Population Management

Managers as detectives

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Introduction

Red pandas in a zoo are individuals: they usually have a name; they have a history of anecdotes e.g. escaped youngsters that are exploring rail-roads next to zoo grounds; and their well-being and breeding reflects the zoo's success with this species. However, one successful zoo does not a breeding program make. Today, breeding a species is no longer an obligatory attraction for zoo visitors. Breeding has become, in the absence of recruitment from the wild, a vital necessity for zoos to maintain their collections. These collections have an educational value but also serve as refuges and sources for re-introduction for many species. At this point, the world of population management starts. It are not the individual zoo successes that count, but the overall situation in zoos. Red pandas (*Ailurus fulgens*) become a population that is characterized by anonymous numbers rather than by individual animals. A population that needs to be managed.

This paper will illustrate the application of two aspects of population management: demographics and genetics. It will focus on why and how several methods are used rather than presenting mathematical backgrounds of these fields of biology. It emphasizes the understanding of possibilities *and* limitations of population management. Therefore, readers may notice a relaxed approach by using terms like 'about', 'more or less', or 'roughly' even in cases when four digit numbers are available. The sequence of applying various techniques is based on the global zoo population of red pandas. Most analyses have been carried out, unless indicated differently, with the Zooresearch Studbook Management version 1.03 (Princée, 1991). Note, however that most of these analyses are also included in the Single Population Analyses and Record Keeping System (ISIS, 1997).

This paper was originally written in 1991. It is used during training courses of co-ordinators of *European Endangered Species Programmes* (EEPs) of the *European Association of Zoos and Aquaria* (EAZA). The major part of this paper includes analyses that have been carried out to develop a global masterplan for red pandas (Glatston and Princée, 1993). These analyses are based on studbook data as available on 31 December 1990. Although these data may appear to be relatively old and also some new analyses have been introduced, the basic approach in developing population management has not been changed. However, more recent literature references in the field of population management have been included in the text, whenever relevant.

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Why population management?

The word breeding program falsely suggests that its ultimate goal is to breed numbers of animals. The more numbers we breed the more successful a breeding program is likely to be considered. This thought might be a remnant of the initial days of studbooks and breeding programs. These programs mainly focussed on species that were rare in captivity, because they were difficult to obtain from the wild (whether endangered or not). Zoos had to breed these species in order to exhibit them. And, especially those species that were difficult to breed established the thought of success that is linked to numbers.

Nowadays, we are not talking about a handful of breeding programs. More and more global and regional programs are being established for 'zoo' species. The zoo world has limited space for maintaining large numbers of populations of various species. Thus we realize that these species starts to compete for this space. This means that each species has a limited amount of zoo-space. It can never be the goal of a program to wipe out another species from the zoo grounds. In the end, we are not playing evolutionary and ecological games.

The amount of available space is determined by a combination of the number of zoos on this planet (logistics) and the wish and will to maintain and/or exhibit a species (politics, ethics). Together these factors determine the maximal number of red pandas that can be housed. Each animal that is born above this maximum is surplus. Surplus in a sense that there is absolutely no place to house these animals in zoos. Unless, we got rid of other red pandas or of other species. It is beyond the scope of this paper to discuss issues as re-introduction[1] or birth-control. But, intuitively, one could state that as soon as surplus occurs more than occasionally, a breeding program can not be called a success. In other words: breeding (or population size) needs to be managed.

So far, the available space has been briefly discussed. But does this equal the required space? This issue focuses more on the 'quality' aspects than the 'quantity' aspects of a population. Have a look at the faces of red pandas on the cover of the 4th volume of the Red or lesser panda studbook (Glatston, 1987). This illustrates the variety of individual characteristics in wild populations. Since, modern zoos tend to present ambassadors of wild species, they should represent the natural variety. Although, environmental conditions have great influences, the base of this variety is the genetic variation that occurs in a species. Thus, preserving genetic variation is the first premise to maintain 'quality' of our ambassadors.

The 'quality' of a population is not limited to features that are visible for human eyes. For instance, O'Brien *et al.* (1985) clearly showed the value of having variation in genes that are involved in immune defence systems. Lack of such variation, as in the cheetah (*Acinonyx jubatus*), can have disastrous effects on a population in cases of epidemics of new or different (as in zoos) mutant viral strains. Basically, this study showed that preservation of genetic variation is essential for maintaining viable populations. Especially, as such populations are the source for re-introduction.

Small populations, like those in zoos, lose genetic variation in each new generation. Soulé *et al.* (1986) proposed that a zoo population should have at least 90 percent of the genetic variation that occurs in the wild population. These authors provided guidelines

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[1] A proper re-introduction program is not based on surplus animals but on animals from planned breeding combinations.

with respect to minimal population sizes that are required to maintain sufficient levels of genetic variation for 200 years (genetic loss and number of breeders are related). Population sizes depend on number of founders (i.e. wild-born animals that reproduced) and generation time (i.e number of generations that are produced within 200 years). The minimal required space for maintaining genetic variation can be determined with this model.

It must be stressed that Soulé *et al.* (1986) provided a model that is used as a guideline. It is based on a model that assumes equal sex-ratio, equal family size, no generation overlap etc.. Who would be surprised that a real population, like red pandas, would differ from this model? Some of these assumptions may not be valid or not feasible to realize in practice. The pedigree chart of *Ailurus f. fulgens* (Princée, 1988) looks like a complex electronic design for a new computer. It illustrates inbreeding, extreme generation overlap and unequal family sizes. This does not mean that theoretic models should be ignored. Population management of a zoo population is a compromise (or balance) between practice and theory.

Compromises become more clear in another part of population management: avoidance of inbreeding (i.e breeding of family relatives) and optimizing founder representation. Several authors have demonstrated the negative effects of inbreeding in both zoo and laboratory and wild populations (e.g. Ralls and Ballou, 1983; Read and Templeton, 1983; van Noordwijk and van Balen, 1988). Negative effects of inbreeding have also been demonstrated in the red panda population (Roberts, 1982). The main reason for avoidance of inbreeding is to limit the chance that (recessive) deleterious alleles are expressed. Optimizing founder representation is a method to (optimally) preserve genetic variation. It is noteworthy to mention that in this part of population management the individual animal (re-)appears: avoidance of inbreeding and optimizing founder representation can only be achieved when genealogies are known. Genetic models can determine what breeding combinations are important for this part of population management. However, if individual red pandas do not like each other.....

What's going on...

Population biology is a science full of models and formulas. It is attempting to dive immediately into sophisticated analyses. But, does this serve a population manager? It makes no sense in knowing growth rates if information on (current) population size is not available. Furthermore, sophisticated models do not a priori present the truth. The more detailed models we use, the more they require from total numbers and quality of data. Studbooks, the major source for population management, do not always present complete and/or accurate data. Important for population management is to get a 'feeling' for trends that occur(ed) in the population. This 'feeling' helps to interpret results from detailed analyses. A first step in this process is to carry out crude demographic analyses. These analyses are free from any statistical background: they just present observations.

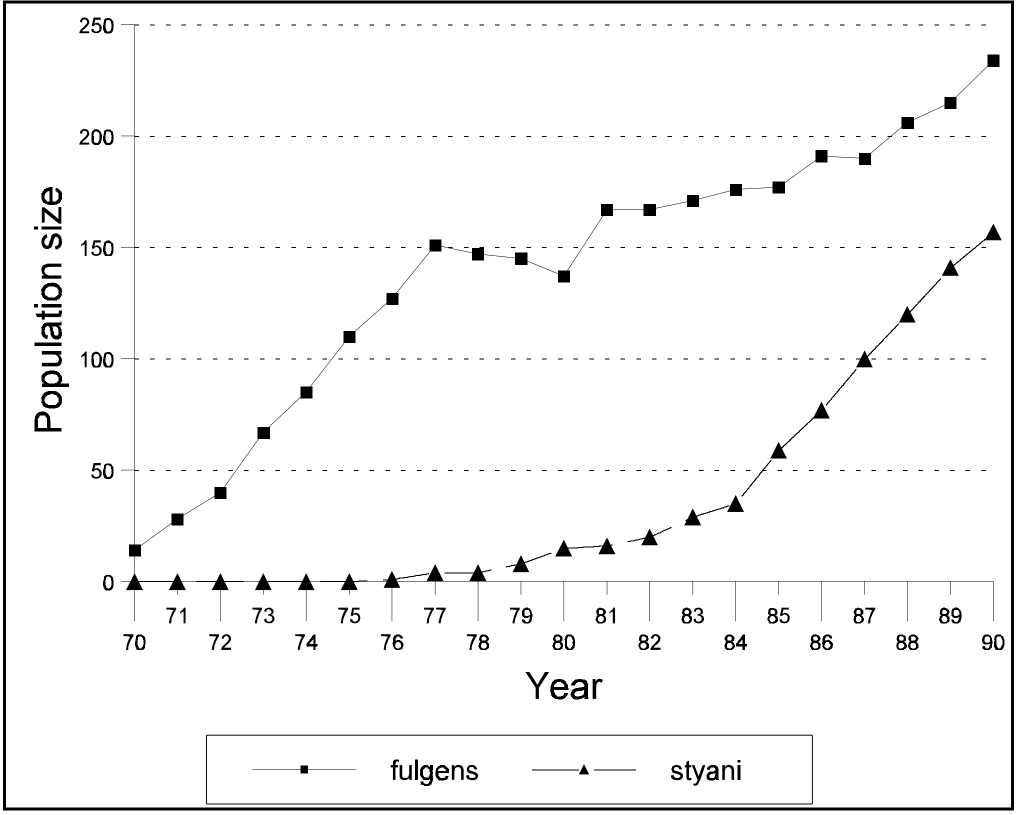

Figure 1 Census at end of each year in zoo populations of the Nepalese red panda (*Ailurus f. fulgens*) and the Chinese red panda (*A. f. styani*).

