

BOOK REVIEWS

Marcy F. Lawton, Editor

Mammalian dispersal patterns: The effects of social structure on population genetics.—B. D. Chepko-Sade and Z. T. Halpin [eds.]. 1987. University of Chicago Press, Chicago. Paper. xviii + 342 p.

This collection of papers, many of them given at a conference in late 1984, is still timely and of great interest for its relevance to evolution, ecology, conservation, and social behavior. The main goal is to see how social structure—particularly who mates with whom and who disperses—affects effective population size (N_e), and especially to see if N_e is low enough that Wright's shifting balance model of evolution holds. A second recurrent theme is to see how much inbreeding there is, particularly whether inbreeding depression and stylized inbreeding avoidance are common. The third theme is a phenomenological survey of dispersal among mammals—who disperses, when, and how far.

A series of chapters on field studies of particular populations provides much of the raw data for the first two themes. Detailed studies of deer, wild horses, wolves, bears, mongooses, prairie dogs, kangaroo rats, voles, pikas, rhesus monkeys, Hutterites, and the Gainj people of New Guinea depict such a wondrous diversity of social structures that one initially despairs of drawing generalizations. Though each of these chapters is an engaging natural history of an interesting social species, most are missing data (as the authors themselves note) that would be required to answer the above questions. Only studies of hominids and some of the rodents contain substantial genetic data, for example, while adequate demographic data exist only for the hominids.

Nevertheless, Chepko-Sade and Shields, with assistance from authors of several of the field studies, are able in a long summary chapter to point to several intriguing preliminary conclusions. First, for most but not all of the populations listed above, estimated inbreeding effective population size is such that, given the appropriate demography, Wright's shifting balance model might be an accurate depiction. However, as the authors note, one would have to be able to calculate F_{ST} (the probability that two homologous genes randomly chosen in a subpopulation are both descended from a single ancestral gene in that subpopulation) in order to clinch the argument. And these data are generally not available. However, it is clear that many mammals typically have a highly subdivided population structure with N_e much lower than censused population size. In any event, the authors' argument that evolution would be faster and "more effective" in a subdivided population than in a homogeneous one needs much more qualification than they provide. The precise reason why N_e is usually so low differs from species to species, though a suggestive result comes from Rood's study of the dwarf mongoose, the only data set allowing calculation of lifetime reproductive success for several individuals. In this species, varia-

tion in this variable has by far the greatest effect in lowering N_e .

Chepko-Sade and Shields also argue that most mammals are characterized by at least mild inbreeding. Templeton takes issue with this conclusion on the grounds that both the theoretical models and the dispersal data (especially intergroup dispersal) are inadequate. This argument, which has previously engaged both Shields and Templeton, is particularly well articulated here and is of importance to conservationists. Templeton points out that, if a species is typically outbred, there is selection for heterotic loci so that, when they are forced to inbreed, inbreeding depression arises because heterozygosity decreases. If, on the other hand, a species is typically inbred, selection removes the very genes that, if homozygous, would cause inbreeding depression. As more and more populations are restricted to small refuges with little gene flow between them, inbreeding will surely increase. Whether this increase in inbreeding entails a substantial inbreeding depression is an empirical matter, and Templeton and Shields make opposite predictions about what the data will show as they become available. From the empirical chapters one gets the impression that there is some degree of inbreeding avoidance in most species but that relatives mate occasionally (or often, in some species). However, Templeton argues that it is difficult to find populations nowadays whose dispersal traits and mating structures are not affected by humans, so that current population subdivision and inbreeding might not reflect the evolutionary lineage from which a species arose. For some populations (e.g., prairie dogs described by Halpin or wolves described by Mech) this caveat seems very pertinent. For others (e.g., Rood's mongooses) it seems less germane.

Some of the empirically oriented chapters, such as those by Smouse and Wood and by Sade et al., have interesting, more general theoretical sections, while three chapters are largely theoretical. Most of the theory is aimed ultimately at effective population size, though many biological traits are treated—the distribution of dispersal distances, kinship among mates, various demographic traits. No synthetic theory is yet available, and, though there is much recent clarification of relative importance of different variables (e.g., Chepko-Sade and Shields' chapter, Wood 1987), any specialist wishing to calculate N_e to assess aspects of a species' evolution or conservation is likely to be uneasy about which model he/she uses and what variables are not included.

