

Local Adaptation, Coadaptation, and Population Boundaries

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Coadaptation can occur either because of local adaptation in a geographically widespread population and/or because of intrinsic adaptation to the state of other genes or chromosomes. In either event, hybridization between animals with differently coadapted gene or chromosomal complexes can result in a decrease in fertility, viability, etc. in the initial hybrids and especially in later generations. This is known as an outbreeding depression. Moreover, releasing animals not adapted to the local environment can seriously hamper the effectiveness of a reintroduction program, and hybridization can also destroy the local adaptation. Coadapted gene complexes are best detected through studies on natural populations because the adaptive nature of the complex is often only apparent in the natural environment. In the absence of information on natural populations (but ideally as a supplement), the presence of coadapted gene complexes and population boundaries can be detected through mating behavior, a pedigree analysis that can detect outbreeding depressions and distinguish them from inbreeding depressions, or genetic and karyotypic surveys. Once an outbreeding depression has been detected, it can be used to redefine the boundaries of the populations to be managed. Basically, the outbreeding depression is avoided by preventing hybridization between animals with the different coadapted complexes. In some cases, formal subspecific designations have been used to define the population boundaries. Unfortunately, many subspecific designations were made before population-thinking influenced taxonomy. It is important to emphasize the need to undertake modern biological studies and to collect additional information useful for systematics. If modern biological studies indicate that the subspecies have little or no biological significance, it is best to treat the animals as a single population and disregard the subspecific designations.

Key words: outbreeding depression, population boundaries

Received for publication September 17, 1985; accepted October 22, 1985.

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INTRODUCTION

The Definition of Coadaptation

The word "coadaptation" was used first by Dobzhansky [1948] to describe the phenomenon that sets of genes derived from different geographical populations of the fruit fly species *Drosophila pseudoobscura* resulted in reduced fitness when brought together by hybridization, particularly in the generations following the initial hybrids. Subsequent work [Brncic, 1954; Templeton et al, 1976; Wallace et al, 1953] revealed that coadapted gene complexes can be found within a large number of *Drosophila* species, although some *Drosophila* species show no evidence for coadaptation despite being widespread geographically [McFarquhar and Robertson, 1963; Richardson and Kojima, 1965, Singh, 1972].

The *Drosophila* studies indicate that coadapted gene complexes are a common but not universal phenomenon. This inference should be applicable to the vast majority of animal species because vertebrates and invertebrates share the same basic type of genetic system and because coadapted complexes evolve under evolutionary conditions common to all animal species [Carson and Templeton, 1984; Shields, 1982]. Moreover, Frankham [1982] could find no case where the results obtained using *Drosophila* have been in conflict with or misleading when applied by animal breeders working with vertebrates. Hence, it is not surprising that coadapted complexes have been found in a wide variety of vertebrate species [see Shields, 1982, for a review of the literature].

These studies reveal two basic, but mutually compatible, mechanisms for the hybrid or recombinant breakdown in fitness. The first major mechanism is adaptation to a local environment. Many species are distributed over a geographical range that encompassed a diversity of environmental conditions that influence the animals' ability to survive or reproduce. Under these conditions, local populations of the species will often adapt to the local environment, particularly if dispersal is limited. Hybridization between different local populations can sometimes destroy the locally adapted gene complex. For example, when the Tatra Mountain ibex (*Capra ibex ibex*) in Czechoslovakia became extinct through over-hunting, ibex were successfully transplanted from nearby Austria [Greig, 1979]. However, some years later, bezoars (*C. ibex aegagrus*) from Turkey and the Nubian ibex (*C. ibex nubiana*) from Sinai were added to the Tatra herd. The resulting fertile hybrids rutted in early fall instead of the winter (as the native ibex did), and the resulting kids of the hybrids were born in February, the coldest month of the year. As a consequence, the entire population went extinct [Greig, 1979].