Census at the end of each year is one of these observations. Figure 1 presents census data for the global studbook populations of *Ailurus f. fulgens* (Nepalese red panda) and *A. f. styani* (Chinese red panda). What do these data tell us? The population of *A. f. fulgens* increased rapidly between 1970 and 1977; a slow growing phase between 1977 and 1988; and an increase in the last two years. The history of the *Ailurus f. styani* studbook population starts somewhere in 1977. But, until 1984, it was a small population. However, since 1984 this population is rapidly expanding. Note that the first edition of the International studbook for red pandas was compiled in 1977. Data from previous years are often difficult to trace. Usually a first edition of a studbook mainly contains data of animals that were alive in the year of survey and data on their ancestors. This implies an under-estimation of actual sizes of the red panda populations before 1977.

Census alone is not a good indicator for breeding success in a population. It does not indicate whether an increase in population size is due to recruitment of the wild or births in zoos. Births, deaths and imports per year should comprise the 'feeling' for trends in

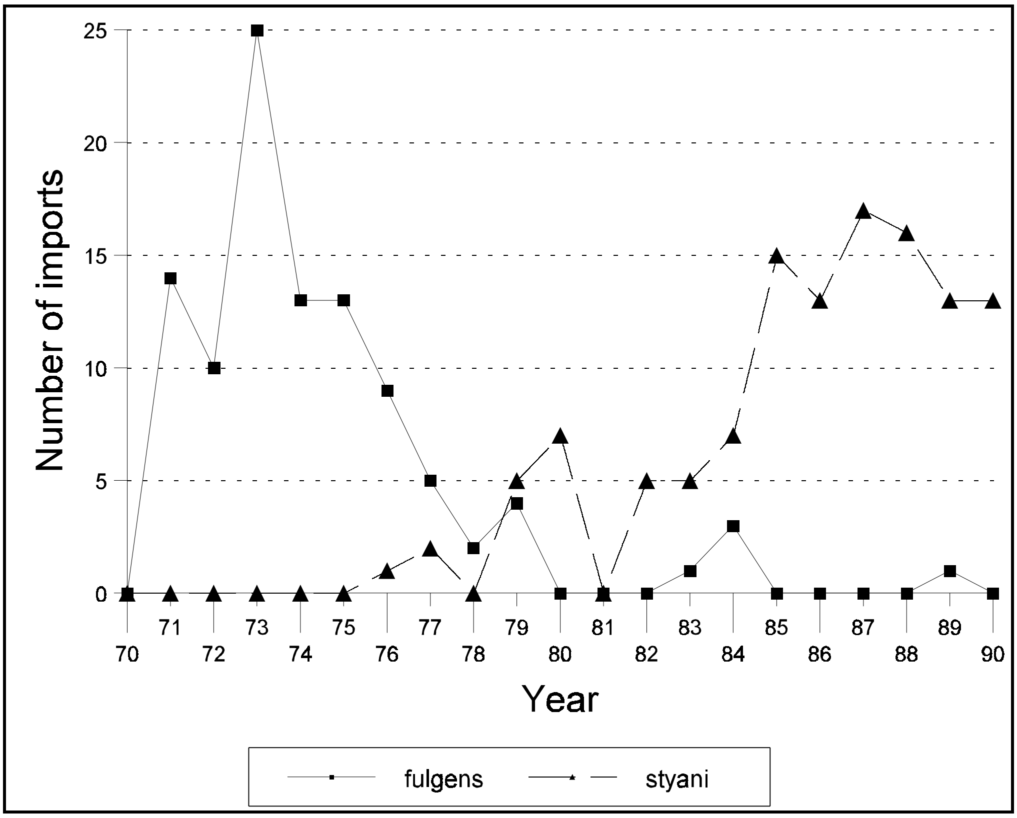

Figure 2 Number of imports of red pandas (*Ailurus fulgens*) from the wild since 1970.

the population. Number of imports from the wild are presented, for both sub-species, in figure 2. Compare these data with the census data in figure 1 and note that imports of *A. f. fulgens* started to decline rapidly around 1977. Since that time population growth is the result of births in zoos. However, recent imports of Chinese red pandas (*A. f. styani*) are the main reason for the rapid increase in population size of this sub-species. This population is in the same phase as its Nepalese relative was during the seventies.

Are we satisfied?

Figures 1 and 2 show that the *A. f. fulgens* population is growing on its own strengths (i.e. by births in captivity) and that we need to wait to follow development of the *A. f. styani* population. It would be wrong to conclude that Nepalese red pandas are doing well. Then, are we really satisfied with population trends in this red panda group? As, mentioned previously, minimal population sizes are required to maintain sufficient levels of genetic variation. Since, the Chinese red panda population mainly consists of wild-born animals we, currently, do not need to worry about genetic variation. But, the Nepalese red panda has been bred for already six generations in captivity. Princée (1989) estimated a minimal population size or *target population size* of 500 individuals for this sub-species (i.e. 125 breeding pairs and 250 offspring) that would be required to maintain 90 percent of the wild genetic variation. This size should be achieved within five to six years (i.e. one red panda generation). The global zoo-population, as on 31 December 1990, consists of 234 animals. So, we are halfway on the road of our genetic goals.

A next step is to determine whether population growth in the Nepalese red panda population is sufficient to meet genetic goals. Thus, a look in the future is required. A quick, but rough, method to determine population growth is using the average birth/death ratio per year. The mean growth in the years 1981 to 1990 is ± 4.5 % per year. Around the year 2004 the *A. f. fulgens* population size is expected to exceed 500 animals (see Figure 3). Birth/death ratios only indicate population growth in the absence of imports and exports. This means that this method would give a rather biased result for the Chinese red panda. Alternatively, the annual *crude rate of change* (CRC) - which is computed as the rate of differences in population sizes between years - can be used. Thus, CRC values also include effects of imports and exports. Note, that projected

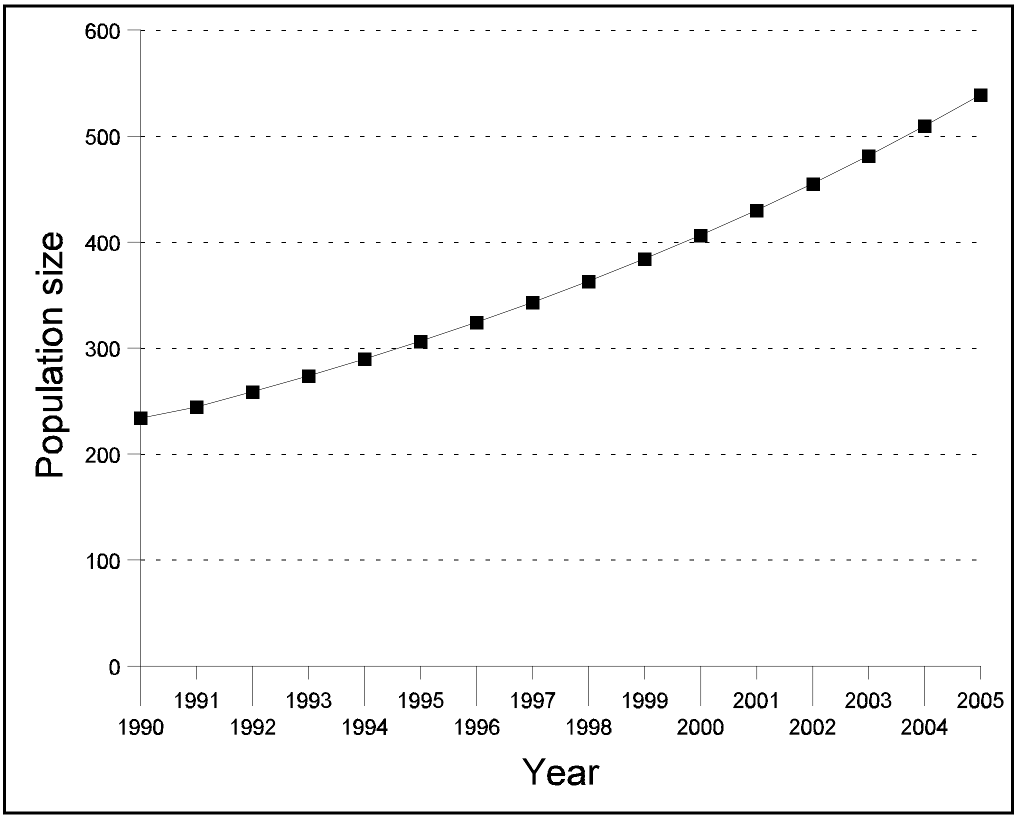

Figure 3 Expected population size of zoo population of the Nepalese red panda (*Ailurus f. fulgens*) based on average birth/death ratio's of 1.045 between 1980 and 1990.

population sizes for future years are *expected* values. This rough method assumes that trends regarding birth/death ratios and/or crude rate of changes do not change in the future. Interpretation of such values will be discussed more extensively in later sections.

Given the rough future projection there is no reason to be satisfied with current population growth in the *A. f. fulgens* population. It takes at least fourteen years (about two generations) before this population reaches its minimal required size. The effect of this slower, than recommended in the guidelines by Princée (1989), population growth on genetic loss will be briefly discussed. Readers are also referred to Soulé *et al.* (1986). First, remind that an objective of genetic management is to preserve at least 90 percent of the 'wild' genetic variation after 200 years. Second, remind that genetic loss is (roughly) related to population size (or better: the number of breeding animals that belong to the same generation group). Thus, the number of generations that occur within these 200 years *and* their sizes determine whether this objective can be achieved.

