necrotic tissue was rare, and even when found, it generally did not support flies. Our impression, where we caught flies, is that the rot was old.

The flies caught, however, were very young. Even after holding flies isolated in vials for almost 1 week before returning to the laboratory, only one female, of 27, laid eggs. None of the others laid until paired with a male, and, because males mature later than females, these pairs required an additional 5 days before offspring were apparent in vials. The second line of evidence of young age is that once captured, only one of the collected flies died within a month.

These observations strongly suggest that when conditions are very bad, adult life-span is short. This conclusion is paradoxical, as for a population to persist, flies must live long enough to mature, which for *D. mojavensis* males is 5-9 days at 25 °C (Markow, 1982). However, if mature flies occurred where we collected, they must respond differently to cactus baits.

The combination of a small population made up predominantly of young flies can have a severe effect on genetic variation within the population. Because in San Carlos, cactus populations are very large, the local population is not likely to disappear, but in areas where fewer organ pipe occur, Sonoran populations could be at risk.

References: Heed, W.B., and R.L. Mangan 1986, In: *The Genetics and Biology of* Drosophila, (M. Ashburner, H.L. Carson, and J.N. Thompson, jr., eds), vol. 3e: 311-345, Academic Press, NY; Hoffmann, A.A., and P.A. Parsons 1991, *Evolutionary Genetics and Environmental Stress*. Oxford Science Publ., Oxford; Krebs, R.A., 1999, Cell Stress and Chaperones 4: 243-249; Krebs, R.A., and K.L. Bean. 1991. Psyche 98: 101-109; Markow, T.A., 1982, Mating systems of cactophilic *Drosophila*. In: *The Cactus-Yeast*-Drosophila *Model System* (J.S.F. Barker and W.T. Starmer, eds.), Academic Press, Sydney, Australia, 273-287.

## New host plants and host plant use for *Drosophila elegans* Bock and Wheeler, 1972.

**Yoshida*, T., H.-w. Chen#, M.J. Toda#, M.T. Kimura* and A.J. Davis#@**

* Environment and Earth Science and #Institute of Low Temperature Science, Hokkaido Univ., Sapporo, Hokkaido, Japan; @ corresponding author current address: Institute of Biology, Aarhus Univ. 8000 Aarhus C, Denmark. biodavis@biology.au.dk

### Introduction

The use of *Ipomoea* spp. by this species has been known for over 20 years (Okada and Carson, 1982; H. Carson, pers. comm.), but little information is available on its use of other flowers. In fact, its use of flowers outside the genus *Ipomoea* was unknown until the recent discovery that it used *Brugmansia* flowers (Sultana *et al.*, 1999). We therefore investigated which species of flowers were, and which were not, used by *D. elegans* in order to clarify the range of host-flowers used by this species. Such information is necessary for a proper understanding of *D. elegans* biology and ecology and forms part of our continuing research on this species (Hirai and Kimura, 1999; Hirai *et al.*, 1999; Kimura and Hirai, 1999).

### Methods

Numerous sites were surveyed in several parts of Iriomote-jima, Japan. This subtropical island is largely covered by secondary forest and associated vegetation. However, since we wanted

to check use of flowers for resting or breeding rather than survey overall *D. elegans* occurrence, we confined our survey to easily accessible forest and field-edge vegetation.

Along a 60km transect from Haemida in the south to Shirahama in the north we examined numerous concentrations of flowering herbs and trees. We concentrated on native plants but also examined flowering cultivated and garden plants when these were accessible. Most sites were examined only once but others were checked several times. For example, of 12 sites containing *Cucurma domestica* examined, four were examined only once and eight more regularly. One of these was examined at least once every day over a 10-day period. Breeding in flowers was also checked by dissecting sample blooms or by keeping blooms in the laboratory to determine whether any adults would emerge.

To determine the numbers and position within the bloom of *D. elegans* eggs and larvae, all the flowers from one *C. domestica* raceme were dissected and the number of eggs and larvae in each bloom and their location in the flower were recorded. Each bloom was classified as either: I) fresh, open flower, II) closed and senescent but still on the inflorescence, and III) senescent flower having fallen to the ground. The larvae found were classified as either S) small, M) medium and L) large, size classes that probably correspond to the three larval instars. We then determined developmental mortality in this flower species by rearing out the adults from these dissected flowers. Two or three blooms were placed on moist tissue paper in cottonwool-plugged culture vials and the emerging adult flies were counted.

