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Elemental stoichiometry of *Drosophila* and their hosts

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Summary

1. Nitrogen (N) and phosphorus (P) availabilities are important ecological determinants of resource use in nature. Despite the wide range of hosts used by species of the genus *Drosophila*, elemental composition of natural resources of these flies has never been investigated.

2. Total body N and P contents were determined in seven species of wild-caught *Drosophila*, their natural hosts, and artificial diets routinely used to rear these flies in the laboratory. The flies tested included *D. hydei, D. arizonae, D. simulans* and *D. pseudoobscura* collected from rotting fruit (melons), and the cactophilic *D. nigrospiracula, D. mojavensis* and *D. pachea* collected from their specific host plants, Saguaro, Organpipe and Senita cactus, respectively.

3. Natural hosts varied in elemental composition, with fruit showing higher N (2·8–4·3% dry mass) and P (0·50–0·67%) levels compared with cacti (0·5–1·6% N; 0·01–0·29% P). No consistent differences in N and P levels were found between healthy and necrotic cactus tissue.

4. Total body N and P also varied among *Drosophila* species. This variation mirrored the levels of N and P found in the respective hosts and laboratory diets. N:P ratios were consistently lower in female flies compared with conspecific males suggesting phosphorus demands during oogenesis are high.

5. Potential mechanisms by which *Drosophila* deal with N or P limitation in nature are discussed.

Key-words: Nitrogen, phosphorus, resource ecology, stoichiometry

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Introduction

Drosophila has become synonymous with the term 'fruitfly', despite the fact that many species are restricted to hosts other than fruit. For example, a number of species exclusively utilize mushrooms or slime fluxes (Carson 1971; Shorrocks 1982) while others are restricted to cacti (Heed 1978) or flowers (Brncic 1983). Some species are highly polyphagous and others are assumed to be completely monophagous. The implications of this host diversity for *Drosophila* biology have been examined at several levels. One approach has been to assess the temporal and spatial predictability of various hosts as they relate to life-history variation among the resident *Drosophila* species (Kambysellis & Heed 1971; Montague, Mangan & Starmer 1981; Lachaise 1983; Heed & Mangan 1986). Other investigations have sought, instead, to understand adaptations of *Drosophila* to secondary plant compounds and macronutrient (protein, carbohydrate, lipid) levels in their hosts (Kircher 1982; Fogleman & Abril 1990). Constituents of some of these resources, such as amanitin in mushrooms and cactus alkaloids, are toxic to most *Drosophila* and thus studies of the tolerance of mycophagous (Jaenike *et al.* 1983) and cactophilic (Kircher *et al.* 1967) species to these substances have been instrumental in understanding the specific host associations of many species in the genus. The microbial communities, especially yeasts, associated with natural *Drosophila* hosts are quite variable, and the importance of this variability in host utilization has also received considerable attention (Begon 1982).

Still, most studies of *Drosophila* nutritional biology have focused on laboratory diets of *D. melanogaster* and have emphasized macronutrient and micronutrient (vitamin) requirements of this species in order to maximize laboratory culture conditions (Sang 1978). Comparative studies, in which the laboratory medium requirements of other *Drosophila* species were determined, although limited in scope, revealed considerable interspecific differences in dietary suitabilities (Royes & Robertson 1964). While useful in designing culture media for maintaining different species in the laboratory and for understanding nutritional biology at one level, this approach does not allow us to test hypotheses about

the ecological and evolutionary implications of nutrient limitation for *Drosophila* at the level of elemental composition often employed in comparative studies of other organisms. It is widely known that for phytophagous insects, host nitrogen (N) levels can directly affect growth and reproduction (Mattson 1980).

Recently Elser *et al.* (1996) have argued that not only N, but the relative levels of N and phosphorus (P) at different trophic levels, may be an important determinant of life-history variation in a given ecosystem. *Drosophila* species exhibit extreme variation in life-history traits (Markow 1996), the origins of which are attributable to both phylogenetic history and recent, but as yet unknown, ecological pressures (Pitnick, Markow & Spicer 1995; Pitnick, Spicer & Markow 1997). We have little information as to what extent natural hosts for *Drosophila* species vary in N and P content, or if either of these elements are so limited as to influence the resource and reproductive ecology of members of this genus. Below we report a study designed to ask the following questions:

1. Do natural *Drosophila* hosts vary in N and P composition?
2. Are adult flies of different *Drosophila* species identical in their elemental compositions?
3. Do male and female flies differ in their elemental compositions?

