Social Subordination, Population Density, and Mammalian Evolution

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Natural selection, operating on phenotypic expressions of the genetic material, is generally held to be of fundamental importance in evolution. Natural selection includes environmental selection, by which is meant here the selection of particular correlated phenotypic-genotypic changes or adaptations that confer better survival, including competitive advantages of the genotype, in a new or changing environment. However, the behavioral characteristics of many, if not most, mammals operate to reduce exposure to new or changing habitats. For example, most mammals are reluctant to go beyond the limits of familiar territory—their home range—and generally must be forced to do so. In addition, socially dominant animals usually occupy and hold the most desirable portions of the habitat and are the most successful breeders. In turn, their offspring tend to be dominant. Moreover, mammals generally occupy the habitat for which they are best adapted, and a given species may occupy similar, if not identical, habitats for many millennia. Therefore, if animals occupy a specific habitat and move with it as the habitat shifts with time and climatic change, how can they be subjected to the selective force of environmental changes, and by which mechanisms does mammalian evolution occur? Mammalian evolution might be expected to be conservative and limited to a rate characteristic of the entire ecosystem. However, mammalian evolution has been explosive with respect to rate and diversity.

I suggest that the conservative influence of social dominance is more than offset by other consequences of hierarchical behavior, and that social behavior is a major force in the evolution of mammals. Mammalian selection and evolution may occur to an important degree through the agency of socially subordinate individuals, and it is these individuals that will provide the genetic material involved in adaptation to new circumstances. An example of the operation of the kinds of force I refer to is provided on the one hand by the social tolerance of bighorn sheep that results in their failure to exploit suitable unoccupied habitats and, on the other hand, by the social intolerance of deer and moose that results in their doing so (*1*). Here I examine some of the methods by which social rank and changes in population density might assume importance in mammalian evolution.

The idea that intra- and interspecific competition are important in evolution is, of course, not new. Interspecific competition generally is assumed to have been, and to be, operative in the evolutionary process, and its possible application to the problem of extinction has received considerable attention (*2*). Intraspecific competition, which must be considered primarily at the local level, often has been considered a factor in evolution in rather general terms. However, the potential importance of social subordination in mammalian evolution has not, to my knowledge, been suggested, although some of Haldane's (*3*) remarks regarding population density are pertinent to some aspects of evolution discussed below. Many authors have commented on the importance of surplus individuals in producing strong pressures for dispersal (*4*). In addition, the proportion of individuals dying is roughly proportional to such pressure. However, the possible role of social rank in evolution has not been mentioned.

Illustrative examples and documentation for this article are taken mainly from the literature on small mammals, partly because of my personal familiarity with them and partly because they have been studied more than most larger mammals, with notable exceptions such as deer. Usually a single, or only a few, species are mentioned. However, much of what is said may be applicable to many other mammals and inframammalian vertebrates.

First, a brief review of pertinent features of social behavior and related population dynamics of mammals is appropriate. Broadly defined, intraspecific competition refers to direct or indirect competition between members of the same species or population, and also includes reproductive and numerical dominance. However, the term *intraspecific competition* often has been used more restrictively to refer to either overt or less obvious agonistic social behavior of members of the same species or population toward each other. Competition for some environmental factors, such as space, food, or nest site, may or may not be implied when *intraspecific competition* is used in the restrictive sense. Nevertheless, in either usage *intraspecific competition* would reflect the social behavior and organization of populations of a species, although to a greater degree when used in the restrictive sense. However, this difference in usage may be inconsequential because the evolution of intraspecific social competition seems to have resulted in bypassing the inherent dangers of direct competition for environmental necessities (*5*).

Hierarchies of Social Rank

The social organization of most mammals may be based, at least in part, on hierarchies of social rank that consist of a series of dominance-subordination relationships between individuals of a group (usually of the same sex), between families, and between coherent groups having bases of organization other than kinship, or on various combinations of these relationships. It should be noted that, while hierarchical social organization probably is common in mammals and birds and occurs in other vertebrates, it is not universal in animals. Therefore, important as social rank may be in the evolution of mammals and some other vertebrates, it is not a necessary mechanism for speciation or change in adaptation. Such hierarchies may vary considerably in details of arrangement from population to

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population. Social organization of rhesus monkeys provides good examples of such relationships (*6, 7*). Individual aggressiveness toward other members of the same species or toward members of other species (intra- or interspecific competition, respectively) is an important overt manifestation of competitive social behavior. Marked differences in aggressive behavior have been observed between individuals, between strains or species, and between sexes. For example, the common meadow vole (*Microtus pennsylvanicus*) is highly intolerant of, and aggressive toward, other members of its species, whereas the prairie vole (*M. ochrogaster*) is highly tolerant of, and nonaggressive toward, other members of *its* species, but is dominant over *M. pennsylvanicus* (*8*). This difference will be referred to again.

