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Genetic Variation in the Zoo Population of the Red Panda Subspecies *Ailurus fulgens fulgens*

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Genetic variation present in the global and regional zoo populations of the red panda is estimated by computer simulations. In this study it is demonstrated that inbreeding depression could occur on the short term in the regional populations. Migration between regional populations is recommended to ensure the future survival of the red panda in captivity. More genealogical lineages should be represented in the breeding program.

Key words: genetic management, computer simulation, GeneFlow

INTRODUCTION

Studbooks of (endangered) animal species in captivity are of the greatest importance to longterm captive management. They provide demographic and pedigree data which are (or should be) the base of management strategies. Information on the current status of a zoo population in respect to its future survival can be deduced by analysis of these data. In this study, the genetic structure of the zoo population of the red panda subspecies *Ailurus fulgens fulgens* is analyzed. The breeding history of this subspecies is well documented in the red panda studbook [Glatston, 1984, 1985].

As of December 31, 1984, the red panda population consists of 142 specimens of *A. f. fulgens* and 16 specimens of *A. f. styani* [Glatston, 1985]. The small captive population of the subspecies *A. f. styani* is not considered in this study. Analysis of the genetic structure of the population of *A. f. fulgens* seems of more importance. Most specimens are captive-born and inbreeding has already occurred. Only 25 wild caught specimens have contributed to the captive-born population. Both genetic drift and inbreeding result in a decrease of genetic variation. Genetic variation in the captive population cannot be increased by introduction of wild caught specimens: the

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red panda is protected by both the government in the lands of origin and the Washington Convention. This means that the captive population of *Ailurus f. fulgens* must be self-sustaining.

The survival of a species in captivity is not guaranteed by its population size alone. Genetic variation as important as well. In this, the cheetah, *Acinonyx jubatus*, is a clear example of the negative effects of low genetic variation. The cheetah shows no variation at the major histocompatibility complex (MHC) [O'Brien et al., 1985]. The MHC is a gene complex in mammals that plays an important role in the defense against viruses. Monomorphism at the MHC will limit a species repertory of defenses against viruses. Cheetahs are extremely sensitive for feline viral diseases [O'Brien et al., 1985]. Glatston [1982b] and Glatston and Roberts [1988] propose breeding programs for the regional zoo populations of the red panda. These regional populations (Australia, Continental Europe, Great Britain and Scandinavia, North America, and "rest" population) are relatively small (5 to 67 specimens). Therefore, the chance that inbreeding depression occurs within a regional population is large. Genetic variation in the regional populations is estimated to determine the extent to which these sub-populations can be regarded as closed demes.

Another purpose of this study is to demonstrate the use of computer simulation models in genetic management of captive populations. To date several models have been designed (e.g., Gene Drop, MacCluer et al., 1986; ColonySim, Dyke et al., 1986) to analyze the genetic structure of zoo populations. The model GeneFlow, used in this study, has been developed to analyze gene flow in populations which are divided in sub-populations and in which generations overlap. The model allows one to simulate the effects of migration of specified individuals between sub-populations.

MATERIALS AND METHODS

The pedigree and demographic data for the red panda population were extracted from the third edition of the studbook and its update report [Glatston, 1984,1985].

The data used in this study include all specimens of the subspecies *Ailurus f. fulgens* which have produced offspring or which are potential breeders. Specimens which were either born in captivity or imported from the wild since January 1, 1975 are regarded as potential breeders. This (arbitrary) criterion is based upon an average life-span of 9 years for red pandas in captivity. Potential breeders which are wild born, are considered as potential founders. Specimens older than 9 years, which have not reproduced, are considered as nonreproductive, i.e., they are assumed to be dead. They are excluded from the simulation experiments as they do not participate in processes of gene flow.

The generation to which each specimen belongs is determined from the pedigree data. The founder group (PO) consists of real founders (i.e., wild specimens which have reproduced) and potential founders. Wild specimens imported after the first captive born specimens were recorded are not regarded as immigrants but as participants of the (potential) founder population (PO).

Specimens which have descended directly from founders are defined as F1. The generation of an individual is determined by the parent from the latest generation, e.g., a F1 $\times$ F2 mating results in F3 offspring.

