

Book Review

The Extended Phenotype: The Gene as the Unit of Selection.
By Richard Dawkins, Oxford and San Francisco: W.H.
Freeman, 1982, \$18.95 hardcover.

Richard Dawkins has provided us with another insightful analysis of evolutionary theory. *The Extended Phenotype* is a collection of ideas and new perspectives advocating the author's gene's eye view of evolution. Much of the book is devoted to clearing up confusion and misunderstanding among evolutionary biologists and colleagues in related disciplines such as developmental biology, ecology, ethology, and genetics. Excellent reviews are presented of kin selection, "genetic determinism," "adaptationism," and "fitness".

The central argument of the book concerns the unit of selection. Dawkins identifies two types of evolutionary entities: "replicators" and "vehicles" (cf. Dawkins, 1976). Replicators produce identical copies of themselves, usually from within the confines of a nested hierarchy of vehicles (chromosomes, organisms, groups?). Because only the bits of DNA or RNA defined as "genes" replicate copies of themselves from generation to generation, Dawkins argues that genes are the 'unit' of selection. Most evolutionary biologists agree (e.g., Williams, 1966).

Dawkins presses the issue further. Noting that genes can have phenotypic effects outside of the organism (e.g., a spider's web), he suggests that "vehicles" such as the organism are superfluous entities. Dawkins proposes a "new central theorem of the extended phenotype: An animal's behaviour tends to maximize the survival of the genes 'for' that behaviour, whether or not those genes happen to be in the body of the particular animal performing the behaviour" (p. 248). For example, the nestling feeding be-

havior of a cuckoo host may be viewed as an extended phenotype effect of genes in the parasitic cuckoo.

Dawkins' argument that evolutionary explanations need not involve the intermediary entities of vehicles has several drawbacks. First, web genes, even though they have effects outside of the organism, are still tied to the reproduction of the individual spider and kin. Similarly, cuckoo genes, although they influence the behavior of the host organism, are still tied to the reproduction of the cuckoo. Moreover, such genes must use their own cuckoo organism to affect the behavior of the host. The feeding behavior of the host is elicited by the begging behavior of the cuckoo. There is no way to eliminate the intermediate step in the path from gene → phenotypic effect in organism → phenotypic affect on other organisms.

The concept of the extended phenotype emphasizes the need to think in terms of evolutionary competition among genes rather than competition among organisms. This point is well taken.

To understand adaptation, however, it is important to consider how differential reproduction at the various levels of life organization (e.g., gene, linked genes, chromosome, genome, gamete, individual, family, group) contribute to the differential representation of genes in future generations (Williams, 1966; Lewontin, 1970; Leigh, 1977; Alexander and Borgia, 1978). Genes may have many phenotypic effects, some of which are favored by selection at one level, but disfavored at another (e.g., Lewontin's dis-

cussion of t-alleles in mice). The emergent properties resulting from gene coalitions (e.g., Leigh's "parliament of the genes" and Alexander and Borgia's "outlaw genes") seem best analyzed from the levels of selection perspective. Dawkins does provoke one to rethink carefully the mechanisms by which natural selection operates.

Dawkins also provokes one to rethink the mechanisms by which the selection of cultural traits occurs. He persists with his concept of the "meme," now defined as the mental construct that generates a cultural trait, similar to Cloak's (1975) concept of "i-culture".

Critical to Dawkins' meme theory, indeed, his view of cultural evolution, is the necessity that a meme be a replicator. Dawkins requires that memes have a "definite structure, realized in whatever physical medium the brain uses for storing information" (p. 109). However, no chemical or synaptic structures in the brain have been found that correspond to specific behaviors or cultural traits (Pribram, 1971). The physical composition of information storage and manipulation probably varies from individual to individual and changes throughout ontogeny.

Dawkins' model is based on the premise that memes culturally evolve to maximize their survival. Like genes, memes are 'selected' on the basis of their effects: "If the phenotypic effect of a meme is a tune, the catchier it is the more likely it is to be copied" (p. 110).

