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Population  
Management  
for Survival  
and Recovery

Analytical Methods and  
Strategies in Small  
Population Conservation



J. D. Ballou  
M. Gilpin and  
T. J. Foose, editors



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# 13

## Monitoring Quantitative Genetic Variation and Evolution in Captive Populations



Stevan J. Arnold

This essay focuses on the genetic aspects of captive management that might ultimately affect the success of reintroduction. Many other aspects influencing the success of reintroduction have recently been discussed by Griffith et al. (1989) and Kleiman (1989). The first consideration is whether the reintroduced population will be able to respond to selection pressures in the wild. Response to selection depends on both the selection that is imposed and the nature and amount of genetic variation in the population (Fisher 1958; Lewontin 1974; Falconer 1981). What types of genetic variation are likely to be important to the population's fate and how can these be monitored and enhanced? Second, the fate of the population may depend on how different the average captive



animal has become relative to the average wild progenitor. Adaptation to the captive regime may mean maladaptation in the wild. What kinds of genetic and environmental modifications can be anticipated under captive propagation and how can they be minimized?

### MONITORING GENETIC VARIATION IN CAPTIVE POPULATIONS

#### What Kinds of Genetic Variation Should Be Monitored?

Not all genetic variation will be equally important in determining whether the reintroduced population can respond to selection in the wild. Genetic variation for selectively neutral traits, for example, will have no bearing on the population's fate. For this reason, most allozyme variation, monitored by protein electrophoresis, has no direct bearing on possible responses to selection, although it may have an indirect bearing. If the population lacks electrophoretic variation, it may have recently gone through a bottleneck and therefore, may also lack genetic variation for adaptively important traits. Abundant electrophoretic variation, however, does not mean abundant genetic variation for the size of the camel's hump, the cheetah's fleetness, or the panda's dentition.

Once the decision is made to monitor genetic variation in traits likely to be important to the population in nature, the problem of choosing them remains. One approach would be to focus on traits likely to be important to any population. The HLA loci are a case in point. The liability here is the potential to miss traits that make tigers different from lions, or dogs different from wolves. Another approach would be to monitor a large number of traits, chosen on largely arbitrary grounds, in the hope that they might be indicators of variation in important traits or that there might be some important traits in the sample. This approach seems only slightly better than focusing on an arbitrary set of allozymes. A third approach, the one that is discussed in this essay, is to tailor the choice of traits to the systematics and ecology of the taxon in question. Even this approach is likely to entail a large amount of guesswork.

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Ecological and systematic studies can be used to suggest the choice of traits for genetic monitoring. Consider three examples. Golden cats (*Felis aurata*) show much geographic variation in their coloration pattern (Kingdon 1977), suggesting that matching the local background plays an important role in prey capture and predator evasion. Lions (*Panthera leo*) displayed pronounced geographic variation in size when they had a nearly world-wide distribution at the end of the Pleistocene (Kurtén and Anderson 1980). Thus, the ability to adapt in body size has apparently been important in the history of lions, and so it is likely to be important in their future. Garter snakes (*Thamnophis elegans*) show polymorphisms and geographic variation in feeding reactions to prey (Arnold 1981). Consequently, genetic variation in feeding reactions is likely to be crucial for adaptation to local ecological circumstances. Pelage and size of felids, or feeding reactions in snakes, are easily scored and could be routinely monitored in captive populations.

Environmental differences between long-term propagation sites and reintroduction sites may suggest traits for monitoring. For example, at the reintroduction site, the population will commonly face a greater variety of predators and greater predation intensity than it did at the propagation site. Does the population show genetic variation for antipredator tactics (Arnold and Bennett 1984; Brodie 1989, 1993)?

The feasibility of monitoring quantitative genetic variation in captive colonies has already been established in the case of primates and rodents. Skeletal remains from rhesus macaques (*Macaca mulatta*) in the Cayo Santiago colony have been systematically preserved over a twenty-five-year period (Buettner-Janusch et al. 1974; Sade et al. 1977). This material was used by Cheverud (1982a, b) to assess the genetic variation in a large number of cranial and postcranial traits. In a similar program, the carcasses of animals dying natural deaths were regularly frozen in a colony of two species of tamarins (*Saguinus fuscicollis* and *S. oedipus*). The skeletal remains of a few hundred animals were later prepared and used in studies of quantitative inheritance (Cheverud 1994; Cheverud et al. 1994). As a third example, skulls and museum skins were routinely prepared from animals in Lee R. Dice's White-footed Mouse (*Peromyscus*) colony at the University of Michigan. Lofsvold (1986, 1988) used that material in comparative studies of morphological inheritance.

