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Authors: Glazier, Douglas S., and Kleynhans, Elsje

Source: African Invertebrates, 56(3) : 729-738

Published By: KwaZulu-Natal Museum

URL: <https://doi.org/10.5733/afin.056.0315>

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Arboreal herbivory by a semi-terrestrial South African isopod crustacean, *Tylos capensis* Krauss (Isopoda: Tylidae), on the bietou bush, *Chrysanthemoides monilifera* (L.) Norlindh

Douglas S. Glazier^{1,2*} and Elsje Kleynhans^{2,3}

¹Department of Biology, Juniata College, Huntingdon, Pennsylvania, 16652
USA; glazier@juniata.edu;

²Department of Conservation Ecology and Entomology, Stellenbosch University,
Matieland, 7602 South Africa;

³South African Subtropical Growers' Association, P.O. Box 886, Tzaneen,
Limpopo, 0850 South Africa; elsje.subtrop@gmail.com

*Corresponding author

ABSTRACT

Most terrestrial isopods are ground-dwelling, scavenging detritivores, and rarely eat live vegetation. Here we report field and laboratory observations of the semi-terrestrial South African isopod, *Tylos capensis* Krauss, feeding above ground on live green leaves of the bietou bush, *Chrysanthemoides monilifera* (L.) Norlindh. The factors involved in the origin of this unusual arboreal feeding behavior are unknown, but we discuss three possible, not mutually exclusive, hypotheses that require testing: (1) Umhlanga beach, South Africa (our study site), provides insufficient detrital food to support the dense populations of *T. capensis* found in this area, thus causing these animals to seek out other food sources, (2) the relatively palatable and abundant *C. monilifera* leaves provide an easily accessible and digestible food source, and (3) few competing insect herbivores feed on *C. monilifera* leaves at Umhlanga beach, thus locally freeing up this resource for *T. capensis*.

KEY WORDS: Afrotropical Region, South Africa, Umhlanga, Asteraceae, Oniscidea, Isopoda, *Tylos capensis*, *Chrysanthemoides monilifera*, behavioral flexibility, ecology, herbivory, marine coastal environments.

INTRODUCTION

Many marine isopod crustaceans are herbivorous, feeding on macro- and (or) microalgae (e.g., Hemmi & Jormalainen 2002), though a wide variety of other feeding types (e.g., omnivory, carnivory, detritivory and parasitism) also occur (Poore & Bruce 2012). By contrast, most terrestrial and freshwater isopods are detritivores that scavenge decaying plant or algal litter (Zimmer 2002; Wilson 2008). Terrestrial oniscidean isopods are typically ground dwelling and rarely feed on live vegetation, though some species will feed on plant seeds (Saska 2008), and when abundant they can be pests on roots, fruits, seedlings or other young plant growth in gardens, greenhouses and crop fields (e.g., Messelink & Bloemhard 2007; Alfaress 2012). On land, the presence of numerous abundant species of insect herbivores may have inhibited the evolution of herbivory by isopods (also see Discussion).

Here we report that the semi-terrestrial South African isopod *Tylos capensis* Krauss feeds above ground on the live green leaves of the bietou bush, *Chrysanthemoides (Osteospermum) monilifera* (L.) Norlindh. This unusual feeding behavior was observed in the field and laboratory. Factors possibly facilitating the origin of arboreal herbivory in *T. capensis* are also briefly discussed.

MATERIAL AND METHODS

Basic biology of Tylos capensis

Tylos capensis is a supralittoral oniscidean isopod (family Tyliidae) (body is oval-elongate reaching a maximum length of 36 mm) that has been described as a burrowing detritivore that nocturnally scavenges algal wrack on sandy beaches from False Bay of the Western Cape Province east to the southern KwaZulu-Natal Province (Barnard 1932; Kensley 1974). However, this trophic description is based largely on observations of the larger western South African congener *T. granulatus*, which has been assumed to be ecologically similar (see Kensley 1974). Actually, the feeding habits of *T. capensis* in the field are not well known. The mouthparts of *T. capensis* are capable of cutting food into pieces (Kensley 1974), thus making leaf-eating a possibility. In the laboratory it eats many kinds of marine algae, as well as the leaves of sour fig (*Carpobrotus edulis* (L.) N.E. Br) and the seagrass *Ruppia maritima* L. (Kensley 1974).

