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Zoo Biology 5:215–232 (1986)

Genetic Monitors of Zoo Populations: Morphological and Electrophoretic Assays

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Zoo populations can be empirically studied and monitored genetically from three distinct and informative prospectives: (1) the careful collection of breeding and pedigree history; (2) biochemical genetic surveys of gene variation from electrophoretic data; and (3) the extent of variation in morphological characters. We present here a summary of the results and conclusions of biochemical genetic surveys performed to date in mammals and indicate those biochemical genetic loci most likely to be informative in management programs. The results of a number of studies of morphological variation (estimated by coefficients of variation or fluctuating asymmetry) as related to the genetic status of biological populations are reviewed. The applications of such measurements to the characterization of the South African cheetah are reviewed briefly with attention to captive vertebrate species. Specific recommendations for the evaluation of captive populations and for the monitoring of breeding programs by using biochemical and morphological characters are proposed.

Key words: morphologic variation, electrophoretic genetic variation, captive population management

INTRODUCTION

The occurrence of deleterious recessive mutations in biological populations is a natural consequence of the evolutionary process which also provides the genetic plasticity necessary for adaptation. Such deleterious mutations are rarely at high frequencies in natural populations, but may become common in small, inbred zoo populations in which heterozygosity is also reduced [Muller, 1950; Wallace, 1968]. For example, the loss of genetic variability following inbreeding is accompanied by numerous congenital abnormalities in man [Cavalli-Sforza and Bodmer, 1971] and by

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

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increased juvenile mortality and decreased fecundity in laboratory animals [Falconer, 1981] and in captive species [Ralls et al, 1979; Ralls and Ballou, 1982a,b; O'Brien et al, 1985]. In natural populations, high heterozygosity is positively associated with growth rate [Singh and Zouros, 1978; Zouros et al, 1980; Pierce and Mitton, 1982; Ledig et al, 1983; Cothran et al, 1983], fecundity [Smith et al, 1975; Johns et al, 1977], body size [Koehn et al, 1973; Boyer, 1974; Garten, 1976; Cothran et al, 1983], and social dominance [Baker and Fox, 1978].

Because of these considerations, a common goal of zoo curators is the avoidance of inbreeding and its resultant genetic homozygosity of deleterious alleles. Such an effort would be facilitated by an a priori assessment of relatedness or an empirical measurement of genetic variability of zoo populations. Although it is not feasible to assess the genetic status of captive individuals with respect to deleterious alleles directly, it is possible to develop an estimate of the extent of genetic variation present in a captive population by using established procedures and principles of population genetics. We suggest two methods that have become common tools in the analyses of populations. Specifically, the extent of genic heterozygosity can be estimated by an electrophoretic survey of allozyme (allelic isozyme) variation. Further, genetic components of phenotypic variation can be determined by morphologic measurements. The use of morphologic and biochemical estimates of genetic variation in a captive population may provide an important adjunct to pedigree, husbandry, nutritional and other management parameters in the establishment and subsequent monitor of captive species. The value of these techniques to the development of captive breeding programs is potentially very great but more electrophoretic and morphologic studies on zoo populations are urgently needed to better establish the relationship of these variables to inbreeding depression. Although neither of these approaches directly samples those specific genes which contribute to inbreeding depression, the results do yield genetic profiles of a population comparable to other populations for which data on mortality, fecundity, and survival are available.

A BIOCHEMICAL ASSAY OF GENETIC VARIABILITY

Allelic variants of soluble enzymes are separated by gel electrophoresis and visualized with histochemical stains. Such variants have been studied for over 20 yr [Lewontin, 1974; Nevo, 1978; Nevo et al, 1984]. During this period, natural populations of over 250 different species of plants and animals have been surveyed for the extent and character of genetic variation. Most of these surveys have revealed abundant genetic variation with frequencies of polymorphic loci (P) ranging from 0.10 to 0.60 and with average heterozygosities (H—the frequency of heterozygous loci in an average individual of the population) ranging from 0.01 to 0.36.