The variance effective size [Kimura and Crow, 1963] is estimated for each parental group. Each parental group consists of all specimens of that generation plus

specimens from previous generations which are involved in backcrosses. For example: The parental group P2 consists not only of all F2 specimens, but also those wild caught and F1 specimens which have mated with F2 specimens.

The expected genetic drift (ΔH_{GD}) per generation is estimated according the following equation:

$$(1)\ \Delta H_{GD} = \frac{1}{2 \times N_{E\,(V)}} \qquad \text{Wright [1931],}$$

where $N_{E(V)}$ is the variance effective population size.

The computer simulation model GeneFlow estimates genetic variation in (captive) populations in which all pedigree patterns are known. Genetic variation can be estimated for generation groups and for living specimens in both whole and subpopulations. The measure gene diversity (or average heterozygosity), as defined in Nei [1975], is used to express genetic variation. The simulation model does not suppose mutation or selection.

The model supposes a very large "wild" population with r independent autosomal loci. At each locus, two alleles A_{1J} and A_{2J}, (J = 1,...,r), are assumed. These alleles have frequencies x_{IJ}, (I = 1,2 and J = 1,....,r).

In each simulation run, Monte Carlo methods are used to draw random genotypes for the (potential) founders and random genotypes, based upon Mendelian segregation of the parental alleles, for descendants. The numbers of founders and offspring and parentage can be simulated according to the observed pedigrees in *Ailurus f. fulgens* or to any other previously assigned pedigree pattern.

Per simulation run the heterozygosity at each locus (h_J) for generation groups and for living specimens of the captive population and/or sub-populations is estimated:

$$(2)\ h_J = 1 - \Sigma\, x_{IJ}^2 \ (I=1,2\ ;\ J = 1,.....,r) \quad \text{Nei [1975],}$$

where x_{IJ} is the frequency of allele I on the J^{th} locus. The gene diversity (H) over r loci is estimated within each group:

$$(3)\ H = \Sigma\, h_J/r \qquad \text{Nei [1975].}$$

Finally the average gene diversity over a number of simulation runs is estimated.

The number of loci (r), the number of simulation runs, and the frequencies of alleles A_{1J} and A_{2J} (J = 1,...,r) can be varied. In the simulation experiments on the captive red panda population, 30 loci were "screened" in 100 simulation runs. The recommendations of Nei and Roychoudhury [1974] are followed for the number of loci which should be tested in studies on protein polymorphisms to estimate gene diversity. The minimal number of loci which is required to yield significant estimates of gene diversity can be determined: First, the estimate of percentage of natural gene diversity ($\%H_{NT}$) in the founder group must not differ significantly from the expected gene diversity according equation:

$$(4)\ \%H_{NT} = (1-1/(2N)) \times 100\ \%, \qquad \text{Frankel and Soule [1981],}$$

where N is the number of founders. Second, genetic drift in the first generation should not differ significantly from the expected genetic drift (ΔH_{GD}).

The frequencies of alleles A_{1J} and A_{2J},(J=1,...,30), in the "wild" population are assumed to be 0.5. This means that gene diversity in the "wild" population is 0.5. Genetic variation in the captive population is presented in terms of percentages of the gene diversity in the "wild" population (i.e., percentages of natural genetic variation).

RESULTS

Pedigree Patterns

Pedigree patterns have been constructed for the red panda population. They are presented in Figure 1. They show that different levels of inbreeding (e.g., full-sib and half-sib matings) have occurred and that the number of specimens reproducing declines with each generation.

Genetic Variation in the Global and Regional Populations as of December 31, 1984

The percentage of natural genetic variation retained in the global population and sub-populations (i.e., regional populations) has been estimated. Genetic variation is also estimated within individual generation groups for both global and regional populations. The rates of decrease in genetic variation are estimated for both (sub)population and generation groups. The genetic variation and decrease rates thereof, as estimated in the computer simulations, are presented in Table 1. The global population has lost 4.6% of the natural genetic variation. The genetic loss in the regional populations is larger than this. The genetic variation estimated in the global population is larger than the arthimetic mean of that of the regional populations. Genetic variation in a regional population is larger than the arthimetic mean of that of generation groups in the regional population.