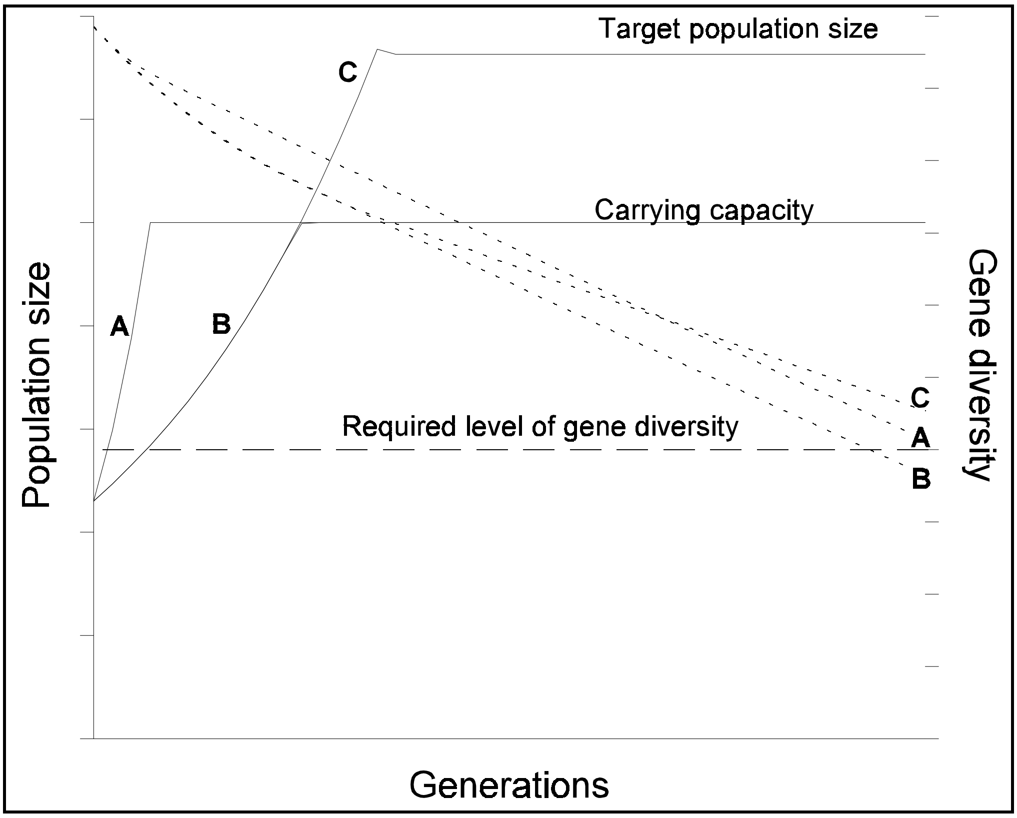

Figure 4 Effect of population growth on preservation of genetic variation in three hypothetical populations A, B and C. Solid lines refer to population sizes ; dotted lines to gene diversity. See text for explanation.

The effects of population growth (and size) on genetic variation are illustrated in figure 4. Population sizes per generation of three hypothetical populations **A**, **B** and **C** are shown as solid lines in figure 4. The corresponding levels of gene diversity which have been maintained in these populations are presented as dotted lines. Population **A** grows very rapidly to the maximal space that is available i.e. *carrying capacity*. This population is managed to be stationary in size after the carrying capacity has been reached. Although genetic variation will still gradually decline at carrying capacity, population **A** will still have enough variation at the end of the 'desired' number of generations. Population **B** has a slower growth rate than population **A** and consequently reaches carrying capacity in a later generation. However, this population has lost too much gene diversity during the initial growth phase to maintain the required level of gene diversity for the 'desired' number of generations. An option to maintain a sufficient level of gene diversity is to allow population **B** to grow above carrying capacity. This strategy requires that the *target population size*, i.e. the population size that is required to maintain sufficient gene diversity for a specific population, is determined. A program like CAPACITY (Ballou, 1992) can be used to compute the target population size. Population **C** in figure 4 illustrates the effect of having population **B** grow to the target population size.

Target population size is a good measure to illustrate whether and how goals regarding minimal levels of gene diversity can be achieved. A target population size that is larger than the carrying capacity indicates that more zoo space needs to be allocated for the population. This can conflict with management programs for other species. Consequently, population growth needs to be increased to reduce genetic loss, within the constraints of carrying capacity, as much as possible. Computer models like CAPACITY can give any answer by manipulating population parameters. However, these answers make only sense when they are based on parameters that reflect the species-specific biology. For example, litter size and gestation length will already determine the maximal population growth.

The crude demographic analyses, as described in the previous section, confirm concerns about optimal husbandry management as is stressed in several papers in editions of the International Studbook of Red pandas. The next section will demonstrate the use of demographics as a tool for analysing and/or detecting specific problems in management of the Nepalese red panda. Result of these analyses will determine whether genetic goals for this species can be achieved.

Playing detective...

The previous section explained that population growth in the Nepalese red panda is not sufficient to meet genetic goals. The first step is to determine whether this slow growth is due to low numbers of births or large numbers of deaths. Figure 5 presents numbers of births and deaths per year in the *A. f. fulgens* population. The population annually produced on the average 22 births per 100 individuals since 1988. If no deaths occurred these births would represent a potential growth of 22 percent per year. Since, population growth is about 4.5 percent per year for the last ten years, death rates in the population (including newborns) must be about 17.5 percent per year.

Considering the fact that twin births occur, less than 22 percent of the population is annually involved in breeding. This gives an impression that breeding success is low. It would suggest that an increase in population growth could be accomplished by optimizing breeding conditions. But, be careful with drawing conclusions from results of crude analyses. For instance, sex-ratio in the red panda population is more ore less equal. This means that annually 22 births per 50 females occur. It implies that, ignoring twin births, almost 44 percent of the females are involved in breeding. Crude analyses will not provide any clue why other females are not breeding. They might be simply too young or too old for reproduction.

More detailed analyses that provide information on ages of animals and fertility in the red pandas are required. This also applies to mortality data. Crude analyses do not indicate whether mortality can be reduced. For this, information on age related types of death are required e.g. juvenile mortality or death in old aged animals (what is old?). Construction of life tables and age distribution are methods that are commonly used to obtain better insight views in demographic characteristics of populations.

Life tables

Intuitively, one can understand that mortality and fertility are related to age. During its lifetime an animal goes through different phases: from juvenile, sub-adult to adult. Juveniles and (often) older animals are physiologically unable to reproduce. Furthermore, risks of death (also in the zoo) may vary throughout different phases of life. Life tables are used to map these differences in age-specific mortality and fertility. A general approach in demography is to categorize a population in *age classes*, e.g. animals of 0 to 1 years old, 1 to 2 years, etc. The width of these age classes is determined by longevity of a species. Using classes of one year for species that have a maximal life-span of two years would hardly provide us information. Weeks or months would be more suitable for short-living species. A rule of thumb is to restrict the number of age classes to 20 (or 10). Mortality and fertility are estimated per age class *and* for males and females separately.

Life tables of studbook populations do not a priori show biological features of a species. Husbandry has a large impact on life tables, e.g. hand-rearing can greatly influence juvenile mortality or curators can decide whether red pandas are allowed to breed. Life tables evaluate zoo management in the past. Having this in mind, life tables preferably should be based on recent data e.g. the last five years. Mortality and fertility rates that are presented in this section are based on events that occurred between 01 January 1986 and 31 December 1991. Such a time-span is called a *window* in demographics. Analyses of the Zooresearch Studbook Management (Princée, 1991) were used to construct life tables for red pandas.

Readers are referred to literature that describe and discuss these techniques more extensively (e.g. Goodman, 1980; Krebs, 1985; Albers, 1989; Begon et. al. 1990). Let it be satisfying that various computerized studbook programs take over the time-consuming job of constructing life-tables.

Mortality rates

The mortality rate (symbol Q_x) of an age class is the proportion of individuals belonging to that age class that die before reaching the next age class. Example: if 20 of 100 newborn male red pandas die within the first year the mortality rate of the first male age class (Q_0) is 0.20. Suppose that 10 males die between 1 and 2 years of age. Since, 80 males survived the first year, the mortality rate for the next class is 10/80 = 0.125.

Figure 5 presents mortality rates in *A. f. fulgens*. Note that the first age class (from 0-1 years) in these figures is indexed as zero (Q_0). The following trends can be observed in mortality rates: mortality in the first year (class 0) is high (0.32 and 0.38 for females and males, respectively); mortality rates for age classes 1 to 9 vary around 0.05; and mortality rates increase, as expected, for higher age classes (i.e. older animals). One might be surprised that the mortality rate of the last age class is not 1 (or 100%). In the end, red pandas are not immortal. This effect is due to the use of a limited number of years of observations (i.e. the demographic window). All animals that were alive at the begin of the window (i.e. 1 January 1986) and all animal that were born before the end of the window (i.e. 31 January 1991) are included in the calculations. The last age class is based on the oldest *observed* age at death or age of living animals between 1986 and 1991. A number of animals that belong to the last age class were still alive as on 1 January 1991. Therefore, mortality rates of these last age classes are lower than 1.0.

Figure 5 Mortality rates in zoo population of *Ailurus f. fulgens.* in the period 01 January 1986 to 31 December 1991. Class width is one year.

Juvenile mortality

Reducing juvenile mortality is, in terms of demographic management, an effective way to increase population growth. At the same time, solving problems in juvenile mortality points to husbandry rather than demographics. High juvenile mortality is not a new phenomena in red pandas (see Roberts, 1982; Glatston and Roberts, 1988; and Glatston,1989). In this, demographics serve as an analytical tool to quantify the negative effects of juvenile mortality on maintaining a self-sustaining population.

The analytical power of demographic techniques can also serve to indicate fields of possible causes of juvenile mortality. Considering the variety of biological and veterinary disciplines that may be involved in husbandry, efficiency in problem solving may be required. Abortions and stillbirths may indicate other problems than deaths that occur at the end of the first year. Therefore, calculation of mortality rates based on smaller classes e.g. months, weeks or days may be more indicative. Mortality rates for different time intervals and class widths are presented in figure 6.