In our laboratory, we have concentrated on mammalian taxa with particular emphasis on the Felidae [O'Brien, 1980; O'Brien et al, 1983, 1985; Newman et al, 1985]. The P and H values of ten feline species were not significantly different from other species (Fig. 1) with one exception, the cheetah. An electrophoretic survey of 55 South African cheetah samples *(Acinonyx jubatus jubatus)* revealed that each animal was homozygous at 52 allozyme loci. A multidisciplinary analysis of the captive cheetah population revealed that they were suffering the consequences of inbreeding as shown by (1) poor breeding success in captivity; (2) a high degree of juvenile mortality in captivity compared to other zoo species; (3) a high frequency of spermatozoal abnormalities in ejaculates; and (4) an extraordinary sensitivity to pathological viruses [O'Brien et al, 1985]. In the case of the cheetah, the allozyme

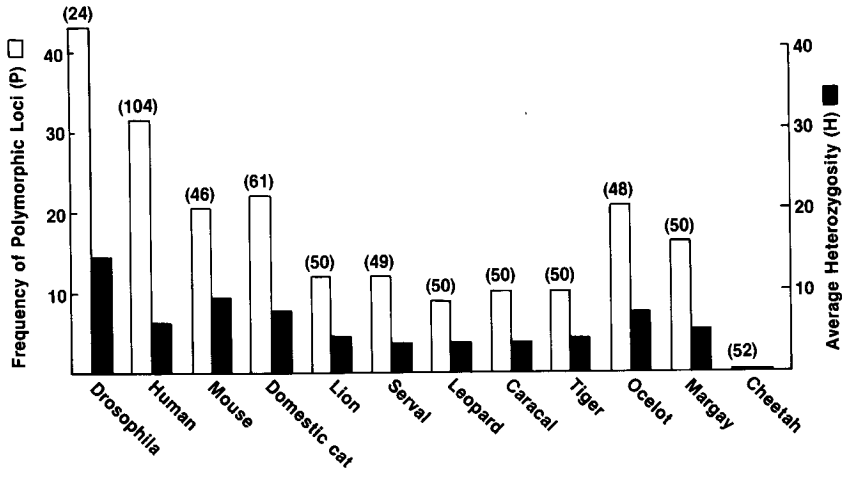

Fig. 1. Proportion of allozyme loci estimated to be polymorphic (P) and the proportion of the genome estimated to be heterozygous (H) in 12 representative species. Number of loci typed in each study is indicated in parenthesis above each histogram. Values are derived from Nevo [1978], Rice et al [1980], O'Brien [1980], Newman et al [1985], and Harris and Hopkinson [1972].

survey was one of the first steps in understanding the breeding problems which had been experienced in management of this species.

Allozyme surveys have been used to identify populations which are genetically variable (eg, lions, domestic cats, see Fig. 1) and genetically deficient (eg, the cheetah). Table 1 presents observed levels of polymorphism and heterozygosity in wild and captive populations of mammals. This table may be used as guideline for evaluating the relative variability of zoo populations with two important caveats. First, lower levels of heterozygosity do not necessarily reflect proportionately higher rates of inbreeding. Second, the species in Table 1 differ in the number and composition of enzyme loci sampled and in the number of individuals composing each survey. The ability to statistically discriminate the level of heterozygosity of wild or captive populations depends on the sample size and number of loci surveyed [Nei, 1978; Hartl, 1980; Avise and Aquadro, 1981]. Thus, considering the small size of most zoo populations, a large number of loci (>40) are required in order to determine whether a particular zoo stock is deficient in enzyme heterozygosity.

In previous surveys, we have examined approximately 50 allozyme loci; however, we now believe that fewer loci are necessary for characterizing a breeding population. The reason is that in mammalian allozyme studies, about 60% of the tested loci are always invariant, while the genetic variation is restricted to the remaining 40% of the enzyme loci [O'Brien et al, 1980; Newman et al, 1985]. We termed this latter group "polymorphic cluster" loci and now routinely sample only these loci for management purposes. The "polymorphic cluster" loci thus far identified in mammals and their incidence of polymorphism in mammalian population genetic surveys are illustrated in Figure 2.

The original description of the polymorphic cluster loci was based on large samples (of loci and individuals) for three species: man, mouse, and cat [O'Brien et al, 1980]. Since the publication of these data, a number of additional mammalian

TABLE 1. Comparison of Electrophoretic Estimates of Biochemical Variation Among Mammalian Species