Number of Specimens per Age Group

The number of living specimens belonging to the same age group is presented in Table 2. These data show that generation groups overlap. The majority of the wild caught and F1 specimens can be expected to die in 3 to 4 years (i.e., they reach the age of 9 years which is assumed, as the average life-span).

The Loss in Genetic Variation per Generation

The percentage of natural genetic variation and its rate of decrease have been estimated for the different generations. Each generation group includes all specimens that have reproduced or are potential breeders. Table 3 shows computer simulations of the genetic variation and rates of decrease rates thereof, as estimated with the computer simulations.

Effective Population Size

The composition and the variance effective population size of each parental

Fig. 1. Pedigree patterns in the zoo population of the red panda subspeciea *Ailurus f. fulgens*. The code used for each specimen corresponds with the studbook code. e.g., m73/02 is specimen FM/00/73/02. The prefix m and f indicates sex (males and females respectively). Specimen m79/07 is specimen m79/06. Breeding pair m77/01 - f79/20 have also produced 84/01 and 84/02 (sex of both specimens is unknown).

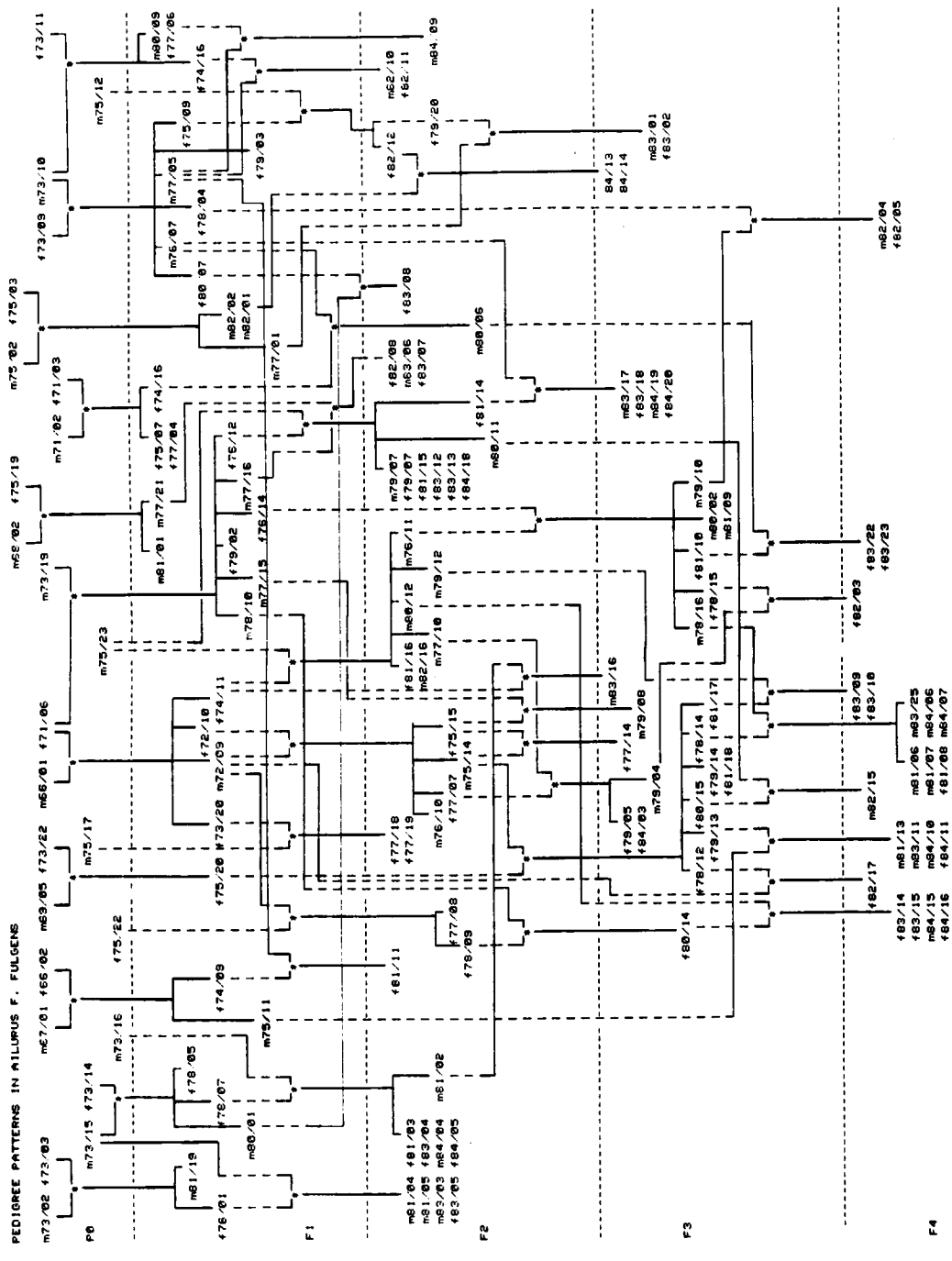
PEDIGREE PATTERNS IN AILURUS F. FULGENS
P0
F1
F2
F3
F4

