Table 1. Radioactivity in brain DNA extracted from frog tadpoles after receiving daily injections of [^{3}H]thymidine during the periods shown. Each range of values is derived from three portions of the total DNA extracted from six pooled brains. Measurements of DNA were done on other portions. All tadpoles received six injections of either prolactin (P), somatotrophin (S), or saline (C) on alternate days, beginning at mid-stage III.

Group	Radioactivity (count/min)	
	Per milligram of DNA	In whole brain
	Mid-stage III to stage VI	
P	40,200 ± 1800	2816 ± 126
S	56,190 ± 510	5900 ± 54
C	33,600 ± 3400	2016 ± 196
	Stage VII to stage X	
P	32,360 ± 2780	3883 ± 333
S	16,056 ± 1656	2240 ± 232
C	17,380 ± 40	1564 ± 4
	Stage X to stage XIII	
P	33,617 ± 1133	7059 ± 238
S	12,092 ± 483	2060 ± 82
C	21,310 ± 2710	2660 ± 337

waned during subsequent development, and was ultimately reduced to a net increase of 15 to 25 percent in the postmetamorphic frogs of the S-group. The labeling experiment (Table 1) showed comparable changes in the accumulation of newly synthesized DNA. Only during the injection period did the S-group animals exceed the controls in uptake of [^{3}H]thymidine into brain DNA.

There are reasons, however, for exercising caution in interpreting the significance of the increased radioactivity in the DNA of the experimental groups. First, increased [^{3}H]thymidine incorporation suggests an enhancement of cellular proliferation, but it does not exclude the possibility that the normal number of polyploid neurons is increased. Moreover, our evidence that both hormones primarily increase DNA synthesis—temporal differences notwithstanding—does not preclude the possibility that cell death is also affected. In particular, neuronal death is extensive in normal animals during the metamorphic stages XX to XXV (*9*); and during this period, P-group tadpoles suffer a mean decrease in brain DNA that is only 25 percent as great as the DNA losses in the other two groups (Fig. 2). This observation suggests either that a diminution of cell death may also occur after prolactin treatment, or that enhanced cell proliferation and normal cell death occur concurrently in P-group animals during metamorphosis.

We have confirmed that purified somatotrophin increased DNA in the developing brain, although our results are not in complete agreement with the hypothesis advanced by previous researchers (*3*). They inferred, from observation of a net DNA change and some histologic estimations, that somatotrophin extends the period of rapid neuronal proliferation. In our experiments, neither prolactin nor somatotrophin, administered during early larval stages, lengthened the period over which brain DNA is normally accumulated (to stage XVI). Rather, somatotrophin induced a very rapid rise in the rate of brain DNA accumulation during the period of its administration; but shortly after the termination of the injections, the rate of rise in DNA content declined to below that of the control group. In contrast, the effects of prolactin on the accumulation of DNA in the brain became manifest only after the injection period: an extraordinarily rapid rate of increase of DNA was maintained through the mid-larval stages, and considerably less brain DNA was lost during metamorphosis than in normal tadpoles.

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Mammalian Evolution: Is It Due to Social Subordination?

The basis of J. J. Christian's (*1*) evolutionary hypothesis is that in certain vertebrate species the available stands of optimum habitat are allocated to socially dominant individuals. Subordinate, chiefly young, animals are compelled to pioneer new kinds of habitat where they may become prospective founders of new evolutionary lineages while the original population is preserving the status quo. Though most of Christian's examples are small rodents, he extends the hypothesis to animals in general and to Darwin's finches in particular.

In spatially shifting but temporally stable habitats (for example, successional communities) the dominant-subordinate social system indeed facilitates the evolutionary status quo as subordinate pioneers are destined to discover newly available stands of the habitat and, as Christian rightly states, become dominant settlers there. Many polymorphic dispersionary systems exist in the animal world (*2*) and some—for example, solitary and gregarious locusts and alate or apterous aphids—function on a phenotypic basis, as Christian claims the cyclically expansive small rodents do (*3*). However, contrary to what Christian claims, I believe this mechanism does not easily lead to evolutionary differentiation. Colonies on secondary or marginal habitats have poor reproductive success, and they owe their prolonged existence to steady reinforcement by surplus individuals from optimal habitats (*4*). Such overwhelming gene flow slows down or prevents local adaptation on whatever basis this could happen (*5*). Christian's hypothesis does not explain how subordinate and surplus mammalian emigrants isolate themselves from the parent population. Yet, without isolation—in the cited cases geographic isolation is the most likely mode—they could hardly have evolved into different species, let alone into different adaptive types.