Overt intraspecific aggressiveness is an important factor in establishing and maintaining rank hierarchies in many species—for example, the house mouse and the meadow vole—but it is not mandatory, as the establishment of rank may involve much more subtle behavioral factors. On the other hand there may be a direct relationship between (i) the degree of overt aggressiveness and (ii) the magnitude of dispersal with increased density, and the associated increase in contacts between animals; the general level of aggressive interaction may be greatly increased and, with it, the force to disperse.

Social hierarchies, as such, also constitute a major force for dispersion. Such hierarchies may be of individuals or of groups, but for simplicity I limit discussion here to the former. Low-ranking individuals are generally forced to emigrate from their birthplace and to find space in suitable habitat unoccupied by higher-ranking members of the same species or by members of dominant competing species. It is almost axiomatic that socially subordinate individuals (usually maturing young animals) that are forced to disperse have an extremely high rate of mortality (*9*). Few find suitable vacant niches and survive. However, some of these pioneers will become socially dominant in the new situation.

Gene-flow may be considerably reduced through the function of hierarchies because (i) some aggressive characteristics productive of dominance can be inherited (*10*), (ii) dominant individuals may account for a disproportionately large share of the breeding in a population (*11, 12*), and (iii) there is restricted genetic interchange between subunits, or demes, of a population associated with territoriality and limited home ranges (*11, 13*). For example, if the offspring of dominant animals are dominant, they too will remain in their territory, thus limiting the spread of traits characteristic of dominant animals. Therefore one might expect to find an increase in the prevalence, and a decrease in the variability, of aggressive behavior in succeeding generations. However, progressively greater aggressiveness has not been observed in natural populations. Moreover, there do not appear to be marked differences in aggressiveness between natural populations of a particular subspecies, or of a species, such as might be expected if dominance was determined solely by genetics. There are a number of possible explanations for the apparent absence of unidirectional selection for aggressiveness. (i) Dominance appears to be, at least in part, a function of time and place, particularly at the local level; the first animals born early in the history of a population or early in each breeding season are likely to be dominant over animals born later (*7, 12, 14*). Age and size may largely determine dominance (*7, 10*). (ii) Dominance is relative and not a function of an inborn absolute amount of aggressiveness. If all low-ranking male mice from a number of populations are placed together, a new hierarchy emerges. The same thing occurs if all dominant males are placed together. (iii) There is probably an optimum degree of aggressiveness for a particular species, beyond which increases in aggressiveness may be incompatible with adequate reproduction and survival. Experimental evidence on physiological responses to increased density and aggressiveness suggests that extreme aggressiveness and high reproductive rates may be incompatible (*15*). The essence of the foregoing considerations is that it is not likely that there is continued selection for increasing genetically determined aggressiveness.

These and other components of population dynamics may exhibit wide variations from year to year, so no hard and fast quantitative rules can be derived that will be valid generally. Details of density-dependent inhibition of maturation and the pertinence of the size of overwintering populations have been discussed in some detail elsewhere (*15, 16*). But, in particular, inhibition of maturation, whether density-dependent or density-independent, of young born late in the breeding season may be a mechanism that has evolved that insures an adequate breeding population an optimum habitat for the succeeding breeding season.

An example of both (i) the relationship between high aggressiveness and inhibition of breeding and (ii) the survival value of inhibition of the maturation of animals born late in the breeding season is given by a population of meadow voles (*Microtus pennsylvanicus*). In the breeding season of a year of high population density, all mature males were scarred from fighting, often severely so, but immature males were completely unscarred (*17*). As soon as the young males began to mature they became scarred, and probably were less likely to breed as a result of such social strife (*15*). Early termination of the breeding season by virtue of inhibition of maturation of animals born late in the season generally accompanies such high densities and the attendant increase in intraspecific strife. Thus, excessive density and aggressiveness may interfere with reproduction. Also it may be surmised from the absence of scars on immature males that they were not attacked and so were not driven to disperse. Thus, males whose maturation is inhibited may remain unattacked in their original territory from the end of one breeding season to the beginning of the next. Such males probably account for 90 percent or more of the breeding population at the beginning of each new season.

Population Densities

Population density acting in concert with intraspecific competition is a major component of the force to disperse (*4, 18*). When densities are very low, a higher proportion of subordinate individuals can find suitable areas in the preferred habitat, the number of dispersing animals is reduced, and the survival of subordinate animals is greatly increased. Broadly speaking, in natural populations of small mammals it is the young each year that comprise the bulk of subordinate animals, and generally only those young that succeed in occupying and establishing themselves in a suitable habitat become dominant. To what degree such dominance is genetically determined is not known.