TABLE 1. Percentage of natural gene diversity in living specimens in different generations per regional population*

	Generation					
Region	PO	F1	F2	F3	F4	Total
Australia						
N	2	3	2	6		13
$\%H_{nt}$	75	77.6	61.4	76		82
ΔH_{nt}	25	22.4	28.6	24.0		16
Europe (Continent)						
N	4	4	6	5	8	27
$\%H_{nt}$	87.5	84.2	87.6	80.0	85.6	94.2
ΔH_{nt}	12.5	15.8	12.4	20.0	14.4	5.8
Scandinavia Great Britain						
N		9	10			19
$\%H_{nt}$		91.6	88.2			91.4
ΔH_{nt}		8.4	11.8			8.6
U.S.A. Canada						
N	2	7	22	18	18	67
$\%H_{nt}$	75	85.2	90.2	87.2	84.6	90.4
ΔH_{nt}	25	14.8	9.8	12.8	15.4	9.6
Rest						
N	5					5
$\%H_{nt}$	90					90
ΔH_{nt}	10					10
Mondial						
N	13	23	40	29	26	131
$\%H_{nt}$	96.2	94.8	93.6	90.8	87.6	95.4
ΔH_{nt}	3.8	5.2	6.4	9.2	13.4	4.6

*N = Living specimens of *Ailures f. fulgens* at December 31, 1984, younger than 9 years. $\%H_{nt}$ = Percentage of natural gene diversity. ΔH_{nt} = Decrease rate in natural gene diversity in respect to the wild population.

TABLE 2. Distribution of age groups in different generations

	Generation					
Age group	PO	F1	F2	F3	F4	Total
9–10	5	3	1			9
8–9	2	3	2			7
7–8	1	6	5	1		13
6–7	1	3	1	4		9
5–6	2	2	4	6		14
4–5		2	2	3		8
3–4		2	8	4	4	17
2–3		2	5		5	12
1–2			8	5	9	22
0–1	2		4	6	8	20

group have been determined. The expected loss in genetic variation caused by genetic drift is estimated for each generation. The variance effective population size of each parental group and genetic drift is also estimated assuming males and females produced the same number of offspring. These results are presented in Table 4. They

TABLE 3. Decrease in natural gene diversity in different generations*

	Generation				
	PO	F1	F2	F3	F4
N	35	35	42	30	26
$\%H_{nt}$	98.6	95.6	93.8	90.6	87.6
ΔH_{gr}		2.9	1.8	3.3	3.3
ΔH_{nt}	1.4	4.4	7.2	10.4	13.4

*N = Number of individuals that have reproduced offspring or are potential breeders (younger than 9 years). $\%H_{nt}$ = Percentage of natural gene diversity, estimated by computer simulations over 100 runs and 30 independent autosomal loci. ΔH_{gr} = Decrease rate in gene diversity in respect to the previous generation. ΔH_{nt} = Decrease rate in gene diversity in respect to the wild population.