The second mechanism for hybrid and recombinant breakdown is coadaptation. Coadaptation occurs when a genetic or karyotypic complex evolves in response to the state of other genes or chromosomes. For example, the process of gamete formation normally requires a matched set of chromosomes (with the exception of the sex chromosomes). As long as the set matches, meiosis is normal, but if the two sets of chromosomes differ in number or structure, abnormal meiosis and attendant fertility problems are possible. An example of this type of karyotypic coadaptation is illustrated by fertility difficulties discovered in captive populations of the Owl monkey, *Aotus trivirgatus* [de Boer, 1982]. Several chromosomal races were detected by karyotyping, and there is evidence that successful reproduction is enhanced when chromosomally similar forms are paired [Cicmanec and Campbell, 1977]. Such chromosomal incompatibility has been found in a variety of vertebrate species [White,

1978; Benirschke, 1983; Ryder, in press]. However, chromosomal differences are not universal indicators of coadaptation because some species are variable for chromosome number and/or structure with no detected fitness problems [Templeton, 1981] or even hybrid superiority [Baker et al, 1983; Christensen and Pedersen, 1982; Patton et al, 1980; Vosselman, 1980].

Another type of coadaptation depends upon interactions between specific gene loci rather than chromosome structure or number. For example, in humans, the sickle-cell allele of the beta-hemoglobin locus tends to cause a crystallization of hemoglobin molecules in the red blood cells of homozygotes [Templeton, 1982]. This crystallization can cause the red blood cells to rupture, thereby leading to a hemolytic anemia that is often fatal. However, in Arabia, these clinical manifestations are virtually absent because many Arabians (unlike most other human populations) do not turn off the synthesis of fetal hemoglobin at birth. As a result, about 10 to 20% of their blood after birth is of the fetal variety, and the presence of fetal molecules disrupts the crystallization and thus eliminates the deleterious effects of the sickle-cell gene [Templeton, 1982]. Hence, the fitness effects associated with the sickle-cell allele are greatly influenced by the fetal hemoglobin gene, thereby illustrating the importance of intrinsic genetic states. However, the reason for the high frequency of the sickle-cell allele in the first place is that it represents a local adaptation by some human populations to the presence of malaria. This fact illustrates that local adaptation and coadaptation are not necessarily exclusive.

IMPLICATIONS

If hybridization between two differently locally adapted or coadapted populations takes place in a captive breeding program, an outbreeding depression may occur. The outbreeding depression is an increase in gametic incompatibility, zygotic and embryonic mortality, stillbirths, decreased fertility, and/or increased mortality that may be manifested in the F_1 or delayed until the F_2 or backcross generations [Endler, 1977; Hedrick et al, 1978; Shields, 1982]. Such an outbreeding depression can severely hamper the reproductive success of a captive breeding program. Indeed, it can be so severe that if hybridization is common in the breeding program, the entire population can be driven to extinction, as illustrated by the ibex example mentioned in the previous section [Greig, 1979].

The occurrence of an outbreeding depression can be used to define the boundaries of a managed population. Frequently, an animal manager is faced with the situation of having a collection of animals whose biological status is ambiguous. Perhaps the population consists of a mixture of more than one species, subspecies, or locally adapted population. Should the manager attempt to unravel this mixture and breed each entity separately, or should the manager simply allow hybridization to occur? Information on local adaptation and/or coadaptation can provide an answer to this question.

DETECTION

Given that locally adapted and coadapted complexes can have an important effect on management of captive populations and upon the very definition of what should constitute the boundaries of a managed population, it is important to detect the presence of such complexes.

The very best sort of detection schemes involve studies on natural populations. These studies are particularly important because the manifestation of local adaptation commonly depends upon the gene complex interacting with the natural environment in which the animals live. Thus, the true adaptive significance of the complex is often apparent only in the natural environment. For example, consider studies on two species of sculpins, *Cottus confusus* and *C. cognatus*, that live in the same river systems of northwestern America [Zimmerman and Wooten, 1981]. Both fish species live in rocky riffles of cold, clear streams, but *C. cognatus* also lives in the open water of larger streams and lakes. The two species are quite distinct ecologically and morphologically, and moreover several diagnostic gene markers allow individuals to be unambiguously assigned to the proper species with 100% accuracy. However, there does exist one population for which this clear distinctiveness breaks down. A population living near a dam represents, in effect, a hybrid swarm. Moreover, there is no evidence for an outbreeding depression in the dam population, and indeed a high frequency of backcross individuals implied that the hybrids had a high fitness. Zimmerman and Wooten [1981] explain this phenomenon in terms of the altered thermal regime induced by the dam. Normally, reproductive activity does not coincide in these two sculpins. However, the altered thermal regime by the dam apparently shifts the period of reproductive activity in both species in such a manner as to cause them to coincide. Thus, in this artificial environment, no barrier to hybridization, including an outbreeding depression, is evident, yet in nature these fish species have distinct ecological roles and never hybridize.

