Room to spare? Is *Drosophila flavohirta* Malloch, exploiting *Eucalyptus gomphocephala* A. DC flowers, in an incomplete guild?

A.J. Davis[1*] & G.D. Tribe[2]
[1]*Department of Biology, The University, Leeds, LS2 9JT, United Kingdom*
[2]*Plant Protection Research Institute, Ryan Road, Rosebank, 7700 South Africa*

Drosophila flavohirta Malloch (Diptera: Drosophilidae) oviposits, and the larvae develop in the flowers of eucalypts (Myrtaceae), among them *Eucalyptus gomphocephala* A. DC. The larvae feed on eucalypt nectar and also ingest pollen (Tribe 1991), and the adults feed on pollen (Nicolson 1994a,b). Feeding by *D. flavohirta* larvae reduces nectar availability and thus curtails the yield of honey from bees foraging on *E. gomphocephala* flowers (Du Toit 1987; Tribe 1991).

Both the tree and the drosophilid are native to Australia, but the tree was introduced into South Africa about 100 years ago (Poynton 1979). Colonization by *D. flavohirta* probably occurred much later, since beekeepers first reported a drop in honey yields from bees foraging on a eucalypt, *E. grandis* Hill ex Maiden, in 1975 (Herrmann 1983), and *D. flavohirta* was discovered in the flowers in 1981. It is likely that the fly arrived a few years before 1975. Other insect species also occur on eucalypt blooms. Adults of several beetle and syrphid species are found from time to time but have a negligible effect on nectar production. Thrips (*e.g. Thrips australis* (Bagnall)) often infest eucalypt blooms but there is no evidence that they significantly reduce nectar production as thrips do not use the nectar (Herrmann 1983) and infested blooms still contain nectar (Herrmann 1985). Considerable amounts of nectar are, however, taken by ants (*Camponotus* spp., *Linepithema humile* (Mayr) and *Pheidole* spp.) and by the European wasp (*Vespula germanica* Fabricius) (Herrmann 1985; Buys 1987a,b; Tribe & Richardson 1994) but these are generalist foragers and are not confined to eucalypts. *Drosophila flavohirta*, on the other hand, is confined to eucalypts and is the single-most important insect affecting nectar production by these trees in South Africa. However, it is not the only drosophilid, nor even the only insect, potentially capable of colonizing flowers (Brncic 1966, 1983; Pipkin *et al.* 1966; Cook *et al.* 1977) and further reducing nectar availability. The current lack of other species exploiting the resource may indicate that there has been insufficient time or opportunity for *Eucalyptus* to accumulate more species since it was introduced into South Africa. It is therefore important to determine whether further colonization of *E. gomphocephala* flowers is likely. The likelihood of further colonization is easier to assess for patchy and ephemeral

*Correspondence: A.J. Davis, Department of Biology, The University, Leeds, West Yorkshire, LS2 9JT United Kingdom (E-mail pab6awd@leeds.ac.uk)

resources like eucalypt blooms than it would be for a more permanent resource, as the number of species able to coexist on patchy and ephemeral resources is strongly influenced by the distribution over patches of each species (Ives & May 1985; Rosewell *et al.* 1990; Shorrocks *et al.* 1990; Ives 1991) and distributions are easy to measure. This model of coexistence, the aggregation model (Shorrocks & Rosewell 1986, 1987), states that coexistence is promoted if species distributions are aggregated and if each species is distributed independently of potential competitors (*i.e.* that the numbers of individuals of each species are neither positively nor negatively correlated over patches). All known *Drosophila* guilds conform to the aggregation model even when non-drosophilid guild members are included in the analysis (Shorrocks 1995; Shorrocks & Sevenster 1995). The modal number of species in a guild is predicted to be six or seven, a prediction supported by the available data on real guild sizes (Shorrocks *et al.* 1990).

If *D. flavohirta* larvae are aggregated over blooms, the aggregation model of coexistence would predict that eucalypt blooms should support a guild of six or seven specialist nectar feeders. As this guild currently contains only one species, *D. flavohirta*, it would appear that there is sufficient space in *E. gomphocephala* flowers for colonization by several additional specialist nectar feeders. This is doubtful, however, since *E. gomphocephala* bears its flowers in large racemes of 10–100 blooms and *D. flavohirta* larvae can move between blooms within racemes. Indeed, movement is necessary as blooms produce nectar for only seven days (Tribe 1991; Nicolson 1994a), but the larvae need 13–14 days to complete development (Du Toit 1987). Movement between blooms would tend to diminish the degree of aggregation as the larvae would be expected to distribute themselves evenly over blooms within racemes. The aggregation model would consequently not apply, and colonization of *E. gomphocephala* by additional species would be less likely. We therefore tested whether *D. flavohirta* larvae were aggregated over

Table 1. Difference of the aggregation statistics v/m (variance to mean ratio) and *j* (standardized crowding index), within racemes, branches and the entire tree, of *Drosophila flavohirta* larvae in *Eucalyptus gomphocephala* blooms from the values expected, respectively 1 and 0, for random distributions. One-tailed, single-sample *t*-tests calculated from bootstrapped estimates of variance.

