University of Massachusetts Amherst

From the Selected Works of Charles Kay Smith

November, 1983

The Domestication of Evolution

Raymond P. Coppinger, *Hampshire College*
Charles Kay Smith

Available at: <https://works.bepress.com/charleskaysmith/133/>

THE DOMESTICATION OF EVOLUTION

RAYMOND P. COPPINGER AND CHARLES KAY SMITH

ABSTRACT

A coming 'Age of Interdependent Forms' seems destined to mark the success of what could be called 'despecialized/interspecific fitness' among neotenic strains (perpetuating juvenile traits) of species such as humans and domestic animals. Humans as well as the first domesticants underwent a neotenic evolution in the wild during the repeated interglacial periods which, acting on a number of mammalian forms, selected against adult species-specific ancestral adaptations to a stable environment. Neotenic species continue to look and behave more like ancestral youths than adults—even after sexual maturity and throughout their life-history. As they retain lifelong youthful dependency motivations, they can easily, under suitable conditions, become interdependent forms. By the time of melting of the last Pleistocene glacier, all the domestic partners had already become more dependency-prone than formerly, and were behaviorally despecialized enough to form the alliance that is now changing the old order of Nature.

ENVIRONMENTALIST VERSUS EVOLUTIONIST VIEWS OF EXTINCTION

The Lascaux cave-paintings in southwestern France illustrate a mute but fascinating tale. A few millennia before the domestication of cattle, early humans drew within their walls, as though all were already members of an extended family, wild species such as Tarpan¹ and Aurochs². Horses, bulls, and humans, were thus poised to play their parts in a macro-evolutionary trend, the drama having begun when intradependent mammals and birds of the Tertiary period replaced more independent reptilian forms at the end of the Mesozoic era. The second act occurred during the million-or-so years of the Pleistocene ice-ages that resulted in the interdependency of some species, such as those painted on the walls together with their human painters. All were eyeing one another just before establishing the domestic alliance of the Holocene, whose current success was about to usher in a new 'Age of Interdependent Forms'—and usher in, too, another swift mass-extinction as large as, if not larger than, that experienced at the end of the Mesozoic.

Both environmentalists and evolutionists must be concerned with extinction, but in different ways. In the hope that it might be of use to environmentalists, the present authors wish to offer an alternative view on the issue of human and domestic animal and plant proliferation, and concomitant wild-species extinction—as discussed in the pages of *Environmental Conservation*, and with particular attention to Arthur H. Westing's (1981) article measuring environmental dangers now and in the near future.

¹ *The post-Pleistocene Eurasian Wild Horse {Equus caballus gmelini}, extinct since 1851 (cf. Zeuner, 1963 pp. 303-13).—Ed.*

² *Bos primigenius, also called Ure-ox, which survived in Poland until 1627 (cf. W. Szafer in Biological Conservation, 1(1), pp. 45-7 & figs, 1968)*

On such issues as clean air or water, and on careful monitoring and regulating of the disposal of toxic or radioactive wastes, the authors support the environmentalist position. However, the endangered species approach, useful as it may be to alert us to anti-ecological folly of the moment and to hector bureaucrats into amending short-sighted industrial and technological policy, may actually mask a needed understanding of the profound revolution in evolution that, by the middle of the next century, seems destined to bring us close to the extinction of at least half of the extant wild terrestrial species. Perhaps, if we could understand better the current evolutionary trends in which we play a part, we could act more reasonably to minimize environmental damage.

The environmentalist sees the almost certain extinction of a species such as the Whooping Crane (*Grus americana*) or wild American Turkey (*Meleagris gallopavo*) as the sole responsibility of human folly that many environmentalists believe could be corrected through moral effort. Extinctions are seen as examples of contemporary decay and degradation of an environment that is presumed to have been better in the past. If humans do not reverse their decadent or thoughtless trend, it is said, and act more responsibly, this environmental decay will lead to an unnatural cataclysm. Because our species is playing a part in the coming extinctions of many wild forms, we humans tend to think that we are the sole cause of such extinctions and must be acting voluntarily. And so, obsessed with guilt rather than struggling to understand, we imagine that extinctions-to-come will soon mean the death of Nature, rather than a re-balancing of the prevailing situation. Such assumptions often seem most persuasive, even though it is known that extinctions of species have occurred naturally and repeatedly in evolutionary history (e.g. Raup & Sepkoski, 1982). Indeed, without the disappearance of some species there could scarcely be the flourishing of others, and to that extent at least there would be little further evolution.

Evolutionists recognize that Nature is always changing—sometimes very swiftly. Change is not assumed to lead towards good or bad so much as towards different interactions of forms and strategies, effecting ever-new balances, each with its own possibilities and limitations (Gould, 1982a). The important point that evolutionists feel compelled to insist upon is that humans do not stand outside evolution, but are players within the drama. Though occasionally we may ad lib a few lines here and there, we do not write the script and are still largely unconscious of the parts we have played and are about to play in evolution.

When writing on extinction, environmentalists usually direct our attention to instances of human folly or cupidity—such as over-hunting, polluting, dumping of toxic wastes, and other misuses of our natural resources. However, environmentalists generally acknowledge (e.g. Ehrlich & Ehrlich, 1981 pp. 131 et seq.) that by far the most important agent of extinction is the sheer biological success of domesticated plants, humans, and other animals. The increase in numbers of humans, and of domestic plant and animal species, is inversely proportional to the number of wild species that can share a limited environment and supply of energy. Westing (1981, 1982) attempts to quantify the alarming increase in biomass of the members of the domestic alliance projected for the next seven or eight decades. That biomass (in this case the total dry-weight of humans together with domestic animals) amounted in 1860 to some 5% of the biomass of all terrestrial species of animals; in 1940 it was 10%, and at present it is nearly 20% (Westing, 1981 p. 180, 1982 p. 39).

As human population may double in a little less than 40 years and cattle in a little over 40 years, before the year 2020 we and domestic beasts may make up approximately two-fifths of the world's terrestrial animal biomass. In the plant kingdom there is already under cultivation 'about 11 % of the global land area that is not continuously covered by ice' or 'some 8% of the world's terrestrial net primary photosynthetic production' (Westing, 1981 p. 180). The world's human population is projected to triple in the next seven or eight decades before it is expected to begin to stabilize—assuming that the birth-rate will not once again accelerate. By the middle of next century, then, we can expect, at the very least, that about three-fifths of all terrestrial animal biomass and about one-fourth of all plant life will be composed of humans and a few domesticated species.