TABLE 4. Variance effective population size and composition of the parental groups*

Parental group	Composition								N	$N_{e(v)}$	ΔH_{gd}	$N_{e(v)}$	ΔH_{gd}*
	Wild		F1		F2		F3						
	m	f	m	f	m	f	m	f					
P0	17	18	—	—	—	—	—	—	35	17.3	2.9	66.4[a]	0.8
P1	5	1	14	21	—	—	—	—	41	17.9	2.9	75.0[b]	0.7
P2	—	—	5	3	20	22	—	—	50	13.4	3.7	98.0	0.5
P3	—	—	2	1	5	—	12	18	38	13.5	3.7	74.0	0.7

*m,f = males, females. N = number of specimens in parental group.
$N_{e(v)}$ = variance effective population size of parental group.
ΔH_{gd} = expected genetic drift from estimated $N_{e(v)}$ (in %). $N_{e(v)}$* = variance effective population size under equal distribution of offspring. ΔH_{gd}* = expected genetic drift estimated from $N_{e(v)}$* (in %).
[a]Variance in distribution over males and females is 0.06 and 0.05, respectively.
[b]Variance in distribution over males and females is 0.13 and 0.12, respectively.

show that the variance effective size of each parental group is smaller than its size. If each individual had produced equal numbers of offspring, the variance effective size would have been approximately twice that of the parental group. The expected genetic drift given an equal distribution of offspring would be less than 1%.

Bloodlines in the Regional Populations

The bloodlines represented by living captive-born specimens in each of the regional populations are shown in Table 5. These data show that the specimens in the Australian population represent 5 bloodlines where as those in Europe (continental), Britain/Scandinavian, and North America represent 17, 14, and 18 respectively. The European and North American populations differ in 5 bloodlines. The British/Scandinavian population differ from the European and North American population in 11 and 13 bloodlines, respectively.

Migration Between Regional Populations

In order to examine the effect of migration on genetic variation in the regional populations, a simulation experiment was undertaken. The migration model, used in the simulation experiment, involved the introduction of specimens which are non-

TABLE 5. Bloodlines in the regional populations*

Founder	Line	Australia	Europe	Scandinavia/Great Britain	U.S.A./Canada
66/01	A		+		+
66/02	B		+	+	
67/01	C		+	+	
68/02	D				+
69/05	E		+		+
71/02	F		+		+
71/03	G		+		+
71/06	H		+	+	+
73/02	I			+	
73/03	J			+	
73/09	K	+	+	+	+
73/10	L	+	+	+	+
73/11	M		+	+	+
73/14	N		+	+	+
73/15	O		+	+	+
73/16	P		+	+	+
73/19	Q		+	+	+
73/22	R		+		+
75/02	S	+		+	
75/03	T	+		+	
75/12	U	+			
75/18	V				+
75/19	W				+
75/22	X		+		+
75/23	Y		+		+

*+ indicates the presence of a bloodline. The code for each founder corresponds with the studbook code, e.g., 66/01 is specimen FM/00/66/01.

inbred and represent at least two bloodlines which are not represented by the specimens of that regional population. The specimens involved in the migration program and the effects on genetic variation in the regional populations are presented in Table 6. This table shows that the percentages of natural genetic variation in the regional populations increases as result of such migrations.

DISCUSSION

Genetic Variation in the Global Population

The percentage of natural genetic variation in the global population (all living specimens which are assumed to be still reproductive as of December 31, 1984) is 95.4% (Table 1). This represents a decrease of 4.6% on the situation in the wild population. The main question is whether this amount of genetic variation is sufficient to establish a viable population. The genetic variation determines the extent to which a population can adapt to environmental changes (e.g., mutant strains of viruses). The current captive population must possess, excluding the small genetic input of mutation, the genes (alleles) which are required to survive under changed conditions. Soulé et al. [1986] suggest that a captive population should represent at least 90% of natural genetic variation over the next 200 years. Given this 90% criterion, genetic variation in the current red panda population would be sufficient to establish a viable population.