The dynamics and consequences of hierarchical social organization have been studied for muskrats (*9*) and woodchucks (*Marmota monax*) (*19*). In a study of *Peromyscus* it was shown that, when maturing males are released into an incompletely filled habitat, they are able to establish themselves between the areas occupied by resident individuals, but when the available areas are filled, other animals released into the same habitat disperse and usually disappear (*20*). Comparable results have been obtained from other studies of populations of *Peromyscus* (*21*). When densities are high, the proportion of dispersing individuals is greater (*18*). Despite the increase in mortality that accompanies dispersal movements, it also follows that increasingly more marginal and submarginal habitats should become occupied as density increases. The ultimate effects of excessive densities on the involved populations are discussed elsewhere (*16, 22*) and are not particularly germane to the subject at hand.

The density of many populations of mammals, particularly that of small mammals with high reproductive potential, fluctuates more or less regularly. With each major fluctuation there is a progressive increase in density from year to year, until some maximum is reached; this is followed by a rapid decline. The general magnitudes of the maxima appear to be characteristics of the species and habitat. In addition to fluctuations from year to year (interannual fluctuations) there are increases and decreases in density within a single year (intra-annual fluctuations). Both intra- and interannual increases result in dispersal of subordinate individuals. Overwintering, usually immature, small mammals form the breeding population early in the breeding season each year. However, their mortality is high, and they are replaced by younger recruits, probably drawn from the first wave of litters in the breeding season. The individuals born subsequently comprise the dispersing populations and are, for the most part, probably subordinate. As density increases interannually, the force for dispersal, on the average, increases intra-annually until, in the final year of a "cyclic" increase of some species, the numbers dispersing may reach staggering proportions.

Similar changes may occur in the densities of populations of large mammals, but the time bases are greater. On the other hand, for many species there is little interannual fluctuation in population size, yet dispersal forces still operate intra-annually. The difference between intra-annual and interannual fluctuation in density is primarily quantitative; much wider dispersal accompanies the latter. In either case the vast majority of mammals forced to disperse fail to survive. Nevertheless, once in a great while a dispersing individual may, one would suppose, harbor a mutation or genetic change that increases its ability to adapt to the new surroundings and improves its chances of survival. It is such individuals that should be the basis for evolutionary changes. A suboptimum area could be invaded repeatedly by countless numbers of individuals before a genetic change permitting adaptation occurred. Thus, the dispersal of large numbers of socially *subordinate* individuals into new environments may provide the wherewithal for natural selection, in contrast to the relative conservatism of dominant individuals in an optimum habitat.

In summary, the important points of the foregoing discussion of competitive social behavior are (i) that populations of mammals are generally organized in social hierarchies; (ii) that low-ranking, predominantly young individuals usually are forced to disperse; (iii) that the genetic variability necessary for adaptation and evolution is carried by subordinate individuals; (iv) that the proportion of low-ranking individuals generally increases in association with an increase in the forces for dispersal with increasing density; (v) that the amount of less-than-optimum habitat occupied increases with increased dispersal; (vi) that dispersing individuals may be forced into competition with members of other species as they move into more or less alien habitats; and (vii) that inhibition of maturation late in the breeding season results in insuring the presence of a breeding population in the preferred habitat the following season.

The selective breeding and dispersal that generally accompany social organization should have important genetic and evolutionary consequences. And if genetic change and its correlated phenotypic expression are the basis of evolution (*23*), genetic change should be an essential component of the mechanism hypothesized here. The role of genetics in evolution and the sources of genetic variation are amply discussed in several recent accounts (*23–26*).

Optimum Habitat

Most mammals at a given time occupy ecological niches within their general ranges to which they are highly, if not maximally, adapted and for which they show a marked preference. Such a niche may be considered a mammal's optimum habitat, and it can be defined further as that habitat which the mammals in question occupy regularly despite seasonal and other relatively short-term climatic changes and at times of minimum population density. In the last instance, such habitats may be considered refugia. For the most part, they are not the only habitats occupied; mammals may regularly disperse into, and occupy, less advantageous habitats under the pressures of increasing population density and intraspecific social competition. In some instances the optimum habitat may be a temporary seral stage, but one that occurs sufficiently frequently to become available for occupancy regularly as other, similar areas pass into the next seral stage and become uninhabitable for a particular species. A successful, dominant mammal will not leave its preferred habitat, and only animals forced to do so will migrate to other, marginal habitats. This is such a well-known and well-documented fact for many species that it has become axiomatic. Dispersing mammals tend to select habitats as much like the original one as possible, but, as dispersal pressure builds with increasing population density, they tend to disperse into a gradient of habitats differing from the original to increasingly greater degrees. As noted above, life expectancy for the vast majority of such mammals is very poor. Thus it seems unlikely that most mammals are subjected directly to the selective force of a significant change in the environment. Selection among dominant animals in an optimum habitat probably can lead only to further specialization, at a slow rate, for that habitat, since there would be no pressure forcing individuals to go in other directions. Optimum habitats rarely and only gradually change in character and only slowly change in location, and dominant individuals move with geographic shifts. For example, with the advance and retreat of glaciers, it is unlikely that the dominant members of a species were forced into new habitats by climatic or environmental changes, and more likely that they remained in their preferred niche as this niche advanced or retreated with changes in climate, whether in a desert, a tundra, or other type of habitat (*2, 27*). With advancing glaciation during the Pleistocene there was a general shift southward of whole faunas that have since retreated northward again (*27, 28*). Arctic shrews (*Sorex arcticus*), northern bog lemmings (*Synaptomys borealis*), and pine martens (*Martes americans*) occurred in Tennessee. Spruce voles (*Phenacomys* cf. *ungava*), yellow-cheeked voles (*Microtus xanthognathous*), and other species of recent boreal mammals were found in Pennsylvania, whereas their present distribution is considerably farther north. During the late Pleistocene period of glacial advance these mammals apparently occupied habitats in Pennsylvania or Tennessee that were quite similar to, but perhaps not completely identical to, those they now occupy either much farther north or as relicts in the boreal zones of higher altitudes. These mammals "moved" with their habitats as the latter changed in latitude (or altitude) with glacial climatic changes. It is reasonable to assume that this continued occupancy of the same type of habitat as it moved, or moves, with major climatic changes was and is the rule for most mammals. Therefore, potential or presumed direct impact of environmental change on a particular species probably is seldom realized, since, as far as the mammals are concerned, significant environmental change probably did not occur. The mammals considered in this article dispersed to areas peripheral to the core of their optimum range instead of changing their habitat.