Species	Common name	Number of Populations	Number of Individuals	Loci	Percent of loci estimated to be polymorphic	Average heterozygosity	References
Primates							
Leontopithecus rosalia	Golden lion tamarin	1	74	47	4	0.010	Forman et al [in press]
Alouatta palliata	Golden mantled howler	1	?	20	5	0.013	Malmgren [1977]
Alouatta seniculus	Red howler	2	196	27	22	0.08	Pope [1983]
Cercopithecus aethiops	Vervet	4	422	32	38	0.034	Turner [1981], Lucotte et al [1982], Kawamoto et al [1982]
Erythrocebus patas	Patas monkey	2	150	33	33	0.072	Lewis [1984], Lucotte and Dandieu [1983]
Macaca mulatta	Rhesus macaque	5	456	39	33	0.102	Kawamoto et al [1982], Melnick et al [1984], Nozawa et al [1977]
Macaca cyclopis	Formosean rock macaque	1	50	29	24	0.041	Nozawa et al [1977]
Macaca radiata	Bonnet macaque	1	7	29	14	0.067	Nozawa et al [1977]
Macaca arctoides[a]	Stump-tailed macaque	1	9	29	21	0.082	Nozawa et al [1977]
Macaca nemestrina	Pig-tailed macaque	1	10	29	21	0.073	Nozawa et al [1977]
Macaca fascicularis	Crab-eating macaque	3	60	29	41	0.069	Kawamoto et al [1982], Nozawa et al [1977]
Macaca fuscata	Japanese macaque	2	1,063	29	37	0.014	Kawamoto et al [1982], Nozawa et al [1977], Nozawa et al [1975], Nozawa et al [1974]
Papio hamadryas	Hamadryas baboon	1	350	36	11	0.032	Shotake et al [1977], Kawamoto et al [1982]
Papio anubis	Olive baboon	3	74	36	13	0.024	Shotake et al [1977], Kawamoto et al [1982]

Rodentia							
Mus musculus	House mouse	9	338	42	34	0.085	Rice et al [1980], Bonhomme et al [1984], Selander et al [1969]
Mus cervicolor	Thai mouse	1	3	42	9	0.032	Bonhomme et al [1984]
Mus minutoides	Ivory coast mouse	1	24	36	27	0.091	Bonhomme et al [1984]
Mus setulosus	Ivory coast mouse	1	3	36	8	0.043	Bonhomme et al [1984]
Mus caroli	Thai mouse	1	12	22	18	0.130	Bonhomme et al [1984]
Mus dunni	Indian mouse	1	5	22	5	0.005	Bonhomme et al [1984]
Cynomys ludovicianus	Marmot	2	592	16	43	0.122	Chesser [1983], Foltz and Hoogland [1983]
Carnivora							
Vulpes vulpes	Red fox	1	282	16	0	0.0	Simonsen [1982]
Ursus americanus	Black bear	6	233	35	18	0.011	Manlove et al [1977]
Thalarctos maritimus	Polar bear	2	52	13	0	0.0	Allendorf et al [1979]
Procyon lotor	Raccoon	23	526	49	33	0.035	Beck and Kennedy [1980], Dew and Kennedy [1980], Forman [1985]
Potos flavus	Kinkajou	1	27	33	39	0.132	Forman [1985]
Mustela erminea	Stoat	1	39	16	0	0.0	Simonsen [1982]
Mustela nivalis	Weasel	1	13	16	0	0.0	Simonsen [1982]
Mustela putorius	Pole cat	1	24	16	0	0.0	Simonsen [1982]
Martes martes	Pine martin	1	2	16	0	0.0	Simonsen [1982]
Martes foina	Beech martin	1	121	16	0	0.0	Simonsen [1982]
Meles meles	Badger	1	5	16	0	0.0	Simonsen [1982]
Felis catus	Domestic cat	1	56	61	21	0.082	O'Brien [1980]
Leopardus pardalis	Ocelot	3	6	48	21	0.072	Newman et al [1985]
Leopardus weidi	Margay	3	11	50	16	0.047	Newman et al [1985]
Caracal caracal	Caracal	2	16	50	10	0.029	Newman et al [1985]
Leptailurus serval	Serval	3	16	49	12	0.033	Newman et al [1985]
Panthera pardus	Leopard	5	18	50	8	0.029	Newman et al [1985]
Panthera leo	Lion	6	42	40	18	0.050	Newman et al [1985]
Panthera tigris	Tiger	5	40	50	10	0.035	Newman et al [1985]
Neofelis nebulosa	Clouded leopard	5	25	49	6	0.023	Newman et al [1985]
Acinonyx jubatus	Cheetah	7	55	52	0	0.0	O'Brien et al [1983, 1985]

(continued)

TABLE 1. Comparison of Electrophoretic Estimates of Biochemical Variation Among Mammalian Species (Continued)