### Monitoring Genetic Variation in Polygenic Traits

The individual traits that make or break the population in its struggle for reestablishment are likely to be affected by many genes (Wright 1968). In such polygenic or multifactorial traits, most genes have such small phenotypic effects that detection is difficult. Despite the difficulty of assaying individual genes (as in protein electrophoresis), the ensemble properties of the many genes that affect a particular trait can be detected (Fisher 1918) by quantifying the phenotypic resemblance between parents and offspring. The essential points are perhaps easiest to see with hypothetical data.

The resemblance between parents and their offspring reflects genetic variance and covariance if there are no confounding environmental sources of resemblance. With hypothetical data, such confounding is removed by assertion, but in the real world it can be controlled by experimental design (e.g., randomization of rearing environments, cross-fostering). Suppose a particular phenotypic attribute—say, skull width—is scored in a set of parents and their offspring. The trait must be scored at the same age in all individuals or at any age after the skull has stopped growing. If the average skull width of each set of siblings is plotted against the average skull width of their parents, any of the relationships shown in figure 13.1 might be obtained. No resemblance is an indication of no genetic variance in skull width; a strong resemblance is a sign of abundant genetic variance. The significance of genetic variance in skull width is that it enables one to predict the genetic consequences of selection on skull width (figure 13.2).

The resemblance between different attributes can also be examined. To do this, one attribute in offspring (e.g., skull depth) is plotted against a different attribute in parents (e.g., skull width). The cross-resemblance in such a plot is an indication of genetic covariance (figure 13.3) and reflects the influence of particular genes on both traits as well as non-random association between genes (i.e., between genes that affect skull width and those that affect skull depth). The genetic covariance between two traits may be negative (e.g., fig. 13.3, graph A), positive, or zero. The significance of genetic covariance is that it enables one to predict whether selection on one trait will have ramifications on other traits (figure 13.3, graph B).

The Mendelian basis of the concepts of genetic variance and covari-



## Monitoring Genetic Variation in Polygenic Traits

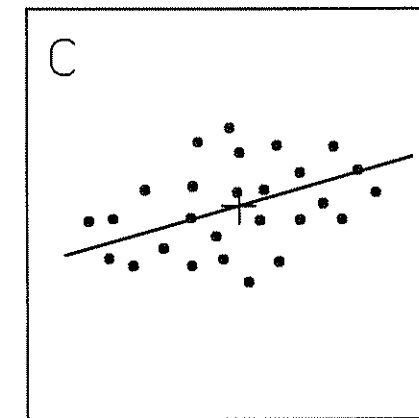
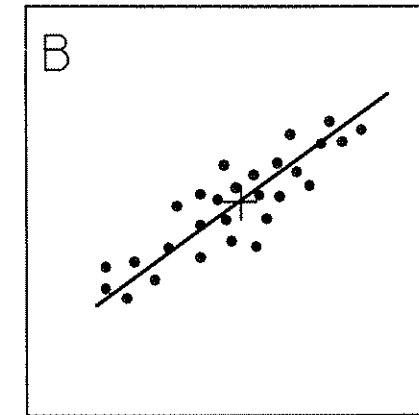
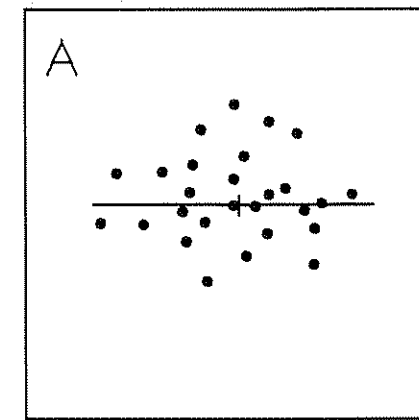
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The Mendelian basis of the concepts of genetic variance and covari-

OFFSPRING SKULL WIDTH



PARENT SKULL WIDTH

Figure 13.1 Resemblance between parents and their offspring is a reflection of additive genetic variance. Hypothetical data are shown in which the average skull width of offspring is plotted against the average skull width of their parents. The least squares regression of offspring values on parental values estimates the standardized genetic variance (heritability) of the trait. The three plots represent different populations with (A) no, (B) abundant, and (C) modest additive genetic variance for skull width.

Figure 13.2 Response to selection is proportional to additive genetic variance. The three panels correspond to the panels in figure 13.1. The horizontal arrows represent the difference between the mean skull width of all potential parents and the mean skull width of parents selected for breeding (open symbols), a measure of the intensity of selection on skull width. (A) With no additive genetic variance, selection produces no shift in the mean of the offspring generation. (B) With abundant additive genetic variance, selection produces a large response in the offspring generation (vertical arrow). (C) With modest additive genetic variance, selection produces a small response in the offspring generation (vertical arrow).

