Elevation gradients of flower visitation on a mesa in the Nama Karoo, South Africa

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Abstract

We investigated the composition of the insect fauna visiting flowers on the mesa of Tafelberg (Eastern Cape, South Africa). During the season-long study, 1825 individuals of 55 insect species were recorded visiting flowers of 28 species plants within permanent quadrats. Four taxa were very common as flower visitors, with between 2-300 individual visits recorded (one species from each of the orders of Hymenoptera, Diptera, Lepidoptera and Coleoptera). Two-thirds of all visits were to the composite *Pencia punctata* (Asteraceae). There was a strong pattern to the diversity of the flower-visiting fauna, with diversity increasing with elevation. This pattern matched the availability of flowers, which were much more abundant on the top of Tafelburg than on its lower slopes.

Keywords: diversity, altitude

Introduction

To understand the complexity and organisation of pollinator relationships and to be able to target conservation efforts effectively, a community approach is required to investigate pollination interactions. Such studies have been infrequently undertaken since the IBP-funded work of Moldenke and colleagues in the USA (Moldenke 1979), with some notable exceptions (e.g. Kato et al 1990, 1993a,b; Kato & Miura 1996). Most published work concentrates on pollinator interactions between particular plants and their specialised vectors. The southern African arid regions, in particular, have been rather neglected entomologically, and hence in pollination research, probably partly because of the difficulty of identifying insect visitors.

We are interested in the possibility of inselbergs/mesas of the Nama Karoo of South Africa and Namibia being conservation islands for the indigenous flora and fauna, including the pollinators of native plants. The extent to which the mesas constitute a network of connected islands forming a metapopulation is yet to be determined, but is clearly important in the context of the restoration project. The more connected they are, the more rapidly they will serve as foci for revegetating and repopulating the degraded landscape of the Nama Karoo. Plant species diversity is higher on the top of koppies/mesas (K.Esler, pers.comm.), but this may not be true for at least some insect groups, which show greater diversity on the flat grazing land between the mesas (e.g. grasshoppers: Gebeyehu & Samways 2005), but this result may well be taxon-specific. Flower-visiting insects are clearly an important group to investigate in the context of restoring degraded land, since the availability of pollinators is known to be limiting in many situations in natural and disturbed habitats (Ghazoul 2002). Lack of pollination service may effectively prevent the spread and maintenance of wild plant populations in even the apparently richly vegetated UK, and may be much more limiting in a landscape degraded by over-intensive human use. Pollination relationships are poorly known in southern Africa (Struck 1994, Esler 1999), and contain many endemic coevolved interactions (Gess 1996, Johnson et al 1998, Johnson & Steiner 2000).

This project seeks to investigate whether there are gradients of insect-visitor relationships along the elevation gradient of the mesas of the Nama Karoo. The occurrence of such gradients may indicate the role of mesas as conservation islands in this landscape.

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Materials & Methods

The study was conducted on the northeast slope of Tafelberg (between 31°30'S, 25°05'E and 31°40'S, 25°15'E), 25 km outside Middelburg, Eastern Cape, South Africa. Tafelberg is 1180 m above sea level: the vegetation is described by Burke et al (2003). The area is situated in the summer rainfall region, with 40% of the rain occurring in summer. The mean annual rainfall for this region is 341 ± 115 mm (W Asher, pers. comm.); the mean annual temperature for January is 20.9°C, while in July is 7.9°C. During the study period of November 1999 - May 2000, rainfall was 360 mm from August to November, regarded as a severe water shortage; in December - April the rainfall increased to 4480 mm. During the first few weeks of the year the total annual rainfall had already fallen. This irregular and unpredictable rainfall has a significant impact on flowering and on the appearance of flower-visiting insects.