Species	Common name	Number of Populations	Number of Individuals	Loci	Percent of loci estimated to be polymorphic	Average heterozygosity	References
Pinnipedia							
Pusa hispida	Ringed seal	1	82	21	19	0.010	Simonsen et al [1982]
Pagophilus groenlandicus	Harp seal	1	6	21	5	0.007	Simonsen et al [1982]
Cystophora cristata	Hooded seal	1	10	21	5	0.008	Simonsen et al [1982]
Odobenus rosmarus	Walrus	1	102	32	9	0.033	Simonsen et al [1982]
Mirounga angustirostris	N. elephant seal	1	159	24	0	0.0	Bonnell and Selander [1974]
Mirounga leonina	S. elephant seal	2	60	18	27	0.028	McDermid et al [1972], Seal [1971]
Artiodactyla							
Odocoileus virginianus	White-tailed deer	2	783	26	50	0.087	Cameron et al [1978], Baccus et al [1983]
Odocoileus hemionus	Mule deer	1	2	17	11	0.053	Baccus et al [1983]
Capreolus capreolus	Roe deer	2	24	17	11	0.024	Baccus et al [1983], Gyllersten et al [1980]
Cervus elephas	Red deer	2	27	18	16	0.047	Baccus et al [1983], Gyllersten et al [1980]
Cervus canadensis	Elk	3	249	28	7	0.081	Cameron et al [1978], Ryman et al [1977], Baccus et al [1983]
Rangifer tarandus	Reindeer, caribou	2	24	17	5	0.007	Baccus et al [1983]
Alces alces	Moose	2	2,303	22	23	0.019	Ryman et al [1980], Ryman et al [1977], Baccus et al [1983], Gyllersten et al [1980]
Antilocapra americana	Pronghorn	1	5	17	5	.011	Baccus et al [1983]
Bos bison	Buffalo	1	7	17	5	.023	Baccus et al [1983]

[a]Formerly *M. speciosa*.

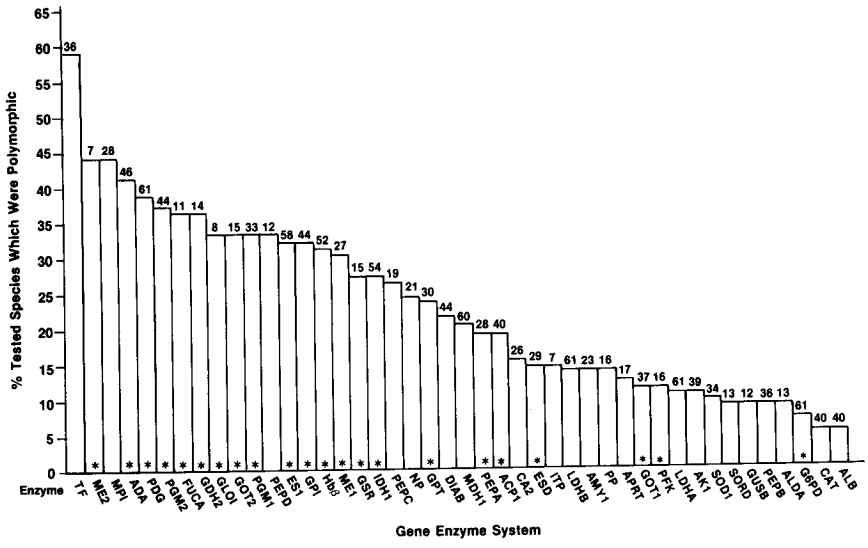

Fig. 2. Polymorphism frequency of homologous enzymes in population genetic surveys of mammals. Data are derived from 149 different populations of 58 mammalian species (see Table 1). The number of populations tested for each enzyme is indicated above each enzyme column. Asterisk indicates those enzymes previously identified as "polymorphic cluster" enzymes by O'Brien et al [1980]. See Harris and Hopkinson [1976] for description and assay methods for each biochemical locus. Abbreviations for allozyme loci are listed in Shows and McAlpine [1984].

species have been genetically surveyed by using similar techniques. We summarize results of genetic estimates from 58 different mammals in Table 1. The studies in this table supplied the basis for our computation of the incidence of polymorphism at individual homologous loci presented in Figure 2. In general, the "polymorphic" cluster loci previously identified appear to be polymorphic in multiple species as predicted, and a few other loci should be added to the group based upon their abundant polymorphism among the 58 mammals examined here.