Many papers plus the summary chapter present data that contrast interestingly with birds. For example, Shields discusses Greenwood's study (1980) showing that, in mammals, young males tend to disperse furthest while in birds young females tend to disperse furthest. Further, as Chepko-Sade and Shields note, mammals typically have lower levels of average het-

erogosity and mean population polymorphism than do many other taxa. The classic examples of virtually homozygous populations include several mammals—elephant seals, cheetahs, wisents—but, to my knowledge, no birds. In general, this volume on mammals covers many of the same topics treated in *Avian Genetics* (Cooke and Buckley 1987), particularly the chapters by Greenwood, Rockwell and Barrowclough, and Findlay, but the timing of both volumes prevented authors in either from commenting on papers in the other. Anyone who found *Avian Genetics* interesting would do well to read *Mammalian Dispersal Patterns* as well.—DANIEL SIMBERLOFF, Department of Biological Science, Florida State University, Tallahassee, FL 32306.

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GENERAL ADAPTATION, ESCALATION, AND PHAGY

Evolution and escalation.—Geerat J. Vermeij. 1987. Princeton University Press, Princeton, NJ. xv + 527 pp. \$47.50.

Phagy? Well, that's a term I just made up to fill an awkward void. It refers to feeding on live organisms, so it includes predation, parasitism, herbivory, and pathogen-caused disease, in case you have so many categories. The adjective is "phagous," and all phagers feed on what we may as well call their prey—it seems better to generalize a familiar word when confusion isn't likely. So a goldenrod is the prey of an aphid and a fungus as well as of a mammal that eats the adult or an insect that eats a seed. Phagers can be mutualistic, like a pollen-eating bee (mutualistic to the parent if not to the haploid individuals it eats) or a coral which protects and nourishes some zooxanthellae while digesting others. Does the cost of nectar make a nectarivorous fly phagous? Most concepts are fuzzy when pressed far enough.

Vermeij has written a clear and very well-documented book on evolutionary progress, although he mostly doesn't call it that. I probably shouldn't either, as the word is inherently value-laden and means quite different things to different people, whatever one happens to give a positive value to. If progress is to represent more than prejudice or aesthetics, which may not be possible, it must at least be measured on a scale causally appropriate for the evolutionary process. Unfortunately this criterion doesn't define a unique scale, although it eliminates some proposals, so we are back to subjectivity. Vermeij prefers current adaptation as the scale. But most usefully, perhaps, it can be regarded as an increase in general adaptation. The concept of

general adaptation was first distinguished and named by Wright (1949, p. 387), as far as I know, but despite Brown's repeated advocacy it isn't widely applied. A pity, for it opens some otherwise invisible doors. It refers to adaptations useful in a wide variety of circumstances, as distinct from special adaptations. The fuzziness of the boundary here doesn't need any pressing but that doesn't make the distinction less useful.

So. Does general adaptation tend to increase in evolution? The challenges of selection are specific sorts of things. Adaptations to one stress may be retained or modified or reversed or allowed to fade away with a later stress. General adaptations can then arise in three ways: by a modification of an earlier adaptation, building on it rather than eroding its earlier function; by diverse stresses acting more or less together on a single population; and as an initially unselected by-product of special adaptation. There is no survey, but I suspect that the third mechanism may be the most common. The "excessive construction" of Gans (1979) is an aspect of this third mechanism.

The origination of an adaptation does not ensure its persistence. I take it as obvious that, *ceteris paribus*, general adaptations are less likely than special ones to decay or be reversed. Furthermore, lineages with more general adaptations should persist longer, and probably diversify more, than comparable lineages with more special adaptations. We should thus expect the average generality of adaptation to increase through geological time.

It is possible, though, to argue rather the reverse: that special adaptations tend to be more useful than general ones over short evolutionary intervals, and that this short-term advantage should permit them to predominate. I gave a general equilibrium theory for long- and short-term adaptations some years ago (Van Valen 1975); although it needs modification to the extent that long-term advantage is episodic rather than continuous, it does show quantitatively how both scales of adaptation can coexist. The coevolution of angiosperms and insects seems to be predominantly of special adaptations insofar as the diversity of the two groups is concerned, which makes the argument of this paragraph a reasonable one.

(At the risk of seeming tendentious, I would like to repeat a hypothesis on coevolution [Van Valen, 1983] which Vermeij and several others have drastically misinterpreted; I hope that I have not returned the favor to him on something else in this review. In the first sentence of that paper I defined coevolution as occurring "when the direct or indirect interaction of two or more evolving units produces an evolutionary response in each." I then gave reasons to suppose that coevolution, in this rather narrow sense, "may comprise most of evolution." This is a fairly radical hypothesis. It may be wrong, but it isn't trivial. Rather than reinterpreting it by stereotyping [shoving an unfamiliar round plug into familiar square categories] and thereby trivializing it, I wish that discussion of it would be on what I actually said. I don't think that I can say it more clearly, although it may indeed be uncomfortable.)

When theoretical arguments conflict and, yes, even when they don't, it is useful to look at evidence. Facts aren't evidence until they are put into a conceptual picture, and all this is what Vermeij's book is about.