The intensity and consistency of flower use was assessed by surveying several different *C. domestica* plants on a single day at a single site near Funaura in the south-east of the island. Intensity of use was assessed by counting the numbers of blooms within each raceme containing flies on 13 June between 09:00 and 09:30. Consistency of use was further quantified by resurveying one particularly large plant 3h later, at 12:40, on the same day and at the same site.

**Results**

*Drosophila elegans* was found in three flower species and breeding was confirmed in two of these (Table 1). Equally importantly, no *D. elegans* were found in five other taxa nor in numerous species of garden flowers.

Flies were not found in *I. pes-caprae* even though this species is plentiful along low altitude roadsides and on beaches and might be expected to attract colonizing flies. No flies were present at Haemida beach where *I. pes-caprae* grows over hundreds of square meters of sandy beach nor on the other side of the island at Uehara where it again covers a large area of seafront. At Uehara flowers were closely examined twice during the day, in the early morning when they first opened and late in the evening after they had closed. No flies were found at any of these times and no eggs or larvae were found when 12 flowers from this site were dissected. Roadside flowers of this species near Shirahama and at a site west of Uehara were also free of *D. elegans*.

The positions of immature *D. elegans* within *C. domestica* blooms varied with their age (Table 2) and consequently also with the age of the bloom. In Stage-I flowers, eggs, empty eggshells and S larvae were found almost entirely at the basal part of flower and on anthers. In stage II flowers, only M larvae were found and these were mostly feeding on the anthers though a few occurred on the apical part of a petal. The larvae found in stage-III flowers were all in class L, with the same distribution within flower as M larvae. More class M larvae were found than S, or L, class but the total number of immatures per flower was relatively constant among five Stage-II flowers, ranging from 11 to 15. The total number of adult flies having emerged from the laboratory culture was 85 (46 females and 39 males), giving an emergence rate of 0.977.

Table 1. Flower use by *Drosophila elegans* on Iriomote-jima, Japan.

| Plant taxon | adults | breeding | notes |
|---|---|---|---|
| *Cucurma domestica* | + | + | Widespread and abundant |
| *Ipomoea indica* | + | + | Widespread and abundant |
| no-botan | + | - | in only one of many flowers examined. |
| *C. manghas* | - | | widespread |
| cultivated cucurbits | - | | two sites |
| *Hibiscus tilaeus* | - | | native species |
| *Hibiscus spp.* | - | | introduced species |
| garden flowers | - | | including *Nicotina* sp. |
| *Ipomoea pes-caprae* | - | | widespread and abundant |
| Malvaceae (not *Hibiscus*) | - | | garden plants at two sites |

Table 2. Distribution of immature *Drosophila elegans* within the blooms of a single *Cucurma domestica* raceme. Larvae were classified into three size-classes: small, medium and large.

| Flower part | Base | Filament | Anther | Petal apex | Total |
|---|---|---|---|---|---|
| Stage | | | | | |
| Egg | 3 | 1 | 4 | 0 | 8 |
| Egg* | 2 | 0 | 3 | 0 | 5 |
| Larva (small) | 5 | 0 | 2 | 0 | 7 |
| Larva (medium) | 0 | 0 | 52 | 11 | 63 |
| Larva (large) | 0 | 0 | 8 | 1 | 9 |
| Total | 8 | 1 | 66 | 12 | 87 |

Egg* = empty egg-shell

Flower occupancy varied between sites as at Takana flies were present in two of the five *I. indica* flowers examined and at a site 2km from Ohara in the south, four of 14 flowers of this species were occupied. Usage of *C. domestica* also fluctuated as flies were not found at all sites nor in all flowers at occupied sites. At Funaura all five plants examined carried some racemes containing adult *D. elegans,* with only 10 of the 62 racemes examined having no blooms containing flies. The mean occupancy rate over all 227 blooms was 56.6%.

Observations from frequently examined sites indicated that neither site, nor flower, occupancy were consistent between visits. Examination of the same flowers more than once in the same day showed that use of individual blooms also changed during the day. Flowers occupied on one visit could be empty later on and, likewise, previously empty flowers could be occupied later on. The minimum change in occupancy was 21.5% among 65 blooms in 17 racemes on the one plant resurveyed after 3 hours. Fourteen of the 65 blooms had changed from empty to containing flies, or *vice versa*, on the second visit.