Extinctions among wild species are already beginning to accelerate. For instance, among mammals the average rate of non-anthropogenic species extinction has been estimated (by J. Fisher et al. as paraphrased in Westing, 1981 p. 181) as approximately one species every 140 years. Yet about 36 mammalian species have vanished in only the past 360 years—a rate of increase since AD 1600 of over 1,400%. With 100 or more mammalian species currently said to be threatened with extinction, we begin already to sense the acceleration of a massive extinction. This brings us to a crucial question. Are humans responsible for creating a Frankenstein monster of domestication that is about to commit mass biocide on natural species? Or is domestication a natural evolutionary phenomenon?

DOMESTICATION AS AN EVOLUTIONARY STRATEGY

Instead of assuming that domestication of animals and plants is but another artificial human invention that is somehow ruining Nature, we hope to show through this paper that the perhaps-too-successful symbiosis among humans, livestock, pets, and plants, is a natural phenomenon—indeed, an adaptive strategy of evolutionary origin and significance. Charles Darwin established the convention of considering domestication apart from Nature by using it in *The Origin of Species* as an instance of artificial selection whereas, implicitly, 'real' evolution proceeds by natural selection. For Darwin (1859, 1868), and most biologists since, domestication has been important primarily as a metaphorical analogue for the way evolution works but is itself not perceived as a natural process. We suggest that current biological 'concepts of what is fit and adaptive in Nature are, as a result, at least 15,000 years out of date. For, these conventional 'fitness' models—models that are still the foundation of much of our environmental as well as of our political, economic, and social, planning--were developed without recognition of the domestic alliance as a natural evolutionary event, which at the same time constitutes an extraordinarily important adaptive strategy.

How successful the domestic allies have become is exemplified by the Orange Tree (*Citrus aurantium*) which, in its vast protected groves, may spread out more widely than any species of wild forest tree. Or again, because of the alliance between man and dog, the total biomass of dogs is already greater than that of all its wild, more self-sufficient, relatives. The same is true of goats, sheep, cattle, horses, camels, etc. Thus, by this criterion the domestic morph has the selective edge over its wild relatives under the global conditions of today—while, paradoxically, appearing maladaptive. Indeed, domesticated forms are often termed 'degenerate' (e.g. Hafez, 1975 pp. 13, 172) because they are interdependent,

despecialized forms rather than being what is considered most fit in the conventional sense of independent and highly specialized.

Practically all the domesticated forms of plants and animals, including humans, are virtually helpless 'in the woods'. Almost all need extensive help at every stage of development--with birth or other origin, food-finding, sheltering, protection from predators and competitors, and so forth. But in consort, these interspecifically socializing forms are especially well adapted to cope with present conditions because they share ecological talents--whether it be fecundity, growth-rate, mobility, or else some speciality such as smell, hearing, photosynthesis, or learning ability. Learning ability has recently made the human species a distinguished member of this alliance. Culture, rather than any apparent genetic change, was the human contribution during this period; but we should swallow our pride and accept our own inextricable interdependency with other domesticants. The culture we pride ourselves on was, and remains, dependent on the success of domestication.

Species outside the interdependent alliance are not able to reproduce as swiftly as domesticated species. Their dwindling populations are thus threatened with extinction. Specialized, self-sufficient species such as the eagle and the Lion (*Leo leo*, 'the King of Beasts'), that we are used to supposing the most fit in Nature, are being vastly out-reproduced by a few interdependent, less specialized forms. The fittest still survive, but despecialized inter-dependencies among species is a newly important strategy in Nature and is redefining the concept of 'fit'.

NATURAL ONTOGENETIC SELECTION DURING THE PLEISTOCENE

The astounding reproductive success of a population of cattle, swine, maize, humans, or wheat, based on a reciprocally dependent sharing of energy, makes possible, for all members of the alliance, often vastly decreased mortality due to a limiting of predation and competition from ecological equivalents. It further enables a range-expansion into additional ecological niches. Yet at first it seems strange that animals which are our natural competitors, either for grain or meat, would or could bond together into a symbiosis. Such a mutually beneficial system implies cooperativeness, as well as the absence of strong species-specific adult drives such as territoriality or dominance-aggression. Not every and perhaps not many animal species would have been behaviorally amenable to inter-species symbiosis. Had early humans attempted to domesticate Black Rhinos (*Diceros bicornis*), for example, they might have faced some insurmountable problems, to say nothing of the difficulty of attempting mutual symbioses with alligators or turtles!

Part of the key to understanding initial domestications is to consider the possibility that those first domesticants were already somewhat neotenic³, or they probably never could have been successfully domesticated. Suppose a species could somehow lose, or at least loosen, its adult drives and retain youthful dependency motivations. An evolutionary process that results in selection for juvenile traits retained into adulthood is called Neoteny (e.g. Kollmann, 1885; Mason, 1968), and neoteny has occurred repeatedly in evolution. Just as youthful mammals and birds join in interspecific play (Fagen, 1981), so, too, even adults of some species can play and live cooperatively.

³ *i.e. remaining indefinitely in an immature state, and commonly applied to genetic strains perpetuating juvenile traits.*

The behaviors of mammalian and avian neotenates are highly social throughout life, displaying strong youthful motivations to solicit one another's care and synchronize with one another's behavior. Furthermore, neotenates lack the strong species-specific recognition that generally inhibits adults from socializing across species-boundaries. As a consequence, interspecific behavior, and in general more cooperative and complex social organizations (Bekoff, 1972; Hendrichs, 1983), are not only possible but likely among neotenic forms. Domestic interdependency is a re-adaptation in neotenic adults of an infant and youthful mammalian motivation--care-soliciting--that was pre-adaptive because it motivated infant mammals to remain in close dependency with parents and their group. The continued activation of care-soliciting, together with the loss of species-specific ancestral drives, would make it probable for a neotenic species to readapt care-soliciting or social-dependency proclivities so as to initiate and enter into symbioses with other neotenic mammalian or avian species with which it shares youthful dependency motivations.

Neotenually evolved species achieve a selective advantage by becoming sexually mature before they complete their development into ancestral adults, thus retaining ancestrally youthful structure and behavior while avoiding full activation of ancestrally adult structures and drives (Haldane, 1932; Hardy, 1954; Beer, 1958; Gould, 1977, all explain structural neoteny; see Coppinger & Smith, 1983, for a brief discussion of the process and significance of behavioral neoteny). The behavioral consequences of systemic neoteny are not only as important as the more commonly discussed physical structures, but we believe that behavioral neoteny may often provide the advantage that Nature acts upon to select the whole genetic package of more youthful physical and behavioral traits in a mammalian population.