Social Behavior as a Force in Mammalian Evolution

However, evolution has taken place, new species have evolved, and the changes do correlate with major environmental changes. What, then, occurs that ultimately results in environmental selection? One must assume that forces for evolution were operative and that these forces promoted exploitation of new environments where the probability of occurrence of adaptive genetic changes was increased and where environmental selection could operate on preexisting as well as new genetic variability. Subsequently geographic and reproductive isolation would complete the requirements for speciation (see, however, *13*). Given the conditions outlined above, it seems reasonable to suggest that social behavior, particularly dominance-subordination hierarchies, leading to dispersal of subordinate individuals constitutes a major force in mammalian evolution and provides a reasonable explanation for a number of features of such evolution, particularly at a local level. The fundamental tenet of the present hypothesis is that dispersal of subordinate individuals into marginal or suboptimum habitats provides an opportunity for environmental selection to operate on the genetic variation in environments which differ from that preferred by the dominant members of a species, and thus to improve chances for species survival and change. If adaptation in a new environment depends on existing genotypic variability in a subordinate animal, the animal might be considered to be "pre-adapted" or prospectively adapted. Since selection operates on phenotypes, any genetic variation or genetic mutation would necessarily have to have an advantageous, or at least neutral, phenotypic expression in order to be selected (*23*). Once a subordinate individual has moved into a less-than-optimum environment, the processes of natural selection and genetic variation presumably operate, as generally described by modern evolutionary theory (*23–26*). It seems likely that the dominant core of a population or species is rarely primarily involved in the evolutionary process. Presumably reproductive isolation must eventually isolate the evolving group in order for speciation to occur (but see *13*).

Such a behavioral mechanism seems appropriate to explain the evolutionary events that have resulted in the present 14 species of finches in the Galapagos Islands. The original invaders occupied a habitat closest to their original habitat. Subsequently, countless subordinate individuals were driven off into other kinds of habitat, unoccupied by competing passerines. Eventually, a mutation occurred in one of these, which provided improved chances of survival in marginal habitat. The rest of the process logically follows, with successive occupancy of, and adaptation to, other habitats. What is new in this account of the evolution of these finches is the proposed role of socially subordinate birds and their enforced dispersal into marginal habitats.

The proposed subordination-dispersal force for evolution has a number of other features. First, it would include the flexibility and adaptive characteristics of behavior, defined as the capacity to learn and to adapt to new environmental situations (*26*). Second, intraspecific competition presumably would become more important as invasion of new environments took place. Interspecific behavioral competition would have the same potentialities, in this situation, as intraspecific competition discussed above. However, interspecific competition has dual potentialities: it may lead to evolution, on the one hand, or to extinction of one of the two competitors, on the other, depending on their relative degree of adaptation and on the intensity of the competition. Intraspecific competition should not lead to extinction unless it became so severe that excessive mortality dominated, rather than reproduction and dispersal. (This conceivably could be the case in some microtines.)