Before we leave the allozyme disucussion, we should emphasize that these genes are unlikely to be the specific loci which confer the deleterious effects on the population. Rather, they are simply markers which indicate the extent of genetic variability within an individual or population. When the values are inordinately low, and this can be statistically determined [Hartl, 1980], they point to a history of inbreeding and would encourage efforts to introduce distinct genetic lineages to a breeding program. It may be important to reiterate that the ability to statistically discriminate differences in population heterozygosities increases with the sample size and the number of loci surveyed [Nei, 1978; Avise and Aquadro, 1981].

MORPHOLOGICAL ASSAYS OF GENETIC VARIABILITY

Morphological variation has been observed to vary inversely with the extent of genetic variation for a variety of species of plants and animals [Lerner, 1954; Thoday, 1956; Waddington, 1957]. In general, inbred domestic and laboratory animals commonly display increased morphologic variation in a variety of characters compared to their outbred counterparts. Lerner [1954] interpreted this increase in morphological

variation as a reflection of increased homozygosity of polymorphic loci which quantitatively affect development. The abundant heterozygosity of these genes in outbred populations provides a developmental buffering effect which minimizes individual variance. Inbreeding thereby would increase the range of extremes in quantitative characters and disrupt what Lerner [1954] termed "developmental homeostasis." Although the specific genetic bases for such effects are still largely obscure, there is ample evidence which demonstrates an inverse correlation between biochemical and morphological variation. We list these studies and summarize their observations in Table 2. The degree of morphologic variation in these studies was estimated either by comparing the coefficient of variation of multiple traits between populations or by comparing the extent of fluctuating asymmetry of individual traits (the magnitude of differences between left and right measurements of bilateral characters). The coefficient of variation is necessarily a measure of population-wide variability while asymmetry is measured for each trait in each individual. The latter may be compared between individuals or averaged across many individuals as a populational measurement of asymmetry.

To continue our example with the cheetah, we have undertaken a comparative morphological analysis of cranial material from museum specimens of wild-caught cheetahs and three other felid species (leopard, margay, and ocelot) which had appreciable levels of genetic variation (Fig. 1). Sixteen bilateral morphologic measurements were made on the right and left sides of skulls from 33 cheetahs and on approximately 20 individuals from each of the three other cat species. Morphologic variation was calculated as the coefficient of variation for each of these measurements, and asymmetry was estimated as the absolute value of the difference between the logarithmically transformed left and right side measurements. The results, which have been described in detail elsewhere [Wayne et al, 1986], are summarized in Table 3. The coefficient of variation was similar in the cheetah and other large cats, but asymmetry is significantly greater in the cheetah. This apparent demonstration of an inverse relationship between morphologic and genetic variation must be interpreted, however, in the framework of the possibly important differences in locality and time frame of the cheetahs sampled in the allozyme study (all South African, 1971–1981) and the morphological analysis (primarily East African, 1890–1950). Should the East African cheetahs, likewise, be found to be genetically uniform, a morphologic/genetic correspondence would be demonstrated. Conversely, the present data might be predictive of probable genetic monomorphism in the East African population.

MORPHOLOGICAL MEASUREMENTS OF CAPTIVE ZOO ANIMALS

Because of the potential value of both morphological and biochemical genetic measurements, an ideal study would include them both. We suggest using the two parameters from both a theoretical perspective and from the insight achieved by the analysis of captive cheetahs. For this reason, we outline briefly certain aspects that should be considered of a morphological study.

The measurement of morphologic variation or asymmetry can be made on skulls, postcrania, or on live animals. Skeletons in museum collections often consist of only cranial material and, hence, only measurements on one morphologic unit, the skull, are possible. Live animals may be preferable because measurements can be made both internally on the skeleton from radiographs and externally on the body. However, these measurements are often not as precise as measurements directly on bones.

Tables 4 and 5 provide a list of measurements to be used on skeletons and on the external body of live or preserved specimens. Most measurements have been used in previous studies and are described extensively in the cited references (see Table 2). Many skeletal measurements can be taken from radiographs, but previous studies have not used this approach since it is often just as easy to skeletonize specimens. In zoos, the widespread use of clinical x-rays suggests that many measurements, such as the length of the left and right molars, metapodials, transverse processes or number of left and right ribs, could be noted as part of a routine radiographic examination. Whenever possible, many different developmental units should be included; eg, teeth, splanchnocranium, cranial vault, basicranium, limb bones, and vertebra. Morphologic measurements, which include a common length or measure the same morphologic unit (eg, bulla length and width), should be avoided because they tend not to be independent and may confound statistical analysis. Moreover, measurements should be chosen for ease of accuracy and reproducibility in the particular species under study.

