AN EVALUATION OF HUTCHINSON'S 'BEETLE-DAISY' HYPOTHESIS

INTRODUCTION

Some Cape Asteraceae species have conspicuous dark markings on their ray florets. Such markings are usually interpreted as 'guides' of various sorts (e.g. Faegri & Van der Pijl 1979). However, Hutchinson (1946) suggested that the dark raised marks on the ray florets of *Gorteria diffusa* Thunb. mimicked herbivorous beetles burrowing head down in the inflorescences. He noted that this species appeared to have few beetle visitors and to suffer less herbivory than other Asteraceae (such as an *Arctotis* sp.) growing nearby. He hypothesised that the marks repelled the beetles. In his review of plant mimicry worldwide, Wiens (1978) considered this an exceptionally intriguing example of Batesian mimicry. Despite this there still appears to be a dearth of information on the interaction between beetle-daisies and beetles. The purpose of this note is to extend the concept of beetle-daisies and to test Hutchinson's hypothesis.

The beetles which commonly burrow into daisy flowers are known as monkey-beetles (Coleoptera: Scarabaeidae: Rutelinae/Hopliinae; Scholtz & Holm 1985). The subfamily to which they belong is largely centred in the Cape. Little is known about their ecology against which to test Hutchinson's hypothesis. The situation regarding the relative absence of monkey-beetles on *Gorteria diffusa* observed 45 years ago by Hutchinson remains unchanged today (pers. obs. in Nieuwoudtville District). I did not see any hopliinid visitors on this species in many hours of observation in the spring of 1990. Since the hopliinids are a large group and they visit many other plant species (Whitehead, Giliomee & Rebelo 1987; pers. obs.), Hutchinson's hypothesis may be of more general relevance. Assuming this, I studied the interaction of *Arctotheca calendula* L. (Cape weed), a weedy daisy without dark markings on the ray florets, and the beetle *Heterochelus sexlineatus* Thunb., a herbivorous species with strong cutting mandibles. This plant species is visited by many hopliinid species (Scott & Way 1990) and I observed *Heterochelus sexlineatus* visiting at least seven other plant species at the study site, suggesting that there is only a diffuse relationship between the two study taxa.

In *Gorteria diffusa*, the so-called beetle-daisy, the 'beetle' mark is a dark raised bump on the ray floret with a white spot in the middle and with yellow 'legs'. Under ultraviolet light this 'beetle' does not appear significantly different (pers. obs.). The number of 'beetles' per inflorescence is very variable (from none to a full ring with marks on all ray florets) within and between individuals (pers. obs.). The 'beetles' on inflorescences with a full ring appear to be the least derived condition because they are poorly differentiated and are similar in appearance to many other Asteraceae with a ring of conspicuous dark basal markings on ray florets (e.g. *Gazania lichtensteinii*). Even *Arctotis* species (e.g. *A. gumbletonii* Hook. f.), which Hutchinson (1946) suggested suffer more predation, have complex dark basal markings on the ray florets.

It is thus possible that any dark marks near the base of the ray floret or darkening of the disc found in other genera such as *Osteospermum*, *Dimorphotheca* and *Ursinia* may be mimicking beetles. In the Still Bay area, J. Vlok and I noted an *Ursinia* species (close to *U. paleacea* (L.) Moench) which also appears to be a beetle-daisy. In this

TABLE 1.—Number of *Heterochelus sexlineatus* beetles on manipulated and unmanipulated inflorescences of *Arctotheca calendula*. For plots 1 and 2 extra beetles were released (see text)

Treatment	Plot 1		Plot 2		Plot 3	
	Sample size	No. (%) with beetles	Sample size	No. (%) with beetles	Sample size	No. (%) with beetles
Control	150	26 (17)	50	11 (22)	250	15 (6)
Black dots	73	15 (21)	24	5 (21)	50	4 (8)
Removed petal	73	10 (14)	23	7 (30)		
Yellow dots					50	2 (4)
Brown dots					50	3 (6)

species some of the ray florets have been lost and through the gaps they have left, large dark involucral bracts appear. This exceptional modification is equally impressive in the field as that of *Gorteria diffusa*. *Ursinia* is placed in the tribe Anthemideae whereas all the other genera mentioned are in the Arctotideae, indicating strong floral convergence. According to K. Bremer (pers. com.) these types of dark markings are probably restricted to the Cape Asteraceae. If all the above modifications are shown to be a response to monkey-beetles then I estimate that about 30 Cape species could display the 'beetle-daisy' syndrome (see Midgley 1991 for photographs of most of above examples).