TABLE 6. The effect of migration on the percentages of natural gene diversity in the regional populations. For each specimen the bloodlines are given*

	Australia	Europe	Scandinavia Great Britain	U.S.A. Canada
Emigrants + Bloodlines	83/01 KLSTU 83/02 KLSTU 84/01 KLSTU 84/02 KLSTU 84/13 KLSTU 84/14 KLSTU	79/06 HQY 83/04 NOP	81/04 IJO 81/11 BCKL 82/02 ST 83/03 NOP	82/16 AHY 83/06 DKQW 83/07 DKQW 83/12 AHY
Immigrants + Bloodlines	79/06 HQY 81/11 BCKL 82/16 AHY 83/03 NOP 83/04 NOP 83/07 DKQW	83/01 KLSTU 83/02 KLSTU	83/06 DKQW 83/12 AHY 84/01 KLSTU 84/02 KLSTU	81/04 IJO 82/02 ST 84/13 KLSTU 84/14 KLSTU
$\%H_{nt}$	82.0	94.2	90.0	91.4
$\%H_{nt}$*	92.6	94.4	91.4	93.0

The code for each specimen corresponds with the studbook code, e.g., 83/01 is specimen FM/AD/83/01. % H_{nt} = Percentage of natural gene diversity in the population on December 31, 1984. % H_{nt} = Percentage of natural gene diversity after migration.

However, this 90% criterion is, as stated by Soulé et al. [1986], arbitrary. How environmental conditions will change in the future is unknown. Thus, it is unknown which genes (alleles) a population must possess to be adapted to future conditions. Furthermore, the minimal percentage of natural genetic variation which is needed to ensure long-term viability of a captive population may differ per species. Even 100% of natural genetic variation does not a priori ensure future survival of a (captive) population. For example: Natural populations which have, in recent times, undergone a severe bottle-neck, have a low genetic variation [Nei et al., 1975]. These natural populations have an already relative low adaptive potential. It seems advisable to preserve more than 90% of the natural genetic variation in a captive population in which the founders originate from these source populations. Further studies are required to set up criteria of minimal genetic variation for different (groups of) species.

In this study the 90% criterion, as suggested by Soulé et al. [1986], is followed. This means that genetic loss in the red panda population should not exceed 5.7% over the next 200 years. The global population of the red panda is represented by a number of different captive-born generations; this overlap is due to the long reproductive life span of the panda [Roberts, 1982]. In addition, the definition used in this study of a captive-born generation leads to an artificial overlap (see "Materials and Methods"). Within the captive-born generations the percentage of natural genetic variation is smaller than that for all generations combined (Table 1). The PO (wild specimens) and F1 groups both represent a relatively large percentage of the natural genetic variation (Table 1). However, in these groups most specimens are older than 6 years (Table 2). Thus, in the near future both groups will die out. If the size of the global population remains stable, the F1 must be replaced by later generations, but these

have a lower genetic variation. This means that the gene diversity in the global population will decline.

Certain measures should be taken to avoid this and these can be deduced from analysis of the processes which have already caused a decrease in genetic variation in the red panda population.