A subordination-dispersal mechanism should affect the rate of evolution, particularly if the rate of mutation is not the limiting factor, which it appears not to be (*23*). The intensity of dispersive forces in a population undoubtedly varies directly as some function of population density and of the degree of mutual intolerance, short of a degree of intolerance resulting in inadequate reproduction or excessive mortality. Therefore the rate of evolution should be enhanced by greater dispersive forces and increased numbers (*29*). That is, the opportunity for adaptive genetic change and for environmental selection would be expected to increase progressively as greater numbers of animals dispersed into increasingly diverse habitats. Of course, the rate of evolution would be on a geologic time scale, although the opportunities for genetic change and selection would occur very frequently. An increase in speciation might be expected in association with increased intraspecific intolerance, provided that occupied areas of optimum habitat were within larger areas having sufficient ecological diversity to allow selection to operate on the genotypes of surviving subordinate individuals, and that reproductive isolation from the central (or parental) population was eventually achieved. Continued survival in a new ecological niche or suboptimum habitat presumably would involve a series of mutations in colonizing animals over a long period. A second, but less rigid, requirement would be that there would be no animals already occupying the ecological habitat into which the migrants moved, or that the migrants with their new adaptive mutations would be dominant over any such occupants. Thus, one would predict a burst of evolutionary change, followed by evolution in situ, upon occupation of a totally new and unoccupied area with suitable and diversified habitats.

Species that experience regular extreme highs in population density might be more likely to exploit, and to evolve in, new environments than those that had evolved sensitive and effective density-dependent mechanisms for limiting population growth at relatively low densities. Also, relatively nonaggressive species would not be expected to evolve as rapidly, or to the same degree, as more aggressive ones. Furthermore, the less aggressive species would be expected to exploit available environments less completely.

Periodic Irruptions

In addition, different species exhibit quantitatively different degrees of population fluctuation. For example, species of the genus *Peromyscus* seldom reach the spectacularly high levels of population that are achieved by some of the microtines. Furthermore, there is great variation among the microtines themselves. Among the most spectacular and most publicized of these upsurges are the great irruptions of lemmings (several species of *Lemmus* and *Dicrostonyx*). Meadow (*Microtus pennsylvanicus*), montane (*M. montanus*), and other voles also may occasionally experience spectacular irruptions and usually exhibit rather marked fluctuations in numbers. On the other hand, prairie voles (*M. ochrogaster*), as well as some other microtines, rarely reach such spectacular numbers, and their reproductive potential appears to be lower than that of many other members of the genus (*30*).

An explanation of the periodic irruptions of a number of microtines may lie in the characteristics of their original habitat prior to deforestation and agricultural use of the land (particularly for hay, fodder, and grains) by man. For example, *Microtus pennsylvanicus,* and possibly some other species of *Microtus* with similar ecological requirements may once have been restricted largely to temporary wet grasslands, such as "beaver meadows" created by abandonment of beaver dams. Such temporary meadows usually progress rapidly through seral stages of reforestation. Therefore a species that depended on such a habitat could not have survived long unless it had evolved mechanisms for discovering and exploiting newly created similar habitats. For example, I recently observed an invasion of a beaver meadow by *M. pennsylvanicus* in less than a week after its creation, in a year when the vole population was very high. Furthermore, the voles had to cross inhospitable forest habitat to invade the meadow. The marked fluctuations in the populations of *M. pennsylvanicus* may have served this end by periodically producing large numbers of migrants. The period between irruptions necessarily would have to be shorter than the temporary grass stage of the beaver meadows. Evolution of a dispersive force would be absolutely essential in such a situation. The development of social hierarchies (with accompanying intraspecific aggressiveness and intolerance) in combination with high population density would create a large number of subordinate individuals that would be driven from the habitat of their birth by dominant individuals, once the available home habitat was filled. The vast majority of such migrants would quickly and inevitably die. A very few would reach unexploited, newly created habitat and survive. Thus, new populations would be established by subordinate migrants, and constant repetition of the process would insure survival of the species as a whole.

Of course, *Microtus pennsylvanicus* has been able to exploit agricultural lands and is extremely common and widely distributed. This vole is much more intolerant of other members of its own species than is *M. ochrogaster,* an inhabitant of the extensive prairie grasslands of North America (*8*), and this may be a pertinent factor. Superficially, this intolerance appears to be a process for selecting social subordination, but, as mentioned above, establishment of social rank in a given population may be more a matter of time and place than of genetics. Similar expansion into man-made habitats has occurred with root voles (*M. oeconomus*) in Finland (*31*). These voles prefer habitats that are very small and discontinuous, but under the pressure of increasing density they may occupy previously uninhabited suboptimum habitat. This dispersion occurs mainly at the time of seasonal change in habitat, and it is young voles that occupy these habitats. In addition, these voles, in years of high population density, drive field voles (*M. agrestis*) from their usual habitats.