Seven species of *Drosophila* were examined in this study. Two, *D. simulans and D. hydei,* are considered cosmopolitan, typically associated with human habitation (Patterson & Stone 1952). Two others are considered to be primarily either cactophilic (*D. arizonae*) or slime-flux breeding (*D. pseudoobscura*) but are polyphagic and often found breeding on decaying fruits and vegetables. *Drosophila nigrospiracula*, *D. pachea* and *D. mojavensis* are all strictly cactophilic, endemic to the Sonoran Desert of North America (Heed 1978). Of these three, *D. pachea* is the only one, because of its nutritional dependence upon a unique sterol in Senita cactus (Kircher *et al.* 1967), that does not switch cactus host species in different parts of its range. To address the questions asked in this study, wild flies were collected directly from their respective hosts for elemental analysis. Samples of each host were also collected and analysed. Progeny of field-caught flies of three species, *D. arizonae, D. simulans* and *D. nigrospiracula*, were reared on laboratory media and these flies and media were also analysed to assess whether elemental composition changed substantially in response to diet.

Materials and methods

COLLECTION AND PREPARATION OF PLANT MATERIAL SAMPLES

Fruit on which wild flies were found breeding and feeding in Tempe, Arizona, included decaying Cantaloupe, Honeydew and Watermelon. When collecting samples of necrotic material, care was taken to remove any immature or adult arthropods. Samples of melon rind were also taken from Watermelon and Cantaloupe. Cactus was sampled from the sites where cactophilic species were collected: Saguaro (*Carnegiea gigantea)* in the Superstition Mountains of Arizona, and Senita (*Lophocereus schottii)* and Organpipe (*Stenocereus thurberi)* in Guaymas, Sonora, Mexico. All arthropods were removed from the necrotic cactus collections and samples of healthy tissue were also taken from the same plants. For Saguaro and Senita, samples of healthy tissue were also taken from several other plants located several hundred metres away. Samples were placed in a drying oven at 60 °C for 1 week before being ground to a fine powder with mortar and pestle for analysis.

COLLECTION AND PREPARATION OF *DROSOPHILA* SAMPLES

Flies were aspirated directly from their feeding sites into vials and taken to the laboratory. Four species, *D. hydei, D. arizonae, D. simulans* and *D. pseudoobscura* were collected from resident populations on the same pile of rotting fruit in Tempe, Arizona, in autumn 1996. All four species had been reared from these substrates on numerous occasions, although the individuals used in this study were aspirated as adults. Three species are cactophilic and were collected from their specific host cacti in the Sonoran Desert. Flies of *D. nigrospiracula* were aspirated from necrotic Saguaro in the Superstition Mountains east of Phoenix, Arizona. The other two species, *D. mojavensis* and *D. pachea*, were found on their respective hosts, Organpipe and Senita, in San Carlos, Sonora, Mexico. In the laboratory, males and females were immediately separated and placed in separate glass vials in a drying oven set at 60 °C for 72 h. Flies, numbering from about 20 to 200, were pooled in order to obtain enough material for analysis. Dried flies were counted and weighed before being ground to a fine powder with a mortar and pestle.

LABORATORY DIET EXPERIMENTS

In three species, *D. nigrospiracula*, *D. arizonae* and *D. simulans*, wild-caught inseminated females were allowed to oviposit on laboratory food and an F_1 generation was reared. Eclosing males and females were separated and, at 3 days of age, were dried for elemental analysis. Each species was reared on a different laboratory medium, as not all species do well on the same food type. *Drosophila nigrospiracula* was reared on Betty Crocker Potato Buds® moistened with distilled water, while *D. arizonae* and *D. simulans* were reared on standard banana or cornmeal culture media, respectively. Samples of the culture media on which the flies were raised were also prepared for

analysis. Decay of fruits and cacti in nature is associated with the presence of a variety of species of yeasts. Because pure samples of these particular yeast species could not be obtained for analysis, samples of live baker's yeast (*Saccharomyces cerevisiae*) were analysed to compare the elemental composition of a yeast with the other dietary material.

ELEMENTAL ANALYSIS

Total N content was determined in a Europa Scientific 20/20 mass spectrometer (Vandalia, OH, USA) using air as the standard. Total P was determined using persulphate oxidation followed by analysis of orthophosphate using the acid molybdate technique (APHA 1992). All element determinations were performed in triplicate on each sample preparation to assess potential experimental error due to processing.