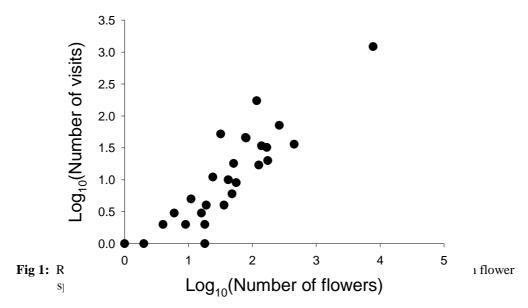
Fieldwork was carried out during November and December 1999 and then again from March to May 2000. A survey of flower-visiting insects was taken in and around five permanent 40 x 15 m plots laid out to record plant species composition. These plots provide a transect from the plains below (one plot, at 1197 m altitude), up the sides (three plots of gradually increasing elevation) to the top of Tafelburg (one plot, at 1649 m). At the beginning of each observation day, one of the five plots was chosen at random for observation. From this plot, higher plots were visited in sequence, and then lower plots visited on the way down. Each of the five plots was observed once each observation day.

The actual quadrat observed in detail measured 5 x 5 m. If no plants in flower were found in the first quadrat selected, a new one was selected: this process was repeated a maxiumum of three times. If no plants in flower occurred in any of the three attempts, then 'no flowering plants' was recorded. Flowers were counted and identified (or voucher specimens taken), and then observed for a ten-minute period. Insects were recorded as visitors if they landed on, or walked across the flower. The number of sets of flowers observed was dependent on the density and distribution of flowers in the quadrat. Observations were normally carried out between 0900 h and 1500 h.

To minimise disturbance, insect visitors were collected when they were observed on flowers outside the quadrat, and morphological data recorded; voucher specimens were kept for subsequent identification. Flowers were measured (corolla depth and width) and a variety of variables recorded (colour, height, whether the corolla restricts visitation [=specialized] or not [=unspecialized], degree of clustering of the flowers, etc).

Results

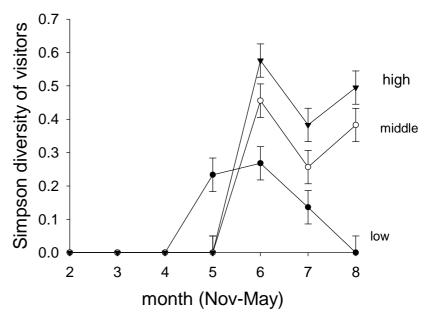
In all, 34 days of observation were carried out, each one involving surveying all five plots on the elevational gradient, and on the quadrats of the plots 611 patches of the various flower species were observed systematically. 28 plant species were recorded flowering in the observation quadrats, with a total of 9766 individual flowers watched for visitors. The most heavily visited by far (67% of all recorded visits) were those of *Pentzia punctata* (Compositae - Anthemidae, Matricariinae). *Pentzia* has upright, open, yellow flowers that can be visited by a very broad range of different visitors, but more importantly it is by far the commonest flower with 80% of the flowers recorded in the plots. Two other species were also relatively heavily visited, *Moraea polystachya* (Iridaceae) and *Pegolettia baccaridifolia* (Compositae, Inuleae). In general there was a strong relationship between the availability of flowers of different species and the number of visits they received (Fig 1).



1825 individual insects of 55 different taxa were recorded visiting flowers in the quadrats. The largest group were Diptera (16 spp), followed by Coleoptera (11), Hymenoptera (9), ants (8) and butterflies (5 spp). Four taxa made between 200 and 300 visits over the year (honeybees, the butterfly *Loxostege frustalis*, a dipteran and a beetle), and two ant species (*Messor barbarus* and an unidentified species) made more than 100 visits each.

The overall visitor diversity in the different months of the study (counting from October) is shown in Fig. 2. There was a pronounced effect of elevation. In the early summer there were very few if any insects recorded visiting the flowers of the pre-Xmas period. Then the lower-elevation plots developed a diversity of visitors early on, peaking in February (month 5), and then this diversity declined. Flowers of the mid- and high-elevation plots started to get visited in March; the mid-elevation plots then declined in visitor diversity, but those at the top of Tafelburg continued to have a substantial diversity of flower visitors right until the end of the season in May. The plot just below the top is omitted from this analysis since it was on a very steep part of the incline, and was shaded for much of the afternoon; it therefore received relatively few visitors.