The failure to detect local adaptation or coadaptation in a captive situation is also illustrated by the ibex example mentioned in the first section. In this case, there would be no difficulty in breeding any of the populations or their hybrids in an environment that protects the newborns from harsh weather. Yet the season of birth, unimportant in the captive environment, was the critical trait causing the failure of the reintroduction program. All of these examples clearly show the importance of understanding the population under natural conditions.

There are several different kinds of studies on natural populations that are relevant here. First is an assessment of how genetic or phenotypic variation is distributed within versus between populations. If most variation is found between individuals regardless of their geographical or subspecific status, the population should be regarded as a single entity. For example, some 77 species and over 94 species and subspecies of grizzly bears have been described for North America alone on the basis of morphological differences [Hall, 1981]. However, much of this variation turned out to be individual or family differences, so today only one species of big brown bear (*Ursus arctos*) is recognized on a global basis, with the grizzly bear being included within this species. This example also illustrates the fact that formal taxonomic status is not always a good indicator of population boundaries. Many of the taxonomic names still in use are holdovers from taxonomic studies done before population thinking had a major impact upon systematics [Mayr, 1982]. As a consequence, many subspecific and some specific (eg, grizzly bears) designations are of dubious validity.

A second type of evidence used to define natural population boundaries stems from biogeography. If two populations can live together or in contact in nature without interbreeding or introgressing, they should be regarded as distinct biological entities. The sculpin example discussed earlier is an illustration of this type of study.

Another common biogeographic pattern is one in which most of the species live in a central, continuous range with peripheral isolates surrounding it (eg, a mainland species coupled with island populations). Many of these isolates show local differentiation, and some had been given subspecific status in the past. However, in many cases this differentiation is due primarily to genetic drift (random genetic changes induced by the small number of animals in the peripheral populations) and does not involve local adaptation or intrinsic coadaptation. For example, the collared lizard (*Crotaphytus collaris*) is found in the American Southwest, but peripheral isolates are found in the rocky glades of the Ozarks of Missouri. About 15 glade populations have been studied so far, and each is genetically unique (Davis and Templeton, unpublished). If this pattern persists, there will be literally thousands of genetically differentiated populations of this lizard in the Ozarks alone. However, the biogeographic pattern of genetic variation among these glade populations suggests random fixation of genes rather than adaptation to local conditions. Consequently, in an ongoing release program of this lizard into previously disturbed glades that are currently unoccupied, no effort is being made to prevent hybridization. Indeed, the release program deliberately maximizes hybridization in order to increase the level of genetic variability in the released populations and to provide genetic markers for monitoring reproductive success [Templeton, in press].

A third biogeographic pattern is one in which two populations are separated for the most part in nature, but contact does occur in some areas, often with the production of a geographically restricted hybrid zone. Endler [1977] and Barton and Hewitt [1981] review a large number of such situations. Although hybridization is occurring in nature in these cases, the restricted nature of the hybrid zone is often indicative of local or intrinsic adaptive differences between the populations. In a few cases it is even possible to see the effects of an outbreeding depression in nature [Woodruff, 1979]. Hence, they should be regarded as distinct and separate biological entities.

A simple type of biogeographic information that is often a rough indicator of the potential for outbreeding depression is the geographic distance separating the birthplaces of potential mates or the populations from which they were derived [eg, Oliver, 1972; Price and Waser, 1979]. In species with wide dispersal relative to the distances separating breeding groups of individuals, outbreeding depression is unlikely to occur except over vast distances. In less panmictic species with more localized dispersal, the probability of outbreeding depression would be higher, so that tests for incompatibility (to be discussed shortly) might be useful in designing a management program. Because of this relationship between geographic distance and the potential for outbreeding depression, it would probably be wise to choose animals (whether they are wild animals for enriching a captive population or captive animals for enriching a wild population) from the same geographic region where a source population occurred, if possible [eg, Shields, 1983].

