy wire anchoring rod, 1.5 m in length, was run vertically through the center of the frame and driven halfway into the sand. Tape around the rod between the net opening and the sand enabled the net to swivel in the wind just above the sand surface. Seven nets were placed along the crest, 10 m apart, with their openings facing the prevailing wind. They were operated for 48 h on 21-22 July, the first day being characterized by light breezes. A strong east wind, averaging ± 50 km/h (Gobabeb weather records) during the 2-3 h of its greatest intensity, dominated during the second day. These conditions are fairly typical of winter weather at Gobabeb.

Population density measurements of *Lepidochora discoidalis* beetles were begun on 17 June. We collected 200 individuals by hand from the slipface base, where most were active that day. Beetles were marked on the elytra with poster paint and released where captured. The procedure was repeated daily, using different colors of paint, for the next 4 d. Proportions of marked and unmarked beetles were recorded on those days and at subsequent intervals (see below). Mark-recapture analysis was performed using Statpak (Anonymous, 1985) software.

Feeding tests

Many initial observations showed that *L. discoidalis* typically selects small pieces of fine diameter detritus. These are pursued during windy periods on steep slopes, and also handled more passively in detritus accumulations at slip face bases. Many of the items are bristle-like *Stipagrostis* spp. awns attached to bracts previously enclosing grass seeds. We observed relatively little feeding on larger items (mainly grass leaves and stems) that comprise the great majority of the accumulated detrital biomass. To test the influence of detritus type (awn or leaf) and diameter on food selection, we first starved field-collected beetles at Gobabeb for 48 h to clear their guts, then placed groups of 10 individuals on sand (2 cm deep) in open plastic containers (length x width: 20 x 15 cm; height: 10 cm).

Using size as a criterion for sex (females tend to be larger than males but otherwise similar in appearance), we employed sex ratios ensuring at least 50 % females (verified by subsequent dissection). Containers with beetles were divided into the following four treatments, each replicated three times: 1) assorted detritus (including awns) collected from the field site, 2) "coarse" detritus from the site consisting only of grass leaves > 5 mm in diameter cut in 5 cm lengths, 3) "fine" detritus from the site consisting only of similar leaves shredded with a scissors to units < 1mm in diameter, and 4) no detritus (control). A second control consisted of beetles collected during their late afternoon foraging and frozen within an hour. All containers occupied a room in which air temperatures approximated those of the study site. Windy weather caused moderate (unmeasured) air movement in the room. Darkness in the room was guaranteed only between 23:00 and 07:00 hours.

Beetles treated experimentally were killed by freezing and then examined under a dissecting microscope after 17-18 d to determine the following: 1) relative amounts of ingested material in the foregut, midgut and hindgut; 2) relative amounts of fat body remaining in the abdominal cavity; and 3) length of the largest remaining eggs in females. Amounts of food in each gut region were ranked as 2 (considerable), 1 (moderate), or 0 (no food). The same system was used to rank amounts of fat body in the abdomen. Egg lengths were measured with an ocular micrometer.

Results of all rankings (summed ranks in the case of ingested detritus) were analysed using the Kruskal-Wallis test followed by the Student-Newman-Keuls multiple range test. A G test for heterogeneity was used to compare egg lengths (Zar, 1984).

RESULTS

Detritus dynamics

The dyed detritus was completely buried by avalanching sand within a month of its redistribution below the slip face. It remained buried for ± 10 mo, when a second sieving collected 78.6 g, of which only 2.9 g were still dyed .

The 7 detritus nets on the dune ridge trapped an average (± SE) of 0.173 ± 0.037 g of mainly fine, wind-borne detritus in 48 h. To compensate for minor losses due to handling and fine particles passing through the mesh, we rounded that value upward to 0.2 g. This resulted in an estimated average per net of 0.1 ± 0.02 g/d and a total estimated catch of 0.7 ± 0.14 g/d. Because the seven nets collectively spanned 2.8 % of the crest's 70 m length, they trapped an estimated 25 ± 5 g of detritus per day over the entire crest (in both directions) during the 2-d collection period.

Beetle populations

The Jolly-Seber mark-recapture estimate for the study site population in mid-June was 1021 individuals (95 % confidence intervals: 630-1412). Of the 675 beetles marked over a 4-d period, 188 (27.9 %) were recaptured at least once by day 5. Marked individuals gradually disappeared from the site, presumably by migration (Fig. 1). Only four of the 81 specimens (4.9 %) collected on day 89 bore marks. Some marked beetles travelled considerable distances, always along the main ridge of the Station Dune system. On day 20, two were seen within 20 m of the system's highest point, nearly 1 km from the study site.