STATISTICAL ANALYSIS

For both plant and fly tissue, subsamples of the same tissue preparation were effectively identical, as evidenced by the small standard errors in Tables 1 and 2. Thus mean percentages of N and of P in both plant and fly tissue were subjected to arcsin transformation prior to statistical comparisons using non-parametric tests (SYSTAT 7·0.1). Because the frugivorous *Drosophila* species all are associated with all three types of melons, unlike the host-specific cactophilic species, the three types of melons were grouped when comparing natural host elemental contents.

Table 1. Nitrogen and phosphorus contents in natural hosts and laboratory diets of *Drosophila*. All values are means (± SE) for three separate determinations on each sample

Hosts or laboratory diets	Nitrogen (%)	Phosphorus (%)	N:P
Fruit (hosts for *D. hydei, D. arizonae, D. simulans* and *D. pseudoobscura*)			
Cantaloupe rind	4·3 ± 0·0	0·57 ± 0·07	7·5
Cantaloupe flesh	3·9 ± 0·2	0·55 ± 0·10	7·1
Honeydew (rind and flesh)	2·8 ± 0·0	0·59 ± 0·12	4·7
Watermelon skin	3·5 ± 0·1	0·67 ± 0·09	5·2
Watermelon flesh	4·1 ± 0·0	0·50 ± 0·05	8·2
Saguaro (host for *D. nigrospiracula*)			
Necrosis (sample no. 1)	0·8 ± 0·0	0·01 ± 0·00	80
Necrosis (sample no. 2)	0·8 ± 0·0	0·02 ± 0·00	40
Healthy tissue (sample no. 1)	0·9 ± 0·0	0·03 ± 0·00	30
Healthy tissue (sample no. 2)	0·7 ± 0·0	0·02 ± 0·00	35
Healthy tissue (sample no. 3)	1·3 ± 0·0	0·03 ± 0·00	43
Healthy tissue (sample no. 4)	0·5 ± 0·0	0·02 ± 0·00	25
Healthy tissue (sample no. 5)	0·8 ± 0·0	0·01 ± 0·00	80
Organpipe (host for *D. mojavensis*)			
Necrosis	1·0 ± 0·0	0·22 ± 0·01	4·5
Healthy tissue	0·6 ± 0·0	0·16 ± 0·01	3·8
Senita (host for *D. pachea*)			
Necrosis (sample no. 1)	1·3 ± 0·0	0·12 ± 0·01	10·8
Necrosis (sample no. 2)	1·5 ± 0·1	0·19 ± 0·02	7·9
Healthy tissue (sample no. 1)	1·4 ± 0·1	0·29 ± 0·01	4·8
Healthy tissue (sample no. 2)	1·6 ± 0·0	0·14 ± 0·01	11·4
Healthy tissue (sample no. 3)	1·4 ± 0·0	0·16 ± 0·02	8·8
Laboratory diets			
Potato medium	1·4 ± 0·0	0·39 ± 0·02	3·6
Banana medium	2·8 ± 0·0	1·98 ± 0·02	1·4
Cornmeal medium	1·0 ± 0·0	0·67 ± 0·02	1·5
Yeast (*Saccharomyces cerevisiae*)	5·7 ± 0·0	0·75 ± 0·03	7·6