Although it is ideal to have information on the natural population, this information often does not exist nor is likely to be forthcoming. In this case, other methods of detection can be used, although ideally even these methods would be used in conjunction with studies on natural populations.

The first method is to allow the animals to identify their own natural boundaries through their mating behavior. If animals are observed in a mate choice situation, sometimes their mating choices can define the proper biological groupings. For

example, Godfrey [1958] demonstrated that bank voles (*Clethrionomys glareolus*) prefer to mate with individuals born on the same island and display a negative correlation between mating preference and the geographical distance separating the birthplaces of potential mates. Similarly, Bateson [1978] has shown that Japanese quail prefer unfamiliar mates but with phenotypic characters similar to those they were reared with. As a final example, Epple and Belcher [1984] have shown that scent marks in the tamarin *Saguinus fuscicollis* differ in the relative concentrations of some compounds between subspecies, and that the animals can readily discriminate between the markings of their own and other subspecies. However, if no mating preference is observed, it does not mean that different coadapted populations do not exist. There are many examples of incompatible populations displaying little or no mating isolation, particularly when brought into a captive situation [eg, see Mayr, 1970; Cade, 1983].

The second method is based upon a pedigree analysis of the captive herd. As mentioned earlier, one manifestation of coadapted complexes is an outbreeding depression. If this depression occurs in the F_1 (often as F_1 sterility), it is easily and rapidly detected in the captive population. However, the outbreeding depression is often delayed into the F_2 and backcross generations. In such cases, a confoundment can arise between outbreeding depression and inbreeding depression because it is common in many zoo populations for the F_2 or backcross generation to also be the first generation experiencing inbreeding. Fortunately, the confoundment is often not complete. For example, F_2 animals at risk for an outbreeding depression can be produced both by breeding full sib F_1 animals, in which case their inbreeding coefficient is 0.25, or by crossing unrelated F_1 individuals, in which case their inbreeding coefficient is 0. Alternatively, F_2 individuals produced by a full sib cross and the offspring of a parent-offspring mating both have an inbreeding coefficient of 0.25, yet a delayed outbreeding depression should be much more severe in an F_2 cross than in a parent-offspring backcross. These various mating types indicate that the inbreeding level can be variable for animals at risk for an outbreeding depression, and alternatively, the outbreeding depression risk can be variable for a fixed level of inbreeding. Hence, it is statistically possible to separate the effects of inbreeding versus outbreeding when examining a fitness depression in a captive population. The details of such a pedigree analysis for the detection of outbreeding vs. inbreeding depression are given in Templeton and Read [1984], who showed that a viability depression in a captive herd of Speke's gazelle was due to inbreeding rather than outbreeding depression. Ralls and Ballou (personal communication) used the methodologies developed by Templeton and Read [1984] to examine the cause of fitness depression in several other captive populations of mammals. In many cases, no resolution between inbreeding and outbreeding depression was possible because the appropriate diversity of crosses was lacking, but in all cases where resolution was possible and the sample sizes allowed statistical significance, the inference was one of inbreeding depression.

This resolution is an important one for the animal manager. If one is dealing with an outbreeding depression, it is important to stop the incompatible outcrossing and redefine the population units to be managed. If one is dealing with an inbreeding depression, two major options exist. First, in some cases it is impossible to avoid or significantly lower the amount of inbreeding due to a restricted availability of unrelated animals. Such was the case with the Speke's gazelle, so Templeton and Read

[1984] initiated a breeding program to adapt the herd to inbreeding in order to eliminate the inbreeding depression. The breeding program outlined by Templeton and Read [1984] actively promotes extensive recombination between all ancestral lines. This is effective in eliminating an inbreeding depression [Templeton and Read, 1984], but would be a disaster if the original depression had been caused by outbreeding. The other option in dealing with an inbreeding depression is to manage the inbreeding to low levels by bringing unrelated or distantly related animals into the herd, given that such animals are available. For example, Templeton and Read (unpublished data) detected a significant inbreeding depression in the gerenuk. Unlike the Speke's gazelle, many unrelated animals existed at other zoos, so breeding exchanges were arranged to bring unrelated animals into the St. Louis herd. This second option also promotes more outbreeding and therefore could have a negative impact on herd management if the original depression had been due to outbreeding rather than inbreeding.