Figure 6 shows that juvenile mortality mainly occurs in the first month after birth (class M0). A further fine-tuning to the first month after birth reveals that major mortality occurs in the first week (class W0). Finally, figure 6 shows that we can restrict major causes of juvenile mortality to the first three days, including abortions and stillbirths (classes D0 to D3). At this point the detective role of demographers, with respect to mortality, stops and pathologists take over. Post-mortem reports should reveal whether causes of death are due to e.g. congenital factors, are due to insufficient mother-care or are disease related. The geneticist can also play a role: Roberts (1982) demonstrated an increased juvenile mortality in inbred red pandas.

Figure 6 Juvenile mortality rates in the zoo population of *Ailurus f. fulgens* in the first year (class width is 30 days), in the first month (class width is 7 days) and the first week (class width is 1 day). Data have been extracted from the studbook for the period 1 January 1986 to 31 December 1990.

Fertility rates

Crude analyses give a rough impression of breeding success in the Nepalese red panda population. Results from these analyses are not sufficient to indicate whether it is feasible to improve breeding success. It was only possible to speculate that females which did not reproduce may be too young or too old. Age-specific fertility rates provide more detailed information on reproduction. The fertility rate (symbol M_x) of an age class is the proportion of number of offspring that are born from parents of the same sex that belong to that age class. Example: 100 female red pandas between 5 and 6 years produced 20 daughters. The fertility rate of this age class (M_5) is 0.20.

Figure 7 Fertility rates in the zoo population *Ailurus f. fulgens* in the period 1 January 1986 to 1 January 1991. Class width is one year.

Figure 7 present fertility rates for males and females. Reproductive life-span in red pandas stretches from 1 to 14 years for males and from 1 to 10 years for females. However, more important information is provided by fertility tables. First, they show that reproductive success differs per age class. Second, reproductive success is not randomly distributed over age classes, but follows a distinct pattern. Have a close look at fertility rates in females (Figure 7). Notice the curve in fertility rates: an increase from age class 1 to 6 followed by an decline. The curve in fertility rates in males is less obvious. There seems to be two curves: one from class 1 to class 7 and one from class 7 to 11.

These two curves not necessarily reflect biological features. First, zoo managers can decide at which age red pandas are paired. Furthermore, life tables in studbook populations are based on relatively small numbers of data. The second curve in male fertility rates may be due to small sample sizes. For example, the high fertility rate in male class 14 may be due to the 'odd' case where a single surviving animal produced offspring.

Reliability

Studbooks are general small in size, rarely exceeding a thousand animals. Furthermore, the number animals that are included in lifetable analyses are restricted by the time window or other view settings (for example to animals born in Europe). Clearly, the number of animals included in these analyses (i.e. sample sizes) determine the reliability. Bingaman and Ballou (1996) present the following rough guideline: sample sizes per age class of less than 10 animals at risk may result in useless results, 10-30 in potentially misleading results, while sample sizes > 30 may be useable. Mortality and fertility rates of especially older age classes tend to be based on small numbers of animals. Therefore, these rates are less reliable than those estimated for younger age classes. A common technique in demographics is to lump the older age classes into one class.

A technique called '*smoothing*' (Tukey, 1997) is applied in the program DEMOG (Bingaman and Ballou, 1996). This technique involves smoothing of data by running medians of threes (i.e. age classes). For example, the smoothed Qx for class 2 would be the median of class 1 to 3. Readers are also referred to Gage (1995), Taylor and Barlow (1995) and Taylor *et al.* (1995) for discussion of smoothing and other techniques.

Litter size

After describing and discussing fertility rates the major question whether reproduction can be improved is still not answered. Fertility rates in females suggest that at the 'optimal' reproductive age, i.e. class 6, one female offspring is born per two females (M_{f6}=0.5) or, assuming equal sex-ratio at birth, one offspring per female. Since red pandas produce, as seasonal breeders, one litter a year this seems to be a high rate. Still, in the absence of data on litter sizes it can not be concluded whether the fertility

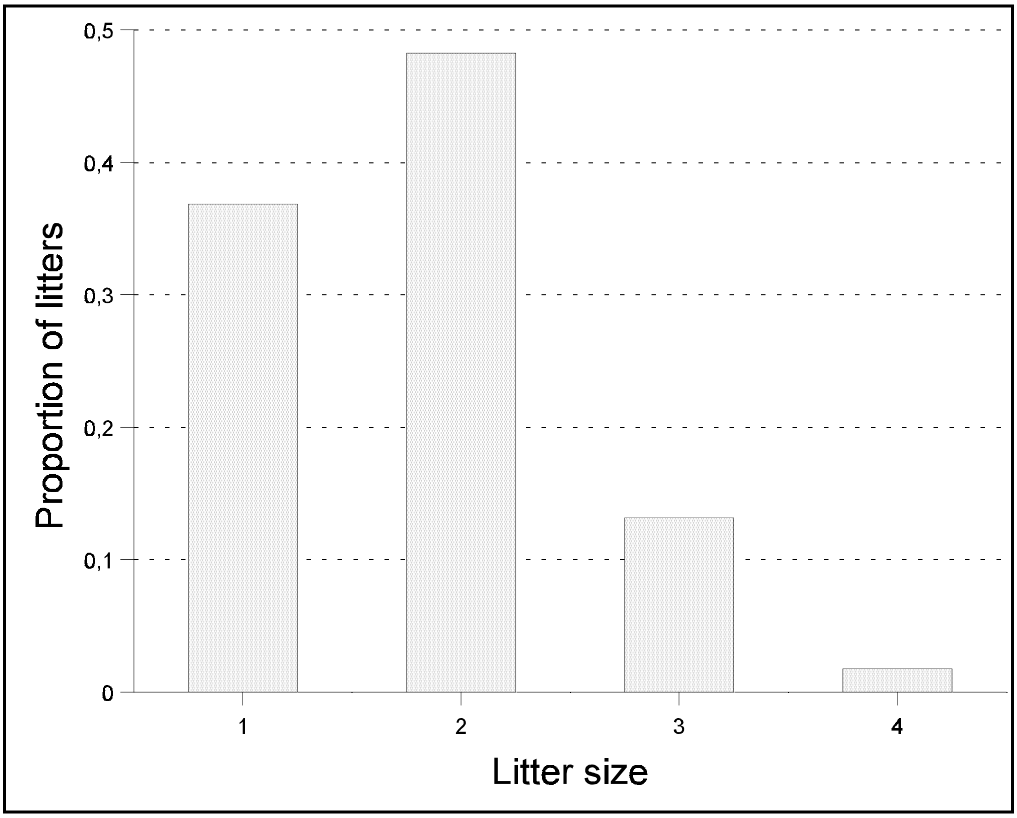

Figure 8 Frequencies of litter size in the zoo population of *Ailurus f. fulgens* (N=114).

rate for age class 6 is reasonable. Figure 8 presents percentages of litter sizes that were observed between 1 January 1986 and 31 December 1990 (*N*=114). Thirty-seven percent of the litters consist of one offspring; 48 percent of twins, 13 percent of three offspring and 2 percent of four offspring.

The distribution of litter sizes allows to determine the maximal fertility rate for an age class. Assume that age class 6 consists of 100 females which all reproduce. According the observed distribution 37 females will produce litters of one (i.e. 37 offspring), 48 females will produce twin litters (i.e. 96 offspring), 13 females produce litters of three (i.e. 39 offspring) and 2 females produce a litter of four (i.e. 8 offspring). This means that these 100 females are expected to produce a maximum of 180 female offspring. The maximal fertility for this female age class could be 0.90 (daughters per female). This is almost twice as high than the observed value for age class 6 in the period 1986-1990.

Maximal fertility rates, as estimated for female age class 6, can only be achieved if zoo management would be the only limitation in reproductive success. But, as mentioned previously, fertility tables are combined results of reproductive biology (e.g. social and physiological features) and zoo management. A study to distinguish between effects of both fields would involve tracing breeding situations for every individual red panda. Furthermore, relations between age and litter size, relations between litter size and survival and inter-birth interval need to be studied. Even in a decade of computerized studbooks, such a study may be a time-consuming job. Therefore, effects of increasing fertility (and decreasing mortality) rates on population growth should be evaluated. The following section will illustrate these effects.

A look in the future...

Birth-death ratios, obtained from crude analyses, can be used to predict population size in future years (see figure 3, page 6). This method is useful in obtaining rough impressions of future prospects for populations. Unfortunately, its results can be misleading. First, no imports or exports should occur. Second, age distribution in the population should be stable. Population growth in a population may for instance be limited to older wild-born individuals. Zoo populations do not, especially in the first years, tend to follow these conditions. Furthermore, this method is not suitable to study effects of age-specific mortality rates and fertility rates on population growth. Therefore, more sophisticated methods are required for future projections.