Dawkins notes several weaknesses in the meme/gene analogy. First, "it is not clear that they [memes] occupy and compete for discrete 'loci,' or that they have identifiable 'alleles' (p. 112). Second, the meme "copying process is probably much less precise" (p. 112). And third, "New 'mutations' may be 'directed' rather than random" (p. 112). He concludes that "These differences may prove sufficient to render the analogy with genetic natural selection worthless or even positively misleading" (p. 112).

In spite of this caveat, Dawkins goes on to argue that the acquisition of cultural traits is independent of biological adaptation: "a meme has its own opportunities for replication and its own phenotypic effects, and there is no reason why success in a meme should have any connection whatever with biological success" (p. 116). I disagree.

The mechanism by which cultural traits increase or decrease in frequency are products of

a history of natural selection on human abilities to utilize the accumulated body of information that comprises culture. The selection of cultural traits by an individual may be independent of the genetic transmission of that individual, but it never can be independent of the past history of natural selection that created and guided the mechanisms of cultural selection (Alexander, 1979; Flinn and Alexander, 1982).

In the final chapter, "Rediscovering the organism," Dawkins analyzes the integrity of the individual. Among other topics, he discusses 'individuality' in regard to asexual reproduction and vegetative growth (cf. Harper, 1977; Janzen, 1977). Dawkins suggests that development and ontogeny are important criteria distinguishing cellular reproduction via asexual propagules (e.g., dandelion seeds) from growth. He further notes that asexual reproduction involves germ-line cell division, whereas growth involves somatic or 'dead end' cell division. This discussion is especially fun for those of us who study relatively mundane species from the animal kingdom. Dawkins conjures up images of "a primitive plant consisting of a flat, pad-like thallus, floating on the surface of the sea . . . spreading into an ever larger circular green carpet, like a monstrous lily pad several miles across and still growing." Although he suggests that this is not "reproduction in an interesting sense," it is characteristic of his writing in an interesting sense. Dawkins makes good use of wit, metaphor, and example throughout the book.

The Extended Phenotype is exciting and very worthwhile reading. Many important issues in evolution and behavior are objectively summarized with thorough and up-to-date references. Dawkins presents his arguments in straightforward fashion and pushes them to their logical ends. He is not afraid to make clear his points, even if clarity causes them to be more vulnerable to critics. I strongly recommend the book to all students of evolution.

Mark V. Flinn
*Department of Anthropology,
 Division of Biological Sciences,
 and Society of Fellows
 University of Michigan*

REFERENCES

Alexander, R.D. *Darwinism and Human Affairs*. Seattle: University of Washington Press, 1979.

- Alexander, R.D. and Borgia, G. Group selection, altruism, and the organization of life. *Annual Review of Ecology and Systematics* 5: 325–383 1978.
- Cloak, F.T. Is a cultural ethology possible? *Human Ecology* 3: 161–182, 1975.
- Dawkins, R. *The Selfish Gene*. Oxford: Oxford University Press, 1976.
- Flinn, M.V. and Alexander, R.D. Culture theory: The developing synthesis from biology. *Human Ecology* 10: 383–400, 1982.
- Harper, J.L. *Population Biology of Plants*. London: Academic Press, 1977.
- Janzen, D.H. What are dandelions and aphids? *American Naturalist* 111: 586–589, 1977.
- Leigh, E. How does selection reconcile individual advantage with the good of the group? *Proceedings of the National Academy of Sciences, U.S.A.* 74: 4542–4546, 1977.
- Lewontin, R.C. The units of selection. *Annual Review of Ecology and Systematics* 1: 1–18, 1970.
- Pribram, K.H. *Languages of the Brain*. Englewood Cliffs, N.J.: Prentice Hall, 1971.
- Williams, G.C. *Adaptation and Natural Selection*. Princeton: Princeton University Press, 1966.