Because the management goals are exactly the opposite for dealing with inbreeding versus outbreeding depressions, it is important that this distinction be made as early as possible after a depression is first observed. One advantage of the pedigree approach is that it requires no a priori knowledge of the status of the natural population nor of the origins of the import animals. However, there are two major limitations to this technique. First, the depression is often measured only through a few fitness components such as birth weight or viability. However, the outbreeding or inbreeding depression may be occurring in unmeasured fitness components such as spontaneous abortion rates or fertility. Consequently, the analysis is limited to determining the cause of a depression in some measured fitness component rather than detecting all possible outbreeding (or inbreeding) depressions. The second limitation is statistical power. The experience of Templeton and Read [1984] indicates that about 20 matings distributed over a variety of mating-type categories is minimally needed to insure sufficient power. For many species, doing the appropriate number and kinds of crosses may require a considerable investment in time, money, or space. However, if a depression is encountered and it is deemed impractical to perform the appropriate crosses, the results of Templeton and Read [1984] and of Ralls and Ballou (unpublished) would indicate that it would be best to manage the herd as if the depression were caused by inbreeding. However, many more examples need to be analyzed to strengthen this trend of inbreeding depressions being much more common than outbreeding depressions in captive mammalian populations. Hence, it is best to perform the appropriate crosses, if at all possible.

Sometimes a breeding program is begun in a total absence of information concerning the founders and with a neglect of the possibilities of either inbreeding or outbreeding depressions. Nevertheless, if a depression is detected in the F_2 or backcross generations of the breeding program, the herd manager can often perform the pedigree analysis using the information gained from crosses already made or by supplementing the existing crosses with crosses of other types in order to generate the diversity of mating types needed to resolve inbreeding versus outbreeding depressions. For this reason, it is very important for all herd managers to keep full and accurate records on the reproductive history of the herd, including stillbirths and birth weights if possible.

An alternative to the pedigree analysis that also assumes no knowledge of the natural population is a direct genetic screening of the captive animals. First, the

karyotypes of the animals could be determined to see if they differ in chromosome number or structure, as was done in the case of owl monkeys mentioned earlier [de Boer, 1982]. If they differ in karyotype, the possibility of a karyotypic coadaptation exists. However, it is known that many species can be variable for karyotype without this variation affecting fitness [Templeton, 1981], so the detection of karyotypic differences only indicates the possibility of an outbreeding depression. Another type of genetic screen involves an assessment of isozyme or DNA sequence differences. In general, if there are large genetic differences between two populations, it becomes increasingly likely that outbreeding depressions will be encountered and that the two populations represent distinct natural units. As with the karyotypic differences, this type of data is suggestive rather than conclusive because there are examples of populations with large genetic distances having no observed outbreeding depression [Ferguson, 1980] and examples of other populations being virtually identical as assayed by genetic screens yet displaying considerable outbreeding depression [Templeton, 1981]. Consequently, genetic and karyotypic screens should be used to identify possible natural population groupings that can then be investigated more directly using pedigree analyses or studies on natural populations.

It is also important to keep in mind that the results of these genetic screens may sometimes be discordant with divergence in external morphological characters among the same groups. For example, the northern and southern races of white rhinoceros have been considered trivially distinct. However, a comparison of mitochondrial DNA restriction site maps of northern and southern white rhinoceros with the genetically distinct black rhinoceros suggests that the divergence of black and white rhinos occurred 3.5 million years ago and that the two races of white rhino diverged 2 million years ago [George et al, 1983]. The extent of this mitochondrial DNA differentiation is fully consistent with their classification as subspecies. Along similar lines, the captive population of the East African Soemmering's gazelles are remarkably diverse karyotypically, with three separate Robertsonian rearrangements and chromosome numbers varying from 34 to 39 [Benirschke et al, in press]. It is not clear at present if this karyotypic diversity is due to cryptic population boundaries within the species' distribution or due to undocumented hybridization of wild-caught stock with other gazelles prior to the establishment of breeding groups in North American zoos. In any case, the lack of reproductive success of breeding groups in captivity underscores the merits of genetic screenings of founder stock for captive breeding programs [Ryder et al, 1981; Ryder, in press].