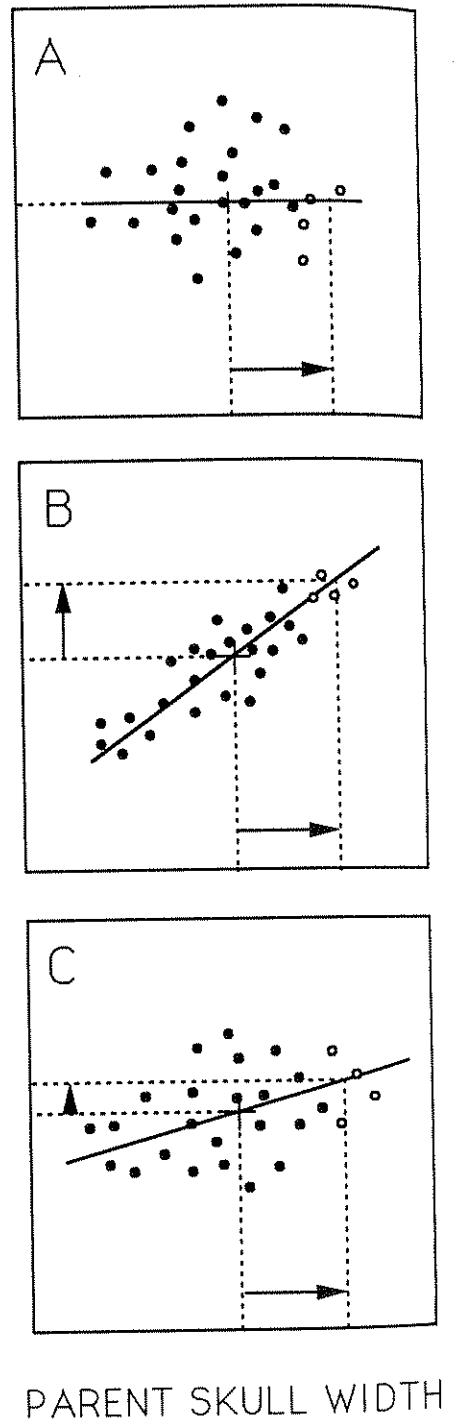


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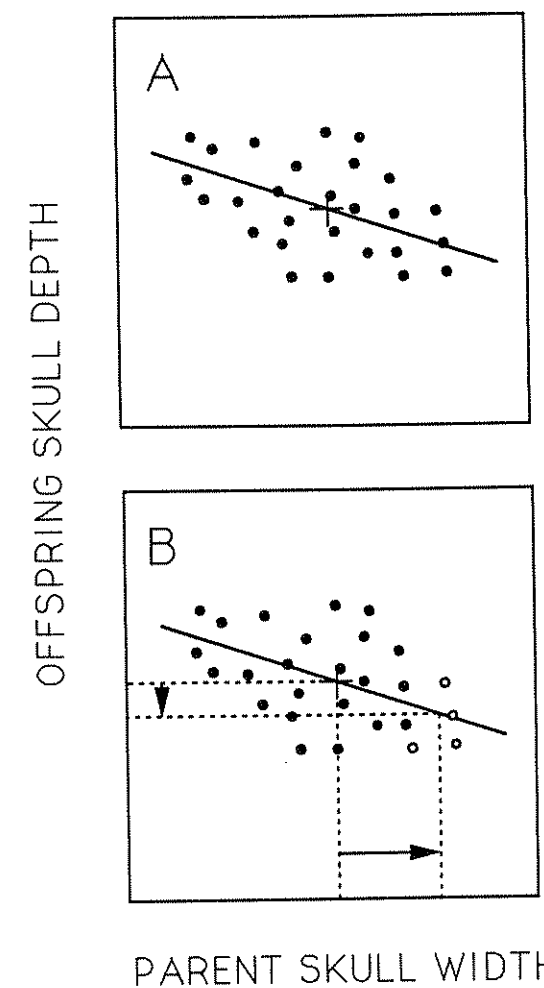
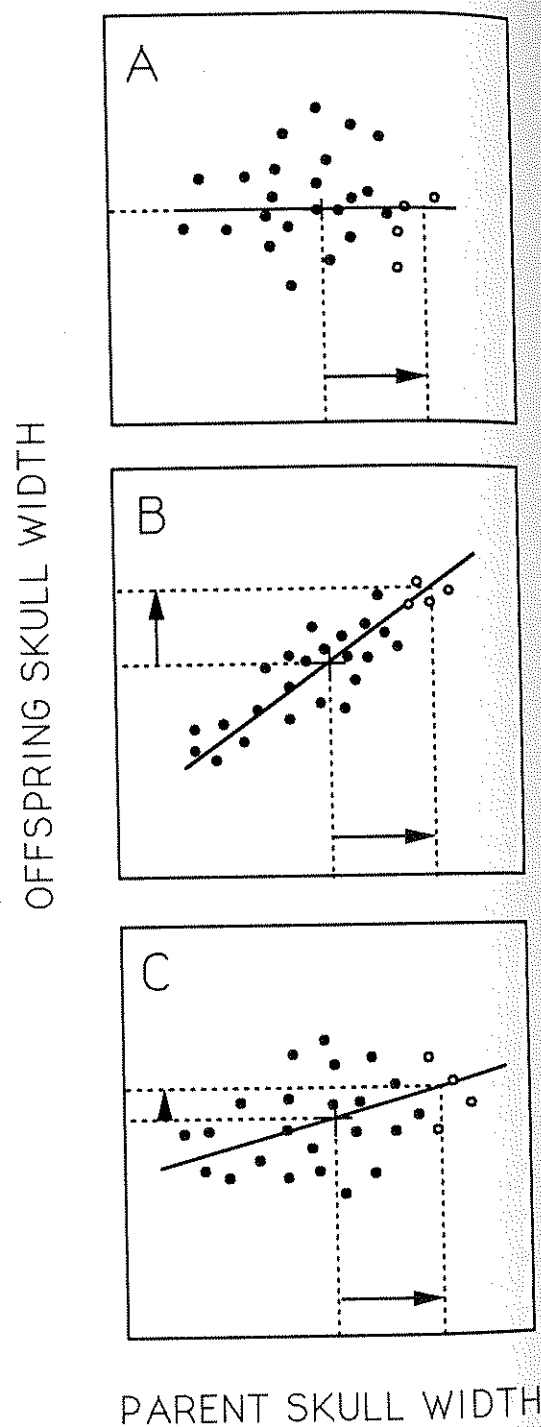