Basic biology of Chrysanthemoides monilifera

Chrysanthemoides monilifera is a daisy (family Asteraceae) that grows as a perennial evergreen woody shrub reaching 3 m or more in height (Blood 2001). It is native to South Africa, and has been introduced to Australia and New Zealand, where it has been frequently planted along sea coasts to help prevent beach erosion, but its extensive increase in distribution and abundance has made it a problematic invasive species in need of biological control (Adair *et al.* 2012; Scott & Batchelor 2014). *C. monilifera* includes six subspecies (Norlindh 1943), two of which are of concern for this study: *C. monilifera monilifera* (often called “boneseed”), which is mainly distributed in the Western Cape Province of South Africa and *C. monilifera rotundata* (often called “bietou” or “bitou bush”), which is chiefly distributed along the southern and eastern coasts of South Africa (Scott 1996; Weiss *et al.* 2008).

Field observations

Field observations of *T. capensis* behavior in association with the bietou bush, *C. monilifera rotundata* were made after sunset (1900 to 2030) on 2 February 2013. The study site included rows of bietou bushes that bordered “The Promenade” and nearby walkways along Umhlanga beach, approximately 17 km north of Durban, South Africa (Figs 1, 2). During the day on 30 and 31 January 2013, a few individuals of *T. capensis* were observed in sandy soil or leaf litter of coastal forest in Umhlanga (between The Promenade and Lagoon Drive).

Laboratory observations

Our laboratory observations at Stellenbosch University served to verify that *T. capensis* not only eats the live leaves of *C. monilifera*, but also can sustain its body mass while feeding only on them. We exposed individuals of *T. capensis* (collected in Umhlanga on 2 February 2013) to five feeding treatments (during 21 February to 23 March, 2013): no food, lettuce, or fresh green leaves of *C. monilifera* from three different localities (collected on 21 February 2013 from Jan Marais Nature Reserve in Stellenbosch, South Africa; on 26 February 2013 at Cape Hangklip, between Pringle Bay and Betty’s Bay, South Africa; and on 5 March 2013 at Yzerfontein, South Africa). The leaves of *C. monilifera* collected from Jan Marais Nature Reserve and Cape Hangklip resembled those described for the subspecies *C. monilifera monilifera* (relatively thin with serrated



Figs 1, 2. Photographs at night of senior author D.S. Glazier near rows of bietou bushes *Chrysanthemoides monilifera rotundata* along walkways near The Promenade of Umhlanga beach, South Africa. These are two of the sites where numerous individuals of the isopod *Tylos capensis* were observed climbing on bietou bushes. Photographs © E. Kleynhans.

edges), whereas those from Yzerfontein were thicker (more succulent) and more smoothly rounded, thus more closely matching those of the subspecies *C. monilifera rotundata* observed at our field site in Umhlanga (cf. Weiss *et al.* 2008). However, the

reader should be cautioned that the subspecies of *C. monilifera* exhibit considerable variation and readily hybridise, and thus identifying them is not clear cut (Blood 2001).

After being fasted for 1 d, 10 isopods per treatment were placed individually in 150 ml plastic cups with perforated tops and containing tissue paper moistened with water to maintain high humidity. Brief fasting was necessary to ensure that feces produced during the trials originated from eating the experimental food. In the food treatments, leaves were supplied *ad libitum*. Ambient air temperature was 21–24°C. The isopods were weighed (± 0.1 mg) using a Mettler Toledo New Classic MF balance at the start and end of an experimental run (duration = 6 d). Survival was also recorded after 6 and 9 d for all five treatments and after 21 d for the no food, lettuce and boneseed leaf treatments. The survival time (d) for 90 and 50% of the individuals in each food treatment group (lethal duration [LD]: LD90 and LD50 respectively) was calculated from the fitted logistic regression in R [using the *dose.p* function (Venables & Ripley 2002) in the MASS library]. The non-linear effect of food source, i.e. no food, lettuce, boneseed leaves (*Chrysanthemoides monilifera monilifera*) from Jan Marais Nature Reserve, boneseed leaves (*C. monilifera monilifera*) from Cape Hangklip, or bietou bush leaves (*Chrysanthemoides monilifera rotundata*) from Yzerfontein, and exposure duration, i.e. 6, 9 or 21 d, depending on food source, on the proportional survival (calculated as the number of individuals alive divided by the total number of individuals) was tested using a logistic regression with a quasi-binomial distribution of errors and probit link function in R (v. 3.1.0, R Development Core Team 2010).