The following information was collected to test Hutchinson's hypothesis; (i) do numbers of beetle visitors differ between inflorescences with artificial beetle marks and those without, (ii) do numbers of beetles on unmanipulated inflorescences suggest that the presence of one beetle deters others?

MATERIAL AND METHODS

The behaviour of the hopliinid *Heterochelus sexlineatus* was observed on a large (>500 individuals) population of *Arctotheca calendula* growing wild in an arboretum at Saasveld, near George in the southern Cape.

Sampling took place on warm days between 15h00 and 16h00 during October 1990. Inflorescences were manipulated by marking the ray florets with brown, yellow and black dots using commercial Artline pens. The yellow marks were not visible (to human eyes) on the yellow ray florets and thus served as controls to determine any other non-visual effects of the marks on beetles. Numbers of dots ranged from two to five and were approximately the same size as the beetle. To simulate the *Ursinia* type model (described above), from three to five ray florets were removed from a sample of inflorescences. Inflorescences were checked the following day for numbers of beetles. In some cases inflorescences became unsuitable subsequent to marking and this accounts for unequal numbers on Table 1. Because the numbers of beetles per inflorescence are low (less than 5%—see Results and conclusions) in some instances beetles were captured from other areas and released in the vicinity of study plots.

RESULTS AND CONCLUSIONS

Surveys indicated that 10 out of 200, six out of 100 and nine out of 300 *Arctotheca* inflorescences had beetle visitors (mean of less than 5% of inflorescences had visitors). *Ursinia anthemoides* (L.) Poir. in the vicinity had less than 2% of inflorescences with visitors. The manipulation experiments indicate that this beetle is virtually indifferent to markings on the ray florets and to the absence of ray florets (Table 1). The fact that considerable aggregation of beetles occurs on inflorescences (e.g. up to eight individuals in Table 2) suggests that the presence of an individual is not inimical to others. Approximately twice as many male beetles as females were found (Table 2). Relative to the number of inflorescences, the beetles, and especially the females, are rare. Consequently males probably visit many inflorescences searching for mates. The males fight for access to females (Midgley 1992). This suggests that this beetle would be an effective pollinator (its hairy body is often covered with pollen) but a relatively insignificant herbivore (a few florets in a few inflorescences in a population are damaged). The results concerning manipulated inflorescences suggest that floral markings have no negative effect on visitation. It is possible that beetles are actually attracted to the marked florets. However, on discovering that there are no real beetles on the florets, they fly off. It was not, however, possible to observe each visitor as it arrived on all manipulated inflorescences simultaneously to see whether this was the case. Although the hopliinid considered in this study is a herbivore with strong cutting mandibles, many other hopliininds are merely pollen feeders (Peringuey 1902). It would make little sense for mimicry to evolve to repel the non-herbivorous, pollen-carrying hopliinid beetles. Also there would be little reason for an evolutionary trend towards reduction in the number of beetle marks, if their function is repulsion.

TABLE 2.—Distribution by gender of *Heterochelus sexlineatus* beetles (M = male, F = female) in three samples of inflorescences of which each had at least one beetle visitor

	Samples		
	1	2	3
1M	27	35	31
1F	1	3	4
1M1F	12	8	7
2F	0	0	2
2M	1	2	0
2M1F	7	4	9
2M2F	5	4	2
1M1F	3	3	1
3M1F	1	0	3
2M3F	1	1	0
3M3F	0	0	1
4M3F	1	0	0
4M4F	1	1	0
4M1F	0	1	0
TOTAL	60	60	60

The above (no repulsion, aggregation and feeding habits) suggest that Hutchinson's hypothesis is not complete. If the markings act as mimics then it is probably to attract beetles, presumably for their role in pollination. This would then be a case of reproductive mimicry (sensu Wiens 1978), similar in a way to pseudocopulatory orchids. Obviously this study of one beetle and daisy species needs to be broadened before Hutchinson's intriguing hypothesis of this little-studied syndrome of Cape plants is fully tested.

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