He proposes that through geological time there is an overall increase in defensive and competitive adaptations, and thus in adaptation to the biological environment. Phagors and competitors increase their own adaptations, with the net result being a progressive (but not monotonic) escalation of the overall level of adaptation. Therefore an average species now should be better than one from the Paleozoic even for a Paleozoic environment, but it doesn't do better now because its "enemies" (competitors and phagors) are better to a comparable degree. Darwin expressed the same viewpoint, but Vermeij's argument has later theory to build on and his evidence is almost incomparably better.

From one perspective the book is a paean to adaptation—a successful one. It should be quite adequate to remove doubts, from those who still have them, about the great preponderance of adaptation in phenotypic evolution. That the same conclusion can be reached in other ways doesn't diminish Vermeij's treatment. He gives both a theory of adaptations (and of the adaptive process), although without mentioning adaptive zones, and a large amount of organized evidence. Constraints on adaptation have their due treatment. Because the main focus of the book is on the evolution of adaptation through geological time, Vermeij critically discusses the nature of the value and of the imperfection of the fossil record, together with problems which arise in studying adaptation in extinct organisms.

Adaptations for survival are usually what we see in fossils. Vermeij, though, tries to make a virtue of this paleontological necessity. He has some discussion of mate competition, a nod to the amount of reproduction, almost nothing on timing of reproduction, and nothing on expansion, dormancy, and such. Even adaptation to enemies, though, is often mostly by reproductive escape. He thinks that fertility increase is "clearly favored only when population size is increasing" (p. 422); I had thought that this sort of misinterpretation of *r*-selection had left us long ago. He notes that mate competition often favors attributes which also enhance survival and implies incorrectly that only survival thus need be considered. Even with respect to survival he implies that selection on phagy-resistance is important only in cases where phagy regulates the population. Competitive exclusion does require that at least the excluded species be regulated by the source of competition, but that there is no such requirement for selection in general should be apparent from any realistic example.

Vermeij is a malacologist, and the book appropriately emphasizes marine mollusks. Some generalizations are therefore less universal than is implied (e.g., whole-body swallowing is not restricted to relatively small prey for some fishes, snakes, and ciliates, at least), and as a mammalogist I noted an expected proportion of minor errors for that group. The emphasis, though, is on a well-known, diverse, and abundant group for which much can be inferred. Thus there is a fine treatment of armor and its usual functional antagonist locomotion, with some appropriate extensions to other phyla. Comparative data on armor breakage give an especially insightful treatment. There is a whole chapter on use of vacated shells by other animals, in no less than seven taxonomic classes. Only snail shells are

discussed in this connection, but I suspect that other taxa will prove to have been providers if they are looked at with suitable criteria.

That evolution tends to favor the maximum rate of energy use consistent with constraints of history and habitat was extensively argued in 1973 by Hamilton. This interesting thesis has oddly been mostly ignored since then, but Vermeij revives it (without citing Hamilton) with several more examples. Such a getting-and-spending economy has to move fast or collapse, and Vermeij properly indicates the several reasons why most kinds of high-energy taxa have an unusually high risk of extinction. Cephalopods are the jet-set of mollusks and have exemplified the relation well. An extension of this argument is that low-energy taxa become progressively obsolete adaptively in environments with a good supply of accessible free energy. They may nevertheless find (or persist in) refuges from their enemies in low-energy environments like caves or the deep sea, below the surface of sediments, among sand grains, in bodies of well-defended organisms, and the like. The invasion of fresh water and land may have been triggered in this way; physical inhospitability has some of the properties of low free energy.

Escalated (high-energy) organisms usually can't survive well in habitats with low free energy, whatever else may be there. Thus occupation of such habitats by relatively unescalated organisms is an aspect of the size of their adaptive zone, and is not *in itself* an indication of a competitive advantage or of the existence of special adaptations for such habitats. An exception, where viability escalation occurs in a low-energy habitat, comes for the high level of defenses of plants living on the white sands of the drainages of blackwater rivers (Janzen 1974). This habitat is low-energy because the low availability of nutrients makes net photosynthesis low. Vermeij notes this pattern but dismisses it as not an anomaly. I think the anomaly is real but can fit comfortably in a somewhat broader approach. What Maiorana (1976) called submergent behavior, reducing one's food intake to minimize phagy, is a related phenomenon. Escalation does have costs, and whether these costs would outweigh the advantage in a biotic environment earlier in the Phanerozoic is not obvious but could perhaps be estimated in some cases. Escalation may not increase average general adaptation after all.

That the freshwater biota, especially the benthos, remains relatively unescalated is a remarkable phenomenon which is first documented here. Lakes are ephemeral things, but large rivers persist for tens of millions of years or more and their inhabitants didn't even suffer noticeably in the Cretaceous/Paleogene extinction, unlike the situation in all other known habitats (Van Valen and Sloan 1977). In the absence of an apparent explanation we should look more closely at the reality of the phenomenon: does escalation occur predominantly in a different way rather than at a lower rate? My cursory survey suggests that reproductive adaptations are not stronger in fresh water than in the sea, though, so we are left with a genuine mystery.