Activation during mammalian ontogeny of adult characters that form a complete system of species-specific structure and behavior by the end of the youthful metamorphic phase, is under genetic regulation. Genetic variations in the completeness, or intensity of activation, of the whole system of adult behavior and anatomy, exist within mammalian species. Variations in the regulatory program that would decrease the rate and degree of activation of a system of genes during a species' development, thus prolonging or even perpetuating the display of a system of youthful characters in descendants, could have been selected for during the periods of fluctuating habitats of the Pleistocene.

During the Pleistocene, the environment underwent both widespread (Denton & Hughes, 1981) and unprecedented changes of the order of 6 times the normal fluctuation of climatic conditions (Kerr, 1981). Such environmental instability would tend to penalize high specialization while rewarding despecialized forms that could more flexibly readapt themselves to diverse conditions in a changing environment. Specialization is not always advantageous to a species. When the environment is changing rapidly, despecialized forms that can adapt themselves to a changing locale (or else can migrate to new habitats) could be more successful than specialized forms. Such despecialization can be newly acquired most quickly and efficiently by a natural selection for mutations that retard the control-system regulating ontogenetic development during a species' life-history. This process of systemic neoteny tends to retain the ancestor's genetically programmed youthful structure and behavior into the derived species' adulthood while at the same time suppressing or destabilizing the

species-specific structures and behavior that are genetically programmed for the adult phase of the ancestral stock.

The neotenic variety or strain of a mammalian species could thus migrate and exploit more new niches in a rapidly changing environment than a stable one, but it would also have, as parts of its neotenic package a number of other youthful motivational systems such as care-soliciting social-dependency needs that, so long as these were not disadvantageous, could persist as a whole new neotenic adult behavior system. A propensity towards social dependency could have helped to establish, by the end of the Pleistocene, the symbioses that led to domestication (further neoteny, as we will soon see). In this way many species that were later domesticated (and some domestic species which were already so tame, so neotenic, that we never needed to neotenize them further--such as camels (*Camelus* spp.), Indian elephants (*Elephas maximus*) but not African elephants (*Loxodonta africana*). Reindeer [*Rangifer tarandus*], and Indian or Water Buffalo [*Bubalus bubalis*]) could have become neotenic in the wild during the Pleistocene. The process of systemic neoteny is known to have played a large part in directing our own human evolution (deBeer, 1958; Montagu, 1962; Gould, 1977), and thus we also became more ready than otherwise to enter into interdependent symbioses—relationships that led to a whole new strategy of survival for all the neotenic partners.

Humans have assumed that they domesticated their animal partners in alliance, and certainly in some way humans seem to be pivotal to the symbiosis. But it should be kept in mind that in most cases of domestication, there is evidence that the neotenic process had started long before domestication was initiated. The argument that Geist (1971) has made for the selective pressures on Bighorn Mountain Sheep (*Ovis canadensis*) during the Pleistocene leading to systemic neoteny of body and behaviour, could be made for other taxa whose ranges expanded between glacial ages—such as of canids (Fox, 1971), camelids, horses, cattle, goats, and rabbits.

The likelihood that future domesticants were first camp-followers of human groups, or crop pests (Zeuner, 1963 p. 58), suggests that the initiation of the symbiotic relationship may not have come from humans. Wolves following hunting parties, wild cattle invading wheat or barley fields, and the African wild cats invading Egyptian granaries in search of rodents, are but a few forms of the camp-followers or crop-robbers. If one looks at the Lapp/reindeer or Eskimo/dog domestication processes, it becomes difficult to distinguish which symbiont is following and which leading. Certainly the picture of the cat by the fire as we go off to work each day belies the common belief that humans derive greater benefit from this symbiosis.

DOMESTICATION BY ONTOGENETIC SELECTION

Without recognition of the evolutionary process of neoteny, successful domestication by prehistoric people, unconscious of genetics, can hardly be anything but a mystery. We have seen why domestic alliances could begin at the end of the Pleistocene. But the domestication process itself is an especially fascinating mystery because similar behavioral changes were induced in a number of domesticated species in several parts of the world at roughly the same time. Some species may even have been domesticated more than once by different human groups but with similar results. The similar results of domestication have been mentioned by

many researchers (e.g. Klopfer & Hailman, 1974 p. 206). These similarities (including attenuation of ancestral adult structures and drives such as territoriality, courtship, parental behavior, dominance-aggression, and the lifelong continuance of youthful structures and motivations such as social-dependency and docility) sound like the behavior of young mammals—or that of 'adults' which have undergone systemic neoteny. Did those species that were already neotenic enough to initiate symbioses at the end of the Pleistocene, in some way undergo further neotenizing to the extent that we now call domestication? What was this process of domestication, and how much did humans have to do with it?

It is likely that prehistoric humans would have preferred and unconsciously preserved, for mating, those captive animals that had retained one or more youthful behavioral complexes such as tameness, docility, or adaptive flexibility, in different interspecific habitats (e.g. farmyard or pen) and social organizations as were imposed by changing modes of life and production. Such behavioral complexes are not single or simple traits but are composed of interactions among a combination of infant mammalian motivational systems, as well as rendered more likely because of the neotenic deactivation of adult ancestral species-typical drives. This kind of selection for linked youthful behavioral complexes and against formerly adult species-specific behaviors makes much more understandable the quantum leap of systemic neoteny and helps to explain how a little unconscious selection for a more pliable youthful behavior or a less disruptive adult behavior could have resulted in a new form of adult—a neotenic behavior-morph in a relatively few generations. In other words we suggest that, aided by the orchestration of systemic neoteny, early human unconscious co-evolutionists could have achieved profound effects in a relatively shorter time, and with much surer success, than would have been possible had humans pursued, according to the conventional model of how domestication occurred, a deliberate sequential selection for one useful physical trait after another.

The likely habit of killing and eating captive animals, particularly of adolescent males, for which there is early fossil evidence (Perkins, 1964), would have occurred when the captives began to display 'difficult' species-specific behavior such as territoriality, courtship, and increased aggressiveness with disruptive fighting that could damage other stock. Destroying young adult males would hardly have been done on the basis of a careful accounting of the age of an animal, but more likely on that of increased difficulty of handling most young adults following the full activation of species-specific behavior. The simple veto of animals that displayed full adult species-specific behavior, and tolerance of animals that did not do so, would unwittingly have assured a differential contribution to the captive gene-pool. Favored animals would be those that continued, even after sexual maturity and mating, to express youthful docility.