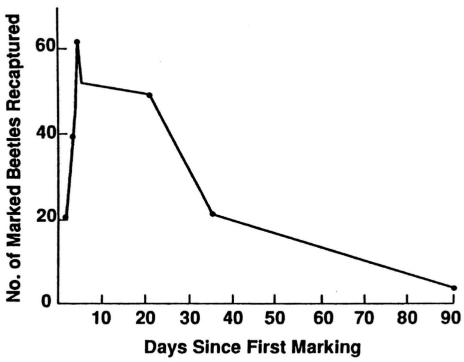

Fig. 1. - Recaptures over time of previously marked *L. discoidalis*. Beetles were not marked after the third date indicated.

Feeding tests

The type but not necessarily the diameter of detritus offered to the beetles had clear effects on the three parameters examined: gut contents, fat body and egg size. Kruskal-Wallis rankings of residual gut contents and fat body condition (Table 1) were significantly lower (H for both = 147.0, 4 df, $P < 0.05$) when "coarse" and "fine" grass pieces were the only foods available than when an assortment of detritus was present. Small amounts of ingested material in the guts of unfed beetles may have originated from airborne particles that

Table 1. - Ranked *L. discoidalis* gut content and fat body condition following feeding test.

Treatment	Kruskal-Wallis average ranks n	Gut contents	Fat body
Detritus with awns	30	88.3[a]	93.6[a]
"Coarse" grass leaves	28	54.8[b]	69.3[b]
"Fine" grass leaves	30	69.8[b]	56.0[b]
No detritus	30	29.3[c]	62.9[b]
Field controls	30	121.1[d]	90.3[a]

Means followed by the same letter are not significantly different (P < 0.05; Student-Newman Keuls multiple range test [Zar, 1984]).

Table 2. - Size (length) comparison of largest eggs remaining in *L. discoidalis* following feeding test.

Treatment	No. females with largest remaining egg: < 1 mm length	> 1 mm length
Detritus with awns	5	4
"Coarse" grass leaves	7	4
"Fine" grass leaves	18	5
No detritus	16	8
Field controls	7	10

settled on the sand, and/or from organic residues already present in the sand.

Treatment effects on lengths of the largest remaining eggs are shown in Table 2. Egg length was not independent of treatment (G = 14.78, 4 df, P < 0.01). The largest remaining eggs from field control females and from females fed detritus containing awns tended to be longer than those of females fed either nothing or detritus without awns.

DISCUSSION

The selective use of available detritus by *Lepidochora discoidalis* appears to have metabolic and possibly reproductive consequences. These beetles consume and utilize detritus containing relatively ephemeral grass awns more effectively than large or small fragments of relatively persistent grass leaves. Tissues associated with plant reproduction may also have special value to other Namib tenebrionids. Thus, *Onymacris plana* (Peringuey) produces more eggs after eating curcubit flowers than after ingesting grass stalks (Seely 1983), and *Physadesmia globosa* (Haag) consistently consumes a high ratio of fallen *Acacia* tree flowers to leaves (Crawford *et al.* 1990).

Because the "preferred" awn-containing food of *L. discoidalis* has potential fitness benefits yet constitutes only a small proportion of available detritus, and because *L. discoidalis* densities can be strikingly different in very similar habitats (many personal observations), we ask whether local densities of this beetle can be limited by the availability of such detritus. In doing so, we acknowledge but have not estimated the possible effects of chance, abiotic factors and biotic interactions on density.

Our study site initially contained about 1000 beetles, many of which remained in the immediate vicinity for more than a month despite their ability to move rapidly to other detritus-rich locations in the same dune system. Individual beetles require 3.7 mg of dunefield detritus per day, and can starve for at least two months (Louw & Hamilton, 1972). If the 3.7 g of detritus required by the 1000 beetles had consisted only of awns and other small items blowing over the dune crest, if 25 g/d was in fact a reasonable average for this flux, and if no other source of detritus had been present, the beetles we observed would have had to trap and eat 14.8% of the blowing material in order to maintain themselves. In reality, this would not have happened because during windy periods, when beetles are active, very few individuals actually catch and eat blowing particles which swirl much faster than beetles run. This suggests that windblown material on the slip face is an insufficient source of food in the long term.

Other foods include occasional scattered pieces of detritus such as tiny particles in the sand (< 1 % of the sand mass-unpublished results) as well as detrital accumulations at slip face bases. If the windblown material is insufficient for 1000 beetles, then these resources take on relative importance. At the Station Dune site, the slip face accumulations should have weighed about 500 g, considering our collection procedures. Most of this material consisted of relatively large grass leaves and stems. How much was consumable is not known; we offer an estimate of 5 %, or 25 g. Without replacement, that amount would have been eaten in about a week, and continuous occupation of the site by 1000 beetles could not have occurred.

The dynamics of this consumer-detritus relationship are clearly complex. They are also difficult to measure and should be monitored over long periods in order to account for climate variation. In our admittedly short-term, winter season study the design and placement of detritus-catching nets may have led to an underestimate of the amount of detritus entering the site. Nonetheless, if our assumptions and calculations are at all realistic, they imply that in ecosystems of very low productivity, the quality and quantity of allochthonous detritus can govern detritivore population densities.

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