In contrast to species such as *Microtus pennsylvanicus,* there are those that originally inhabited continuous and extensive areas of relatively similar habitat, such as the extensive deciduous forest of eastern North America and the great plains of central North America prior to the advent of Europeans. Some members of the genus *Peromyscus* (for example, *P. maniculatus*) may be representative of such species. They seldom irrupt, and their population densities seem to be under much more effective control than is the case with regularly irruptive species. Their reproductive function evidently is much more sensitive to inhibition than is that of those microtines and other small rodents that have been tested (*15, 17*). Differences in food requirements usually appear not to be an important contributing factor in accounting for the different degrees of regulation of population size in *Microtus* and *Peromyscus.* Therefore, we have an interesting situation: one species, *M. pennsylvanicus,* may have survived because it did not evolve an efficient negative-feedback control of population size, whereas *P. maniculatus,* for example, may have survived because it did, and thereby avoided the potential danger of overexploitation of the environment. However, *M. pennsylvanicus* has taken advantage of the vast grasslands created by agriculture, but it has retained its characteristic fluctuations in population, which are inappropriate now. If the foregoing hypothesis is valid, and if present agricultural practices persist long enough, the meadow vole should eventually evolve more effective control of its population densities. In the interim it would face the threat of extinction if it should reach such low numbers after a peak that it was unable to recover from the decline. Social dominance of meadow voles by the grassland inhabitants (*M. ochrogaster*) (*8*) and *Peromyscus maniculatus bairdii* (*32*), by the woodland inhabitants *P. leucopus* (*32*) and *Clethrionomys gapperi* (*33*), and probably by other socially dominant species may limit the expansion of meadow voles into other habitats. *Peromyscus leucopus* also is dominant over *Microtus ochrogaster* and may limit the latter to cultivated fields (*34*).

Somewhere in between the group of mammals represented by *Microtus* and those represented by *Peromyscus maniculatus* are house mice and Norway rats, which appear to be essentially opportunistic in their ability to exploit man-made habitats and to irrupt under favorable conditions. In other words, they are potentially, but not regularly, irruptive.

Arctic and Subarctic Species

In the case of the Microtinae, the problem of those species that inhabit the extensive and relatively uniform arctic and subarctic tundras remains to be considered. Lemmings of the genera *Lemmus, Phenacomys, Synaptomys,* and *Myopus* are generally considered to be among the more primitive of the microtines (*35*). It is conceivable that at one time the ancestral predecessors of today's arctic lemmings —*Lemmus, Dicrostonyx,* and, to a lesser extent, *Phenacomys, Synaptomys (Mictomys),* and *Myopus*—inhabited temporary grasslands and evolved a mechanism for exploiting new and temporary habitats similar to the mechanism proposed for *Microtus*. For example, *Dicrostonyx*, while highly evolved for its arctic habitat, seems to have occupied similar less boreal and discontinuous parklike habitats, and later to have survived only in more purely arctic habitats. There is recent evidence that a relatively boreal parkland-coniferous forest existed in Pennsylvania during the late Pleistocene, and that *Dicrostonyx* did indeed occupy these discontinuous grassy parklands that were interspersed in a region of boreal coniferous forest (*27, 36*). *Dicrostonyx* disappeared with the subsequent gradual transition of boreal parkland to boreal forest and is now restricted to the arctic tundra. If such is the case, then one must assume that the collared lemming (*Dicrostonyx* sp.) adapted to and occupied the arctic much earlier than *Lemmus* and closely related forms did, since the collared lemmings exhibit much greater adaptive specialization for arctic conditions and also appear to have diverged from ancestral microtine-like stock very early in the evolutionary history of the group (*35*). Subsequently they may have survived only in increasingly boreal habitats as a result of competition from more newly evolved, dominant species, possibly microtines, which replaced them in the temporary and more temperate habitats, much as field voles (*Microtus agrestis*) are driven from man-made habitants in Finland by root voles (*M. oeconomus*) in years when population density of the species is high (*31*). Other lemmings, such as species of *Synaptomys*, now occur in several types of habitat other than grassland, but they appear to be subordinate to *Microtus* where the two occur together, and *Synaptomys* is rarely found in the preferred habitats of *Microtus*. The arctic lemmings also may have retained the social characteristics and population responses that are necessary for colonizing new habitats, responses which now are inappropriate for most of their range. However, lemmings (*L. lemmus*) may invade essentially alien habitats and regions in years of high population density, and may even drive regular inhabitants from their customary habitats (*31*). Whether these events actually occurred in the evolution of arctic lemmings may never be determined, but it is a possible explanation for their apparently useless and violent fluctuations in population size. It seems likely that genetic exchange could take place in lemming populations without extreme fluctuations, as it does in many other species.