DEALING WITH OUTBREEDING DEPRESSIONS

Given that an outbreeding depression has been encountered, what should the herd manager do? Basically the existence of an outbreeding depression indicates that the population can be subdivided into two or more biologically meaningful entities. Hence, the first action should be to identify which individual animals should be placed in the same subdivision. Thereafter, each subdivision should be treated as a separate breeding population as, for example, has been recommended for the various chromosomal races of owl monkeys [de Boer, 1982].

However, suppose that studies on natural populations and/or pedigree analyses indicate that two groups of animals are fully compatible and display no outcrossing depression. In this case, it would be appropriate to integrate the two populations into a single breeding program. However, if the two populations represent different formal subspecies, should the populations remain separated or not? As mentioned earlier,

some subspecific designations were assigned before modern population-thinking had been integrated with taxonomic studies. As a consequence, some designated subspecies are of dubious biological reality. Hence, if a contradiction exists between modern biological data of the sort outlined in this paper and formal taxonomic status, precedence should be given to the biological data. This is particularly important because a large number of species are currently endangered while the capacity of zoos to serve as "arks" is severely limited. Hence, this precious, limited resource of zoo space should not be wasted preserving "subspecies" that have no or little biological significance according to modern studies. If the modern biological evidence is absent or ambiguous, it is still best to treat the subspecies as distinct entities until their status can be resolved.

If a subspecies is judged to be artificial, it is probably best to cross it into other herds of the same species. The reason is that each founding animal represents a potential source of new genetic variants that should not be lost. Other papers from this workshop explain in more detail why maximizing genetic variation within reasonable constraints is the primary goal of any breeding program involving an endangered species. The exact details of how such pseudo-subspecies should be integrated into a single herd is beyond the scope of this article because specific recommendations will have to be formulated on a case-by-case basis.

CONCLUSIONS

1. Coadapted complexes can occur because of either local adaptation and/or intrinsic adaptation to the state of other genes or chromosomes.

2. Locally adapted and coadapted complexes can lead to difficulties in a breeding program by creating an outbreeding depression and to failures in reintroduction programs because of maladaptation to the local environment.

3. Locally adapted and coadapted complexes are ideally detected through studies on natural populations, but can be detected in a captive population as well through observations on mate choice, pedigree analysis of the causes of fitness depression, and genetic and karyotypic surveys.

4. It is important to distinguish between inbreeding and outbreeding depression because the management options for dealing with these two types of genetic depression are mutually incompatible. Initial results indicate that inbreeding depression is the more common phenomenon.

5. If a population is judged to be subdivided into two or more differently coadapted entities, the boundaries of the population must be redefined in order to prevent hybridization between the subdivisions.

6. Formal subspecific designations are not always good indicators of biologically meaningful subdivisions, so if a contradiction exists between formal subspecific status and modern studies indicating that the subspecies are of little or no significance, the subspecific designations should be ignored in managing the herd so as to maximize genetic variability and to efficiently utilize the space available in zoos for breeding endangered populations.

ACKNOWLEDGMENTS

This paper arose out of a panel discussion by the same name that was held during the workshop on Genetic Management of Captive Populations at Front Royal,

VA on August 7–10, 1984. Although the authorship of this paper is limited to the panel members, many of the ideas incorporated into this paper stemmed from the general discussion that occurred during the workshop. Hence, we would like to thank all of the participants at the workshop, and we especially appreciate the efforts of Jonathan Ballou and Katherine Ralls in organizing the workshop. We also wish to thank Oliver Ryder and two anonymous reviewers for their valuable comments and suggestions on an earlier draft of this paper.