Units	*d.f.*	$t_{v/m}$	$P_{v/m}$	t_j	P_j
Racemes					
A	9	9.9	<0.001	10.2	<0.001
B	9	19.4	<0.001	23.3	<0.001
C	9	16.3	<0.001	19.0	<0.001
D	9	17.7	<0.001	20.7	<0.001
E	9	28.9	<0.001	26.6	<0.001
F	9	14.3	<0.001	19.8	<0.001
Branches					
1	9	13.9	<0.001	18.1	<0.001
2	9	38.9	<0.001	88.3	<0.001
Tree					
1	9	28.3	<0.001	27.8	<0.001

Table 2. Aggregation statistics v/m (variance to mean ratio) and *j* (standardized crowding index) within racemes, branches and the entire tree for larvae of *Drosophila flavohirta* in *Eucalyptus gomphocephala* blooms. In brackets ±1 S.D. calculated from bootstrapped estimates of variance.

Racemes	A	B	C	D	E	F
v/m	26.2 (7.79)	15.9 (2.42)	6.7 (1.08)	19.5 (3.99)	11.8 (1.18)	8.0 (1.23)
j	4.5 (1.30)	1.2 (0.16)	0.7 (0.11)	4.6 (0.72)	2.2 (0.26)	0.9 (0.13)
n	50	36	58	28	23	18
Branches		1			2	
v/m		15.3 (2.67)			12.8 (0.95)	
j		1.7 (0.26)			2.1 (0.08)	
n		144			69	
Tree			1			
v/m			14.9 (1.55)			
j			1.9 (0.07)			
n			213			

E. gomphocephala blooms within racemes and within branches. We show that *D. flavohirta* is part of an incomplete guild and that colonization of the resource by additional species is therefore likely.

Six racemes, three from each of two branches, containing a total of 213 blooms, were collected on 13 March 1995 from an *E. gomphocephala* tree on the border of the Cape Point Nature Reserve, Cape Peninsula, South Africa (34.35S 18.24E). The site is about 38 km due south of Cape Town. As each raceme was cut from the tree, each individual bloom was removed and placed in a separate vial preventing the larvae from moving between blooms after collection. The blooms were stored at 5 °C to slow larval development until they could be examined, but no blooms were stored for more than 21 days. Each bloom was dissected under a binocular microscope and the larvae and puparia in each bloom were counted. The aggregation of larvae was calculated first between all blooms within each raceme, then within the two branches and, finally, for all blooms examined. We calculated the degree of aggregation as the standardized crowding index *j* (Ives 1991; Jaenike & James 1991) and, for comparison, as the variance to mean ratio v/m. Because only a single aggregation statistic can be calculated for each raceme or branch, our comparisons of aggregation are carried out using bootstrapped estimates of variance. Each bootstrapped estimate was calculated from 10 random subsamples each of 90 % of the total data.

The larvae of *D. flavohirta* were significantly aggregated at all levels of the analysis (Table 1) with variance to mean ratios much greater than one and *j* much greater than zero (Table 2). Furthermore, there was great heterogeneity in the degree of aggregation with significant differences between racemes (parametric ANOVA, Table 3) and between the two branches for *j* (*t*-test, 2-tailed, corrected for unequal variances, $n_1 = n_2 = 10$, $t = -8.13$, $d.f. = 10.63$, $P < 0.001$) although not for variance to mean ratio (*t*-test, 2-tailed, corrected for unequal variances, $n_1 = n_2 = 10$, $t = 0.12$, $d.f. = 11.25$, $P = 0.907$).

Table 3. Parametric ANOVAs using bootstrapped estimates of variance of the aggregation statistics v/m (variance to mean ratio) and *j* (standardized crowding index) between racemes for larvae of *Drosophila flavohirta* in *Eucalyptus gomphocephala* blooms.

	n	*d.f.*	*F*	*P*
v/m	60	5	35.35	<0.0001
j	60	5	73.41	<0.0001

It is evident that *D. flavohirta* larvae are aggregated over eucalypt blooms within racemes, despite the possibility of larval movement between blooms. The observed aggregation was more than sufficient to facilitate the coexistence of several species on the resource (Shorrocks 1995). The within-raceme aggregation was compounded by the heterogeneity between racemes and between branches and additional heterogeneity can be expected between trees. Further colonization of the eucalypt-bloom resource is thus likely to occur given the arrival in South Africa of suitable floricolous species. The arrival of additional species would add to the reduction of eucalypt nectar production already caused by *D. flavohirta*. This threat implies that import restrictions against floricolous species that are potential colonizers should be strictly enforced and it gives added urgency to the search for control measures for *D. flavohirta* (Tribe 1991).