Fig 2: Mean Simpson diversity (± SE) of the insect visitors to all plants of the bottom (plots 1 and 2), middle (plot 3) and top (plot 5) permanent quadrats of Tafelburg from November (month 2) to May (month 8). There significant effects of month $(F_{5,138} = 9.7, p<0.001)$ and an interaction between month and level $(F_{10,138} = 2.03,$ p < 0.05).



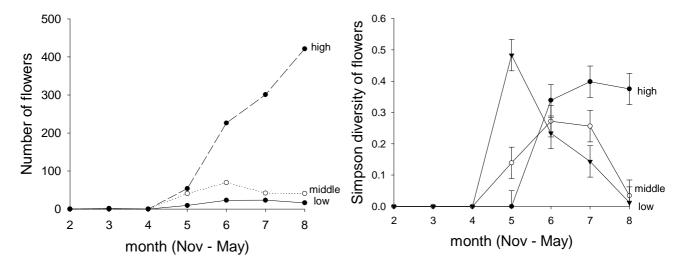


Fig 3: Availability of flowers (of all species) at the bottom, middle and top levels of Tafelburg over the season from November to May. There is a highly significant interaction between month and level ($F_{10,175} = 3.72$, p<0.001).

Fig 4: Simpson diversity $(\pm SE)$ of flowers at the three levels over the season.

It is also interesting that this pattern of insect visitation does not follow the availability of flowers (Fig 3), which show a very pronounced difference between the low- and mid- as opposed to the high-elevation plots. The overall Simpson diversity of flowers was not related to elevation ($F_{2,138} = 0.7$, n.s.); there was a 'nearly significant' interaction with season ($F_{10,138} = 1.83$, p=0.06). Interestingly this is in the opposite direction from insect visitor diversity, with the highest elevation peaking in diversity earlier in the year than middle and lower elevations (Fig 4).

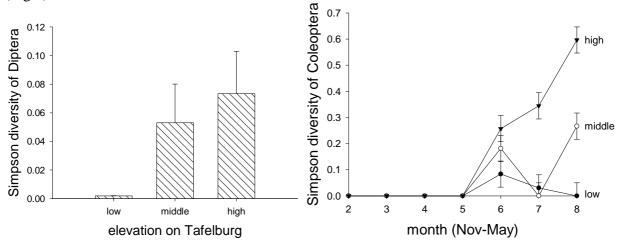


Fig 5: Simpson diversity (± SE) of the Dipteran visitors to flowers along an elevation gradient of Tafelburg from 1=low (plots 1 & 2) through 2=mid- (plot 3) to 3=top (plot 5). Plot 4 was omitted for the reasons stated above.

Fig 6: Simpson diversity $(\pm SE)$ of beetle visitors to flowers along an elevation gradient on Tafelburg.

When the data were separated into the five main taxa, a clear difference was seen. Butterflies were only found on the top of Tafelburg. There was no effect of elevation level on bee diversity ($F_{2,136} = 0.1$, n.s.) and no interaction with season ($F_{10,136} = 0.001$, n.s.). In the ants

there was a slightly greater diversity at the top than elsewhere, but again this was a non-significant effect of level ($F_{2,137} = 0.4$, n.s.) and there was no interaction with season ($F_{10,136} = 0.8$, n.s.). A stronger pattern was shown by dipteran diversity, where there was an increasing diversity with elevation (Fig 5), although again this was not significant as a main effect ($F_{2,138} = 1.0$, n.s.) nor as an interaction ($F_{10,136} = 1.5$, n.s.). It was among the beetles that a very strong and significant pattern of increasing diversity with elevation was shown (Fig 6) as a main effect ($F_{2,135} = 3.6$, p<0.05) and also interacting with season ($F_{10,135} = 1.83$, p = 0.06).

Flowers that are specialized received on average fewer visits (17.0 \pm 8.3, n=7) than those that are unspecialized (89.5 \pm 70.0, n=19), but this difference was not significant (H = 1.3, n.s.) because of the great variation among the unspecialized group. Specialized flowers were relatively rare in the observation plots (25 \pm 10) compared with unspecialized ones (500 \pm 400), but again this difference was not significant (H=3.6, n.s.). Specialized flowers tended to be smaller flowers (n.s.), and were more likely to contain just nectar rather than just pollen ($\chi^2_4 = 11.2$, p<0.05) and be held at an angle or pendulous ($\chi^2_6 = 16.4$, p<0.01).