Whole systems of behavior can be radically altered by selecting mutations of a few genes that regulate developmental allometries. In neoteny, the genes that change the proportions of an animal's body and behavior during the metamorphic phase from infant to adult, are regulated to decrease the rate and degree of development. As the animal grows to adulthood, its characteristically youthful anatomical proportions and its behavior remain less altered than in the ancestor. When the neotenate reaches a certain overall growth-threshold, its reproductive system is activated. The same reproductive hormones shortly bring the whole metamorphic phase to an end. Thus both structural and behavioral allometry is halted at a stage, relative to the ancestor's ontogeny, that would be described as youthful or incompletely

adult; and this genetically-programmed youthful anatomy and behavior, as its possessor becomes reproductively mature, would tend to be passed on to progeny. Moreover, provided there is some favorable selective pressure, the slightly neotenic genes could soon be accumulated to produce a neotenually domesticated new breed.

Furthermore, the unconscious selection of an abridged ontogenetic stage in a captive mammalian stock by prehistoric humans would have resulted in a bonus that they could hardly have known or appreciated. The bonus was a completely new system of adult structure and behavior achieved swiftly without the usual very high risk of accumulating deleterious genes in the process. For the infant, youth, and adult, of a species share the same genotype even though they undergo a metamorphosis owing to the rate and degree of expression of those same genes.

The metamorphic changes that most mammals undergo in their behavior from infant to adult are surprisingly profound and predictable (Lorenz, 1965; Eibl-Eibesfeldt, 1970; Brown, 1975), especially when we examine this development not only qualitatively in terms of the kind of behavior performed, but also quantitatively in terms of the relative frequency with which species-specific patterns and sequences are expressed. The changes consist, in part, of more stereotyped motor patterns of species-specific adult drives, expressed more frequently and organized into longer and more fixed sequences of behavior than are generally to be found in the young of that species (Fentress, 1983). These typical ontogenetic changes serve to adapt the mammal, when finally adult, to a specific role in a relatively stable society and habitat.

Because of these important changes in behavior and structure during the ontogeny of most mammalian species, it is sometimes difficult to remember that it is not the genotype that changes during metamorphosis. And the same is true of ontogenetic selection for neoteny--the genotype of the neotenic breed remains essentially the same as that of the parent stock, except for rather slight mutation of the system that regulates the rate and degree of genetic expression during development. In phylogenetic terms, a great change in the appearance and behavior of the new neotenic species is achieved with a minimum of change in the genotype. A new genotype, constructed entirely of random mutations selected by early humans, would, we believe, almost certainly not have enabled one successful domestication ever to have taken place, let alone a considerable number of them.

However, this does not mean that all differences between modern domesticants and wild ancestral stock are due to systemic neoteny.- We wish to emphasize that, in the initial domestications, the package of ancestrally youthful behavioral and structural characteristics retained into adulthood was merely a 'rough first draft', 'edited' and modified thereafter by mating with members of the wild ancestral stock, or by human selection for individual traits. Over the past few thousand years, less adaptive neotenic characters were excised or amended, and new traits, having nothing to do with neoteny, were added. For instance, when neoteny went so far in domesticants that they lost adult parental behaviors, and would trample their own offspring in the farmyard, early humans could have reversed the effect of neoteny by simply breeding domesticants back to the wild ancestral stock for a generation or two. According to Ratner & Boice (1975), ancient documents indicate that domesticated animals such as sheep and dogs were frequently 'refreshed' by breeding with the ancestral stock.

Nevertheless, it is well known by observers of domestication that the neotenic package still accounts for the most important structural and behavioral differences between the ancestral stock and the domesticated stock— that domesticants relative to their ancestors display youthful motivations even after sexual maturity is achieved, while ancestrally adult drives are expressed in diminuendo (Lorenz, 1961; Zeuner, 1963 p. 73; Hafez, 1975 pp. 9 et seq.; Clutton-Brock, 1981 pp. 21,25,39). For example, domesticated mammals are all more likely than their wild ancestors to display, with greater frequency and intensity, the typical youthful mammalian motivational systems of play, care-soliciting, social-synchrony, docility, investigativeness, and a propensity for close social proximity or touching. Most of these behaviors are social-dependency traits that help a young mammal to stay in dependent contact with parental and social groups in order to survive its vulnerable infancy and youthful phase. In addition to retaining youthful behavior, the neotenic 'adult' would express diminished dominance-aggression and territoriality, and highly specific routines of predation, courtship, or parental protectiveness that, if fully activated in ancestral adult intensity, would end youthful tameness and might well disrupt social processes in the restricted area of a domestic enclosure.

The process of neotenic domestication in mammals has, in addition to changing behavior, tended to make the anatomy of adult domesticants more like the structures expressed earlier in ontogeny in the ancestral stock. For instance, the proportions of a domesticated adult horse are somewhat more like those of the long-legged, long-necked colt of the wild horse than of its adult ancestral form. One can attribute a pattern to the process of neotenic domestication in mammalian species that has rendered the domesticants relative to the wild stock: less specialized, more tame and docile, more dependent, and more youthfully adaptive even when adult. The degree to which cattle, pigs, horses, dogs, or sheep, have undergone systemic neoteny often, we suggest, determines much of the difference between one breed and another (Fox, 1978 table on p. 129; Coppinger & Coppinger, 1982).

So far we have placed our emphasis on mammalian domestication, but what we have suggested for mammals appears also to apply more or less closely to the early domestication of chickens, ducks, geese, turkeys, and other birds. Like mammals, most avian species display infant/youth motivational systems such as care-soliciting dependency and, later in ontogeny, a metamorphic onset of species-specific structures and drives such as courtship, parental care, and territoriality designed to adapt them to a particular habitat. By selecting against adult drives and in favour of motivations characteristic of very young birds, they, too, could have been domesticated quickly and easily without knowledge of breeding. And there is evidence of neoteny in domesticated fowl. For example, 72-hours-old- Peking (domesticated) ducklings display approximately the same maturity of response as that shown by only 24 hours-old wild Mallard (*Anas platyrhynchos*) ducklings (Miller & Gottlieb, 1981). Also, it is likely that some birds which were later domesticated, such as ducks and geese, had already become less specialized and more dependent in the wild through a naturally selected neotenic process when their ancestral habitats began to change swiftly during the Pleistocene. There might well have been a selective advantage for birds, too, in quickly abridging highly specialized adult behavior in order to expand their niches and migrate to new habitats as their old habitats changed or became unlivable during the expanding and melting glacial conditions. As part of the neotenic package, they would have continued to display the structures and motivations of youth, and thus have been ready in the early Holocene to act as partners in establishing domestication with humans.