Figure 13.3 One trait can respond to selection on another trait if the two traits are genetically coupled. (A) Association between the average skull depth of offspring and the average skull width of their parents is a sign of genetic coupling (genetic covariance). In the case shown the association is negative. (B) Because skull depth and width are genetically coupled, selection on skull width in the parental generation (horizontal arrow) will shift the mean skull length in the offspring generation (vertical arrow). Because the genetic coupling is negative, selection for increased skull width in the parental generation results in reduced skull depth in the offspring generation.



ance are lucidly discussed by Falconer (1981). Using these two concepts and the concept of selective force shown in figures 13.2 and 13.3, the simultaneous evolution of multiple traits can be modeled (Lande 1979, 1988). Moving from two to three to dozens of traits requires no new concepts. Furthermore, a large body of techniques developed for genetic analysis of economically important traits in commercial animal breeding (Turner and Young 1969) could be applied to captive propagation programs.

The concepts of genetic variance and covariance, and their consequences, are easiest to understand from plots comparing offspring with their parents, but these genetic parameters can be estimated from other combinations of relatives (e.g., sets of full sibs, sets of half sibs, etc.). Some kinds of relationships give much better estimates of genetic variance and covariance than others (e.g., parent-offspring data are usually better than just full-sib data). The estimation theory was developed by Kempthorne (1954) and Cockerham (1954, 1963), building on Fisher's seminal 1918 paper, and it is reviewed by Falconer (1981). Complications arising from maternal effects have been recently discussed by Lande and Price (1989) and Kirkpatrick and Lande (1989, 1992). Genetic variances and covariances can also be estimated from pedigrees if the scores of polygenic traits are known for all or most individuals. For overviews of theory and methodology see Barton and Turelli (1989) and Arnold (1992, 1994).

It is difficult to say how many sets of relatives will be required to estimate genetic variances and covariances because standard errors of these parameters depend on the magnitude of the parameters themselves. Small genetic variances have large standard errors; large genetic variances have small standard errors. The usual approach in planning a quantitative genetic analysis is to work on a worst-case basis. Suppose that genetic variance is only 10% of the phenotypic variance (10% heritability). How many families would be needed to show that genetic variance is nonzero at the 0.05 level? Robertson (1959a, b) and Falconer (1981) give formulas for solving this and similar problems. Generally speaking, one can expect to need dozens or scores of families to detect heritabilities as low as 10 or 20%. If heritability is as high as 70% (as is often the case for linear dimensions in large mammals), only a couple of dozen families would be needed. On the dark side, if only one or a few offspring are available in each family, hundreds of families may be needed to detect low heritabilities (Klein et al. 1973; Arnold 1994).

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### How Often Should Genetic Variation Be Monitored and When?

Because of the sample sizes needed, it may be possible to estimate genetic variation only periodically, pooling data over several or many generations. In the case of intensively managed, small populations of large vertebrates, traits might be scored from photographs or from records taken at autopsy. Many generations might elapse before records are compiled on, say, a set of fifty parents and their offspring. In animals maintained in larger populations, it may be possible, with appropriate planning, to estimate quantitative genetic variation in any particular generation. In this case, it would be possible to track genetic variation. In either case, however, the crucial juncture for estimation may be the generations that precede reintroduction. If genetic variation should turn out to be discouragingly low, the manager would have the option of supplementing variation by infusion from other captive or wild populations (Lande, essay 14 of this volume).