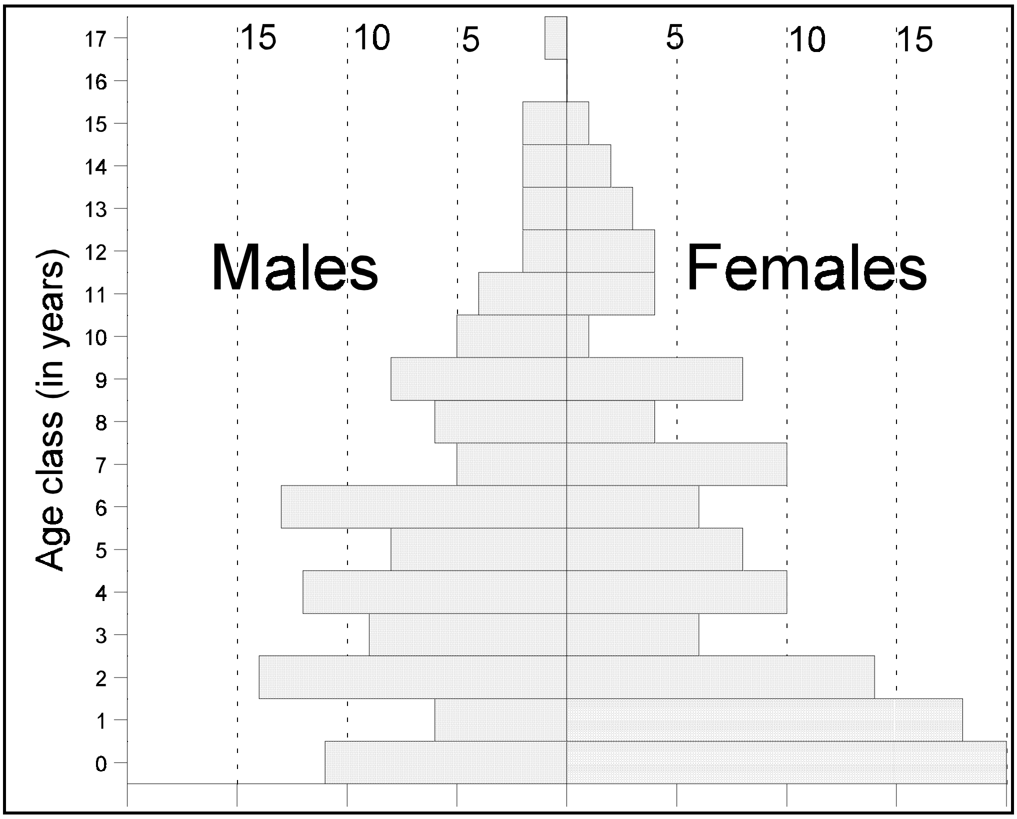

Figure 9 Age distribution in the zoo population of *Ailurus f. fulgens* as on 31 December 1990. Numbers of red panda per age class are indicated next to dotted lines.

Leslie matrices (Leslie,1948) are in common use to estimate future population sizes. This technique uses life tables and age distribution. Life tables for red pandas have been described and discussed in the previous sections. Age distribution is basically nothing more than counting living males and females per age class. Figure 9 presents male and female age distribution for Nepalese red pandas as on 31 December 1990. Analysing shapes of age distributions can be considered as a type of crude analyses. Pyramid shapes, (i.e. younger age classes are larger than older age classes) indicate that a population is either stable in size or growing.

The methodology behind Leslie matrices is relatively simple. Starting with the age distribution at last census date, the number of animals that are expected to survive to the next year (i.e. age class) can be computed from the mortality tables. The number of births that are expected within a year can be computed on the basis of fertility tables for

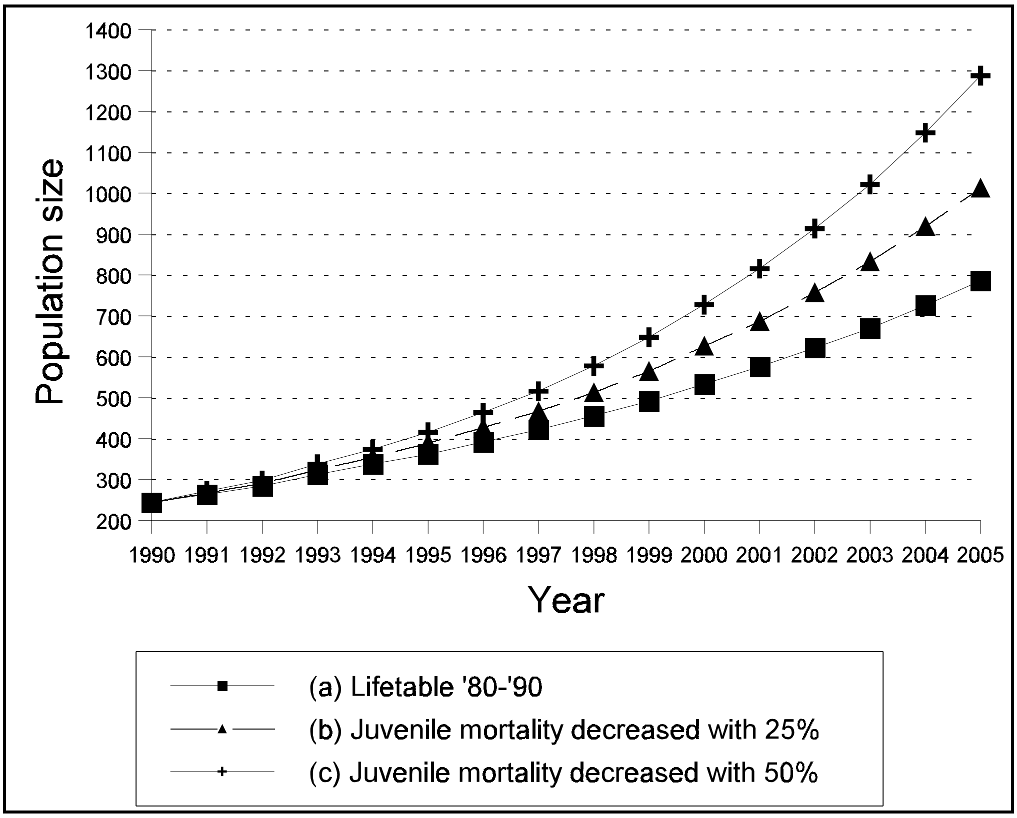

Figure 10 Effects of reducing juvenile mortality on population growth in the zoo population of *Ailurus f. fulgens*. See text for details.

each age class. Traditionally, wildlife managers and ecologists only use female age distribution and female life tables in future projections (see e.g. Caughly, 1977; Krebs, 1985). Total expected population sizes can be computed as, assuming equal sex-ratio, twice the female population size. This approach is also used in the following future projections.

Effects of manipulating mortality and/or fertility rates can be evaluated with Leslie matrices. Figures 10 and 11 present future projections of *A. f. fulgens* for different assumptions on fertility and/or mortality rates.

The population size that is required to preserve 90 percent of genetic variation in 200 years is established after 10 years for rates of fertility and mortality as estimated for the period 1980-1990 (figure 10). The two years difference with the value estimated from birth/death ratios (figure 3) is partly due to the fact that population growth in females is larger than male population growth. Furthermore, the average of male and female birth/death ratios between 1980-1990 is used. This also results in a lower annual growth rate.

Reducing juvenile mortality rate (i.e. M_0) with 25 percent results in establishing the required population size in 8 years. (see scenario b, Figure 10). A population size of 500 can be reached in 7 years if juvenile mortality can be reduced with 50 percent (see scenario c, Figure 10). Same results can be achieved by increasing the overall fertility rates (see scenarios’ d, e and f, Figure 11). Increasing current fertility rates by 10% can be compared with a 25 percent decrease in juvenile mortality. An increase of 25% in fertility equals the result of an 50 percent decrease in juvenile mortality. A combination of 25 percent decrease in juvenile mortality and 10 percent increase of fertility rates will result in 500 red pandas in 7 years. Note that increasing breeding success of females in

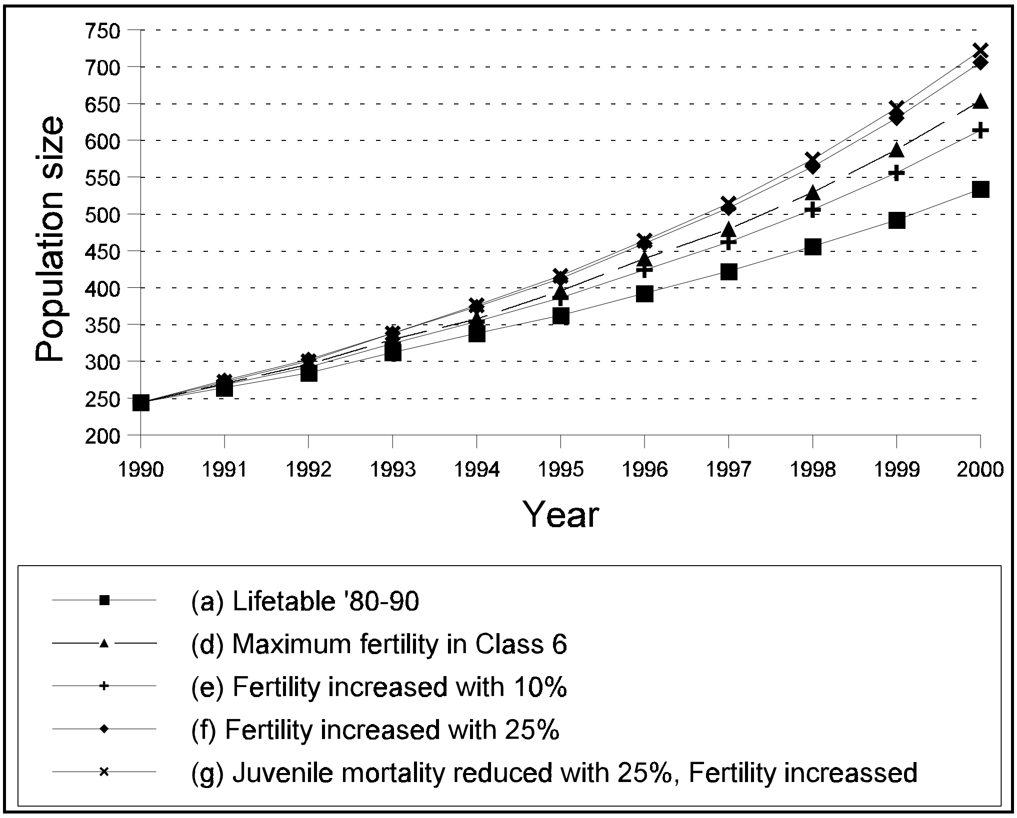

Figure 11 Effects of reducing juvenile mortality and/or increasing fertility on population growth in the zoo population of *Ailurus f. fulgens*. See text for details.

age class 6 to the theoretic maximum rate of 0.90 has a same effect as increasing the overall fertility by 10% (see Figure 11).