Discussion

It was obvious in the data that diversity increased with elevation among flower-visiting insects. This was reflected in the availability of flowers, whose density greatly increased on the top of the mesa. However, floral diversity was not related to elevation. There were clear indications that some taxa of flower visitors are restricted to the top of Tafelburg, and hence possibly to mesas in general. This certainly appears to have implications for pollination. The strong increase in beetle-visitor diversity with elevation needs further study, together with a detailed look at exactly which species are involved. The restriction of most butterflies to the top of Tafelburg is equally noteworthy. Many butterfly species are well known to be long-distance transporters of pollen (e.g. nymphalids and pierids), although equally well many species have been recorded as dispersing less than 100 m in their lifetimes (e.g. many lycaenids). The butterfly taxa recorded as visitors to Tafelburg flowers do not appear to be highly sedentary species, and hence gene flow among mesas could be extensive if the relevant plants are pollinated by butterflies. However, butterflies are known to be rather poor pollinators. The metapopulation implications of these results could be very interesting and important, and deserve detailed study.

Acknowledgements

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Appendix 1: Flower species

Appendix 2: Insect species

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Family	Species	Order	Family	Name
Acanthaceae	Belpharis mitrata	Arachnida	Salticidae	Salticus
Apocynaceae	Carrisa haematocarpa	Arachnida	Thomisidae	Thomisus
Asteraceae	Chrysocoma ciliata	Arachnida	(2 unident.)	
Asteraceae	Felicia filifolia	Coleoptera	Chrysomelidae	
Asteraceae	Felicia muricata	•	Coccinellidae	Chelomenes lunata
Asteraceae	Geigeria ornativa	Coleoptera		
Asteraceae	Osteospermum sinuatum	Coleoptera	Coccinellidae	Exochomus flavipes
Asteraceae	Pegolettia baccaridifolia	Coleoptera	Coccinellidae	(2 unident.)
Asteraceae	Pegolettia baccaridifolia Pegolettia retrofracta	Coleoptera	Lycidae	Lycus
Asteraceae Asteraceae	Pencia punctata	Coleoptera	Meloidae	Mylabris oculata
Asteraceae	Pentzia quinquafolia	Coleoptera	Melyridae	Astylus atromaculatus
Asteraceae	Senecio erysimoides	Coleoptera	Scarabaeidae	Heterochelus (hairy)
Asteraceae	Veronia pinifolia	Coleoptera	Scarabaeidae	Heterochelus
Brassicaceae	Heliophila suavissma	Coleoptera	Silphidae?	
Capparaceae	Cadaba aphylla	Coleoptera	(3 unident.)	
Caryophyllaceae	Dianthus basuticus	Diptera	Asilidae	Hoplistomerus nobilis?
Crassulaceae	Crassula lanigulosa	Diptera	Calliphoridae	Chrysocoma chloropyga
Crassulaceae	Crassula setulosa	Diptera	Calliphoridae	Chrysomya regalis
Cucurbitaceae	Cucumis zeyheri		•	
Fabaceae	Indigofera sp.	Diptera	Calliphoridae	Stegosoma
Fabaceae	Lessertia pawifolia	Diptera	Calliphoridae	(unident.)
Geraniaceae	Oxalis commutata	Diptera	Muscidae	Musca lusoria
Geraniaceae Geraniaceae	Pelargonium abrotanifolium	Diptera	Muscidae	(2 unident.)
Iridaceae	Pelargonium dichondrifolium Moraea polystachya	Diptera	Muscidae/Calliphoridae	Polietes?
Lamiaceae	Stachys aymbalaria	Diptera	Mutillidae	
Mesembryanthemace	2 2	Diptera	Syrphidae	Eristalis crassipes?
Mesembryanthemaceae <i>Trichodiadema rogersiae</i>		Diptera	Syrphidae	Eristalis tenax
Scrophulariaceae	Jamesbrittenia tysonii	Diptera	Syrphidae	Eumerus sp
Scrophulariaceae	Striga sp	Diptera	Syrphidae	Eupeodes
Scrophulariaceae	Sutera atropurperea	Diptera	Tabanidae	Philoliche
Scrophulariaceae	Sutera halimifolia	Diptera	Tabanidae	Philoliche aethiopica
Selaginaceae	Selago albida	Diptera	(5 unident.)	The state of the s
Selaginaceae	Walafrida geniculata	Formicidae	Formicinae	Camponotus fulvipilosus
Selaginaceae	Walafrida saxatilis	Formicidae	Myrmicinae	Linepithema?
Sterculiaceae Sterculiaceae	Hermannia cuneifolia		•	*
Verbenaceae	Hermannia linearifolia Lantana regosa	Formicidae	Myrmicinae	Messor barbarus
verbenaceae	Laniana regosa	Formicidae	Myrmicinae	(unident.)
		Formicidae	(4 unident.)	
		Hemiptera	Coreidae	(unident.)
		Hemiptera	Miridae	(unident.)
		Hemiptera	Pentatomidae	Agonoscelis versicolor
		Hemiptera	Pentatomidae	(unident.)
		Homoptera	Cercopidae	Locris
		Hymenoptera	Apidae	Allodapula
		Hymenoptera	Apidae	Apis mellifera adansonii
		Hymenoptera	Apidae	Lasioglossum
		Hymenoptera	Braconidae	(unident.)
		Hymenoptera	Chrysididae	Chrysis lyncea
		туппепория	Cin yordidac	Citi ysis i yiweu