Morphologic variation can be evaluated in two ways. The amount of morphologic variation should first be measured by using the coefficient of variation (CV; std/mean $\times$ 100). Measurements are made on individuals from a population and the variability about the mean is calculated. To compare the variability of measurements (eg, tooth length vs skull length) or to compare populations or species of different body size, we standardize the variation by dividing by the character mean. The resulting coefficient of variation (CV) is therefore a population parameter. Different zoo populations can be compared on the value of the CV for each measurement or the CV may be averaged over all measurements, providing a single value to be compared between populations. There are a number of statistical tests to assess the significance of interpopulation differences in the CV [Lewontin, 1966; Jackson, 1973; Lande, 1977; Sokal and Braumann, 1980; Zar, 1984].

A second parameter for estimating morphologic variation is the measurement of fluctuating asymmetry of bilateral traits. To estimate asymmetry for metric characters the absolute value of the difference between logarithmically transformed left- and right-side measurements is calculated. Each individual, therefore, has an asymmetry value for each of the morphologic measurements. These values may be averaged for each individual and compared to other individuals within the same population for an estimate of intrapopulational variability in asymmetry or averaged across the entire population and compared to other zoo stocks. The same procedure may be applied to meristic measurements but logarithmic transformation is not generally needed, since these characters are counted, not measured (eg, the number of cat whiskers), and are somewhat size independent. Leamy [1984] and Wayne et al [1986] present other multivariate approaches for reducing the dimensionality of the data set and procedures for assessing the significance of asymmetry differences. Fluctuating asymmetry has the advantage over CVs for measuring variance in an individual and, as such, may be particularly informative for detecting developmental imbalance resulting from inbreeding.

CONCLUSIONS

There are three diagnostic approaches which should be considered for the genetic management of captive species. The first is the careful collection and analysis of pedigree data for formulating a theoretical assessment of the level of genetic variation within a population. The second approach is an estimation of genetic

TABLE 2. Summary of Recent Studies on the Relationship of Genetic and Morphologic Variability*

Organism	Generic name	Number of		Population type	Number of		Coefficient of variation	Fluctuating asymmetry	Reference
		Individuals	Populations		Isozyme loci	Morpho-logical traits			
Inbred mouse	*Mus*	252	18	H,I	ND	10	ND	+	Leamy [1984] (1)
Face fly	*Musca*	159	8	W,O	14	14	+	ND	Bryant [1984]
House sparrow	*Passer*	621	6	W,O	6	14	+	ND	Fleischer et al [1983] (2)
Rainbow trout	*Salmo*	50	1	O	13	5	ND	+	Leary et al [1983] (3)
Clam	*Lampsilis Elliptio*	260	13	W,M	12	1	ND	+	Kat [1982]
Fish	*Poeciliopsis*	90	6	W,A/S	25	8	ND	+	Vrijenhoek and Lerman [1982] (4)
Anolis lizard	*Anolis*	1,278	142	W,O	24	7	ND	+	Hertz and Zouros [1982] (5)
Fruit fly	*Drosophila*	NR	NR	W,O	ND	ND	ND	+	Soulé and Cuzin-Roudy [1982] (6)
Housefly	*Musca*								
Butterfly	*Coenonympha*								
Lizard	*Uta*								
Human	*Homo*								
Mouse	*Mus*								
Rat	*Dipodomys*								
Sparrow	*Passer*								
Deermouse	*Peromyscus*	129	8	W,I/M	29	15	+	ND	Aquadro and Kilpatrick [1982] (7)

Cotton rat	*Sigmodon*	647	16	P/C	23	16	−	ND	McClenagen and Gaines [1982] (8)
House mouse	*Mus*	252	9	H,I	ND	18	+	ND	Thorpe and Leamy [1982] (9)
Sparrow	*Zonotrichia*	NR	2	W,O	4	11	−	ND	Handford [1980] (10)
Lizard	*Uta*	NR	15	I/M	18	4	ND	+	Soulé [1979] (11)
Bush-rat	*Rattus*	129	13	I/M	16	18	+	ND	Schmitt and White [1979] (12)
Teiid lizard	*Cnemidophorus*	NR	22	A/S	6	14	+	ND	Parker [1979] (13)
Killifish	*Fundulus*	560	6	W,O	12	7	+	ND	Mitton [1978] (14)
Monarch butterfly	*Danaus*	1,400	NR	W,O	6	2	+	ND	Eanes [1978]
Honey bee	*Apis*	1,200	8	M,A/S	4	3	ND	+	Brucker [1976]
Rat	*Rattus*	229	14	I/M	37	9–14	+	ND	Patton et al [1975] (15)
Lizard	*Uta*	NR	22	I/M	6	14	+	ND	Soulé et al [1973] (16)
House mouse	*Mus*	19	NR	O,H,I	ND	3	ND	+	Bader [1965] (17)
Cheetah	*Acinonyx*	86	4	W	52	19	−	+	Wayne et al[1986] (18)
Leopard	*Panthera*								
Ocelot	*Leopardus*								
Margay	*Leopardus*								