Given the difference between the observed and the theoretic fertility rate in age class 6, increases of 10 and 25 percent for all age classes seems to be low. However, it is to husbandry whether reducing juvenile mortality and/or increasing fertility is feasible. These future projections only show potential effects of measures in increasing population growth significantly.

A different future?

Some general comments need to be made on use of future projections in demographic management. Population sizes as shown in figures 3, 10 and 11 are *expectations*. Life tables in future projections are probabilities. A juvenile mortality rate of 0.38 means that every newborn has a *risk* of 38 percent to die in the first year. Fertility rates present the average number of offspring that are born per individual (of the same sex) in a specific age-class. But, as shown in figure 8, probabilities are also involved in litter size, varying from 0 to 4 offspring per female. Unfortunately, Leslie matrices do not support the use of probabilities in litter size. For this, so called stochastic demographic models are required.

Life tables are, as is stressed in previous sections, based on conditions that occurred in the past. Changes in management can largely influence population growth and, therefore, make a future projection, based on current conditions worthless i.e. actual population growth will differ from expected growth. This effect is clearly illustrated by future projections that are based on manipulated fertility and mortality rates in figures 10 and 11. Furthermore, all kind of known and unknown *stochastic* (i.e random) processes can occur, e.g. skewed sex-ratio, annual variation in mortality and fertility, or catastrophes such as extreme hot summers. These processes can influence, whether temporary or not, population growth. In this, the stochastic computer model VORTEX (Lacy, 1993), which is generally used within the context of wildlife a management, could also applied in zoo management.

The following basic guidelines should be followed in applying future projections: (1) base life tables on the most recent 'zoo' conditions, e.g. past five years; (2) do not base management measures on long-term future projections and (3) repeat future projections on a (bi)annual base to evaluate changes in husbandry and effects of stochastic processes (that have occurred).

Avoidance of inbreeding

Inbreeding can increase juvenile mortality and reduce fertility (see for example Roberts, 1982; Ralls and Ballou, 1983; Ralls *et al.*, 1988; Laikre and Ryman, 1991; Lacy et al., 1993) and, therefore, can negatively influence population growth. As soon as (small) populations decrease in size, inbreeding levels will automatically increase. This can result in a further decline in population growth. The population may come in a irreversible process of extinction. This over-simplified model illustrates the interaction between genetic and demographic management: inbreeding can directly influence the future of a population!

Table 1 Inbreeding coefficients for hypothetical matings in the zoo population of *Ailurus f. fulgens*. Numbers of males and females refer to studbook codes. This table was generated with GENES (Lacy,1994).

Females	**Males**						
	8811	8822	8814	8813	8835	8818	8829
8802	0.0293	0.0274	0.0498	0.0498	0.0567	0.0274	0.0098
8863	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
8864	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
8824	0.0450	0.0430	0.0684	0.0684	0.1046	0.0625	0.0664
8810	0.0508	0.1055	0.0948	0.0948	0.1602	0.0587	0.0118
8809	0.0274	0.1797	0.0733	0.0733	0.0684	0.0352	0.0156
8812	0.2578	0.0274	0.0400	0.0400	0.0518	0.0821	0.0215
8827	0.0410	0.0274	0.0479	0.0479	0.0518	0.0508	0.0664
8823	0.0274	0.3008	0.0733	0.0733	0.0684	0.0352	0.0196

Inbreeding coefficients for hypothetical matings can be easily calculated from additive matrix analyses (Quaas, 1976; Henderson, 1976). See also Ballou (1983) for an illustrative explanation of this technique. Current studbook software provide facilities to calculate inbreeding coefficients, either using the additive matrix technique or the GeneDrop model (MacCluer *et al.*, 1986). Using these tools, tables of mating combinations can be constructed. Table 1 presents a part of mating tables for red pandas as produced by the computer program GENES (Lacy, 1993). Such tables allow species managers to recommend breeding pairs that are composed of unrelated animals. This table already illustrates that a number of animals can not be paired unless inbreeding is tolerated. Before discussing the practical implications of pair recommendations some notes on inbreeding have to be made.

Inbreeding coefficients are no magic numbers with vague defined levels of acceptation or rejection. These values are probabilities (or risks) that two alleles on a locus originate from one ancestor. Assume, that this ancestor is heterozygous for an unique recessive deleterious allele. The only other animals that can possess this allele are descendants from this ancestor. The only animals that can be homozygous for this 'family' allele are offspring of family related parents (thus inbreeding). Since, heritage of alleles is, according Mendelian segregation, a matter of chance, inbred animals do not a priori posses this rare recessive allele (either in heterozygous or homozygous state). Inbreeding coefficients indicate the risks that an (inbred) animal will be homozygous for this deleterious allele: e.g. offspring of siblings have a chance of 25 percent (f=0.25) of being homozygous. The effect of expression of deleterious alleles is called inbreeding depression.

Given the fact that inbreeding coefficients are risks, levels that can be tolerated are a matter of taste: do we accept risks of 1, 5 or 7.978 percent? In this, it must be mentioned that, low inbreeding coefficients must occur in natural populations since they are not infinitely large. It is also important to stress that inbred animals should not be condemned as not important for a breeding program. Certainly, inbreeding may have affected fitness of these animals. But, as long as they can reproduce, pairing with unrelated partners will reverse the risk on inbreeding depression. However, unnecessary risks in species management, like inbreeding, should be avoided or kept to minimal levels whenever possible. Breeding schemes, that are called Maximal Avoidance of Inbreeding (*MAI*), have been developed to keep levels of inbreeding in small populations as low as possible (e.g. Flesness, 1977; Princée, 1986; 1995).

Given the previous comments, combinations in table 1 that result in inbreeding are not preferred. Fortunately, this table only presents matings between yearlings that are born in 1988. This means that combinations with older animals (that are in reproductive ages!) or younger animals may be possible. In this, features of social and mating structure of red pandas are important. Differences in ages between male and female may play a role in reproductive behaviour. Re-arrangement of breeding pairs in favour of avoidance of inbreeding may have reverse effects on reproduction or it may even stimulate reproduction. These factors have to be taken into account in implementation of breeding recommendations. Furthermore, it is important to create breeding situations before red pandas reach their optimal reproductive age (see figure 7). This makes it possible to evaluate social behaviour of pairs and, when necessary, re-arrange non-reproducing breeding pairs.

Preservation of genetic variation

The basic philosophy behind preservation of genetic variation is that all alleles that occur in a natural population are important for adaptation to long-term *and* short-term environmental changes. Humans tend to classify certain genetic characteristics as disadvantageous. This is fundamentally wrong since we can not foresee the future: alleles that are deleterious today may be advantageous tomorrow. The example of sickle-cell anaemia in human populations in East-Africa illustrates that deleterious alleles can be advantageous in for example heterozygous state (Harris, 1980). The important goal of genetic management is to preserve as much of the natural genetic variation in zoo populations as possible. In this, not only the number of different alleles but also their frequencies in the wild population need to be maintained.

Good or bad?

An important guideline in genetic management is to avoid selection against alleles that WE consider disadvantageous or vice versa to avoid selection in favour of "advantageous" alleles. We are not only unable to decide what is good or wrong but fitness of individuals is also determined by composition of the entire genome rather than one (dis-)advantageous allele. This means that selection against one allele can result in losing a number of "advantageous" alleles. Unintentional selection can not be avoided as zoo conditions have to be considered as an (short-term) environmental change. New selection pressures start at the day wild-born animals are captured, transported and brought into zoos. Those wild-born red pandas that survived and reproduced may (genetically) be better adapted to zoo conditions. This would imply that genetic characteristics that are only advantageous under natural conditions *and* highly disadvantageous under other conditions are lost. Unfortunately, hardly anything can be done to prevent this type of selection. This is an argument to store sperm and/or embryos of wild-born red pandas that do not reproduce themselves. "Wild" alleles in the population can be restored at the time re-introduction is considered feasible. This approach may be appropriate for the *A. f. styani* population that is composed of a relative large number of wild-born animals that have (yet) not reproduced.

All founders are equal

Genetic characteristics of individuals and populations are, except for some strains of laboratory species, completely unknown. This seems to make preservation of natural genetic variation a rather obscure part of population management. However, we can follow, in the absence of hard genetic data, a preventive approach and assume that each wild-born red panda has an unique genome. This approach involves management that aims at an equal representation of the genome of these wild-born animals in their descendants in each zoo-born generation. This means that each founder (i.e. a wild-born animal that has produced offspring) and its descendants in following generations should produce equal numbers of offspring. In reality, this is hardly the case. Each zoo population has its own history where some zoos were successful in breeding while other zoos were still struggling in keeping a species alive. Nowadays, exchange of information on husbandry, for example by a studbook, has given each zoo the potential for successful breeding. Unfortunately, a breeding program inherits the history of a population. Effects of this history on genetic composition of the population needs to be evaluated. The same methods that were described for calculation of inbreeding coefficients (i.e. additive matrix or GeneDrop simulations) can be used to determine