REFERENCES

- Baker, R.J.; Chesser, R.K.; Koop, B.F., Hoyt, R.A. Adaptive nature of chromosomal rearrangement: Differential fitness in pocket gophers. *GENETICA* 61:161–164, 1983.
- Barton, N.H.; Hewitt, G.M. Hybrid zones and speciation, pp. 109–145 in *EVOLUTION AND SPECIATION*. W.R. Atchley; D.S. Woodruff, eds. Cambridge, Cambridge University Press, 1981.
- Bateson, P.P.G. Sexual imprinting and optimal outbreeding. *NATURE* 273:659–660, 1978.
- Benirschke, K. The impact of research on the propagation of endangered species in zoos, pp. 402–413 in *GENETICS AND CONSERVATION*. C.M. Schonewald-Cox; S.M. Chambers; B. MacBryde; L. Thomas, eds. Menlo Park, California, Benjamin/Cummings, 1983.
- Benirschke, K.; Kumamoto, A.T.; Olsen, J.H.; Williams, M.M.; Oosterhuis, J. On the chromosomes of *Gazella soemmerringi* (Cretzschmar, 1926). *ZEITSCHRIFT FÜR SAUGETIERKUNDE*, in press.
- Brcic, D. Heterosis and the integration of the genotype in geographical populations of *Drosophila pseudoobscura*. *GENETICS* 39:77–88, 1954.
- Cade, T.J. Hybridization and gene exchange among birds in relation to conservation, pp. 288–309 in *GENETICS AND CONSERVATION*. C.M. Schonewald-Cox; S.M. Chambers; B. MacBryde; L. Thomas, eds. Menlo Park, California, Benjamin/Cummings, 1983.
- Carson, H.L.; Templeton, A.R. Genetic revolutions in relation to speciation phenomena: A debate. *ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS* 15:97–131, 1984.
- Cicmanec, J.C.; Campbell, A.K. Breeding the owl monkey (*Aotus trivirgatus*) in a laboratory environment. *LABORATORY ANIMAL SCIENCE* 27:517, 1977.
- Christensen, K.; Pedersen, H. Variation in chromosome number in the blue fox (*Alopex lagopus*) and its effects on fertility. *HEREDITAS* 97:211–215, 1982.
- De Boer, L.E.M. Karyological problems in breeding owl monkeys, *Aotus trivirgatus*. *INTERNATIONAL ZOO YEARBOOK* 22:119–124, 1982.
- Dobzhansky, T. Genetics of natural populations. XVIII. Experiments on chromosomes of *Drosophila pseudoobscura* from different geographical regions. *GENETICS* 33:588–602, 1948.
- Endler, J.A. *GEOGRAPHIC VARIATION, SPECIATION, AND CLINES*. Princeton, NJ, Princeton University Press, 1977.
- Epple, G.; Belcher, A. Chemische Untersuchungen der Zusammensetzung der Duftmarken einiger Krallenaffenarten (Callitrichidae), pp. 12 in *HAUPTVERS. DEUTSCHE GES. F. SAUGETIERKUNDE*. Berlin, Parey, 1984.
- Ferguson, A. *BIOCHEMICAL SYSTEMATICS AND EVOLUTION*. New York, NY, John Wiley & Sons, 1980.
- Frankham, R. Contributions of *Drosophila* research to quantitative genetics and animal breeding. 2ND WORLD CONGRESS ON GENETICS APPLIED TO LIVESTOCK PRODUCTION 5:43–56, 1982.
- George, M.; Puentes, L.A.; Ryder, O.A. Genetische Unterscheide Zwischen den Unterarten des Breitmanlnashorns, pp. 60–67 in *INTERNATIONAL STUDBOOK OF AFRICAN RHINOS*. H.G. Klos; R. Frese, eds. Berlin, Zoological Garden, 1983.
- Godfrey, J. The origin of sexual isolation between bank voles. *PROCEEDINGS OF THE ROYAL PHILOSOPHICAL SOCIETY OF EDINBURGH* 27:47–55, 1958.
- Greig, J.C. Principles of genetic conservation in relation to wildlife management in Southern Africa. *SOUTH AFRICAN JOURNAL OF WILDLIFE RESEARCH* 9:57–78, 1979.
- Hall, E.R. *THE MAMMALS OF NORTH AMERICA*, Vol. II, 2nd Edition. New York, NY, John Wiley & Sons, 1981.
- Hedrick, P.; Jain, S.; Holden, L. Multilocus systems in evolution. *EVOLUTIONARY BIOLOGY* 11:101–183, 1978.
- Mayr, E. *POPULATIONS, SPECIES, AND EVOLUTION*. Cambridge, MA, Belknap Press, 1970.
- Mayr, E. *THE GROWTH OF BIOLOGICAL THOUGHT: DIVERSITY, EVOLUTION, AND INHERITANCE*. Cambridge, MA, Belknap Press, 1982.
- McFarquhar, A.M.; Robertson, F.W. The lack of evidence for coadaptation in crosses between races of *Drosophila subobscura* Coll. *GENETICAL RESEARCH* 4:104–131, 1963.
- Oliver, C.G. Genetic and phenotypic differentiation and geographic distance in four species of Lepidoptera. *EVOLUTION* 26:227–241, 1972.
- Patton, J.C.; Baker, R.J.; Glenoways, H.H. Ap-