*Plus sign indicates an inverse association between genetic and morphologic variability or asymmetry, as revealed through isozyme surveys or breeding data. Minus sign means absence of an inverse correlation. ND means measurement not done in that study. NR—not reported. Population type: W=wild, O=outbred, H=hybrid, I=inbred, M=mixed inbred and outbred, I/M=island and mainland, P/C=peripheral and central, A/S=asexual and sexual. Numbers in parentheses are keyed to Table 4.

TABLE 3. Comparative Analysis of Morphological Variation of 19 Cranial Characters From Four Species of Felidae (19–33 Skulls per Species)*

Measures of variation and fluctuating asymmetry	Cheetah	Leopard	Ocelot	Margay
Coefficient of variation	7.2	7.2	7.3	7.2
Average asymmetry (times 1,000)	7.8	5.8	5.5	5.8
Average asymmetry per skull (times 1,000)	8.2	6.2	5.5	5.4

*The mean of each character was determined and the coefficient of variation for each trait was computed. The mean of the coefficients of variation for all traits in each species is presented on the first line of this table. Asymmetry is calculated as the absolute difference between logged left and right side paired measurements. The values on the second line represent an average for each species over all traits and skulls. A single measurement of asymmetry was calculated for each skull by summing the asymmetry values for each measurement on its skull and dividing by the number of measurements. The numbers in line 3 represent an average of these values for each species. The cheetah is significantly greater than the other three cat species in both measures of asymmetry. A more thorough description of this analysis is presented elsewhere [Wayne et al, 1986].

variation based upon electrophoretic resolution of enzyme loci known to be polymorphic in mammalian populations. The third genetic assay measures the extent of morphologic variation based upon both the coefficient of variation and the asymmetry differences in bilateral traits.

We feel that the combined use of these genetic measurements will be useful to zoo animal managers in at least four specific applications:

(1) To identify genetically homozygous zoo populations. Captive populations which have been extensively inbred may be identified by departure from common patterns of allozyme and morphologic variability found in other populations of the same or related species. For example, of the 27 biochemical loci which were variant in one or more cat species (Table 1), ten of the loci were polymorphic, and for the same allele, in three to seven cat species [Newman et al, 1985]. The cheetah was monomorphic for all ten allozymes [O'Brien et al, 1983]. Furthermore, the cheetah sample was found to have significantly greater levels of asymmetry compared to other Felidae species (Table 3). However, as discussed below, increased morphological variance may not itself be conclusive evidence for genetic homozygosity because environmental components can influence morphological variation as well.

(2) To resolve enviromental components of morphological variance. In addition to genetic causes, changes in morphologic asymmetry have also been associated with various kinds of environmental stress [Bailit et al, 1970; Valentine et al, 1973; Seigel and Doyle, 1975; Beardmore and Ward, 1977; Soulé et al, 1982]. Since this is not the case with allozyme variation, high levels of morphologic variability combined with average to high levels of allozyme heterozygosity may be suggestive of increased environmental stress on a zoo population. Therefore, morphologic asymmetry can be