RESULTS

Field observations

At night numerous individuals of *T. capensis* were observed climbing on the stems and leaves of *C. monilifera rotundata* as high as 1 m or more above the ground (Fig. 3). Evidence of feeding included many leaves with holes or cut out margins and the frequent observation of isopods at or near eaten leaf margins. No other kinds of nocturnal or diurnal herbivorous animals were seen on *C. monilifera* at the time of our observations.

Laboratory observations

In the laboratory, individuals of *T. capensis* ate the fresh green leaves of lettuce and both boneseed and bietou bush (both subspecies of *C. monilifera*), as indicated by the appearance of holes or cut out margins of the supplied leaves (as observed in the field) and the presence of dark feces in containers with food, but not in containers with no food. The isopods did not have significantly different mean body masses among the treatment groups at the start of the experimental runs (ANOVA: $F_{4,45} = 1.70$; $P = 0.17$; Table 1). Since some isopods died during the testing period, comparisons of start and end mean body masses were made only for individuals that survived until the end of an experimental run. Only isopods given no food showed a significant decrease in mean body mass during the experiment (Table 1). All other treatment groups with food showed no significant change in mean body mass after 6 d (Table 1). All of the treatment groups showed 20–70% mortality by 6 or 9 d, except for the treatment group with bietou bush leaves as food, where all individuals survived (Table 2). For the treatment groups that were followed for 21 d (not including the bietou bush leaf treatment, which was run for only 9 d), only those with boneseed leaves showed any survivors (Table 2). Logistic

survival assays showed that there were significant differences among the different food treatments (GLZ: $x^2=14.13$, d.f.=4, $P=0.007$), and a significant interaction effect between food treatment and exposure duration (GLZ: $x^2=33.35$, d.f.=4, $P<0.001$) on the proportional survival. However, the main effect of exposure duration did not have a significant effect on survival ($x^2=0$, d.f.=1, $P=1$). The calculated time (d) for 50% of the population to die whilst exposed to the different food treatments, as determined from the logistic regression, were (means \pm one standard error) 8.9 ± 1.1 d for no food (Fig. 4A), 7.5 ± 0.9 d for lettuce (Fig. 4B), 13.1 ± 3.3 d for boneseed leaves (*C. monilifera monilifera*) from Jan Marais Nature Reserve (Fig. 4C), 15.6 ± 5.5 d for boneseed leaves (*C. monilifera monilifera*) from Cape Hangklip (Fig. 4D) and undetermined for bietou bush leaves (*Chrysanthemoides monilifera rotundata*) from Yzerfontein since survival estimates were 100% across the logistic regression exposure duration (Fig. 4E). The estimates for the survival of 90% of the populations are indicated on the logistic regression graphs (Figs 4A–D).

DISCUSSION

Tylos capensis exhibits an unusual behavior for a terrestrial isopod: it not only eats live leaves still connected to a plant (rather than dropped as litter), but also climbs up stems as high as 1 metre or more above the ground to reach them. Furthermore, it can



Fig. 3. Photograph at night of individuals of the isopod *Tylos capensis* climbing on stems and leaves of the bietou bush *Chrysanthemoides monilifera rotundata* along a walkway near The Promenade of Umhlanga beach, South Africa. Note the holes and cut-out margins of some of the leaves indicating feeding activity. Photograph © E. Kleynhans.