Density-Dependent Inhibition of Reproduction

A high reproductive potential and the ability to realize it rapidly are characteristic of microtines and of many other irruptive species of mammals. Nevertheless, reproduction is progressively inhibited as density increases, and may be totally suppressed if densities become sufficiently high (*15*). The inhibition of reproduction is part of a density-dependent endocrine response that also may include increased adrenocortical activity and its sequelae. This density-dependent feedback is believed to operate through social intolerance and aggressiveness in conjunction with increased numbers (*16*). Therefore, if social intolerance and relatively high numbers constitute a force for dispersal and exploitation of new habitats by mammals basically adapted to discontinuous habitats, one might expect more conspicuous changes in adrenocortical and reproductive function with changes in population density in these mammals than in more socially tolerant mammals adapted to continuous habitats. The adrenocortical responses associated with social rank and increased density—and their sequelae, such as decreased resistance to disease—may be considered nonadaptive in terms of individual survival and a disadvantageous by-product of social intolerance and high densities. On the other hand many species adapted to continuous habitats seem to have evolved greater social tolerance, and a more sensitive regulation of reproductive function that serves generally to maintain their populations at relatively lower densities than those of irruptive species. Thus, in mammals adapted to continuous habitat, with their greater social tolerance and more moderate population densities, one might expect much less adrenocortical response to changes in density than one expects in irruptive or potentially irruptive species such as many microtines, house mice, and rats. The lack of correlation between adrenocortical activity and rank or density, together with the marked sensitivity of reproductive function to inhibition by subordinate rank or increased density, in the prairie deer mouse (*Peromyscus maniculatus bairdii*) (*10, 15*) may reflect adaptation to a continuous habitat, with evolution of an efficient feedback mechanism to limit population growth well below irruptive levels. On the other hand, behavioral intolerance and adrenocortical and other density-dependent physiological responses occur in the white-footed mouse (*P. leucopus*) that inhabits serally temporary brushlands and forest edges, as well as in *Microtus pennsylvanicus* and lemmings that, presumably, are basically adapted to discontinuous habitats (*15, 37*). Extensive continuous habitats, which do not impose the necessity for regular dispersal and exploitation of new sites, may have resulted in selection against social intolerance and the adrenocortical and related reactions that accompany it in favor of more benign behavior and more direct and sensitive regulation of reproductive function that usually curtails population growth at levels well below those often achieved by microtines exhibiting extreme fluctuations in population.

A Unifying Hypothesis

Consideration of these problems has led to a unifying hypothesis concerning the direct and important role of social competition—in particular, the role of the subordinate individual—in natural selection and evolution. The essence of this hypothesis is that intraspecific competition is a major force in evolution and that genetic changes on which selection operates are found in these socially subordinate individuals. The probability that an adaptive genetic change will occur will be greater in an environment less favorable than that occupied by the central or parent population. The odds will automatically be increased, in many species of mammals, by the great numerical predominance of subordinate migrants over dominant core residents. Thus, the raw material for speciation by way of natural selection is the rare subordinate migrant that survives in a new habitat. It may be that in these individuals, in suboptimum habitats, genetic change can improve the chances for survival and increase adaptation by selection. It is also suggested that more effective density-dependent control of population growth has evolved in continuous habitats than in discontinuous habitats, where marked social intolerance leads to dispersal and to marked density- and rank-dependent adrenocortical responses. Finally, it is suggested that inhibition of maturation of mammals born late in the breeding season may have evolved as a means of insuring an adequate breeding population in the following breeding season.

References and Notes

1. V. Geist, *Natur. Hist.* **76**, 24 (1967).
2. J. E. Guilday, in *Pleistocene Extinction, The Search for a Cause*, P. S. Martin and H. E. Wright, Jr., Eds. (Yale Univ. Press, New Haven, Conn., 1967), p. 121.

J. B. S. Haldane, *Proc. Roy. Soc. Ser. B Biol. Sci.* **145**, 306 (1956).

4. P. J. Darlington, Jr., *Zoogeography: The Geographical Distribution of Animals* (Wiley, New York, 1957).

J. J. Christian, *Proc. Nat. Acad. Sci. U.S.* **47**, 428 (1961); V. C. Wynn-Edwards, *Animal Dispersion in Relation to Social Behavior* (Oliver and Boyd, Edinburgh, 1962).

6. S. A. Altman, *Ann. N.Y. Acad. Sci.* **102**, 338 (1962); C. H. Southwick, *ibid.*, p. 436.
7. C. B. Koford, *Science* **141**, 356 (1963).

L. L. Getz, *J. Mammalogy* **43**, 351 (1962).

9. P. L. Errington, *Iowa Agr. Exp. Sta. Res. Bull.* **320**, 797 (1943); *Quart. Rev. Biol.* **21**, 144 (1943); *ibid.*, p. 2 *Ecol. Monogr.* **24**, 377 (1954).
10. A. M. Guhl, J. V. Craig, C. D. Mueller, *Poultry Sci.* **39**, 970 (1960); R. E. Wimer and J. L. Fuller, in *Biology of the Laboratory Mouse*, E. L. Green, Ed. (McGraw-Hill, New York, ed. 2, 1966), p. 631.
11. P. K. Anderson, in *Mutation in Population* (Akademia, Prague, 1965), p. **17**; C. R. Terman, *Ecology* **46**, 890 (1965).