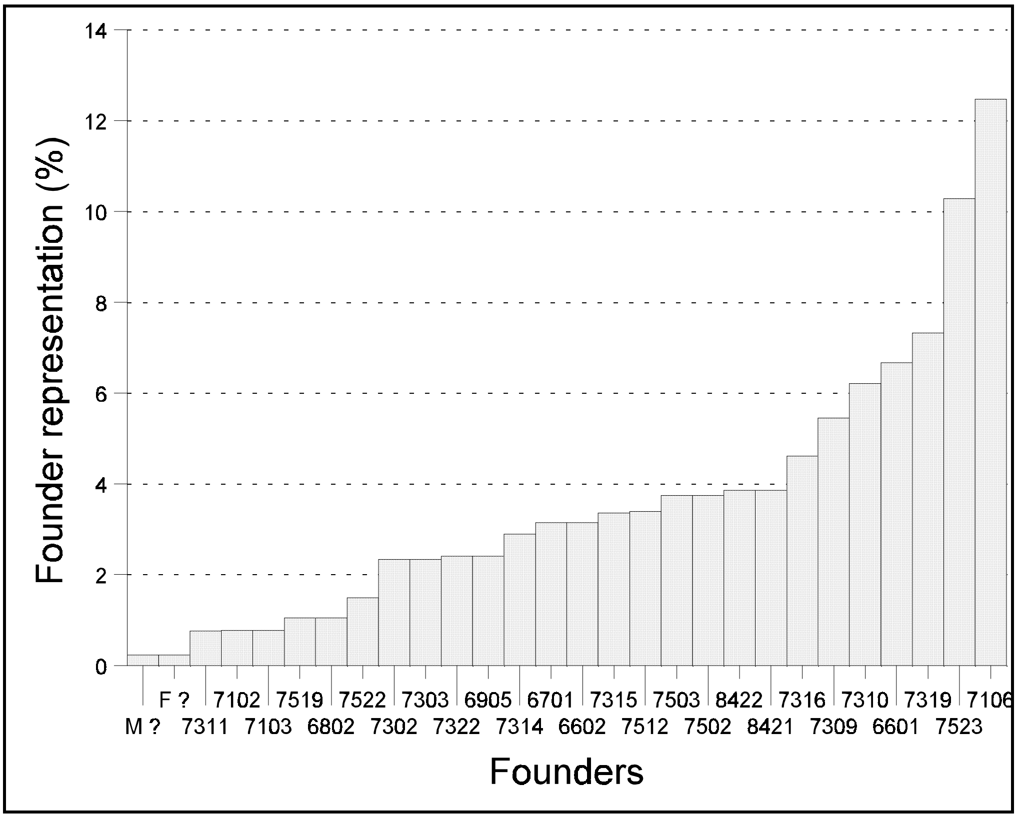

Figure 12 Founder representation in the global zoo population of *Ailurus f. fulgens* as on 31 December 1991. Numbers refer to studbook codes of founder individuals. Codes M? and F? refer to contribution by unknown sires and dams, respectively.

founder representation in the population.

Figure 12 presents founder representation in the global population of *Ailurus. f. fulgens* as on 31 December 1990 (Note that only the sequential part of the studbook code is used in this figure). The history of the red panda population is reflected in this figure. A small group of founders is highly over-represented in the population. These animals and their descendants refer to a small number of zoos like the National Zoo and Rotterdam Zoo that were successful in breeding red pandas since the early seventies. Exchanges of zoo-born animals were initially limited to zoos that already had reproductive success with red pandas. This, of course, increased the contribution of a small number of founder lineages to the zoo population. However, do not forget that population management was not introduced in the zoo world until the eighties. Many zoo populations will show the same features as the red panda population. This species is certainly not an extraordinary example of zoo history.

Genetic management often involves corrections of measures that have been taken in the past. A next step is to develop a management plan to equalize founder representation. The emphasis of such a plan is to breed all living wild-born animals that have never reproduced (potential founders) and all offspring of founders that are under-represented. Potential founders can be easily traced from the studbook. Offspring of under-represented (non-living) founders are more difficult to trace. Founder representation in each living individual need to be determined by using the previously described methods. However, evaluation of importance of individuals for a breeding program is a complex job for (relatively) large populations: some individuals may descent from ancestors that are under-represented *and* ancestors that are over-represented in the population.

Table 2 Example of report of program GENES (Lacy, 1994) presenting mean kinship values in male and female *Ailurus f. fulgens* ordered by rank. Numbers of males and females refer to studbook codes.

Rank	Males	Mean kinship	Known genome	Females	Mean kinship	Known genome
1	7602	0.0000	1.0000	7916	0	1.0000
2	7915	0.0000	1.0000	8932	0.0000	1.0000
3	8421	0.0000	10000	7704	0.0053	1.0000
4	8101	0.0119	1.0000	7601	0.0116	1.0000
5	8105	0.0149	1.0000	8422	0.0150	1.0000

Species co-ordinators of large populations who had to puzzle for days on breeding recommendations continued to study and develop new methods. One of these methods is to determine important animals by calculation of *mean kinships* (see e.g. de Boer, 1990; Ballou and Lacy, 1995). Mean kinship can be described as the mean genetic (family) relatedness (or *kinship coefficient*) between an individual and all other living individuals in the population (including itself). Individuals with mean kinships of zero have no living relatives in the population. They are either wild-caught or single descendants from founders. Table 2 presents the top five of genetical important males and females in the *A. f. fulgens* population as on December 1990. Breeding recommendations are based on pairing the highest ranking male with the highest ranking female, the second ranking male with the second ranking female, etc.. Mean kinship tables do not indicate whether two breeding partners that both have a mean kinship larger than zero are related (e.g. male 8101 and female 7601 in table 2). This means that inbreeding coefficients should be calculated for such breeding combinations. The entire mean kinship table is checked, starting with the top ranking males or females, until an acceptable partner is found. Thus, in the case that combination 8101 x 7601 would result in inbreeding the next combination, i.e. 8101 x 8422, will be evaluated.

Male 7601 and female 7602 both have high ranking positions in the mean kinship tables. However, given data on mortality and fertility (see figures 5 and 7) these animals have belong to the postreproductive age classes. Thus, it would be doubtful to include these animals in breeding recommendations. Since mean kinship does not consider age, this measure will also not detect the genetic importance of an individual that only has relatives in the postreproductive age classes. A way to tackle these problems is to weight mean kinship values for reproductive value. This measure is the expected number of offspring that an individual of a given age is expected to produce until the end of its life-span. This measure combines the risk to die and the chance to reproduce. Ballou and Lacy (1995) have combined mean kinship and reproductive values in the measure *kinship value*. This measure has ‘taken over’ mean kinship. The program DEMOG (Bingaman and Ballou, 1996) produces Fishers reproductive values which can be included in the program GENES (Lacy, 1994). Note, however that the validity of reproductive values depend on the quality of life tables.

Although, mean kinship tables are primarily developed to serve genetic management they can be very indicative for husbandry. Individuals that have never reproduced or have no living descendants will have low values for mean kinship (thus, high ranking positions in mean kinship tables). Therefore, histories of these individuals should be evaluated prior to any breeding recommendation.

Following these guidelines can result in a more balanced founder representation in the red panda population. However, it is must be stressed that it will be virtually impossible to equalize founder representation. First, founder genomes have been lost e.g. non-living founders that have produced one offspring. Second, animals that are important for the breeding program may descend from under-represented lineages *and* over-represented lineages. Third, it is disputable to exclude animals with over-represented lineages from breeding in a population with insufficient reproductive success that needs to grow rapidly. Last but not least, individual red pandas do not bother about our beautiful management plans...

Measures of genetic variation

The objective of genetic management is to preserve as much of the original genetic variation that exists in a wild population as possible. This leads us to the question what is genetic variation? The term 'unique genome' may have suggested that each individual has unique allelic variants at each locus. It would be attempting to describe genetic variation in terms of allelic variants. In that case genetic management should aim at preserving at least 90 percent of the allelic variants that occurred in the wild population. However, a large number of allelic variants in a population are shared by several individuals. Some of these variants occur in high frequencies and are, therefore, shared by the majority of individuals, others are rare (even individual specific). Electrophoretic studies as e.g. in the red panda (Gentz, 1989) illustrate this.

Differences in allele frequencies are the result of selective forces in the original habitat. (genetic drift plays a more important role in neutral selective alleles). Conservation of a species means that as much of the original genetic composition of a wild population is preserved. This means that both the number of allelic variants and their frequencies are important. Any shift in allele frequencies at a certain locus, even without actual loss of allelic variants, can be considered as genetic loss. A measure that expresses this genetic composition of a population is required for genetic management.

Gene diversity or *average expected heterozygosity* (Nei, 1975) is a measure of genetic variation that is based on numbers of allelic variants per locus and their frequencies. It is calculated as one minus the sum of squares of allele frequencies at a given locus. The average gene diversity in a population is the sum of gene diversity at all loci divided by the number of loci. This measure has been discussed by Allendorf (1986) as it can 'honour' a gene with two equally distributed allelic variants with higher values than a locus with one common allele and several rare alleles. A measure like the number of polymorphic loci is more sensitive for rare alleles but would not indicate changes in frequencies.

The basic lesson that can be learned from these discussions is that genetic variation can not be described by one measure. Therefore, genetic management should not be restricted to the use of one measure or one method. Especially, since most of the zoo populations do not fit in the model of ideal (i.e. Hardy-Weinberg) populations, several measures need to be used. For example: gene diversity is under random mating conditions equal to the proportion of heterozygous loci. However, gene diversity is not equal to the observed proportion of heterozygous in populations that are divided in regional sub-populations like the red panda (see for example Princée, 1988, 1995). A strategy based on equal founder representation enhances the chance that rare alleles and original frequencies of alleles are preserved. However, founder representation itself does not inform us on genetic variation in terms of numbers of allelic variants and their frequencies. Models that determine genetic drift based on effective population size are used to obtain this information.

A leaking gene pool

Small populations will loose genetic variation in each generation due to genetic drift. This loss occurs due to the random character of Mendelian segregation. Fir example: an individual that produces two offspring will on the average pass 75 percent of its genome to the next generation. Thus, by chance 25 percent of this individuals genome is lost (see for more detailed information de Boer, 1990). The total loss in a population, due to genetic drift, is lower than the loss per individual as allelic variants are shared by other individuals. Effective population size that is calculated from the total number of breeding individuals and number of offspring per individual determines genetic drift (see for example Frankel and Soulé, 1981; Lande and Barrowclough, 1987).