REFERENCES

BRNCIC, D. 1966. Ecological and cytogenetic studies of *Drosophila flavipilosa*, a Neotropical species living in *Cestrum* flowers. *Evolution* **20**: 16–29.

BRNCIC, D. 1983. Ecology of flower-breeding *Drosophila*. In: Ashburner, M., Carson, H.L. & Thompson, J.N. (Eds) *The Genetics and Biology of* Drosophila. Vol. 3d. 171–220. Academic Press, London.

BUYS, B. 1987a. Argentine ants may collect twice as much nectar as bees. *South African Bee Journal* **59**: 90.

BUYS, B. 1987b. Competition for nectar between Argentine ants (*Iridomyrmex humilis*) and honeybees (*Apis mellifera*) on black iron bark (*Eucalyptus sideroxylon*) *South African Journal of Zoology* **22**: 173–174.

COOK, R.M., PARSONS, P.A. & BOCK, A.R. 1977. Australian endemic *Drosophila*. II. A new *Hibiscus* breeding species with its description. *Australian Journal of Zoology* **25**: 755–763.

DU TOIT, A.P. 1987. Nectar flies, *Drosophila flavohirta* Malloch (Diptera: Drosophilidae) breeding in *Eucalyptus* flowers. *South African Forestry Journal* **143**: 53–54.

HERRMANN, J.M. 1983. Fruit flies and the eucalypt nectar flow. *South African Bee Journal* **55**: 25–33.

HERRMANN, J.M. 1985. Die bloekom-nektarvlieg *Drosophila flavohirta* in Oos-Transvaal. *South African Bee Journal* **57**: 8–14.

IVES, A.R. 1991. Aggregation and coexistence in a carrion

fly community. *Ecological Monographs* **61**: 75–94.
IVES, A.R. & MAY, R.M. 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. *Journal of Theoretical Biology* **115**: 65–92.
JAENIKE, J. & JAMES, A.C. 1991. Aggregation and the coexistence of mycophagous *Drosophila*. *Journal of Animal Ecology* **60**: 913–928.
NICOLSON, S.W. 1994a. Pollen feeding in the eucalypt nectar fly *Drosophila flavohirta*. *Physiological Entomology* **19**: 58–60.
NICOLSON, S.W. 1994b. *Eucalyptus* nectar – production, availability, composition and osmotic consequences for the larva of the eucalypt nectar fly, *Drosophila flavohirta*. *South African Journal of Science* **90**: 75–79.
PIPKIN, S.B., RODRIGUEZ, L. & LEON, J. 1966. Plant host specificity among flower-feeding neotropical *Drosophila* (Diptera: Drosophilidae). *American Naturalist* **100**: 135–156.
POYNTON, R.J. 1979. *Tree Planting in Southern Africa Vol. 2: The Eucalypts*. Department of Forestry, Pretoria.
ROSEWELL, J., SHORROCKS, B. & EDWARDS, K. 1990. Competition on a divided and ephemeral resource: testing the assumptions. I. Aggregation. *Journal of Animal Ecology* **59**: 977–1001.
SHORROCKS, B. 1995. Local diversity: a problem with too many solutions. In: Hochberg, M.E., Clobert, J. & Barbault, R. (Eds) *The Genetics and Maintenance of Biological Diversity*. Oxford University Press, Oxford.
SHORROCKS, B. & ROSEWELL, J. 1986. Guild size in drosophilids: a simulation model. *Journal of Animal Ecology* **55**: 527–541.
SHORROCKS, B. & ROSEWELL, J. 1987. Spatial patchiness and community structure: coexistence and guild size of *Drosophila* on ephemeral resources. In: Gee, J.H.R. & Giller, P.S. (Eds) *The Organisation of Communities: Past and Present*. BES Symposium **27**: 29–51. Blackwells, Oxford.
SHORROCKS, B., ROSEWELL, J. & EDWARDS, K. 1990. Competition on a divided and ephemeral resource: testing the assumptions. II. Association. *Journal of Animal Ecology* **59**: 1003–1011.
SHORROCKS, B. & SEVENSTER, J.G. 1995. Explaining local species diversity. *Proceedings of the Royal Society: Series B, Biological Sciences* **260**: 237–244.
TRIBE, G.D. 1991. *Drosophila flavohirta* Malloch (Diptera: Drosophilidae) in *Eucalyptus* flowers: occurrence and parasites in eastern Australia and potential for biological control on *Eucalyptus grandis* in South Africa. *Journal of the Australian Entomological Society* **30**: 257–262.
TRIBE, G.D. & RICHARDSON, D.M. 1994. The European wasp, *Vespula germanica* (Fabricius) (Hymenoptera: Vespidae), in southern Africa and its potential distribution as predicted by ecoclimatic matching. *African Entomology* **2**: 1–6.

Accepted 26 March 1996