TABLE 1

Mean \pm SEM live individual body masses (mg) of the isopod *Tylos capensis* at the start (0 d) and end (6 d) of being exposed to five different food treatments (sample sizes in parentheses): no food (NF), lettuce (L), boneseed leaves (*Chrysanthemoides monilifera monilifera*) from Jan Marais Nature Reserve (BSM), boneseed leaves (*C. monilifera monilifera*) from Cape Hangklip (BSH), or bietou bush leaves (*Chrysanthemoides monilifera rotundata*) from Yzerfontein (BBY). Paired t-test results are shown, comparing the mean body masses of individuals at 0 and 6 d that survived an experimental run (d=day(s), t=t statistic, df=degrees of freedom, and P=probability that the body-mass difference between 0 and 6 d is the result of chance). The t value that is statistically significant ($P < 0.05$) both before and after correction for multiple comparisons (based on Šidák's multiplicative inequality: Rohlf & Sokal 1995) is shown in bold.

Treatment	0 d (all)	0 d (only 6 d survivors)	6 d	t	df	P
NF	54.0 \pm 1.5 (10)	54.2 \pm 1.9 (8)	51.0 \pm 1.8 (8)	-5.76	7	0.00069
L	54.5 \pm 2.1 (10)	53.8 \pm 2.7 (7)	54.0 \pm 1.8 (7)	0.12	6	0.91
BSM	54.7 \pm 2.0 (10)	53.5 \pm 2.3 (8)	51.3 \pm 1.8 (8)	-2.17	7	0.067
BSH	51.6 \pm 2.5 (10)	50.7 \pm 2.2 (7)	54.0 \pm 2.4 (7)	2.31	6	0.061
BBY	59.8 \pm 3.1 (10)	59.8 \pm 3.1 (10)	60.1 \pm 3.3 (10)	0.26	9	0.80

TABLE 2

Number of individuals (out of a starting total of 10 per treatment) of the isopod *Tylos capensis* that survived 6, 9 and 21 d while exposed to five different food treatments: no food (NF), lettuce (L), boneseed leaves (*Chrysanthemoides monilifera monilifera*) from Jan Marais Nature Reserve (BSM), boneseed leaves (*C. monilifera monilifera*) from Cape Hangklip (BSH), or bietou bush leaves (*Chrysanthemoides monilifera rotundata*) from Yzerfontein (BBY). The bietou bush leaf treatment was run for only 9 d.

Treatment	6 d	9 d	21 d
NF	8	5	0
L	7	3	0
BSM	8	5	3
BSH	7	6	4
BBY	10	10	–

sustain its body mass while feeding on fresh leaves, including lettuce and the green leaves of the bietou bush *Chrysanthemoides monilifera rotundata* (Table 1), the plant that was eaten at our Umhlanga field site (Fig. 3). *T. capensis* can also sustain its body mass while feeding on leaves of boneseed, another subspecies of *C. monilifera* (ssp. *monilifera*) (Table 1). However, *T. capensis* appears to survive better on leaves of bietou bush than those of boneseed (Table 2). Over a 9 d period, no isopod mortality was observed for the bietou bush leaf food treatment, whereas all other food treatments (no food, lettuce, and boneseed leaves from two different localities) showed substantial isopod mortality (40–70%; see Table 2). For the treatment groups that were run for 21 d, only those with *C. monilifera* leaves showed survivors (Table 2). Better survival for the isopods fed *C. monilifera* leaves was also indicated by their survival curves (Fig. 4C, D)