SILVER FOX RECENTLY DOMESTICATED BY SYSTEMIC NEOTENY

Few domestications have been achieved after the initial ones, several thousand years ago, in spite of our scientific knowledge of genetics. Ill-fated attempts, imitating the way we thought domestication (and Nature) worked, relied on a selection of one physical trait at a time—rather than selecting for or against an ontogenetic behavior complex which allowed regulator genes to produce a systemically organized package. All humans needed to do then, and now, to domesticate some mammals was to select for tameness, or docility, and systemic neoteny will, in a few generations, produce a viable neotenic domesticant. Indeed, by following just this simple selective principle, D.K. Belyaev (1979) has in only two decades produced a domesticated Silver Fox (*Vulpes fulvus* Desm.) that continues to look and act like a youthful fox after attaining sexual maturity.

For breeding, animals were selected that consistently displayed tame behavior with respect to people' (Belyaev, 1979 p. 302). After the fifth generation of breeding for tame behavior, some changes were already seen, and after 20 years the domesticant is decidedly different from other foxes. 'Such foxes are quite tame, not as a result of training or taming but due to prolonged selection for a tame genotype. Moreover, several other genetically linked ethological characters have appeared, unusual even in the tamest animals bred on ordinary farms. Like dogs, these foxes seek contact with familiar persons, tend to get close to them, and lick their hands and faces. In moments of emotional excitement, they even sound like dogs... at the sight of even a strange person, they try actively to attract attention with their whining and wagging of tails...' (Ibid. p. 303).

However, it is not the continuation of youthful motivational systems that Belyaev emphasizes in his description of the domestic fox, but rather the deactivation of ancestral adult species-specific behavior and physiology, which he calls 'destabilization' effects, as he does not appear to recognize the systemic neoteny that packaged his successful domestication. 'Thus we observe an undoubted disturbance of the reproductive system, a complex of changes associated with domestication, particularly incipient di-estrousness⁴. These changes reflect a destabilization of normal reproductive patterns that developed and were stabilized in the process of evolution' (Belyaev, 1979 p. 304).

'In addition to changes in behavior and reproduction, the selection for domesticated behavior has brought about other physiological and morphological changes. For example, the time of molting in tame foxes is longer than in non-selected populations.' 'In some of the tame foxes, even from unrelated pedigrees, quite new morphological characters appeared that are not found in wild animals but are quite characteristic of some breeds of dogs.' He mentions, for example, piebald coat coloration and 'drooping ears characteristic of young dogs' (Belyaev, 1979 p. 305).

Even though Belyaev does not name neoteny as indispensable to his domestication process, he does have considerable insight into the kind of systemic help which he was getting in the

process: '...selection for tame behavior seems to result in breaking of previously integrated ontogenetic systems and thus leads to multiple phenotypic effects that seem genetically unrelated to the selected character, namely tame behavior.' In a genetic and biochemical sense, what may be selected for are changes in the regulation of genes--that is, in the timing of and the amount of gene expression rather than changes in individual genes. 'Selection having such an effect is called by me destabilizing selection' (Belyaev, 1979 p. 307).

Owing to the important work of D.K. Belyaev, the systemic neoteny model of initial domestications that we proposed in the previous section has received some experimental verification. The first domestications resulted from systemic neoteny linking a complex genetic composition in response to a very simple direction by humans selecting only for tameness, which brought with it the whole system of youthful traits. This same process of systemic neoteny orchestrating a more youthful behavior-morphic⁵ composition had, as we explained, already occurred in the phylogeny of human and potential domesticants by natural selection. The selective advantage in both cases was at least one trait of continued youthful behavior, which brought into being a new form of adult with a system of lifelong youthful characteristics.

This ontogenetic selection theory of domestication explains the mystery of why it began at the end of the Pleistocene, and why it occurred in a number of diverse locations with similar success to unskilled breeders. It also explains why mammalian domestic stock share a surprising similarity of traits even though of different species. For youthful motivations, such as care-soliciting, are class-common in very young mammals and probably common in infant birds.

ONTOGENETIC SELECTION OF DOMESTIC GRAINS

Ontogenetic selection in plants is somewhat different from that of mammals or birds, because plants do not share the mammalian/avian youthful behavior system for dependency. However, plants as well as mammals undergo a metamorphosis effected by differential rates of change in traits as they mature. It has been suggested that angiosperms—flowering plants that would include wheat or Maize (the grasses *Triticum* spp. and *Zea mays*)—were derived from ancestral gymnosperms by a process of neotenic evolution during the Cretaceous, giving them much-increased adaptive versatility (Takhtajan, 1969, 1976). And cases of neoteny in the more recent evolution of plants have been investigated (e.g. Guerrant, 1982). It is likely that some plants, such as wild wheat and Barley (*Hordeum vulgare*), and the Maize-like teosinte (Beadle, 1981) in the new world, radiated into varieties owing to the unusual fluctuations in climate and terrain during the Pleistocene. Some of the important changes from wild to domestic wheat and Maize seem to have been youthful traits carried into maturity, or the result of ancestral adult traits that have not been activated in the more

⁴ *After a few generations of selection for tameness, female foxes began to display the physiological changes and behavioral propensities to reproduce twice a year, rather than the single spring birth the timing of which had been adaptive in the wild adult.*

⁵ *A term which links behavior and structure to make clear that the neotenic species or variety is not characterized by ancestrally youthful physical structures alone but, in addition, retains throughout life an ancestrally youthful behavior-system as well.*

neotenic domestic plant. These traits can be assumed to be under the control of regulator genes whose mutated deceleration of development, if selected, might dictate a whole system of changes in a neotenic plant variety--changes that could include growth of seeds and seed-head, multiplication of rows in the latter, retention of youthful softness of kernels well into maturity, and inactivation of ancestral triggering of seed-pods to drop at maturity--with concomitant inability to reseed.

Grain could have been domesticated fairly easily and unwittingly if humans had simply found a more neotenic variety than they did in the wild, judged it to be more productive for their use, and then continued to prefer any neotenic trait such as kernels that remained longer on the seed-head at maturity. Some varieties, perhaps those with larger seed-heads or less hard and inedible kernels, or those whose seeds were more resistant to falling or popping off the head, were likely to have been picked and planted by humans at the very end of the Pleistocene or beginning of the Holocene. Such a simple principle of preference could have selected for a more and more neotenic variety of grain that would have brought even the unconscious domesticator a whole package of other youthful traits. These could have included more tender mature kernels, larger growth, and further inactivation of dropping or triggering seeds from their heads at maturity, which would make it easier than otherwise to harvest the grain from the seed-head when ripe.