- parent chromosomal heterosis in a fossorial mammal. *AMERICAN NATURALIST* 116:143-146, 1980.
- Price, M.V.; Waser, N.M. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *NATURE* 277:294-297, 1979.
- Richardson, R.H.; Kojima, K. The kinds of genetic variability in relation to selection responses in *Drosophila* fecundity. *GENETICS* 52:583-598, 1965.
- Ryder, O.A. Genetic investigations: Tools for supporting breeding program goals. *INTERNATIONAL ZOO YEARBOOK* 24/25, in press.
- Ryder, O.A.; Brisbin, P.C.; Bowling, A.T.; Wedemeyer, E.A. Monitoring genetic variation in endangered species, pp. 417-424 in *EVOLUTION TODAY*. G.G.E. Scudder; J.L. Reveal, eds. Pittsburgh, Hunt. Institute for Bot. Document., 1981.
- Singh, B.N. The lack of evidence for coadaptation in geographic populations of *Drosophila ananassai*. *GENETICA* 43:582-588, 1972.
- Shields, W.M. *PHILOPATRY, INBREEDING, AND THE EVOLUTION OF SEX*. Albany, NY, State University of New York Press, 1982.
- Shields, W.M. Genetic considerations in the management of the wolf and other large vertebrates: An alternative view, pp. 90-92 in *WOLVES IN CANADA AND ALASKA; THEIR STATUS, BIOLOGY AND MANAGEMENT*. L.N. CARBYN, ed. Edmonton, Alberta, Canadian Wildlife Service Report, Series No. 45, 1983.
- Templeton, A.R. Mechanisms of speciation—a population genetic approach. *ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS* 12:32-48, 1981.
- Templeton, A.R. Adaptation and the integration of evolutionary forces, pp. 15-31 in *PERSPECTIVES ON EVOLUTION*. R. Milkman, ed. Sunderland, MA, Sinauer, 1982.
- Templeton, A.R. Coadaptation and outbreeding depression in *CONSERVATION BIOLOGY: SCIENCE OF DIVERSITY*. M. Soule; D. Hales, eds., Sunderland, MA, Sinauer, in press.
- Templeton, A.R.; Read, B. Factors eliminating inbreeding depression in a captive herd of Speke's gazelle. *ZOO BIOLOGY* 3:177-199, 1984.
- Templeton, A.R.; Sing, C.F.; Brokaw, B. The unit of selection in *Drosophila mercatorum*. I. The interaction of selection and meiosis in parthenogenetic strains. *GENETICS* 82:349-376, 1976.
- Vosselman, L. Fitness of a translocation homozygote in cage experiments with the onion fly, *Hydomya antiqua* (Meigen). *THEORETICAL AND APPLIED GENETICS* 58:79-85, 1980.
- Wallace, B.; King, J.C.; Madder, C.V.; Kaufmann, B.; McGunnigle, E.C. An analysis of variability arising through recombination. *GENETICS* 38:272-307, 1953.
- White, M.J.D. *MODES OF SPECIATION*. San Francisco, CA, W.H. Freeman & Company, 1978.
- Woodruff, D.S. Postmating reproductive isolation in *Pseudophryne* and the evolutionary significance of hybrid zones. *SCIENCE* 203:561-563, 1979.
- Zimmerman, E.G.; Wooten, M.C. Allozymic variation and natural hybridization in sculpins, *Cottus confusus* and *Cottus cognatus*. *BIOCHEMICAL SYSTEMATICS AND ECOLOGY* 9:341-346, 1981.