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WHAT ARE DANDELIONS AND APHIDS?

WHAT IS A DANDELION?

The study of dandelion ecology and evolution suffers from confusion of the layman's "individual" with the "individual" of evolutionary biology. The latter individual has "reproductive fitness" and is the unit of selection in most evolutionary conceptualizations. Henceforth I will refer to it as the "evolutionary individual," or EI. Instead of viewing the set of short-lived dandelion plants in a habitat as a many-membered population with a very high growth rate, I suggest a quite different view. I suggest that the dandelion population contains a small number of highly subdivided EIs with very long lives and very low population growth rates and which exist through the harvest of a highly predictable resource. For the purposes of this discussion, a nonevolutionary individual dandelion plant is that small green thing that grows on a small bare spot in your lawn. For the sake of generalization, assume that nearly all of its flowers produce a "seed" by apomixis, with the resultant plants being genetically identical to the plant that produced them. Further, assume that on very rare occasions a dandelion plant produces a seed from an ovule fertilized by pollen from a different EI than the one it belongs to.

With these two assumptions in mind, the EI dandelion is easily viewed as a very long-lived perennial organism. At any time, it is composed of parts that are moving around ("seeds" produced by apomixis), growing (juvenile plants), dividing into new parts (flowering plants), and dying (all ages and morphs). Natural selection could just as well have produced an organism with all these parts in physiological contact, but in view of the type of resource on which the EI dandelion specializes, this alternative arrangement of parts is clearly optimal. The EI dandelion survives by the harvest of resources most easily described as 6-square-inch bare bits of ground. Its searching strategy is to repeatedly spread itself very thinly over an area that is likely to have a number of these resource bits. The bits are ephemeral and unpredictable in exact

location (just as are mice in a field to a fox), but their number per large unit time and area is quite predictable (again, as are total mice to be captured per month per acre per fox). Those parts of the EI dandelion that land on a resource bit harvest it as rapidly as physiologically possible and then again spread out over the habitat in search of more bits.

In effect, the EI dandelion is a very large tree with no investment in trunk, major branches, or perennial roots. It has a highly diffuse crown. Such a generalization is often countered by the observation that the individual dandelions cannot contribute to each other's welfare. In fact, the individual parts of more conventional EI plants are connected at all levels, along a gradient from where the fortunes and losses of one part are heavily capitalized on and catered to by other parts, to where the physiological connection is virtually nonexistent. Even at this end, group phenomena still occur, such as pollinator attraction, allelopathy, interspecific interference, etc., by the disconnected but closely spaced members of a conventional clone.

The conceptualization of a clone of dandelions as an EI allows a number of interesting observations:

a) Imagine a new dandelion mutant with fierce spines, growing in a habitat plagued by tender-tongued goats. As its crown grows from occupying one resource bit to covering most of the resource bits, it is competing with several other diffuse crowns of EI dandelions, not with thousands of interbreeding individuals, some of which pick up the fierce-spine gene with each generation. The properties of this competition will be quite similar to that between, for example, the overlapping crowns of four large conspecific tropical rainforest vines, one of which is newly resistant to defoliating insects.

b) If there is a population explosion of groundhogs in the habitat occupied by an EI dandelion, and hence a population explosion of small piles of dirt, the sudden increase in abundance of resource bits will result in a great increase in the size of the EI, not in a population explosion with all the attendant genetic/evolutionary changes expected when a population suddenly is confronted with superabundant resources. To say otherwise would be like saying that a bear encountering a large acorn crop undergoes a population explosion. The EI dandelion is not a member of a fugitive species nor does its population have a high growth rate.

c) It is likely that each EI dandelion occupies a natural habitat much to the exclusion of other EI dandelions. It should be locally adapted, an adaptation brought about through many (hundreds of ?) years of competition between EIs, a competition in which the most locally adapted EI gradually ends up as the nearly unremovable resident (such as when male animals contest for breeding territories that are maintained year after year by one individual). On the other hand, recent severe habitat disturbances by humans should result in severe mixing of EI dandelion crowns, and there may even be natural habitats in which there is too much microheterogeneity for a single EI to consistently capture all the resource bits.