However, if a neotenic variety of wheat or maize does not have some method of reseeding itself at maturity, it becomes entirely dependent on other organisms for its survival. It was nothing new for the highly-adaptive angiosperms to which grasses etc. belong, to have established another symbiosis with the animal kingdom to assist in its reproductive process, when we consider the parts that insects, birds, and even snails or mammals (such as bats), play in propagating and pollinating many species of plants. But these symbiotic systems among neotenic plants, neotenic humans, and neotenic domesticated animals, were something rare in the sense that they formed among despecialized, extraordinarily adaptive, habitat-flexible organisms with a propensity for entering into ever-more mutual dependencies between orders, classes, and even kingdoms, of biota.

EVOLUTIONARY SIGNIFICANCE OF THE DOMESTIC ALLIANCE

A new evolutionary strategy began to accelerate during the Pleistocene, brought about by ontogenetic selection that no longer exploited resources in the environment by the more usual trend of producing highly-specialized forms of which each occupied its own niche. The newly evolved interdependent forms have redefined predator/ prey relationships in their domestic alliance, so that trophic levels are hardly recognizable: the old ecological relationships have been profoundly altered. This revolution in evolution began because of a newly important despecialized interdependency among a few neotenic species. The revolution has meant enormous biological success for the few symbiont species. At the same time it threatens highly specialized, more independent, life-forms with imminent mass-extinction. As in earlier mass-extinctions, the loss of vast populations of some forms will be rebalanced, but this time not by radiations of more highly specialized species as the principle of diversity would predict. Domestically allied neotenic forms represent a strategy that brings into question the principle of diversity's claim to universality. These neotenic species have moved in despecialized and interdependent directions, so that relatively few species can

exploit many niches by either their own adaptive flexibility or by symbioses with other species that can exploit a different range of niches.

When Darwin (1859) framed his principle of divergence or diversity, he was assuming that the environment normally remains relatively stable, or else changes only uniformly and slowly, with catastrophes and wide fluctuations occurring rarely (Kohn, 1981). In such an environment, the more highly specialized forms should be at an advantage, and the pattern of evolution would be a story of more and more varied radiations, and more highly specialized forms exploiting as many of the ecological niches in the environment as were available, but no two species occupying exactly the same niche. Darwin was of course aware that speciation could take sudden leaps (Penny, 1983), but many present-day biologists accept Darwin's ideal equilibrial environmental assumptions as unquestioned fact. MacArthur & Wilson (1967) even calculated from these assumptions a predictable increase in numbers of new species as they slowly optimize fitness—radiating, according to the principle of diversity, into new equilibria of divergent forms in an ever-rigidly-balanced environment.

The difficulty with the principle of diversity and the conventional equilibrial model of the direction and function of evolution is that they rely too heavily on uniformitarian beliefs. Except for a few hints (e.g. Garstang, 1922; Hardy, 1954; Gould, 1982 p. 385) that over-specialization was probably a central though neglected evolutionary phenomenon, the conventional wisdom has fixed its gaze in the opposite direction. It has been assumed that equilibrial efficiency is always accomplished by means of a radiation of highly specialized forms or species to exploit more niches in the environment. Evidence has been overlooked that would point to a theory of neotenic despecialized/interdependency as a survival strategy that was selected for in a number of mammalian and avian species during the extended period of Pleistocene environmental fluctuation, and resulted naturally in the domestic alliance of the Holocene and the ultimate prospect of mass extinction of less interdependent, more specialized forms.

Highly specialized forms cannot live the way humans and domesticants do. They need to be alone to hunt and forage, to court mates, and to care for young. Even if we are willing to share the growing proportion of the environment used by ourselves and domestic plants and animals with wild species, the point is that most wild species cannot share with us. Cooperating youthfully in close proximity with many other species is our forte, but not theirs. As the domestic alliance continues to increase to as much as 60% of the total terrestrial biomass, it will, without our realizing it, be strongly tilting Nature's direction of selection to favor varieties of wild species which can share our space. The domestic symbioses will so dominate the ecology of the next century that varieties of species which display the most highly specific adult behavior-patterns will likely be forced to extinction.

We are only beginning to be aware of the historical relations of past ecologies to patterns of extinction (Lewin, 1982). Perhaps it is too early to predict the relation of present ecology to current evolution; but it seems likely to us that the only alternative to extinction of wildlife in the 21st century will be a despecialized, interdependent fitness. As we have already seen, a swift way that some animals have evolved such fitness, at least for those appropriately genetically predisposed mammalian and avian species, is through the lifelong youthfulness of systemic neoteny. There may be other ways to evolve despecialized interdependency, but a conventional evolution would take much too long to save independent species before the

coming extinctions. Indeed, Nature would seem to be nodding towards the domestication of evolution.

Are we at long last about to witness the biblical prophesy of a 'peaceable kingdom' where the neotenic big cats that survive shall lie down with the lamb? The more domestic nature of the likely future will not necessarily be a catastrophe or necessarily represent degeneracy from the late 19th century myth of a ruthless predatory battle between animals 'red in tooth and claw'. Instead, the fittest strategy of the future may be a system of more cooperative, interdependent relationships among species that are more efficient and more reproductive than the highly specialized self-sufficient competitors which we used to imagine were Nature's fittest. The King of Beasts will have been out-competed by the cooperative strategy of the house-cat. And the Bald Eagle (*Haliaeetus leuco-cephalus*), if it is to survive, may become dependent on human garbage-dumps, as a flourishing group is recently reported to have become in the Aleutians (Johnson, 1983). The period in which giant dinosaurs shook the Earth in search of flesh or flora may seem no more strange to our great-great-grandchildren than the world of self-sufficient, highly specialized 'dinosaurs' of our day, stalking their prey or marking their territories.

Before we pridefully magnify our own human power . and responsibility for bringing about what has happened and what is to come, let us remember that humans are as indirectly responsible for the coming domestication of evolution as they were for the initial, unconscious neotenic domestications of a few already dependency-prone neotenic Pleistocene forms. Something has happened in Nature that is much bigger than we are. Now that we begin to understand one or two pages of script in this current evolutionary drama, and a little of the nature of our limited role in it, perhaps we are ready to ask ourselves, 'What will be the most rational course of environmental action in the next few decades?'

CONCLUSION

There have been many theoretical discussions in the last decade of the punctuated equilibrium model of evolution (e.g. Eldredge & Gould, 1972; Alberch, 1980; Lewin, 1981; Stanley, 1981; Gould, 19826). In this paper we have sketched a macroevolutionary trend in which ontogenetic selection in the wild during the past two million years and under domestication in the past decamillennium (these ontogenetic selections may both be seen as examples of punctuated natural selection) have produced dramatic changes in the morphology and behavior of many species, as well as a massive punctuation of the ecological relationships among species, and a likely mass-extinction of more conservative forms that cannot share in those redefined ecological relationships.