Results

ELEMENTAL COMPOSITION OF NATURAL AND LABORATORY *DROSOPHILA* DIETS

Nitrogen and phosphorus found in natural and artificial *Drosophila* diets are presented in Table 1. Natural host types (melon, Saguaro, Organpipe and Senita) were found to differ significantly in their contents of both N (Kruskal–Wallis test statistic = 14·0345, P = 0·001, df 3) and P (Kruskal–Wallis test statistic = 16·1211, P = 0·003, df 3). Samples from different plants of the same cactus species exhibited only minor variation in levels of both elements. There were no consistent differences between healthy and necrotic cactus tissue, indicating that microbial flora in decomposing tissue did not alter element levels. Nitrogen content was higher in fruit (2·8–4·3%) than in cactus (0·5–1·6%). Cactus species varied in N content such that Senita had the highest N (mean = 1·4%) and Saguaro and Organpipe the lowest (mean = 0·8% fbr both). P varied in a similar way to N, but the magnitude of the difference between fruit and cactus was much greater. The fruits examined here were strikingly higher in P (0·50–0·67%) than the cacti (0·01–0·29%), and of the cactus species, Saguaro had the least P (mean = 0·02%). Of the artificial diets, banana was the richest in P, followed by cornmeal and potato. The banana medium was richer in P than any natural host. Pure laboratory yeast, *Saccharomyces cerevisiae*, was also higher in P and N than natural hosts. The relationship between N and P content in the natural hosts and laboratory diets is shown in Fig. 1. Nitrogen:phosphorus ratios were somewhat variable in the different hosts (Table 1). Owing to its low P content, the highest N:P ratios were found in Saguaro. For the natural hosts, resources low in N generally tended also to be low in P. This reduction was generally stronger for P relative to N and therefore tissue N:P ratios were elevated considerably for cactus relative to fruits. Thus the answer to our first question is that hosts differ significantly in levels of these elements.

ELEMENTAL COMPOSITION OF FLIES OF DIFFERENT *DROSOPHILA* SPECIES

Nitrogen and phosphorus in males and females of seven *Drosophila* species, expressed as percentage of dry body mass, are presented in Table 2 and Fig. 2. Frugivorous species had significantly higher N (Mann–Whitney U = 3·0, P = 0·007, df 1) and P

(Mann–Whitney $U = 5{\cdot}5$, $P = 0{\cdot}017$, df 1) than cactophilic species. Some species were enriched over others in N or P by about 30% or 40%. Two cactophilic species, *D. mojavensis and D. pachea*, showed the lowest N (6·5–6·9%) and P (0·77–0·87%) contents. Sign tests revealed that N did not differ between males and females of the same species, but females always had higher P contents. This difference also is reflected in the consistently lower N:P ratios in females than in conspecific males.

Table 2. Nitrogen and phosphorus contents of wild-caught *Drosophila*. All values are means (± SE) for three separate determinations on each sample

Species	Sex	Nitrogen (%)	Phosphorus (%)	N:P
Frugivorous				
D. hydei	F	7·4 ± 0·0	0·89 ± 0·01	8·3
	M	7·9 ± 0·9	0·87 ± 0·02	9·1
D. arizonae	F	8·8 ± 0·3	1·07 ± 0·04	8·2
	M	8·8 ± 0·0	0·92 ± 0·00	9·5
D. simulans	F	9·3 ± 0·1	1·16 ± 0·02	8·0
	M	9·7 ± 0·0	1·02 ± 0·07	9·5
D. pseudoobscura	F	9·0 ± 0·0	1·14 ± 0·02	7·9
	M	8·7 ± 0·0	0·86 ± 0·01	10·1
Cactophilic				
D. nigrospiracula	F	8·0 ± 0·1	0·92 ± 0·02	8·7
	M	7·8 ± 0·0	0·78 ± 0·02	10·0
D. mojavensis	F	6·6 ± 0·0	0·87 ± 0·02	7·6
	M	6·8 ± 0·0	0·81 ± 0·03	8·4
D. pachea	F	6·9 ± 0·0	0·86 ± 0·01	8·0
	M	6·5 ± 0·1	0·77 ± 0·01	8·4