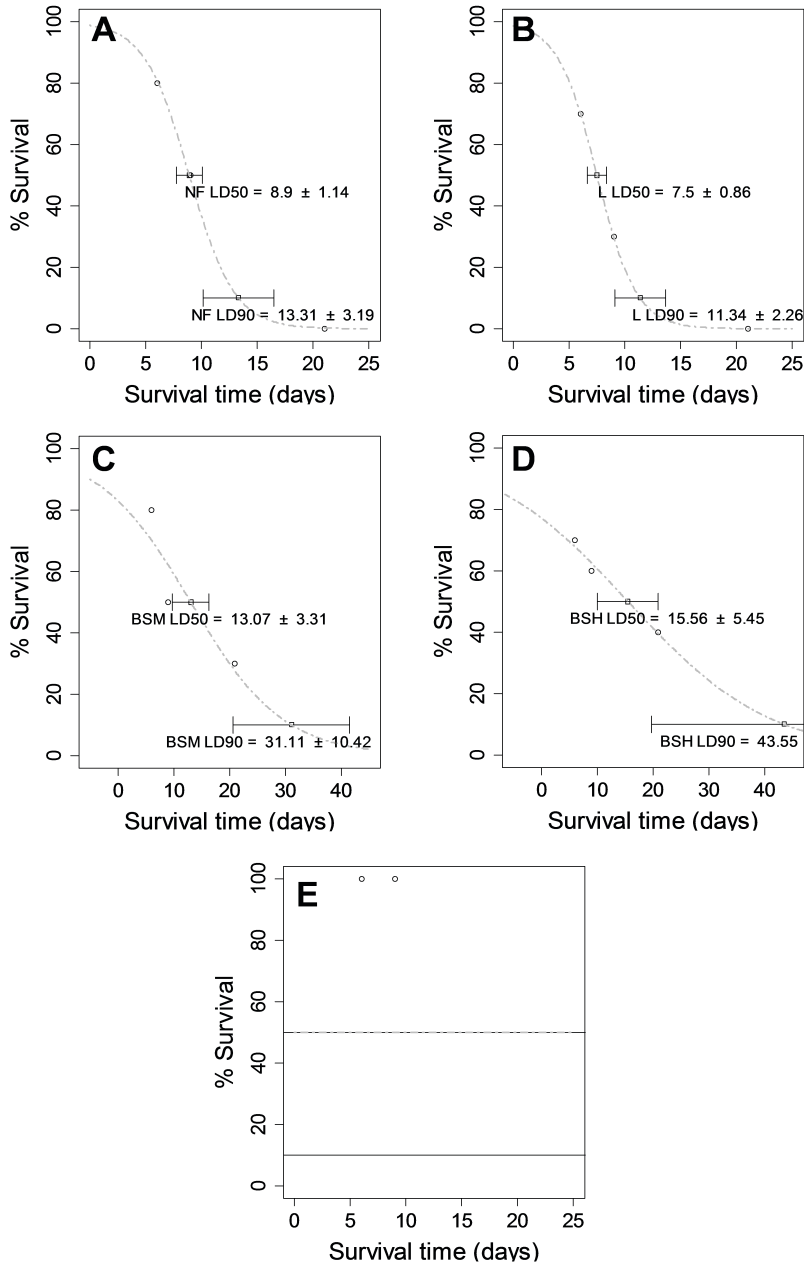


Fig. 4. Logistic curves of the survival of the isopod *Tylos capensis* (expressed as a percentage) as a function of time for five different food treatments: (A) no food (NF); (B) lettuce (L); (C) boneseed leaves (*Chrysanthemoides monilifera monilifera*) from Jan Marais Nature Reserve (BSM); (D) boneseed leaves (*C. monilifera monilifera*) from Cape Hangklip (BSH); or (E) bietou bush leaves (*Chrysanthemoides monilifera rotundata*) from Yzerfontein. The logistic regression lines are plotted through the raw survival data (shown as unfilled circles) and the estimated mean survival times for 50 and 90% of each treatment group (LD50 and LD90 respectively) are shown with \pm one standard error of the mean.

being significantly different from those of isopods fed lettuce or given no food (Fig. 4A, B). Further survival and body-condition studies are needed to verify and extend these preliminary results. Comparative energy-budget analyses of *T. capensis* feeding on *C. monilifera* leaves and other food sources likely encountered in nature (e.g., algal wrack and leaf litter) would also be especially useful.

Whether *T. capensis* in nature feeds on the live leaves of other plants besides *C. monilifera* is unknown and remains to be determined. Why arboreal herbivory occurs in *T. capensis* is also unknown. However, three not mutually exclusive hypotheses requiring testing may help explain this unusual behavior. First, paucity of detrital food on Umhlanga beach may have 'forced' *T. capensis* to seek out other food sources. This hypothesis is supported by the scarcity of algal wrack (a major food source for *T. capensis*, according to Kensley 1974) observed by us on Umhlanga beach during 30 January to 2 February 2013, though more extensive year-round surveys are needed.

Whether *T. capensis* feeds on leaf litter in the coastal forest of Umhlanga, where the senior author observed a few of these isopods, is unknown. A useful test of the 'paucity of detrital food' hypothesis would be to compare the food habits of *T. capensis* along beaches with different amounts of algal wrack, leaf litter and edible live vegetation elsewhere in the geographic range of this species.