## Discussion

Our results clearly show that *Drosophila elegans* is not confined to *Ipomoea* flowers as breeding sites since it makes extensive use of *C. domestica.* Neither, however, is it a complete generalist, since many apparently suitable flowers are not used. We were particularly surprised not to find *D. elegans* in *Ipomoea pes-caprae* even when, in some cases, *I. indica* within 50m were occupied and when the fly breeds in several other species of *Ipomoea* in south-east Asia. It therefore appears that *D. elegans* is making complex host-plant, or habitat, choices so producing the observed mosaic of plant use.

The reasons for these choices are unclear. It cannot be entirely phylogenetic since *C. domestica* is not at all closely related to *Ipomoea* and yet is heavily used. On the other hand *I. pes-caprae* was not used despite its close relationship, and frequent proximity, to *I. indica.* However, there may be chemical or phenological differences between *Ipomoea* species of which we are not aware. *Ipomoea pes-caprae* exudes a particularly viscous sticky latex when damaged which might prevent its use as a substrate for larval feeding whereas *I. indica* does not. *Drosophila elegans*

is also not choosing flowers on the basis of similar growth form since, whereas *I. indica* is a vine, *C. domestica* is a woody herb and *Brugmansia* a small tree. *Cucurma domestica* flowers are, however, like those of *Ipomoea* spp. in being bell-shaped, as is *Brugmansia* in which the species breeds in Indonesia (Sultana *et al.,* 1999). Nevertheless, flower shape cannot be the complete answer, because the beautifully bell-shaped *I. pes-caprae* and *C. manghas* both yielded no flies.

The failure of *D. elegans* to use flowers of the one native and several introduced *Hibiscus* species is perhaps not surprising, because these flowers have separate petals and so are not strictly tubular. However, *Hibiscus* flowers are effectively enclosed except for the brief period when fully open and in other parts of their ranges are used by other flower-breeding species (Bock and Parsons, 1979; Starmer *et al.,* 1997, 1998). The barriers to their use by *D. elegans* would therefore appear slight.

The finding of immatures of similar ages within flowers suggest synchronized development originating in a limited oviposition period for each bloom. This period is likely to be in young blooms, since adult flies are then present. The eggs are laid, and young larvae start to feed, at the base of the bloom only moving to the petals in later instars. Our finding of more medium sized larvae may reflect changes in ovpositiin intensity over time or perhaps that young flowers had not received their full complement of eggs before they were sampled and that some older larvae had already left the flower to pupate. Developmental mortality is remarkably slight with practically all larvae completing development to the adult.

Since a low percentage of all blooms is occupied at any one time, particularly in *C. domestica*, oviposition sites do not appear to be limited. Flower use changes frequently over time, however, probably much more so than our minimum figure of 21.5% suggests. The likely degree of movement implies that adults are continually leaving blooms in which they have mated or oviposited in order to search out new ones. This in turn suggests that there is considerable scope for sophisticated bloom and flower species choice by *D. elegans*.

Whatever the reasons underlying it, *D. elegans* complex mosaic of flower use for resting and breeding poses interesting questions and must form the background for continued research on its biology and ecology.

Acknowledgments: Accommodation and research facilities on Iriomote-jima were provided by the Field Station of the University of the Ryukyus. AJD thanks ILTS and Hokkaido University for financial support and research facilities in Japan, and the Royal Society (UK) and Genetics & Ecology Department, Aarhus University for support during data analysis. Colleagues at Aarhus and Leiden provided useful criticism of earlier versions of this paper.

References: Bock, I.R., and P.A. Parsons 1979, Aust. J. Zool. 27: 219-301; Hirai, Y., and M.T. Kimura 1999, Zool. Sci.16: 417-421; Hirai, Y., H. Sasaki, and M.T. Kimura 1999, Zool. Sci. 16: 211-214; Kimura, M.T., and Y. Hirai 1999, Tropics, (in press); Okada, T., and H.L. Carson 1982, Kontyû 50: 511-526; Starmer, W.T., L.L. Wolf, J.S.F. Barker, J.M. Bowles, and M.-A. Lachance 1997, Biol. J. Linn. Soc. 62: 459-473; Starmer, W.T., M. Polak, L.L. Wolf and J.S.F. Barker, 1998, Evolution 52: 806-815; Sultana, F., M.T. Kimura, and M.J. Toda 1999, Entomol. Sci. 2, 121-126.