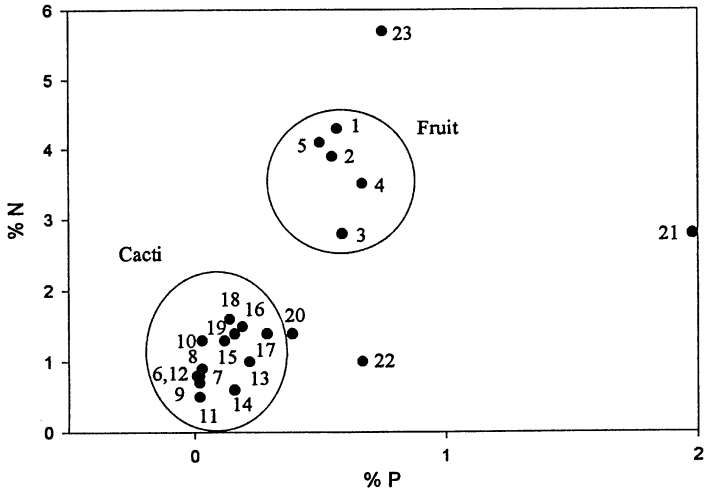

Fig. 1. Nitrogen (N) and phosphorus (P) contents of natural hosts and laboratory diets of *Drosophila* and yeast (*Saccharomyces cerevisiae*). Key to samples: 1, Cantaloupe rind; 2, Cantaloupe flesh; 3, Honeydew (combined rind and flesh); 4, Watermelon skin; 5, Watermelon flesh; 6, Saguaro necrosis (sample no. 1); 7, Saguaro necrosis (sample no. 2); 8, Saguaro (sample no. 1); 9, Saguaro (sample no. 2); 10, Saguaro (sample no. 3); 11, Saguaro (sample no. 4); 12, Saguaro (sample no. 5); 13, Organpipe necrosis (sample no. 1); 14, Organpipe; 15, Senita necrosis (sample no. 1); 16, Senita necrosis (sample no. 2); 17, Senita (sample no. 1); 18, Senita (sample no. 2); 19, Senita (sample no. 3); 20, potato medium; 21, banana medium; 22, cornmeal medium; 23, yeast (*Saccharomyces cerevisiae*).

Differences in the N and P contents of artificial foods compared with natural hosts raise the question of whether changing to a diet altered in elemental composition can change the elemental compositions of the flies. Our laboratory typically maintains cultures of a large number of species and uses different standard foods for rearing, depending upon which ones have been found, through trial and error, to support particular species. Thus when progeny of wild-caught flies of *D. nigrospiracula*, *D. arizonae* and *D. simulans* were reared for this experiment, the food recipes typically used for these three species were employed. It was not our intent, at this stage, to design an experimental assessment of the effects of dietary N and P on body composition, because the extreme differences in host elemental compositions were not known. Nonetheless it can still be asked whether the differences between laboratory and natural foods influence adult elemental composition.

In the case of *D. nigrospiracula*, the potato food was much richer in P, and slightly higher in N, than their Saguaro hosts (Table 1), suggesting that if the N or P composition of *D. nigrospiracula* is limited by these elements in nature, laboratory-reared flies will show higher levels of these elements. Both sexes of *D. nigrospiracula* showed an increase in P as predicted, with the effect being most pronounced in males (Fig. 3). N composition of females of *D. nigrospiracula* increased slightly, while in males it decreased slightly. The fruit *D. arizonae* used in nature was high in both elements, while the banana medium was similar to the natural fruits in N but even higher in P (Table 1). Rearing *D. arizonae* on banana food was expected to produce an increase in body P, which it did, with the greatest increase seen in females (Fig. 3). Cornmeal medium used for *D. simulans* has the same amount of P as fruit, but it was surprising to learn that it has less N than their natural hosts. As predicted, the N content of both males and females of *D. simulans* decreased when reared on cornmeal food (Fig. 3). Interestingly, females of *D. simulans* also showed a substantial decrease in P content.

Discussion

Natural *Drosophila* hosts vary dramatically in N and P contents, with melons containing significantly higher concentrations of both N and P than cacti. How does the variability in elemental composition of *Drosophila* hosts compare with the hosts of other phytophagous insects? Reported N and P contents of some representative resources were compiled and are given in Table 3. Our values for fruit compare closely with the fruits of wild plants surveyed at Brookhaven, New York (Woodwell, Whitaker & Houghton 1975). Flowers clearly show the highest levels of N and are

rich in P as well. Foliage elemental content is known to be strongly influenced by various factors, including soil nutrient supply, temperature, light and growing season. Desert soils are characterized by low N levels (Brady 1990). Clearly, cacti are the lowest in N and P of any of the hosts (Table 1), but this is not surprising given that cacti are slow growing and that N content is positively correlated with plant growth rate and herbivore defence (Mattson 1980; Schmidt-Nielsen *et al.* 1996).