## EVOLUTION IN CAPTIVE POPULATIONS

### Will the Population Evolve in Response to the Captive Situation?

In experimental studies, it is not uncommon to detect responses to selection after only three or four generations. Furthermore, the response may be sustained over many generations (Robertson 1980). Selection on body size in flour beetles (*Tribolium*) increased the mean by over 17 phenotypic standard deviations over a period of 108 generations (Enfield 1980). In a worst-case scenario, therefore, a population might evolve appreciably in just a few generations of captive propagation. Consistent selection, even if not deliberate, could produce sustained change for a hundred generations or more.

Even more troubling is the possibility that substantial genetic change might occur during the first generation or two of captive management (Briscoe et al. 1992). To the extent that traits (e.g., athletic ability, shyness, and nervousness) are heritable, the population may experience considerable response to the unconscious selection imposed during capture and transport, because these procedures usually involve escapes and mortality at nearly every stage. It is, therefore, easy to imagine that

founders of the captive stock are a biased sample of the native population. In addition, the means of other traits may be shifted by the small sample of founders (Wright 1931, 1948; Lynch and Lande 1993). By chance sampling, the mean of the captive population may drift away from the mean of the wild population. Such changes are usually greatest during the first few generations, when the population is small.

Once the captive population builds in numbers, the propagation regime may impose selective pressures different from those in nature and so induce a steady, but artificial, evolution. Effects of the latter kind are the easiest to anticipate and counteract.

### How to Determine Whether the Captive Population Has Evolved

By monitoring the means of quantitative traits each generation, changes in the captive population can be detected. The evolutionary change might be erratic or progressive. In intensively managed small populations, the best strategy might be to score several traits on every animal. Autopsy is one conspicuous occasion for trait scoring. If the veterinarian or pathologist is unable to do more than routine photography (for coloration traits) and measurement, the skull and other body parts might be frozen for later preparation and scoring. If the population is so large that it is not feasible to score every animal, a sample of even ten to twenty animals per generation would provide considerable statistical power to detect trends.

In light of the possibility that substantial change may occur in the first few generations, it is especially critical to score the traits of founders and their immediate descendants. Since the numbers are likely to be small, perhaps the best policy is to preserve as much of each specimen as is feasible (photographs, skins, skulls, postcranial skeletons, and frozen tissue samples). This could be accomplished at autopsy after natural death without jeopardizing the propagation program. Should genetic change be suspected after several or many generations of propagation, the traits in question could be examined in founders and their immediate descendants.

The wild population of origin is also an important reference in testing for progressive change, so traits might be scored in animals not brought into captivity (e.g., by photography of free-ranging animals or



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by measurement in the course of field work involving capture). Such nondestructive scoring in the wild population is especially important if the taxon is not well represented in museums. Most large research museums maintain a computer inventory of vertebrate holdings and can quickly respond to inquiries.

A shift in the phenotypic mean of the captive population from generation to generation or in relation to the wild progenitor may have environmental as well as genetic causes. Rearing temperature, for example, can have dramatic effects on body proportions in domestic swine (Weaver and Ingram 1969). The usual tests for environmental effects on the mean are either to rear populations in the same environment and then compare means (common garden experiment) or to cross the populations and see if the first and second generations of hybrids meet Mendelian expectations (East 1916; Turesson 1922). Generally, only tests of the first kind will be a feasible supplement to a captive propagation program. A variety of the common garden experiment is to contrast the mean of wild stock during the first few generations in captivity with the mean of long-propagated stock kept under the same environmental conditions during the same time period. Under the environmental effect hypothesis, the phenotypic mean of the wild stock should immediately converge on the mean of the captive stock. Another form of data analysis is to test for shifts in the mean of the captive stock while holding the environment constant or to restrict tests to time blocks within which conditions are constant, or virtually so.

