conditions. But the high activity enzyme in the laboratory clone French R and the very high activity enzyme in the highly Op-resistant glasshouse clone PirR (electrophoretically identical to that in the highly resistant clones from northern England and western Scotland[4]) both stain after electrophoresis in a single band with an electrophoretic mobility slightly but distinctly different from E4(MS1G) and from each other.

Because of this electrophoretic distinctiveness it is unlikely that either of these high activity mutant esterases could have arisen by a duplication of the E4(MS1G) gene, or that the higher activity esterase (E4(PirR)) could have arisen by a duplication of the gene for the lower (E4(French R)). A more reasonable explanation would be that E4(MS1G), E4(French R) and E4(PirR) arose independently in separate mutations in different Op-susceptible aphids.

JOHN BAKER
Tom Hood Senior High School,
Terling Close,
Leytonstone,
London E11 3NT, UK

1. Devonshire, A. L. & Sawicki, R. M. *Nature* **280**, 140–141 (1979).
2. Baker, J. P. *Annls appl. Biol.* **86**, 1–9 (1977).
3. Baker, J. P. *Annls appl. Biol.* **88**, 1–11 (1978).
4. Devonshire, A. L., Foster, G. N. & Sawicki, R. M. *Plant Path.* **26**, 60–62 (1977).

DEVONSHIRE REPLIES—The simple model of "a succession of tandem duplications of the structural gene" is based on the measurement of insecticide hydrolysis[1], and not simply on the subjective assessment of electrophoresis gels stained for naphthyl acetate-hydrolysing enzymes. The enzyme, E4, has been shown to be identical in susceptible and resistant aphids, and differences in activity are a direct consequence of the production of more of the same enzyme[1].

Esterase E5 (which probably corresponds to 'the satellite[2] to E4') is present in MS1G and French R, but not in the other five clones examined[1] and seems to occur only in untranslocated variants. Any association of this band with E4 is speculative, and our studies have shown that it plays no part in insecticide hydrolysis. Baker suggests that the six specimens from two sites, in which "the electrophoretic band (E4) *appeared*[3] to be slightly retarded in mobility and without a satellite (E5?)" are associated with glasshouses. We have never detected such decreased mobility of E4 in slightly resistant variants among the several thousand insects examined from the field and glasshouses throughout the UK. The biochemical and toxicological significance of this putative electromorph has not been investigated, and it has little bearing on our conclusions. Although very resistant aphids (with 32 or 64 times as much enzyme) appear to have E4 with slightly lower mobility, on dilution the enzyme reverts to the characteristic mobility either when run alone or when coelectrophoresed with E4 from susceptible insects. It is therefore an artefact of the electrophoresis probably arising from the larger amount of protein present.

In view of the convincing biochemical evidence, and lack of 'electrophoretic distinctiveness' of E4 in the seven variants examined, we believe gene duplication to be the most likely cause of the overproduction of E4 by resistant aphids. This, however, does not preclude hitherto undiscovered mutations at this structural locus.

A. L. DEVONSHIRE
Department of Insecticides and Fungicides,
Rothamsted Experimental Station,
Harpenden, Herts AL5 2JQ, UK

1. Devonshire, A. L. *Biochem. J.* **167**, 675–683 (1977).
2. Baker, J. P. *Annls appl. Biol.* **86**, 1–9 (1977).
3. Baker, J. P. *Annls appl. Biol.* **88**, 1–11 (1978).

Spider feeding behaviour optimises dietary essential amino acid composition

GREENSTONE[1] showed that dietary mixing occurs in the lycosid *Pardosa ramulosa* (McCook) and claimed that the spiders optimise their intake of essential amino acids. He took the optimal proportions of amino acids to be those present in the spiders and estimated the ingested nutrients from the amino acid composition of 'appropriate extracts' of the prey. I suggest that the extracts he used were inappropriate so that the data cannot be used to test the hypothesis that they forage optimally for essential amino acids.

The appropriate extract used by Greenstone was prey haemolymph "because spiders do not consume their prey intact and therefore do not ingest skeletal material" (see Table 2 of ref. 1). However, spiders pour digestive fluids onto their prey and ingest the fluid products and the haemolymph but discard the cuticle. In *Tegenaria atrica* Koch these digestive fluids contain a wide range of proteolytic enzymes as well as esterases and carbohydrases[2]. A similar range of digestive enzymes must be expected in all spiders.

Except for the haemolymph, the distribution of amino acids in insects is poorly known but the information available shows no correlation between the amino acid composition of insect protein and that in the free pool amino acids[3]. In addition the amino acid composition varies between tissues as well as between sexes[4]. Consequently the amino acid composition of ingested material will reflect that of both the haemolymph and of those tissues digested externally. The proportion of each tissue digested will vary because spiders consume different amounts of individual prey items according to, *inter alia*, disturbance, prey type, and hunger and/or prey density. The relationship between the amino acid content of prey haemolymph and the food ingested needs to be established before the hypothesis can be tested.

W. F. HUMPHREYS
School of Biological Sciences,
Bath University,
Bath, Avon BA2 7AY, UK

1. Greenstone, M. H. *Nature* **282**, 501–503 (1979).
2. Mommsen, T. P. *Comp. Biochem. Physiol.* **60A**, 365–382 (1978).
3. Levenbrook, L. & Dinamarca, M. L. *J. Insect Physiol.* **12**, 1343–1362 (1966).
4. Chen, P. S. *Monographs in Developmental Biology* Vol. 3, *Biochemical Aspects of Insect Development* (Karger, Basle, 1971).

GREENSTONE REPLIES—As Humphreys intimates, the most appropriate extract for the dietary studies is not an easily extractable fraction, but rather the difference between the total amino acid composition of the insect and that which remains in the carcass after the spider has fed upon it. At the time the amino acid studies were begun it was not possible to initiate a feeding study. Large stocks of the insects, however, were on hand, from which two types of extracts were potentially available: haemolymph alone, which might underestimate the spiders' amino acid consumptions, and macerates of whole insects, which might overestimate them. I chose to risk underestimation because the spiders' evolutionary history has predisposed them to having low prey utilisation efficiencies.

Pardosa species are small and live in open habitats[1]; this exposes them to heavy density-independent mortality. *P. ramulosa* spiderlings generally have a high ballooning frequency (my unpublished data), which is a correlate of habitat instability[2,3]. Open and unstable habitats are r-selecting, and among the expected traits of r-strategists is low food utilisation efficiency[4]. *Pardosa* species have been shown to have lower prey utilisation efficiencies[5], and jumping spiders to feed for less time on each prey item[6], when food is abundant, as was the case in the study area during my field work[7]. These facts suggested that the spiders would be more apt to take only haemolymph than to consume all of the extractable amino acids.

The use of haemolymph has the additional advantage that material from a large random sample of an insect population can be pooled, thereby averaging out some of the age and sex differences in amino acid composition.

MATTHEW H. GREENSTONE
Department of Ecology and Evolutionary Biology,
University of California,
Irvine, California 92717

1. Greenstone, M. H. *Am. Midl. Nat.* (in the press).
2. Gadgil, M. & Solbrig, O. T. *Am. Nat.* **106**, 14–31 (1972).
3. Southwood, T. R. E. *Biol. Rev.* **37**, 171–214 (1962).
4. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography*, 149 (Princeton University Press, 1967).
5. Kessler, A. *Oecologia* **8**, 93–109 (1971).
6. Gardner, B. T. *Psyche* **72**, 133–147 (1965).
7. Greenstone, M. H. *Symp. zool. Soc. Lond.* **42**, 183–193 (1978).

0028–0836/80/150578—01$01.00