Hymenoptera Ichneumonidae (unident.) Hymenoptera Sphecidae (unident.) Hymenoptera Vespidae *Polistes*

Lepidoptera Danainae Danaus chrysippus aegyptius

Grammodes stollida Lepidoptera Noctuidae Nymphalidae Lepidoptera Acraea neobule Lepidoptera Nymphalidae Hypolimnas misippus Lepidoptera Pieridae Colias electo Lepidoptera Pieridae Colias electo electo Lepidoptera Pieridae Colotis antevippe Lepidoptera Pyralidae Loxostege frustalis

Lepidoptera (3 unident.) Mantodea Empusidae

Mantodea Empusidae Empusa
Mantodea Mantidae Episcopomantis nymph

Thysanoptera (unident.)

الملخص العربى

تأثير التدرج في الإرتفاع على زيارات الحشرات للنباتات في منطقة ناما كارو _ جنوب أفريقيا

فیلیب کیرك _ فرانسیس جلبرت

قسم العلوم البيولوجية _ جامعة نوتنجهام _ المملكة المتحدة

تم خلال هذا البحث دراسة العشائر الحشرية التى تزور النباتات البرية فى منطقة تافيلبيرج بجنوب أفريقيا. تم تجميع 1825 فرد من الحشرات والتى تقع فى حوالى 55 نوع من الحشرات والتى تواجدت على أزهار 28 نوعا من النباتات داخل المربعات التى تم تحديدها بصورة دائمة لإجراء الدراسة. تم رصد أربعة أنواع من الحشرات شائعة التواجد والانتشار على أزهار النباتات وترواحت أعداد أفرادها ما بين 2-300 فرد وكانت تلك الأنواع تابعة للرتب الحشرية: رتبة غشائية الأجنحة _ رتبة غمدية الأجنحة _ رتبة غمدية الأجنحة). أظهرت الدراسة أن حوالى ثلثى الحشرات الزائرة قد تركزت على أنواع نباتات الفصيلة المركبة. أيضا أوضحت الدراسة أن كثافة الحشرات الزائرة للنبات قد ازدادت مع زيادة الإرتفاع عن مستوى سطح البحر وكان هذا متوافقا مع زيادة أعداد الأزهار على النباتات المتواجدة في الاماكن المرتفعة من منطقة تافيلبيرج مقارنة بقلتها في الأماكن المنخفضة.