The degree to which the *Drosophila* species studied differed in their N and P contents was surprising. An earlier study reported the N content for adults of laboratory strains of *D. melanogaster* and *D. subobscura* to be about 10% (Burcombe & Hollingsworth 1970), close to the average of 8·6% reported for insects (Mattson & Scriber 1987). While many things can conceivably influence the elemental composition of wild-caught flies, it is probable that the interspecific differences observed are likely to reflect real physiological differences between species. Nitrogen content does not vary with age in either *D. melanogaster* or *D. subobscura* (Burcombe & Hollingsworth 1970), so, while flies in our samples may have been of varying age, differences in age are unlikely to account for the species differences in body N observed. P content as a function of fly age has not been examined and may, in fact, decrease with female age and reduced reproductive output, but the likelihood of collecting samples of mixed ages seems equally probable for all seven species in the study. Even though larval and adult *Drosophila* have the opportunity, in nature, to raise their N and P intake by consuming both bacteria and yeasts (Starmer 1982), the amounts of these elements in wild-caught flies of each species still closely mirrors the levels present in their natural hosts. Species of *Drosophila* with low body N and P were associated with low N and P hosts. Furthermore, even when reared on N- and P-rich laboratory medium, *D. nigrospiracula* continues to have low body N and P compared with species that use fruit, suggesting that flies do not store excess N or P. This observation raises the question of whether flies of different species have adapted to the levels of these elements in the bulk tissues of their usual hosts.

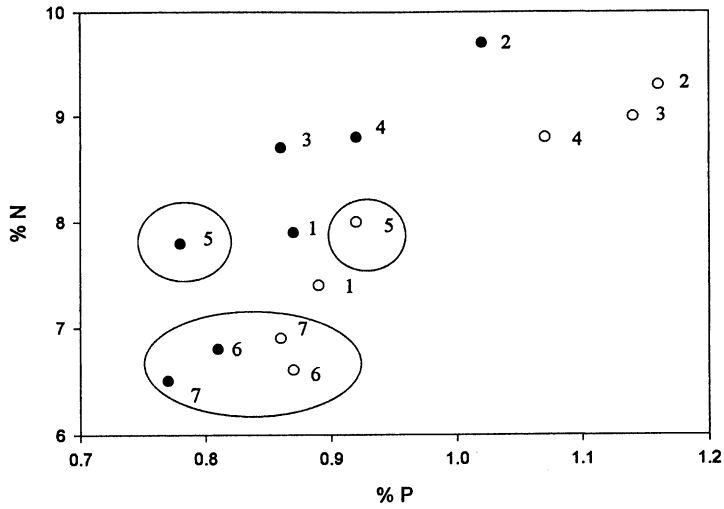

Fig. 2. Nitrogen and phosphorus contents of wild-caught *Drosophila*. Key to species: 1, *D. hydei*; 2, *D. simulans*; 3, *D. pseudoobscura*; 4, *D. arizonae*; 5, *D. nigrospiracula*; 6, *D. mojavensis*; 7, *D. pachea*. Solid circles = male; open circles = female. Cactophilic species are circled.

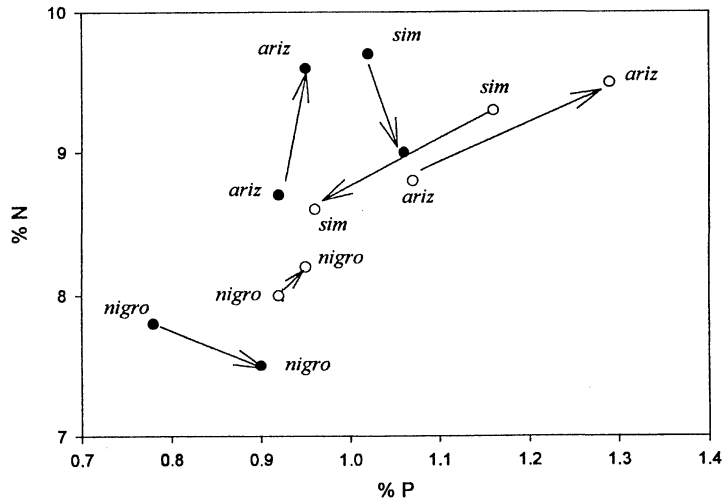

Fig. 3. Differences in nitrogen and phosphorus contents of wild-caught *Drosophila* compared with their laboratory-reared offspring. Solid circles = male; open circles = female. *ariz* = *D. arizonae; nigro* = *D. nigrospiracula; sim* = *D. simulans*. Arrows show shifts in values from wild-caught flies to those of their offspring.

Total N levels in plant biomass can be misleading because many factors influence the actual availability of N, such as the nature of the plant compounds in which the N is found. Furthermore there are several strategies that insects can use to adapt to conditions of N limitation (Tauber, Tauber & Masaki 1986; Mattson 1980). These include increasing feeding rate or efficiency, varying feeding sites on the same host or moving to different hosts of the same species, modifying the physiology of the host to increase nutrient supply, utilizing different species of hosts, and changing phenological responses to be inactive at times when host quality is poor.