#### What Sorts of Phenotypic Change Might Occur Under Captive Propagation?

*Trends Under Domestication.* The study of domestication provides some expectations about the kinds of change that might accompany captive propagation. Captive propagation with the intent of eventual release should produce less extreme effects than domestication. Nevertheless, a consideration of trends under domestication is illuminating (Darwin 1882). Zeuner (1963), for example, lists the following common trends in domesticated species: (a) smaller size; (b) greater variation in size; (c) coloration altered and more variable; (d) facial part of skull shortened relative to cranial part; (e) limb bones usually shorter

but sometimes longer; f) length of hair changed (shorter or longer); (g) skin more flabby (skin folds characteristic of juveniles retained in adults); (h) smaller relative brain size; (i) reduced musculature (but sometimes hypertrophied); (j) increased docility. This list suggests three generalizations: (1) characters are often favored that would be pathological in nature; (2) growth rates are often affected with resultant change in body proportions; (3) juvenile characters persist in adults. The last two kinds of trends have been studied for many years by researchers at the Russian Academy of Science's Institute of Animal Morphology in Moscow. Scott (1954) stresses the point that an increase in variability among breeds has accompanied the domestication of dogs from wolf ancestors. Some dog breeds are less vocal than wolves, but some are more vocal. The same observation applies to among-breed variation in size, aggressiveness, and many other attributes (Darwin 1882). Domestication seems to have quantitative rather than qualitative effects on behavior, e.g., by changing response thresholds (Ratner and Boice 1975; Price 1984).

In an experimental study of the domestication process in rats (*Rattus norvegicus*), King (1939) and King and Donaldson (1929) founded a laboratory colony from 20 female and 16 male wild-caught rats and then tracked changes in behavior and morphology for 40 generations. After this long period of captive propagation, the colony showed an earlier age of first reproduction in females, longer duration of reproductive life, an increase in adult mass, and an increase in docility. But, even after 40 generations, the colony rats were not as docile as typical laboratory stock. Behavioral change (e.g., increased docility) is a major concern in captive propagation.

*Environmental and Hereditary Wildness.* Wildlife managers often anticipate a loss of wildness during captive propagation. Leopold (1944) defined the general meaning of wildness as "the sum of the various behavior patterns and other inherent adaptations which permit the successful existence of a free population." Wildness is an ensemble of attributes, not a single, unitary characteristic. Rearing conditions can affect some aspects of wildness without affecting others (Galef 1970); an animal or population can be tame in some aspects and still wild in others. The tragedy of tameness (the loss of wildness) is that the population, as well as the individual, may be ill-suited to sustain itself in na-

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ture. A few studies of rearing effects on wildness and of hereditary transmission have been conducted, but we know almost nothing about how wildness promotes fitness in nature or, conversely, how tameness results in maladaptation.

An exception is Leopold's (1944) study of why the release of 14,000 hybrid turkeys in Missouri failed to produce sustaining populations. Leopold compared the behavior of wild and hybrid turkeys (*Meleagris gallopavo*) in the field. He concluded that the failure of hybrid birds could be attributed to their tranquility, early breeding, and the scattering, rather than hiding, response of chicks to the warning note of the hen.

Wild turkeys are wary and shy, which are advantageous characteristics in eluding natural and human enemies. They breed at a favorable season of the year. The hens and young automatically react to danger in ways that are self-protective. Reproductive success is high. Collectively these and associated actions and reactions literally adapt the native wild birds to existence in their ancestral environment. . . . Birds of the domestic strain, on the other hand, are differently adapted. Many of their physiological reactions and psychological characteristics are favorable to existence in the barnyard but many preclude success in the wild. (Leopold 1944)

In studies lacking a field component (such as the ones discussed below), we can only guess about the adaptive significance of wildness.

Studies with rodents indicate that some aspects of wildness can be quickly restored simply by changing rearing conditions. Clark and Galef (1977, 1980, 1981) found that shelter can be important for morphological and behavioral development in rodents. Gerbils (*Meriones unguiculatus*) reared without shelters showed accelerated development, lacked a fear response to novel stimuli, and were easier to handle than gerbils that had access to shelters during rearing. Galef (1970) found that handling during rearing affects some aspects of wildness in wild rats but not others. Rearing wild rats with domesticated mothers had no effect on any aspect of wildness.

Although rearing conditions can have immediate effects on wildness, heredity can have effects as well. Environmental and genetic effects are not mutually exclusive. Most genetic studies of wildness have been con-



ducted with rodents, including the earliest studies in the discipline of behavioral genetics. Yerkes (1913) compared the behavior of domestic and wild-caught rats (*Rattus norvegicus*) as well as the behavior of their first and second generation hybrids by scoring a variety of responses to handling by a human investigator (e.g., biting, teeth gnashing, defecation, etc.).  $F_1$  hybrids were intermediate in behavior but also more variable than either parental population.  $F_2$  hybrids were more docile than  $F_1$ s, but very few  $F_2$ s were as wild as rats in the wild-caught parental population.

Coburn (1922) patterned a study of behavior in mice after Yerkes' study. Here,  $F_1$  hybrids showed intermediate behavior with a mean shifted toward the wild parental population and hardly any mice showing scores typical of domestic parents. Both grandparental types were recovered in the  $F_2$  generation, which showed more variance than the  $F_1$ . Dawson (1932) compared the running speed in wild and domestic mice as well as in first and second generation hybrids.  $F_1$  hybrids resembled wild mice. The expansion of variance in the  $F_2$  generation indicated that at least three segregating factors (genes or blocks of genes) were responsible for the differences between the wild and domestic strains. Selection for slower speed over four generations produced a response, but selection for faster speed did not. The results of these studies suggest polygenic inheritance, sometimes with directional dominance for wildness.