With Belyaev (1979) we have the first experiment in conscious ontogenetic selection. It might save some endangered mammalian and avian species from extinction if we could use our growing knowledge of ontogenetic selection in order to facilitate a few species' adaptation to a redefined interdependent ecological alliance. We might do this by aiding small groups in evolving somewhat less ancestrally species-specific adult forms than have been customary in the past. Although this might be the only swift and effective way of saving some species, it would constitute a conscious and deliberate human intrusion into Nature that would be quite different from the unconscious part we have played on Nature's stage up to

now. Are we ready even to contemplate such responsibility, or would we rather console ourselves in imagining that we are doing Nature's work when we intrude in order to preserve more independent forms?

Indeed, some might rather have the Bald Eagle go extinct than see it become, let alone aid it in becoming, interdependent enough to share our living-space. Many still have fixed in mind a myth of the superior fitness of the splendidly self-sufficient wild beast that has really been extinct since the last days of the age of reptiles, if indeed it ever existed even then (see Brink, 1956, for some interesting speculation from fossil evidence on mammal-like structures and behavior in late Mesozoic reptiles). More environmentalists than evolutionists assume that evolutionary transformations have always been brought about by gradual, persistent changes in the environment and that only this kind of slow evolution is natural. In this paper we have attempted to offer an alternative view of some very important issues.

ACKNOWLEDGEMENTS

The authors wish to thank Professor Arthur H. Westing, of Hampshire College, for useful suggestions and for writing the essay 'A World In Balance', published in *Environmental Conservation* (1981), that provoked our essay in response. For their very helpful suggestions after reading early drafts of this paper, we wish to thank Professor Lynn Miller of Hampshire College, Professor Lorna Coppinger of Hampshire College and the New England Farm Center, and Katherine Conway of Thornton Burgess Middle School.

SUMMARY

A coming 'Age of Interdependent Forms' seems destined to mark the success of what could be called 'despecialized/interspecific fitness' among neotenic strains (perpetuating juvenile traits) of species such as humans and domestic animals. Humans as well as the first domesticants underwent a neotenic evolution in the wild during the repeated interglacial periods which, acting on a number of mammalian forms, selected against adult species-specific ancestral adaptations to a stable environment. Neotenic species continue to look and behave more like ancestral youths than adults—even after sexual maturity and throughout their life-history. As they retain lifelong youthful dependency motivations, they can easily, under suitable conditions, become interdependent forms. By the time of melting of the last Pleistocene glacier, all the domestic partners had already become more dependency-prone than formerly, and were behaviorally despecialized enough to form the alliance that is now changing the order of Nature.

Humans did not 'create' domestication. Without knowing it, they induced even more neoteny than formerly in species that had already initiated symbioses with them as camp-followers or crop-robbers. By unwittingly favoring tamer genotypes in captive animals, humans were selecting for a whole system of youthful behavior and an attenuation of adult species-specific behavior. The success of this naturally-evolving domestic alliance, which includes, but is not the creation of, humans, may soon be marked by the seventh major mass-

extinction in the last five hundred million years of evolution. And the species which suffer diminished populations and possible extinction this time will have become the least fit, precisely because they do not seek interdependent alliance. Natural selection is no longer favoring independent, self-sufficient wild animals—the 19th and 20th century stereotype of the 'fittest'. Environmentalists who would save them must not simply curb the excesses of thoughtless human polluters but out-maneuver the momentum of evolution.

REFERENCES

- ALBERCH, PERE (1980). Ontogenesis and morphological diversification. *American Zoologist*, 20, pp. 653-67, illustr.
- BEADLE, GEORGE W. (1981). Origin of corn: pollen evidence. *Science*, 213, pp. 890-2, illustr.
- BEER, SIR GAVIN DE (1958). *Embryos and Ancestors* (3rd edn). Clarendon Press, Oxford, England, UK: ix + 197 pp., illustr.
- BEKOFF, MARC (1972). The development of social interaction, play and metacommunication in mammals: an ethological perspective. *Quarterly Review of Biology*; 47, pp. 412-34, illustr.
- BELYAEV, D.K. (1979). Destabilizing selection as a factor in domestication. *Journal of Heredity*, 70, pp. 301-8, illustr.
- BRINK, A.S. (1956). Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles. *Palaeontologia Africana*, 4, pp. 77-96, illustr.
- BROWN, JERRAM L. (1975). *The Evolution of Behavior*. W.W. Norton, New York, NY, USA: xix + 761 pp., illustr.
- CLUTTON-BROCK, JULIET (1981). *Domesticated Animals from Early Times*. University of Texas Press, Austin, Texas, USA: 208 pp., illustr.
- COPPINGER, RAYMOND P. & COPPINGER, LORNA (1982). Dogs in sheep's clothing guard flocks. *Smithsonian*, April, pp. 64-73, illustr.
- COPPINGER, RAYMOND P. & SMITH, CHARLES KAY (1983). Forever young. *The Sciences*, 23(3), pp. 50-4, illustr.
- DARWIN, CHARLES (1859). *The Origin of Species* (1967 Facsimile of 1st edn). Atheneum, New York, NY, USA: ix + 502 pp., illustr.
- DARWIN, CHARLES (1868). *The Variation of Animals and Plants Under Domestication*. John Murray, London, England, UK: 2 vols., illustr.