Colonization by barrier crossing is an essential phenomenon in island or archipelago situations where geographic speciation occurs on a grand scale, often followed by adaptive radiation. Christian suggests that social pressure seems appropriate to explain the events that led to the evolution of 14 species of Galapagos finches from one common ancestor: new species were formed when population pressure forced subordinate individuals into marginal habitats. Social pressure might be one, but only one, of the many reasons, and the many dispersive mechanisms, whereby these birds were induced to occupy strange habitats. But without geographic isolation—without reaching another, hitherto uninhabited island—they could not have evolved into different species.

The Hawaiian Drepaniidae (*6*) also accomplished a spectacular adaptive radiation where barrier crossing by flight played a decisive role. For example, in the large drepaniid genus *Loxops* we find three heavily differentiated species (*L. virens*, *L. maculata*, and *L. coccinea*), and each of these evolved a different subspecies on each of the islands they inhabited. On the other hand, two other drepaniid genera, *Himatione* and *Vestiaria*, are monotypic, and all their populations on the seven main Hawaiian islands belong to the same subspecies. Both types of drepaniids crossed the water barrier. But while the *Loxops* species mentioned are inner canopy feeders and seldom venture to the lofty heights, *Himatione* and *Vestiaria* feed on nectar high in the outer canopy of the widespread ohia tree. Their flocks are often seen flying over the forest in search of flowering trees, and such flocks are often carried by stormy winds from island to island, a dispersion that presumably hinders local differentiation, by steady mixing of the gene pool (*7*).

A locomotor habit employed in feeding thus enabled one group of drepaniids to subspeciate, to speciate, and, no doubt, eventually to radiate into new niches while a different locomotor habit, also connected with feeding, causes other drepaniids to pioneer much more often and across longer distances (*8*) but prevents their adaptive evolution. There is no need here to speculate on the role of social outcasts, or to postulate that greater dispersive forces necessarily lead to enhancement of the rate of evolution.

In continental evolution the major mode of speciation is not barrier crossing but splitting of the distributional area by ecogeographic barriers. For instance, out of the 24 *Microtus* voles in North America, ten species are monotypic. Two of these are isolated relicts; four have a very small distribution area geographically isolated from the large area of a polytypic, closely related species, the surmised ancestor; and four are similar endemics likewise with a polytypic, neighboring mainland relative. Thus geographic speciation could be postulated in all cases that could be analyzed. The 14 polytypic species consist of 129 subspecies; 26 of these (that is, 20 percent) are geographically isolated from the main distribution area of the species—an indication that geographic speciation is now in progress. Microtine and other mammalian isolates are in good general correlation with avian, reptilian, insect, or even plant counterparts in relict habitats (*2, 5, 9*).

It is more difficult to find examples of incipient, major, adaptive radiation. Out of the three species of *Herpestes* (Viverridae, Mamm.), the mongoose *H. edwardsii* is unique in possessing greatly enlarged, extraordinary transverse processes of the lumbar vertebrae (*10*). These seem to have evolved together with the rolling-up behavior unique to this species—an effective defense posture against a larger predator. I see in this behavioral-structural novelty a new adaptive feature that possibly opens up a new niche—another animal rolling up in defense, much resembling, functionally, the armadillo, hedgehog, and scaly pangolin, among the mammals. Adaptive radiation of such a novel animal is highly plausible, but the basic mechanism does not necessitate the invocation of subordinate behavior here, either.

Though social hierarchy systems may be useful dispersionary mechanisms, Christian failed to recognize that their evolutionary impact strongly necessitates geographic isolation.

Examples of archipelago evolution show that, though behavioral mechanisms could become instrumental in speciation, many complications may arise. Mainland examples of evolution are more easily explained by geographic speciation on refugia and by such adaptive changes as do not warrant dispersive action of dominant-subordinate social systems.

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In reply to Udvardy's comment I first wish to state that I did not intend to extend my hypothesis to all animals or even to all mammals. Presumably it would apply to only those species with hierarchical social organization of one degree or another. Also it would not necessarily exclude other mechanisms. On the other hand, a genetic change resulting in greater adaptation of a subordinate mammal to a marginal habitat previously not permanently occupied, or unoccupied, by the species in question could also result in ecological, behavioral, or reproductive isolation.

I am aware of the avian and mammalian examples Udvardy gives, but do not see that they necessarily conflict or exclude my hypothesis. Also the Galapagos finches were mentioned as a case where such a social mechanism *may* have operated, although I would, in general, expect that such a mechanism probably would be more applicable to mammals, since they generally are less mobile than birds.