Rate of Decrease in Genetic Variation per Generation

The processes which have caused a decrease in genetic variation have to be studied in complete generation groups. This means that each group must include all dead specimens which have produced offspring. The results of this analysis are presented in Table 3. The processes that have caused a decrease are discussed per generation. 1) Founder group (PO); The number of wild specimens which have produced offspring (i.e., founders) or are potential breeders is 35 (Table 3). This group represents 98.6% of the genetic variation that exists in the wild population (assuming that all individuals are unrelated). This percentage can be seen as the genetic input on which the current captive population is built. Unless mutations occur, the percentage of natural genetic variation in the captive population will never exceed 98.6%. 2) F1 generation; The loss in genetic variation in the F1 generation is due to genetic drift (Table 3). The estimated decrease rate per generation (ΔH_{GR}) of 2.9% in the simulation experiment agrees with the predicted expected genetic drift (ΔH_{GD}) from the estimated $N_{E(V)}$ of the founder population (Table 4). Genetic drift in the F1 generation is too large. Frankel and Soulé [1981] argue that the loss in genetic variation should not exceed 1% per generation. Thus, the (variance) effective population size should be at least 50 (see Equation 1). The variance effective size of the founder group is 17.3 (Table 4). This small size is due to the unequal distribution of offspring over the founders. If the distribution of offspring were equal, a variance effective size of 66.4 would have resulted. Then genetic drift would have been limited to 0.8% (Table 4). 3) F2 generation; The decrease rate of 1.8% in the F2 generation is lower than would be expected from the $N_{E(V)}$ of the parental group P1. This group contains F1 specimens and some wild caught specimens (Tables 3 and 4). Genetic drift in this group is expected as 2.9%. Full-sib and half-sib matings have occurred (Fig. 1). However, the effect of both inbreeding and genetic drift has been limited by back-crossing with founders. In fact these founders can be regarded as immigrants. A part of the natural genetic variation is directly introduced into the F2 by the founders. However, the loss in genetic variation in this generation is still too large. Although the F2 generation is larger than the F1, the $N_{E(V)}$ is too small. This is due to the unequal distribution of offspring per specimen. 4) F3 generation; The $N_{E(V)}$ of the parental group P2 is small, resulting in a large genetic drift of 3.7% (Table 4). The loss in genetic variation is limited by the back-crossing with F1 individuals. Even so the net result (ΔH_{GR} is 3.3%) is less satisfactory than for the F2 generation. Analysis of pedigree patterns (Fig. 1) shows different levels of inbreeding, in which some of the "introduced" F1 specimen are involved. Inbreeding increases the loss of genetic variation. 5) F4 generation; The small $N_{E(V)}$ of the P3 group has resulted in a genetic drift of 3.7% (Table 4). The introduction of specimens of previous generations has limited the decrease rate to 3.3% (Table 3). The effect of introducing specimens becomes smaller. The size of the breeding group has decreased with each generation. This results in a higher degree of relatedness between specimens introduced into the parental group P3 and the specimens of the F3 generation than such introduction in previous generations. In these cases back-crossing results in inbreeding.

Guidelines for the Maintenance of Genetic Variation in the Global Population

Three guidelines can be deduced from the above analysis. It must be stressed that the management presented here is purely based upon population-genetics. Other important aspects such as demographic trends [Glatston and Roberts, 1988] and individual behaviour are not considered in this study.

1. Where possible avoid inbreeding. Roberts [1982] demonstrated a positive correlation between juvenile mortality and inbreeding coefficient in the red panda. Since a studbook on the red panda population is available [Glatston, 1980, 1982a, 1984], this should not be difficult to organize.

2. Limit genetic drift by increasing the effective size of the parental groups PO, P1, P2, and P3. To date, a number of wild specimens have not participated in the breeding population. Since these potential founders provide genes for the captive gene pool, it is important to breed with these specimens soon. In the F1 generation some specimens, which will soon reach the age of 9 years, have not yet bred. This limits gene flow to the later generations. Thus, these specimens should also be bred with soon. Genetic variation in the F3 and F4 generation group is relatively low. This could endanger the viability of the zoo population in the near future. Effective size of both the P2 and P3 group (which produce F3 and F4, respectively) must be increased. The gene flow from F2 to F3 and F4 has not yet been completed. Not all specimens in the F2 and F3 generation (which form the P2 and P3 respectively) have reached the reproductive age (Table 2). Incorporation of F2 and F3 specimens in the breeding population will increase the effective size of the parental groups P2 and P3. This will reduce the loss in genetic variation. In this it is also important to optimize effective size by keeping red pandas in pairs. Then a more equal distribution of offspring per specimen is achieved. Equal distribution of offspring reduces genetic loss (Table 4).

3. Analysis of the pedigree patterns (Fig. 1) shows that the current F4 generation is only based on a few genealogical lineages, and that in these inbreeding has occurred. Thus breeding with these F4 specimens might cause inbreeding depression resulting in a less viable F5 generation. F4 specimens should be outbred with specimens from previous generations. The 13 wild specimens that are still in the reproductive age group must be incorporated in the breeding program.