*Change in Fitness Components and Other Traits Due to Inbreeding Depression.* Some degree of inbreeding is inevitable in captive populations because of their small size. Inbreeding has a systematic effect on the means of traits affected by dominant genes; the mean shifts progressively downward (Crow and Kimura 1970; Falconer 1981). This downward shift is known as inbreeding depression. Polygenic traits in which a preponderance of loci show dominance (directional dominance) as well as single-locus traits are susceptible to inbreeding depression. Fitness components (juvenile mortality, longevity, fertility, fecundity) are notoriously prone to inbreeding depression (Darwin 1882; Slatis 1960; Ralls et al. 1979; Falconer 1981; Charlesworth and Charlesworth 1987). Traits that are the immediate determinants of survival and reproductive success are thus prime candidates for monitoring in captive populations, as is any trait showing dominance or directional domi-

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nance. For example, in a survey of genetic literature on activity in mice, Henderson (1986) found that many behaviors (nipple attachment in pups; jumping, running, and pole climbing in older mice) show directional dominance in crosses between strains. Usually  $F_1$  hybrids resemble the more active parental strain. Consequently, on inbreeding a mouse population, we might expect nipple attachment in pups and activity at various ages to decline in succeeding generations.

At present, there is no reliable way to predict which traits (aside from fitness components) are likely to show directional dominance and hence inbreeding depression. One school of thought argues that traits long exposed to directional selection will show directional dominance, whereas traits long under stabilizing selection will not (Mather 1949, 1955). The prediction is based on Fisher's theory of the evolution of dominance, which is still fraught with controversy (Fisher 1928, 1929, 1934; Wright 1929 a-c; Charlesworth 1979). Empirical tests of the directional selection/directional dominance prediction are plagued with failure to actually measure the selection that is being predicted a posteriori from the genetic architecture. The best guide to traits showing directional dominance is the genetic literature in which dominance is directly accessed.

#### How Can Methodical, Unconscious, and Incidental Selection in the Captive Situation Be Minimized?

*Selection in Captivity.* Darwin (1882) distinguished two kinds of artificial selection: methodical and unconscious. Methodical selection prevails when the breeder directs the stock toward some conscious goal. Unconscious selection prevails when the breeder selects the best stock and prevents the worst from breeding, not with the aim of improving the stock, but of simply maintaining it. To these categories we might add a third, namely, incidental selection, to refer to the artificial selection resulting from the captive environment rather than from the direct actions of the propagator. These modes of selection overlap, but the distinctions are useful if they alert the manager to deleterious ongoing selection. Finally, as Darwin (1882) points out, natural selection is not suspended in captivity; it continues to act, either in line with or against the direction of artificial selection.

Minimizing artificial selection is an important goal during captive propagation (Lacy et al., essay 4 of this volume), but one that requires constant vigilance. Methodical selection is worrisome because it holds the threat of gradually shaping the animal into an unnatural form. Even without a stated phenotypic goal for the stock, the threat of methodical selection remains. The stock managers may have their own ideas, for example, of what a Przewalski's horse (*Equus przewalskii*) should look like or how it should behave. A standard strategy in captive breeding programs is to minimize both selection and drift by equalizing family sizes (Lande and Barrowclough 1987; Allendorf 1993; Borlase et al. 1993; Lande, essay 14 of this volume).

Unconscious selection is almost inevitable, since, for example, malformities are bound to arise. Perhaps the safest guideline is to curtail the breeding of only those individuals that would certainly die or fail to breed in nature. The middle ground is the most treacherous. In a large sample of newborn snakes, for example, a few percent will inevitably have slightly kinked vertebral columns. Should these individuals be excluded from the breeding stock? Probably they should since only a small percentage of the newborns are involved, even though it is by no means clear that the trait is heritable. What about variants that are less obviously deleterious, e.g., melanism and other pigment variations, pattern variants, etc.? A good guide here is the natural population. If the variants exist in nature, there may be no reason to weed them out of the captive population. In general, the best practice may be to ask whether a particular form of methodical or unconscious selection, if practiced over a long time period, is likely to transform the population away from the natural phenotype. That natural phenotype, of course, may be variable and polymorphic.