Second, the leaves of *C. monilifera* appear to be an abundant, palatable food source that should be readily accessible to *T. capensis*. Bietou bushes are very common along Umhlanga beach. Furthermore, *C. monilifera* is readily eaten by a variety of animals, including domestic livestock (Weiss *et al.* 2008). Terrestrial isopods generally avoid eating fresh leaves or algae until they have been leached of defensive chemicals (toxic secondary compounds) and (or) have been conditioned by protein-rich fungi and other micro-organisms (Warburg 1993; Pennings *et al.* 2000; Zimmer 2002). Perhaps the live leaves of *C. monilifera* are nutritious and digestible enough to make them attractive to *T. capensis*.

Third, although insects are the dominant arthropod herbivores on land, and thus may have inhibited the evolution of herbivory in terrestrial isopods, the apparent scarcity of insect herbivores on bietou bushes at Umhlanga may have opened up an advantageous local ecological opportunity for *T. capensis*. This hypothesis is inspired by only casual observation and requires more extensive faunal surveys. Various insects are known to feed on *C. monilifera* (over 100 species have been identified: Scott & Adair 1992), but most of these species apparently feed on the ovules, seeds, stems and buds, rather than on full-grown leaves (Scott & Adair 1992; Scott 1996). In a study involving 12 sampling sites across South Africa, defoliation of *C. monilifera* by herbivores averaged only 9% (Scott 1996). However, during outbreaks *Tortrix* moths and *Chrysolina* beetles may cause extensive damage (Scott & Adair 1992; Scott 1996).

So far we have focused on factors that may have favored the herbivory of *T. capensis*, but equally interesting is the fact that this herbivory also requires that these isopods be able to climb considerable heights to reach leaves of the bietou bush. Most terrestrial isopods spend their lives on or in the ground or associated detritus. This prompts the question: has *T. capensis* evolved special adaptive features fostering its climbing behavior, or is this behavior simply a phenotypically plastic extension of an ability to crawl on the stems and blades of detrital macro-algae, a primary food source for supralittoral isopods? The robust and powerful legs and claws of *T. capensis* that are

essential for its burrowing behavior may also be of secondary importance in allowing it to hold onto stems and leaves of the bietou bush without falling.

Brown (1996) has suggested that the survival of animals that inhabit sandy beaches, which present harsh conditions for life, is favored by their considerable behavioral plasticity. The unusual feeding behavior exhibited by *T. capensis* may be an example of this flexibility. Brown (1996) discusses presumed cases of behavioral plasticity based on intraspecific variation in microhabitat selection, locomotor behavior and diurnal activity patterns (including *Tylos* species), but our study suggests that plastic changes in food habits and foraging mode may also be important. Other species of oniscidean isopods inhabiting a variety of terrestrial environments have also been reported to show diet shifts in response to various environmental (e.g., seasonal or weather) changes (reviewed in Warburg 1993).

CONCLUSION

Evidence is presented that the isopod *T. capensis* engages in arboreal herbivory. This behavior is unusual for terrestrial isopods, which are mainly ground-dwelling detritivores. It may represent an important example of how the survival of beach-dwelling animals is facilitated by behavioral flexibility. Furthermore, herbivory of *T. capensis* on bietou bushes raises the question of whether this species could be used as a biological control agent for these plants, which have become invasive “weeds” in Australia and New Zealand. Limitations for this purpose include problems of introducing still another invasive species, the ecological restriction of *T. capensis* to sandy beach habitats, and the apparently small effect that it has on bietou bushes, as indicated by the low amounts of defoliation that we observed along Umhlanga beach (though this needs to be quantified). Nevertheless, further research on the herbivory of this isopod species may not only add to our understanding of how animals make major ecological shifts, but also may have important practical applications.

ACKNOWLEDGEMENTS

We thank Dr Karen J. Esler for help with identifying *Chrysanthemoides monilifera*, Prof. John Terblanche for use of his laboratory and supplies at Stellenbosch University, and Prof. John Terblanche, Dr Susana Clusella-Trullas and Prof. Martin Zimmer for helpful comments on earlier versions of this paper.

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