Genetic Variation in the Regional Populations

For practical reasons breeding programs should act at the regional rather than at the global level [Glatston,1982b]. However the current situation in the red panda population means that such a strategy is not suitable in the short term. The percentages of natural genetic variation in the subpopulations are too low to ensure their future survival (Table 1). The future viability of a sub-population is determined by the percentage of natural genetic variation in the latest captive-born generation. These percentages are low given a minimal genetic variation of 90% as criterion (see Genetic Variation in the Global Population). To avoid inbreeding depression within the sub-populations, new specimens should be introduced. These specimens do not necessarily have to be imported from the wild. Migration between sub-populations will increase genetic variation sufficiently. Since genetic drift is a random process, the qualitative effect will differ in each sub-population. In different sub-populations different alleles will get fixed. In the red panda population, the percentage of natural genetic variation

in the global population is larger than the arthimetic mean for the sub-populations (Table 1). This implies that there is tendency towards the fixation of different alleles in each sub-population. Migration between sub-populations will result in a better distribution of the various alleles over the global population. This means that the percentage of natural genetic variation in the different sub-populations will increase. It is therefore desirable to implement a migration program between the sub-populations.

Migration Program

In order to illustrate the results of a migration program on genetic variation at a regional level, the results of a simulation program are presented here.

The main goal of this migration program is to increase the percentage of natural genetic variation in the Australian population. The future survival of this regional population is in jeopardy as genetic variation in the F3 generation is 76%—this is very much lower than the 90% suggested. The F3 specimens in the Australian population represent only 5 bloodlines (Table 5). Furthermore they are all related to each other (Table 6). New bloodlines have to be introduced into this sub-population in order to avoid inbreeding and to increase the percentage of natural genetic variation.

The F3 specimens in the Australian population represent the bloodlines S,T,U (Table 6). These three bloodlines are not present in the European and North American populations, while U is not present in the British and Scandinavian population. The introduction of Australian F3 specimens will increase genetic variation in the European, North American, British and Scandinavian populations.

The second goal of the migration program is to expand the number of bloodlines in the British and Scandinavian population. This sub-population contains two bloodlines which are not present in the other sub-populations; these could be exchanged for "new" bloodlines.

The migration program proposed involves the introduction of two Australian F3 specimens into each of the regional populations (except for the "Rest" population) and the introduction of 6 specimens, which represent "new" bloodlines, into the Australian population. In addition an exchange of two specimens between the British and Scandinavian and the North American population is proposed. The specimens involved in this migration program are presented in Table 6.

Migration will increase genetic variation in each regional population (Table 6) above the criterion of a minimal natural genetic variation of 90%.

The migration program presented in this section is only an introducing example. The specimens involved are younger than 6 years, non-inbred, and have not yet reproduced. Wild specimens which have not yet reproduced are excluded from the program. These criteria limit the number of specimens which can participate in the migration program . Therefore the introduction of "new" bloodlines into a regional population is limited. Furthermore, the regional populations have only been screened for the presence of bloodlines (Table 5). No account has been taken as to founder representation in each sub-population. A further increase in the percentage of natural genetic variation in each regional population can be achieved by an equal distribution of bloodlines. In this the founder representation in each specimen has to be taken into account. The migration program will be more intensive, in which all potential breeders are involved. However, while an intensive migration program will result in a further increase of the percentages of genetic variation, the regional populations can

still not act as closed breeding demes. Genetic drift in the regional populations will be large, due to the small population size, therefore migration must take place in each generation.

CONCLUSION

The zoo population of the red pandas could be threatened by inbreeding depression in the near future. Although the genetic variation present in the global population on December 31, 1984 might be sufficient to establish a viable population, it gives no guarantee for future survival. In the short term genetic variation will decrease rapidly as the generation groups which represent relatively large genetic variation (wild-caught and F1) die out (Table 2). Genetic variation present in later generation groups (especially F3 and F4) may be insufficient to ensure future survival.

Regional populations cannot act as closed breeding demes. Inbreeding and genetic drift have resulted in low natural genetic variation in these populations.

Increasing effective size by incorporating all potential breeders into the breeding population and by keeping red pandas in pairs, and avoiding inbreeding and migration between sub-populations are the essential measures to reduce genetic loss in the captive population of the red panda.

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