Unconscious selection can arise from the most pragmatic aspects of propagation. Spurway (1955) notes that the practice of breeding just those pairs judged to be in the best sexual condition, with swapping of partners if pairs do not breed, will impose selection for phenotypes that are: (a) the least disturbed by transplantation and human proximity; (b) the least exacting about environmental requirements; (c) the least disturbed by separation from previous partners; (d) the least dependent on social facilitation; (e) the least discriminating in mate choice; and (f) the most stimulating to sexual partners. Many of these differences distinguish domestic strains from their wild ancestors (Lorenz 1940). On the



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morphological side, many of the changes in body proportions associated with domestication (see Zeuner's list, above) may be a consequence of selection for early sexual maturity (Berry 1969). Alteration of developmental timing can have far-reaching consequences on adult form (Alberch et al. 1979), with the captive animal gradually becoming a paedomorph.

The artificiality of caging, food, and social contacts could exert incidental selection. In simple cages, some behaviors are never expressed. Gerbils do not show foot-thumping, a form of social communication, unless provided with tunnels (Clark and Galef 1977). Behaviors that are not expressed may eventually deteriorate because natural selection does not maintain them. Other aspects of captivity may evoke evolutionary change in the direction of adaptation to captivity and maladaptation to the wild. Domestic turkey hens vocalize in response to approaching danger and their chicks disperse. Perhaps this signal-response system has benefits in the barnyard, but in the field it alerts and attracts predators. Wild turkey hens and their chicks crouch and hide in response to danger at a distance (Leopold 1944).

*Countering or Minimizing Artificial Selection.* Could we impose methodical selection to reverse deleterious trends observed in captive stock? In theory yes, but in practice probably not. Genetic coupling between traits presents a serious obstacle in methodical selection. With accurate estimates of the genetic covariances among traits (and their genetic variances), we could, in theory, design a selection protocol to accomplish almost any desired objective; however, the requisite genetic information is unlikely to be available. The more practical and safer alternatives are to reverse the trends by infusion of new stock or by letting natural selection do its work.

Artificial selection can be minimized by implementing a captive breeding program that focuses on maintaining genetic diversity by maximizing effective population size (Lacy et al., essay 4 of this volume). Careful control of which animals breed, with an emphasis on equalizing reproduction among all breeders, will mitigate the effects of methodical and unconscious selection.

Propagation in large natural or seminatural enclosures has the advantage of eliminating some forms of artificial selection while maintaining many forms of natural selection. The most pernicious aspects of me-

thodical, unconscious, and incidental selection arise because breeding is in the hands of the manager and because of the artificiality of the environment. In a population of reasonable size, housed in a sufficiently large enclosure, success in life and in reproduction could be more directly determined by the form and behavior of the animals themselves without the selective hand of the manager. Furthermore, if selection is eliminated, a smaller effective population size is required to maintain genetic variation (Lande, essay 14 of this volume).

### SUMMARY

Genetic variation for phenotypic traits, such as body size, skull shape, or coloration pattern, could be monitored in captive populations in order to determine whether the population could respond to selection in nature and whether genetic variation should be supplemented (e.g., by bringing in additional stock from nature). An arbitrary set of phenotypic traits could be monitored in the hope that representative genetic variation will be assessed. Alternatively, the choice of traits for monitoring could be tailored to the population in question. Traits that are liable to evolution in nature or are ecologically important could be monitored so that the loss of critical kinds of genetic variation can be minimized. Genetic variation can be estimated by assessing the phenotypic resemblance between offspring and parents or between other sets of relatives. A large body of techniques developed for genetic analysis of economically important traits in commercial animal breeding could be applied in captive propagation programs.

In addition to monitoring genetic variation, the phenotypic means of important traits could be scored in each generation to determine whether the captive population is evolving. The results of long-term selection experiments provide some basis for predicting how much evolution might occur per generation. In general, we can expect a captive population to change by only a fraction of a phenotypic standard deviation in each generation. More pronounced evolutionary change, however, might occur during the first few generations in captivity due to the inevitable bottleneck attending establishment of the captive population and to unconscious selection under the new regime in captivity. The litera-

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ture on common evolutionary trends in domesticated species provides some clues about the kinds of traits that are likely to evolve in captivity (e.g., tameness, fatness, etc.). These traits might be included in the monitoring program as well as traits liable to inbreeding depression (e.g., fitness components and behaviors that tend to show directional dominance).

Artificial selection could have the twofold disadvantage of depleting genetic variation and causing unfortunate evolutionary responses. Usually there is not enough genetic information to design a selection program to counteract these evolutionary trends. Furthermore, the captive population is usually so small that measurement of artificial selection becomes imprecise or impossible. Under these circumstances, the best remedy may be to minimize selection as much as possible or, at least, to avoid manifestly artificial selection. This can best be achieved through a captive breeding program that emphasizes the maintenance of genetic variability and equal reproduction. In addition, large natural or semi-natural enclosures have many advantages over small, unnatural enclosures or cages.

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