The important point is that genetic change is required, and this, coupled with selection in a new habitat, could result in speciation. Also, if such a change occurred, albeit rarely, it does not follow that continued reinforcement by other dispersing individuals is mandatory, especially since territoriality, social rank, and other behavioral devices result in a large degree of reproductive isolation and exclusion of aliens. However, if continued mass immigration occurs, one can imagine a situation in which reinforcement might consist of selection of only a particular portion of the total range of genetic variability as well as a genetic change. This would be directional or progressive selection and gradual transformation of the species in situ (*1, 2*). Thus, if a mammal normally inhabited a mesic environment and was forced to immigrate, or otherwise moved, into a sodium-deficient or arid habitat, one can reasonably imagine that only those individuals would survive that had the greatest ability to secrete aldosterone and to concentrate urine. Behavioral patterns for conserving water would also be selected. Thus, even if there were repeated immigration, only those individuals would survive which represented a particular genotype. Continued selection would follow. Selection of a particular portion of a genotype in this manner would require sufficient genetic variability to include the portion selected. Therefore Ayala's statement (*3*) that the rate of evolution of a population becoming adapted to a new environment will be positively correlated with the genetic variability of a population is applicable. On the other hand, if an animal has moved across an ecologically inhospitable habitat to reach one that is more suitable but different from the original habitat, continued immigration into the new habitat may not occur, or may occur at such low rates that the gene flow between populations will be exceedingly slow. Even with contiguous populations of the same subspecies and variety of mouse, gene flow between individual breeding demes is very slow (*4*).

If a mammal has evolved a mechanism enabling it to exploit newly developed habitats similar to those from which it emigrated, it seems reasonable to assume that occasionally a genetic change would occur which would increase the adaptability of an individual to a different habitat. Furthermore, it is not necessarily true that such individuals have poor reproductive success. Udvardy's criticism seems to rest primarily on the presumed occurrence of repeated overwhelming gene flow that prevents isolation and local adaptation. However, repeated overwhelming gene flow does not necessarily follow, particularly if some adaptive changes have occurred, as presumably they must. One might consider behavioral, physiological, or other differences between different subspecies that may illustrate the development of such mechanisms (*5*). For example, it has been reported to me recently that one subspecies of *Peromyscus maniculatus* occupying discontinuous habitat is much more aggressive than an adjacent subspecies which occupies continuous habitat. If this report can be confirmed by future studies, it can readily be seen that reproductive isolation of populations in habitats that are ecologically different—in this case different also in the sense that one is continuous and one discontinuous—can occur and that speciation can ensue. Also there is increasing evidence that reproductive isolation may occur between local populations of a subspecies, particularly through assortative mating, partial or complete hybrid sterility, differences in social behavior, or differences in reproductive organs (*4–6*). Furthermore, positive exclusion of alien migrants by residents is known to occur in *Mus* and *Peromyscus* (*6, 7*), and probably is a widespread phenomenon in mammals. Thus gene flow is much slower than would be predicted by random processes.

If, through genetic change, an animal is adapted to a new *kind* of habitat and if this adaptation is accompanied by reproductive isolation through behavioral or other mechanisms, a major step toward speciation will have occurred. Of course, this is particularly likely to occur in peripheral populations, and Mayr (*8*) has pointed out that ecologically or microecologically marginal habitats may be considered peripheral. He cites the example of a grasshopper, whose main distribution is in the lowlands, that has developed a deviant type of genital structure in the ecologically different Appalachian Mountains, a habitat that can be considered peripheral.

I think some confusion may exist with regard to what I considered, in my article, to be "different" habitats. My intended meaning was, different in the ecological sense and not merely another location of the same kind of habitat, except when I was speaking of the need to exploit newly created discontinuous habitat. However, if the new habitat also is ecologically different, no problem arises. Diversifying selection is one mechanism that probably would be operative when closely related populations or a large homogenous population occupy different habitats (*2*). The various publications cited here delve into these various methods of reproductive isolation in relation to subspeciation, and to speciation, in considerable detail.

I think the important point, emphasized by Mayr (*8*), is that geographic or ecological isolation are one and the same and can occur with "microecological" differences. Thus, speciation presumably can occur as a result of the postulated mechanisms. But, as I originally emphasized, pioneers in an ecologically new or submarginal habitat with new genetic composition would surely be rare, and the vast majority of dispersing animals will not survive. Of course, if geological or climatological events result in physical geographic isolation of a peripheral [in Mayr's (*8*) sense] population of a species, it is generally accepted that speciation may follow. Also, if only a portion of the normal variability is selected from the total genetic composition of a species, linear evolution may occur.

The potential importance of behavioral reproductive isolation of subpopulations for speciation needs considerably more study and evaluation. However, if it occurs in ecologically distinctly different and adjacent habitats, as suggested above, it seems likely that it can facilitate speciation. Also the increasing evidence of behavioral reproductive isolation may add another dimension to the process of speciation, and it may prove to be of considerable significance in mammals if accompanied by other necessary conditions. If dispersion occurs across an ecological barrier, and if some immigrants carry an adaptive genetic change, there again seems to be no particular barrier to speciation.

I do not see that Udvardy's comments necessarily invalidate my hypothesis. However, it *is* a hypothesis, and its acceptance or rejection in toto or in part will depend on the results of future investigations.

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