- DENTON, GEORGE H. & HUGUES, TERRENCE J. (Ed.) (1981). *The Last Great Ice Sheets*. Wiley-Interscience, New York, NY, USA: xviii + 484 pp., illustr.
- EHRlich, PAUL & EHRlich, ANNE H. (1981). *Extinction*. Random House, New York, NY, USA: xiv + 305 pp.
- EIBL-EIBESFELDT, IRENAUS (1970). *Ethology*. Holt, Rinehart & Winston, New York, NY, USA: xiv + 530 pp., illustr.
- ELDRIDGE, NILES & GOULD, STEPHEN JAY (1972). Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82-115 in *Models in Paleobiology* (Ed. T.J.M. Schopf). Freeman, Cooper, San Francisco, California, USA: vi + 250 pp., illustr.
- FAGEN, ROBERT (1981). *Animal Play Behavior*. Oxford University Press, New York & Oxford: xvii + 305 pp., illustr.
- FENTRESS, JOHN C. (1983). A view of ontogeny. Pp. 24-64 in *Advances in the Study of Mammalian Behavior* (Ed. John F. Eisenberg & Devra G. Kleiman). Special Publication No. 7, American Society of Mammalogists, xvi + 753 pp., illustr.
- FOX, MICHAEL W. (1971). *Behavior of Wolves. Dogs and Related Canids*. Harper & Row, New York—Evanston—San Francisco—London: 220 pp., illustr.
- FOX, MICHAEL W. (1978). *The Dog: its Domestication and Behavior*. Garland STPM Press, New York & London: vii + 296 pp., illustr.
- GARSTANG, WALTER (1922). The theory of recapitulation: a critical restatement of the biogenetic law. *Journal of the Linnean Society of London, Zoology*, 35, pp. 81-101
- GEIST, VALERIUS (1971). *Mountain Sheep: A Study in Behavior and Evolution*. University of Chicago Press, Chicago & London: xv + 383 pp., illustr.
- GOULD, STEPHEN JAY (1977). *Ontogeny and Phylogeny*. Harvard University Press, Cambridge, Massachusetts, USA: ix + 501 pp., illustr.
- GOULD, STEPHEN JAY (1982a). Free to be extinct. *Natural History*, 91(8), pp. 12-6.
- GOULD, STEPHEN JAY (1982b). Darwinism and the expansion of evolutionary theory. *Science*, 216, pp. 380-7.
- GUERRANT, EDWARD O., jr (1982). Neotenic evolution of *Delphinium nudicaule* (Ranunculaceae): a hummingbird-pollinated larkspur. *Evolution*, 36(4), pp. 699-712, illustr.
- HAFEZ, E.S.E. (Ed.) (1975). *The Behaviour of Domestic Animals* (3rd edn). Bailliere Tindall, London, England, UK: xii + 532 pp., illustr.
- HALDANE, J.B.S. (1932). The time of action of genes and its bearing on some evolutionary problems. *American Naturalist*, 66, pp. 5-24.

- HARDY, SIR ALISTER C. (1954). Escape from specialization. Pp. 122-42 in *Evolution as a Process* (Ed. Julian Huxley et al.). George Allen & Unwin, London, England, UK: 367 pp., illustr.
- HENDRICH, HUBERT (1983). On the evolution of social structure in mammals. Pp. 738-50 in *Advances in the Study of Mammalian Behavior* (Ed. John F. Eisenberg & Devra G. Kleiman). Special Publication No. 7, American Society of Mammalogists, xvi + 753 pp., illustr.
- JOHNSON, JOHNNY (1983). The garbage eagles. *Natural History*, 92(8), pp. 42-5, illustr.
- KERR, RICHARD A. (1981). Milankovitch climate cycles: old and unsteady. *Science*, 213, pp. 1095-6, illustr.
- KLOPFER, P.H. & HAILMAN, J.P. (1974). *An Introduction to Animal Behavior* (2nd edn). Prentice-Hall, Englewood Cliffs, NJ, USA: xiv + 332 pp., illustr.
- KOHN, DAVID (1981). On the origin of the principle of diversity. *Science*, 213, pp. 1105-8.
- KOLLMANN, JULIUS (1885). Das Überwintern von europäischen Frosch-und Triton-larven und die Umwandlung des mexikanischen Axolotl. *Verhandlungen der Natur-forschenden Gesellschaft* (Basel), 7, pp. 387-98.
- LEWIN, ROGER (1981). Seeds of change in embryonic development. *Science*, 214, pp. 42-4, illustr.
- LEWIN, ROGER (1982). Extinction leaves its mark on ecology. *Science*, 218, pp. 42-3.
- LORENZ, KONRAD (1961). *King Solomon's Ring: New Light on Animal Ways*. Thomas Y. Crowell, New York, NY, USA: 202 pp., illustr.
- LORENZ, KONRAD (1965). *Evolution and Modification of Behavior*. University of Chicago Press, Chicago & London: 121 pp.
- MACARTHUR, ROBERT H. & WILSON, EDWARD O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, USA: xi + 203 pp., illustr.
- MASON, WILLIAM A. (1968). Early social deprivation in the nonhuman primates: implications for human behavior. Pp. 70-101 in *Environmental Influences* (Ed. David C. Glass). Rockefeller University Press and Russell Sage Foundation, New York, NY, USA: ix + 304 pp., illustr.
- MILLER, DAVID B. & GOTTLIEB, GILBERT (1981). Effects of domestication on production and perception of mallard maternal alarm calls: developmental lag in behavioral arousal. *Journal of Comparative and Physiological Psychology*, 92(2), pp. 205-19, illustr.

- MONTAGU, M.F. ASHLEY (1962). Time, morphology, and neoteny, in the evolution of Man. Pp. 324-42, illustr., in *Culture and the Evolution of Man* (Ed. M. F. Ashley Montagu). Oxford University Press, New York, NY, USA: xiii + 376 pp., illustr.
- PENNY, DAVID (1983). Charles Darwin, gradualism, and punctuated equilibria. *Systematic Zoology*, 32(1), pp. 72-4.
- PERKINS, D.H. (1964). The prehistoric fauna from Shandar, Iraq. *Science*, 144, pp. 1565-6, illustr.
- RATNER, S.C. & BOICE, R. (1975). Effects of domestication on behaviour. Pp. 3-19, illustr., in *The Behaviour of Domestic Animals* (3rd edn, Ed. E.S.E. Hafez). Bailliere Tindall, London, England, UK: xii + 532 pp., illustr.
- RAUP, DAVID M. & SEPKOSKI, JOHN J. (1982). Mass extinctions in the marine fossil record. *Science*, 215, pp. 1501-3, illustr.
- STANLEY, STEVEN M. (1981). *The New Evolutionary Timetable*. Basic Books, New York, NY, USA: xvi + 222 pp., illustr.
- TAKHTAJAN, ARMEN (1969). *Flowering Plants: Origin and Dispersal* (English edn). Oliver & Boyd, Edinburgh, Scotland, UK: 310 pp., illustr.
- TAKHTAJAN, ARMEN (1976). Neoteny and the origin of flowering plants. Pp. 207-19 in *Origin and Early Evolution of Angiosperms* (Ed. C.B. Beck). Columbia University Press, New York, NY, USA: 341 pp., illustr.
- WESTING, ARTHUR H. (1981). A world in balance. *Environmental Conservation*, 8(3), pp. 177-83, illustr.
- WESTING, ARTHUR H. (1982). Environmental quality: the effect of military preparations. *Environment*, 24(4), pp. 2-3, 39-40.
- ZEUNER, FREDERICK E. (1963). *A History of Domesticated Animals*. Harper & Row, New York, NY, USA: 560 pp. illustr.