d) An EI dandelion produces a very large number of insect-visited inflorescences, and one wonders why it does not dispense with this behavior and

use the inflorescence solely as an organelle to generate apomictic "seeds." This may occur for the same reason that a large tree produces a large flower crop even if it can self-pollinate and will produce only a small number of seeds irrespective of how many flowers are pollinated. To obtain even some foreign pollen, it has to produce a flower crop large enough to attract insects that already have other large flower crops to visit. If dandelion EIs were originally much more microgeographically separated than in contemporary sites disturbed by humans, such a situation would be even more likely. I might also note that there should be selection for only minimal outcrossing among EI dandelions, since the habitats and resource bits for an EI dandelion are highly invariant. I have trouble thinking of a more monotonous resource than 6 square inches of new mud. In short, if we count the sexually produced seeds as reproductive effort, the ratio of reproductive to vegetative expenditure by the EI dandelion is exceedingly low, being among the lowest among plants. By adding to the seed value the cost of nectar and color of the inflorescence, a structure that is primarily a growth mechanism, the ratio would be little increased.

WHAT IS AN APHID?

It should be evident that an aphid is the annual dandelion of the insect world. In short, individual aphid eggs hatch in the spring into a relatively small number of EIs. Each EI grows rapidly by parthenogenesis, with occasional pieces (aphids) being bitten out of it by parasites (in conventional discussions these would be called parasitoids or predators). Only very rarely is an EI preyed upon (i.e., all of it eaten), since part of its growth pattern is to spread itself very thinly over the surface of the plants in the habitat, so thinly that a potential predator is very unlikely to find all of it at once. Once much growth of the EI aphid has occurred, it is essentially indestructible as long as there is some food in the habitat. In short, the EI aphid population density should gradually decline at a decreasing rate as the summer progresses.

By being spread very thinly, the EI aphid is not only almost impossible to locate and consume in entirety, but it can suck nutrients out of many plants without killing any one of them. The diffuse body means that little energy is expended hauling support tissue from plant to plant, yet a tiny daily meal is obtained from each of the many individual host plants in the habitat.

When the autumn arrives, each EI aphid then makes as many male and female EI aphids as it can, which in turn mate and produce eggs for the next year's generation. In short, the summer generation of EI aphids is made up of individuals that are close to being the largest of (subdivided) insects, have a very stable population density during the summer months, and certainly have a very low rate of population growth in the presence of superabundant food. With this view in mind, not only does apparent altruistic behavior by certain individual aphids take on the very ordinary aspects of individual selection, but it can be seen that the population ecology of aphids, like that of dandelions, is virtually unknown.

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LOW PREFERRED FORAGING TEMPERATURES AND NOCTURNAL
FORAGING IN A DESERT HARVESTER ANT

Bernstein (1974) showed that three species of harvester ants in the Mojave Desert, *Veromessor pergandei*, *Pogonomyrmex rugosus*, and *P. californicus*, have their peaks of abundance at different altitudes. The preferred foraging temperatures of each of these species coincide with the prevailing daylight temperatures at the seasons when seeds are most abundant within the altitudinal range of each species. These preferences result in ants in the high deserts foraging at higher temperatures than ants in the low deserts, because seeds in the high deserts are most available during the hot summer months, while in the low deserts seeds are in greatest abundance in the cooler months (Bernstein 1974).

For *V. pergandei*, which has its peak abundance at lower elevations (Bernstein 1974), nocturnal foraging has been reported as nonexistent (Creighton 1953) or very rare (Tevis 1958). Bernstein developed her model of resource partitioning on the assumption that none of the above species of ants forages at night.

On all six summer nights when we visited our study site (July 22 and 23, August 13 and 17, October 11, 1974; and August 24, 1975), we observed nocturnal foraging of *V. pergandei* near Salton City, California (elevation approximately 30 m). In 20 checks of 10 colonies while the moon was out or shortly after it had set, we found in all cases well-organized foraging columns with seed being transported nestward. For 20 cases, when these same 10 colonies were checked prior to moonrise, only three had active foraging columns and these were poorly organized. In contrast, on the 12 nights between November and May when we visited the study site, no nocturnal foraging was seen.

Workers of *V. pergandei* were observed conducting nocturnal foraging when air and soil temperatures ranged from 21.5° to 31° C. In contrast, daytime foraging in winter may commence in sunlight with air and soil temperatures of 13.5° and 11.5° C, respectively. *Veromessor pergandei* ceased daytime activity in July and August between 08:00 and 09:00 when air and soil temperatures