J. A. Lloyd and J. J. Christian, *J. Mammalogy* **50**, 49 (1969).

13. P. R. Ehrlich and P. H. Raven have recently discussed the relationship of gene flow to differentiation of populations and have emphasized the overriding importance of selection [*Science* **165**, 1228 (1969)].
14. J. B. Calhoun, *Science* **109**, 333 (1949); R. Mykytowycz, *CSIRO (Commonw. Sci. Ind. Res. Organ.) Wildlife Res.* **4**, 1 (1959)
15. J. J. Christian, *Bull. Sinai Hosp. Detroit* **47**, 108 (1970).
16. ———, *Proc. Nat. Acad. Sci. U.S.* **47**, 428 (1961); ———, in *Physiological Mammalogy*, W. V. Mayer and R. G. Van Gelder, Eds. (Academic Press, New York, 1963), vol. 1, p. 189.
17. ———, "Fighting, maturity, and population in *Microtus*," in preparation.
18. D. B. Van Vleck, *J. Mammalogy* **49**, 92 (1968).
19. F. H. Bronson, thesis, Pennsylvania State University (1961) ———, *Ecology* **44**, 637 (1963); ———, *Anim. Behav.* **12**, 470 (1964); D. E. Davis, J. J. Christian, F. H. Bronson, *J. Wildlife Manage.* **28**, 1 (196 E. D. Bailey, *J. Mammalogy* **46**, 438 (1965).
20. L. H. Metzger, paper presented before the 47th Meeting of the American Society of Mammalogists (1967).
21. M. C. Healey, *Ecology* **48**, 377 (1967).
22. See, for example, C. Elton, *Voles, Mice and Lemmings* (Clarendon, Oxford, 1942 D. Chitty, *Phil. Trans. Roy. Soc. London Ser. B Biol. Sci.* **236**, 505 (1952); O. Kalela, *Ann. Acad. Sci. Fenn. Ser. A IV Biol. No. 34* (1957); F. Pitelka, "Arctic biology," paper presented at the 18th Biology Colloquium, Corvallis, Oregon, 1957; K. Murray, *Ecology* **46**, 163 (1965).
23. G. G. Simpson, *The Major Features of Evolution* (Simon & Schuster, New York, 1953).
24. ———, *The Geography of Evolution* (Capricorn, New York, 1965); E. Mayr, *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, Mass., 1963).
25. T. Dobzhansky, *Genetics and the Origin of Species* (Columbia Univ. Press, New York, 1941).
26. J. M. Smith, *The Theory of Evolution* (Houghton Mifflin, Boston, Mass., 1966).
27. J. E. Guilday, P. S. Martin, A. D. McCrady, *Bull. Nat. Speleol. Soc.* **26**, 121 (1964).
28. C. W. Hibbard, *Mich. Acad. Sci. Arts Lett. Rep.* **44**, 3 (1959); J. E. Guilday and M. S. Bender, *Ann. Carnegie Mus.* **35**, 315 (1960); J. E. Guilday, H. W. Hamilton, A. D. McCrady, *Palaeovertebrate (Montpellier)* **2**, 25 (1969).
29. S. Wright [*Genetics* **16**, 97 (1931); *Amer. Natur.* **74**, 232 (1940); in *The New Systemics*, J. Huxley, Ed. (Clarendon, Oxford, 1940), pp. 161–183] has pointed out that there is an optimum inter-deme gene flow and population size for evolution. For example, it could be argued that, if *Microtus pennsylvanicus*, an organism found in discontinuous habitat, did not undergo explosive population growth and dispersion, it would have speciated over its range into a variety of other species. I cannot deal here with the influence of social behavior on these optima; suffice it to say that mechanisms to which I draw attention in this article are assumed to work in parallel with those which classically have been thought to determine evolutionary rates, although I expressly wish to point out the simplifying nature of this assumption.
30. S. A. Asdell, *Patterns of Mammalian Reproduction* (Comstock, Ithaca, N.Y., 1946).
31. J. Tast, *Ann. Zool. Fenn.* **3**, 127 (1966); *ibid.* **5**, 230 (1968); *Ann. Acad. Sci. Fenn. Ser. A IV Biol. No. 136* (1968).
32. J. O. Murie, thesis, Pennsylvania State University (1967).
33. A. W. Cameron, *Evolution* **18**, 630 (1965); G. C. Clough, *Can. Field Nat.* **78**, 80 (1964).
34. J. O. Whitaker, *Ecology* **48**, 867 (1967).
35. E. T. Hooper and B. S. Hart, *Misc. Publ. Mus. Zool. Univ. Mich. No. 120* (1962).

J. E. Guilday, *Amer. Midland Natur.* **79**, 247 (1968).

J. J. Christian and D. E. Davis, *J. Mammalogy* **47**, 1 (1966); ———, in *Comparative Endocrinology*, A. Gorbman, Ed. (Wiley, New York, 1959), p. 71; R. V. Andrews, *Physiol. Zool.* **41**, 93 (1968).

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