Vermeij, like Darwin, seems to go out of his way to find counterexamples to his views. He discusses several trends and their absence which seem to oppose escalation, of which he finds the most serious to be that the evolution of adaptations for and against predation

is quite variable over the Phanerozoic. It is especially high in the early Cambrian (the beginning of taxonomically widespread skeletons), the Silurian-Devonian, and the late Mesozoic, and it even seems to have reversed direction overall in the late Devonian and late Permian extinctions. Why this pattern should oppose Vermeij's argument escapes me. Mass extinctions select for the opportunistic, as noted otherwise above, and unless some group makes a major advance, which can't happen frequently by definition, escalation can proceed in small fits, as it does. However, in making and testing some predictions on extinction, Vermeij neglects to consider to what extent the predictions would also be made by other views. He does overall consider what we don't know as well as what we do. An index entry for puns is actually useful; I thought that one was a misprint on first reading. The density of puns in this review is actually higher than in the book, although they are perhaps less obtrusive.

One conclusion is that the biotic part of the environment is more important than the physical part in the evolution of adaptation. However, another conclusion is that changes in the physical environment often stimulate evolutionary change. Vermeij sees no difficulty in the conjunction of these propositions, nor do I, although part of the recent literature assumes their incompatibility. It should suffice to recall that interaction with enemies and mutualists can vary with the physical environment. Vermeij finds warming, and so a usually greater primary productivity, the most favorable for the evolutionary heat of escalation, together with an increase of moist forest or shelf seas and a joining of previously separated biotas. Conversely, cooling and other causes of decrease in primary production are most important in extinction. He makes some original calculations to find that more heavily armored mollusks are usually selected against by extinction during cooling.

Large warm regions tend to have more escalation than smaller or cooler regions, as Vermeij documented in an earlier book. Boucot (1975, 1978, 1984), though, has found that common and widespread species tend to evolve less than rarer ones, and Maiorana (1979) has found that abundant species tend to have fewer defenses than do less common species. While Boucot's explanation (drift) is clearly unimportant here, there are both absolutely and proportionally more uncommon species in large warm regions than elsewhere. Moreover, niche width is inversely related to species turnover (Vrba 1980), and niches tend to be narrower in warm regions. It may also be that energetic dominance reduces the variation in realized fitness within a species; I know of no relevant evidence, but suitable data may exist for birds. The relation of abundance and distribution to the probability of speciation by splitting is also relevant.

Vermeij doubts that competition causes much extinction. He gives two sorts of evidence for this: an inappropriate analogy with predation and the effect of some natural and artificial introductions. Other introductions, though, have resulted in appreciable extinction (Mooney and Drake 1986). The nature of the difference between the sets of cases remains to be determined; I suspect it is related to what I called the pressure of competition (Van Valen 1976), with low-

pressure competition, as of clams and plants, tending to be more diffuse and so with less of an immediate effect on individual species. The mammalian fossil record also has a moderate number of cases of apparently competitive replacement.

For Vermeij, escalation occurs because more escalated lineages diversify more, and because extinction is overall less important than diversification. The latter proposition is especially shaky. Pelecypods did replace brachiopods because of a lower probability of extinction, not a greater probability of origination (Van Valen and Maiorana 1985). Mass extinctions select against the escalated, but I strongly doubt that normal extinction does and the book ignores the topic. Even the differential diversification of more escalated lineages could conceivably be entirely a result of a lower probability of normal extinction rather than including a component of higher probability of successful branching. Nobody knows yet because it hasn't been studied.

Individual adaptation interacts with lineage adaptation: the properties which make a lineage successful or not come from lower-level, especially individual, selection, and what lineages are available for individual selection to act in are determined by higher-level, especially lineage, selection. And how an evolving biota, on any time scale, changes its distribution of energy use is as much an aspect of evolution as is the change in its taxonomic or genetic makeup and deserves as much study.

It would be interesting to know more or less how much of the energy used by some community or some guild is devoted to its actual life and how much to defenses and aggression of one sort or another. Boundaries would be fuzzy (perhaps too much so), endotherms would differ from ectotherms, etc., but escalation has an immediate cost as well as a long-term one and this is a suitable measure. We can apply it to our own species as well, a bit differently: How much of our productivity goes for defense against (and loss to) our conspecific phagors, i.e., criminals of one sort or another, the military, the merely unethical? How does this compare with that in quite different cultures? It is surely no surprise to us that mass extinction selects against the escalated.—LEIGH M. VAN VALEN, Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637.

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