Values for effective population size are difficult to calculate for populations with non-random mating systems and generation overlap. This situation occurs in the zoo population of red pandas (Princée, 1988,1989). Genetic drift can not be calculated in cases that effective size is unknown. Alternative methods involving computer simulation models, e.g. GeneDrop (MacCluer *et al.*, 1986; Lacy, 1994) or GeneFlow (Princée, 1988,1989, 1995) have been developed to estimate genetic loss in populations with complex pedigree structures.

The model GeneFlow has been used to analyse genetic processes in the *A. f. fulgens* zoo population. Gene diversity was estimated for generation groups and in the world and regional populations as on 31 December of the years 1984,1985 and 1986 (Princée, 1988,1989). It was concluded from these experiments that the zoo population of this red panda sub-species maintained sufficient genetic variation to develop a long-term preservation program. However, genetic loss in the population was considered too high: roughly 2.5 percent per generation time of about 4½ years (Princée, 1989). Recommendations involved rapid increase of population growth to a population of 500 individuals to limit this genetic loss.

This objective has not been reached in terms of population growth (see section 'Are we satisfied?'). Therefore, genetic loss may be larger than allowed. Population management involves, as mentioned in previous sections, continuous monitoring of the population and evaluating of measures and strategies. Therefore, effects of population growth on genetic processes in the population need to be analysed. Gene diversity in the living *A. f. fulgens* population at end of the years 1980 to 1990 has been estimated with an extended version of the GeneFlow model (Princée, 1995). This method of simulation has an advantage over estimation of genetic variation in zoo-born generation groups. Since generations in red pandas largely overlap, genetic processes in the population can not be easily evaluated in a historical perspective. The results of GeneFlow simulations are, expressed as percentages of gene diversity in the source (i.e. wild) population, presented in figure 13.

Strategies for preservation of genetic variation in the Nepalese red panda population were based on genetic processes that occurred until 31 December 1986. Gene diversity in 1986 and 1990 are 96.12 and 95.92 percent respectively. This means that the population lost 0.2 percent of gene diversity in 4 years time. This loss is considerably smaller than the rough estimate of 2.5 percent loss per generation as occurred in the past (Princée, 1989). Reproductive success of the population increased with respect to the period before 1986. This resulted in a larger effective size and, thus, in a smaller genetic loss than predicted.

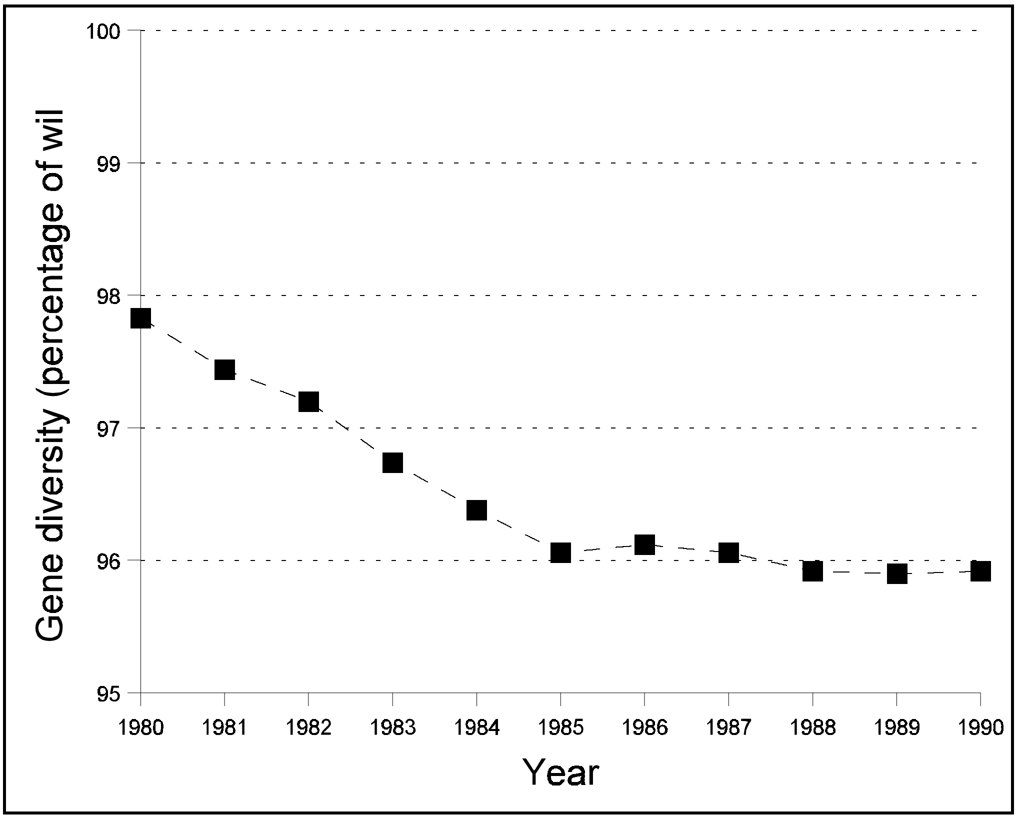

Figure 13 Percentages of original gene diversity in the zoo population of *Ailurus f. fulgens* as on 31 December of the years 1980 to 1990. Values estimated with simulation model GeneFlow (Princée, 1988,1995). GeneFlow specifications: 25 loci, 5 allelic variants per locus, equal allele frequencies and 50 iterations.

Co-ordination of co-ordinators

Analyses and discussions in this paper refer to management of global zoo populations of the Chinese red panda and the Nepalese red panda in particular. In reality, red pandas are, partly, managed on a regional level. Initially, management of the international studbook population was divided in five regions: Australasia, British Isles, Continental Europe, North America and a rest population (mainly Asia) (Glatston, 1982). Since that time zoos in several regions, including Asia, established organizations or 'movements' (e.g. EEP, SSP) to coordinate breeding programs. The goal of these regional programs is to establish or maintain self-sustaining zoo populations of various species for educational reasons and as a source of last resort. These goals may suggest that each regional population of red pandas should be self-sustaining and meet the '90 percent - 200 years' criterion. However, this criterion refers to one population that is managed. As soon as other regions establish breeding programs, the combined sub-populations should maintain 90 percent of genetic variation over 200 years.

Regional approaches could even lead to controversial management measures in the case of *A. f .fulgens*. Regional populations do not have sufficient levels of genetic variation to be self-sustaining (Princée, 1988, 1989). Consequences of management of independent regional populations would imply recruitment of new individuals from the wild. The global population, however, has the potential to be self-sustaining. This has, among other problems, been recognized by the international studbook keeper and regional co-ordinators of red pandas. They formed in 1992 the Global Red Panda Management Group. This group even urged international organizations to establish a moratorium on acquisition of red pandas from the wild.

Although, quarantine regulations were an important reason for establishing management on a regional level, exchange of red pandas should occur in cases that inbreeding levels are considered too high. Mating tables for the global population need to be constructed. Recommendations, that also take logistic aspects into account need to be based on these tables. Therefore, coordination between regional programs is of great importance.

Future prospects

The previous section(s) showed that population management of zoo populations is a dynamic process. Studbook populations do not only change as a result of biological processes or altered zoo conditions but also by discovering 'new' zoos that have red pandas or by acquiring additional data on individuals. Furthermore, the science of management of small populations is still evolving. New techniques and models are developed that allow more detailed analyses of demographic and genetic processes in populations.

The dynamics of population management may be illustrated by the fact that shortly after analysing genetic processes in the *A. f. fulgens* population, new and additional information on missing data was available: individuals that were previously not reported dead; offspring that are sired by other parents; unknown parentages are resolved; a zoo with three wild-caught individuals has been discovered and one living wild-caught individual seems to belong to the *styani* sub-species. The result of all these changes: gene diversity in the world population as on 31 December 1990 is 95.86 percent of the wild population. This value is slightly lower than presented previously.

These latest data will be used to (re-)evaluate future prospects with regard to the '90 percent - 200 years' criterion. The space required to meet this criterion has been estimated as 500 animals (Princée, 1989). This value, however, was not based on the demographic and genetic conditions (e.g. growth rate and effective population size) in the 1986 population. It was estimated to show that the red panda population has the potential to be self-sustaining under conditions of rapid population growth within one generation to the required population size and equal family sizes. Since loss of genetic variation between 1986 and 1990 is small the *A. f. fulgens* population has still the potential to be self-sustaining. Last but not least: the Chinese Zoo Association appointed a coordinator for the Chines e red panda (after the analyses in this paper were carried out). Consequently, a lot of data from Chinese zoos became available to the international studbook (see Lu *et al.*, 1993)

It must be stressed that the term potential does not mean that the *fulgens* population **is** self-sustaining. Current growth rates and effective population sizes largely differ from the conditions that are required. The annual population growth (8) during the last five years is 1.075. The N_e/N ratio is 0.75 per year (approximately 0.2 per generation). A computer model, based on the CAPACITY program of Ballou (1992), is used to estimate genetic variation in the population after 200 years. The space available in zoos for *A. f. fulgens* is about 500 animals. The model allows the population to grow to this carrying capacity. Initial size and genetic variation are based on the status of the population as on 31 December 1990. Genetic variation after 200 years is expected, under current conditions, to drop to 72 percent of 'wild' variation. The target population size is, under current conditions, about 4000 individuals (see also the section 'Are we satisfied?'). Given the space that is required for *A. f. styani*, but also dozens of other species, we should not even discuss whether such a population size is feasible.

Demographic and genetic models can be used to evaluate trends in populations, predict future developments and analyse effects of management measures. We may conclude from these models that (juvenile) mortality needs to be reduced and fertility needs to be increased. However, demographics and genetics will not solve these problems. All improvements need to be achieved in the field of husbandry. This will be a hard task that requires combined efforts from zoo keepers to directors of those institutions that keep red pandas. Since one zoo does not a breeding program make....

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