Despite the differences between frugivorous and cactophilic *Drosophila* species in N and P percentages, the N:P ratio was fairly similar for all seven species, ranging from 7·6 to 10·1. Thus, relative to values for insects in general of 8·6% N and 0·9% P (Mattson & Scriber 1987), *Drosophila* are unremarkable. The most striking pattern observed for N:P ratios is the consistently lower ratio for wild females (Table 2). N:P ratios will be strongly influenced by the relative amounts of proteins and nucleic acids (Elser *et al.* 1996). During oogenesis in *Drosophila*, ovarian nurse cell chromosomes are endoreduplicated such that each chromosome is present in 1024 copies (Ashburner 1989). Nucleic acid amplification is increased further by the intensive transcription of maternal message destined for the growing oocytes to

support early embryogenesis (King 1970). Thus the P associated with increased nucleic acid investment by reproductively mature females is expected to alter the N:P ratio in the direction observed in our data.

Females therefore appear to have a disproportionate requirement for P compared with males. How do females ensure adequate P supplies in the face of P-poor resources such as cacti? As with N limitation, discussed above, several options exist. Females may seek P-rich resources to a greater extent than do males, but owing to the small size and great mobility of *Drosophila,* direct monitoring of the visits of males and females to different feeding sources is difficult.

It is suggested that male seminal fluid may serve as one source of limited nutrients in some *Drosophila* species. Males of a number of species engage in 'seminal feeding' of females through the non-sperm portion of their ejaculate, components of which are rapidly incorporated by females into their somatic and ovarian tissues (Markow & Ankney 1984; Pitnick *et al.* 1997). Originally this phenomenon was detected in *D. mojavensis* (Markow & Ankney 1984) using radiolabelled amino acids, suggesting that proteins were involved. Copulatory transfer of P in these species has not been assessed, but in male *Drosophila*, the reproductive tract, especially the accessory glands and ejaculatory bulb, contains highly concentrated levels of P (King 1954). Male reproductive maturity in many of these species is delayed by several days compared with females, perhaps in order to sequester limited ejaculatory nutrients, such as P, prior to mating.

Other ways in which animals deal with nutrient limitation is through altered physiological processes, namely by reducing metabolic rate and slowing development (Mattson 1980; Mattson & Scriber 1987). The *Drosophila* species examined in this study show substantial variation in adult body size and in development time. *Drosophila nigrospiracula*, growing in the poorest host (Saguaro), is the largest species. *Drosophila hydei*, however, is also large but is highly polyphagous. Furthermore, some cactophilic species are smaller and develop quickly even though they are associated with nutrient-poor hosts. The ability to make any definitive statements about the extent to which mineral nutrient limitation has shaped or constrained these traits in *Drosophila* awaits more comprehensive comparative studies of body size, metabolic rate, elemental requirements and development time that control for the effects of phylogeny. It is also possible that nutrient limitation selectively influences growth of specific tissues rather than overall development rate. For example, polytenization of ovarian nurse cell DNA begins during late larval life and pupation, and *Drosophila* species vary considerably in the stage of oogenesis typically present in eclosing females (Kambysellis 1968). If P is limited, and if flies have responded to this limitation, females emerging from P-poor substrates should have less advanced ovarian chambers than females of species using P-rich resources. This prediction is currently being tested.

Table 3. Some representative nitrogen and phosphorus contents of insect resources

Resource	Nitrogen (%)	Phosphorus (%)	N:P
Bacteria	9·6[a]	3·00[a]	3·2
Fungi	5·1[a]	1·40[a]	3·6
Yeast (*Saccharomyces cerevisiae*)	5·7[b]	0·75[b]	7·6
Pollen (various)	2·9[c]	0·43[d]	6·7
Foliage (8 species)	8·5[e]	0·63[e]	13·5
Fruit (5 species)	4·3[e]	0·83[e]	5·2
Flowers (5 species)	17·4[e]	2·4[e]	7·3
Roots (8 species)	3·5[e]	0·94[e]	3·7
Bark (7 species)	4·2[e]	0·45[e]	9·3

[a] Mattson & Scriber (1987).
[b]Present study.
[c]Levin & Haydak (1957).
[d]Vivino & Palmer (1944).
[e]Woodwell, Whitaker & Houghton (1975).

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