TABLE 4. Skeletal Measurements for Monitoring Morphologic Variation†

Skull	Postcrania
Birds	Birds
Bill length (10)	Carpometatarsus weight (6)*
	Humerus weight (6)*
	Ulna weight (6)*
Mammals	Mammals
Basilar length (15)	Femur length (1,9)*
Basonasal length (7)	Humerus length (1,9)*
Braincase width (12,15)	Ilium length (1,9)*
Bulla length (12,18)*	Innominate length (1,9)*
Bulla width (18)*	Length clavicle*
Cranial depth (7,12,15,18)	Length hyoid*
Diastema length (15)*	Length terminal phalanx*
Foramen magnum depth (12)	Number of ribs*
Foramen magnum width (12)	Obturator foramen length (1,9)*
Inside M1 width (12)	Radioulna length (1,9)*
Interorbital width (9)*	Scapula length (1,9)*
Interorbital constriction width (7)	Tibia length (1,9)*
Interorbital width (12)	Transverse processes on thoracic vertebra*
Interparietal length (12)	Dental
Interparietal width (12)	Canine length
Length auditory meatus (6)*	M1 length (17)*
Length of incisive foramen (6)*	M1 length and width (17,18)*
Length of mandibular ramus (6)*	M2 length and width (17,18)*
Mandible length (1,9,18)*	M3 length (17)*
Maxilla width (18)*	P3 length (18)*
Maxillary tooth row length (7,12,15,18)*	P4 length (18)*
Occipital-nasal length (15)	
Orbit length (12)*	
Palatal length (7,9,18)	
Premaxilla width (12,15)	
Pterygoid breadth (7)	
Rostral length (15)	
Skull length (7,9,12,18)	
Skull width (9)*	
Total length of tooth row (7,18)*	
Width across upper molars (7,15)	
Zygomatic fenestral length (1,9)*	
Zygomatic width (7,15,18)*	

†Numbers in parentheses refer to references in Table 2. Asterisks indicate bilateral traits of use in estimating fluctuating asymmetry.

used to determine if changes in the captive environment of zoo populations might be physiologically detrimental providing that allozyme and morphologic estimates of variability are employed concurrently.

(3) To identify individuals for optimum success of breeding programs. Individuals with low heterozygosity, based on either low allozyme levels or significantly higher asymmetry, may also be homozygous for genes affecting fertility and fecundity. If these animals must be included in the breeding program they should be paired with genetically distinct lines in order to decrease the expression of deleterious recessive genes.

TABLE 5. External Measurements for Monitoring Morphologic Variation†

Head	Body
Fish	Fish
Number dentary inner teeth (4)*	Dorsolateral scale count (4)*
Number dentary outer teeth (4)*	Number rays anal fin (14)
Number gill rakers, lower brachial (3)*	Number rays caudal, dorsal fin (14)
Number gill rakers, upper brachial (3)*	Number rays pectoral fins (3,4)*
Number mandibular pores (3)*	Number rays pelvic fins (3,4)*
Number premaxillary inner teeth (4)*	Number scales on lateral line (4,14)*
Number premaxillary outer teeth (4)*	Number scales below lateral line (14)
Reptiles	Reptiles
Head length (13)	Hindleg length (13)*
Number mandibular teeth (13)*	Longest articular scale length (11)*
Number maxillary teeth (13)*	Number canthal scales (5)*
	Number circumorbital scales (11,16)*
	Number digital laminae 3rd toe (13)*
	Number digital laminae 4th toe (5,13)*
	Number femoral scales (6,11,13,16)*
	Number infralabial scales (13)
	Number loreal rows (5)*
	Number subinfralabial scales (13)
	Number supralabial scales (5,13)*
	Number supraocular scales (6,11,16)*
	Snout vent length (13)
Birds	Birds
Tail length (10)	Tail length (10)
	Tarsus length (10)*
	Toe length (10)*
	Wing length (10)*
Mammals	Mammals
Canine length*	Body length (7,9,12,15)
Diastema length*	Fingerprint whorl count (6)*
Ear length (6,7,9,15)*	Frontfoot length*
Molar length and width*	Hindfoot length (7,12,15)*
Number mustacial vibrissae (6)*	Hock length*
Premolar length and width*	Length palmer pad*
Tooth row length*	Number of ribs*
	Number of teats*
	Tail length (7,12,15)
	Weight (9)

†Meristic (countable) characters are those which begin with "Number . . .".
Numbers in parentheses refer to references in Table 2. Asterisks indicate bilateral traits of use in estimating fluctuating asymmetry.

(4) To monitor progress of a breeding program. It is important to determine whether breeding programs are affecting average genetic variability. Therefore, allozyme and morphologic variabilities need to be assessed periodically throughout the course of a breeding program. If heterozygosity declines over several generations, then the breeding program can be modified according to allozyme and morphologic data.

We must first document the relationship between inbreeding and morphologic and electrophoretic variation before these techniques yield their potential value for captive management programs. We advocate their application to questions concerning zoo populations because we believe that such documentation will increase the power of pedigree analysis and the likelihood of successful management procedures.

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