sex ratio bias. Furthermore, the bias goes in opposite directions for colour banded males and females, which is hardly to be expected under the age/experience hypothesis. Although she cannot rule out factors associated with possible differential parental abilities to rear sons and daughters, Burley concludes that the most likely cause of the effect is parents adjusting the sex ratios of their broods to produce attractive offspring[9]. This interpretation is based on the assumptions that differences in attractiveness are normally heritable, and that brood reduction is adaptive under normal circumstances.

But what is so special about leg band colour? Burley believes that the answer may lie in the evolutionary history of the species. Band colours preferred by zebra finches were compared with those chosen by the closely-related double bar finch (*Poephila bichenovii*)[10]. Burley found that birds with bands of colours absent from the beak and plumage of conspecifics but similar to those naturally occurring on the other species tended to be less attractive. On the other hand, bands of similar colour to those characteristic of opposite sex conspecifics are more likely to be attractive. Song and courtship behaviour are quite similar among the elstrildrid finches while plumage and beak coloration can vary markedly among species. Perhaps, Burley surmises, some of the preferences she has demonstrated 'reflect strong selection for species identification mechanisms in a group in which colour pattern appears to have played an important role in speciation'[10].

These findings must be considered preliminary. Sample sizes are fairly small, possible confounding factors can sometimes be envisaged, proximate mechanisms are little understood, and the number of extra-pair copulations is unknown. Nevertheless, many of the patterns seem robust and, if they can be demonstrated under more natural conditions, they beg evolutionary interpretation.

References

1 Burley, N. (1981) *Science*, 211, 721–722
2 Immelman, K., Hailman, J.P., and Bayliss, J.R. (1982) *Science*, 215, 422–423
3 Thissen, D., and Martin, E. (1982) *Science*, 215, 423
4 Burley, N. (1982) *Science* 215, 423–424
5 Burley, N., Krantzberg, G., and Radman, P. (1982) *Anim. Behav.* 30, 444–455
6 Burley, N. (1985) *Auk*, 102, 647–651
7 Burley, N. (1986) *Am. Nat.* 127, 415–445
8 Trivers, R.L. (1985) *Social Evolution* Benjamin/Cummings
9 Burley, N. (1986) *Evolution* (in press)
10 Burley, N. (1986) *Anim. Behav.* (in press)

Species Conservation and Systematics: the Dilemma of Subspecies

Oliver A. Ryder

Zoos are gaining recognition as potential *ex situ* conservators of the gene pools of threatened species. The zoo directors, curators, geneticists and population biologists who attempt to pursue the elusive goal of preservation of adaptive genetic variation are now considering the question of which gene pools they should strive to preserve. There are no illusions that zoological parks can conserve but a very small proportion of biotic diversity; charismatic megavertebrates are their stock-in-trade.

Space, or captive habitat as some call it, is limited in zoos. Conway's optimistic estimate[1] suggests that 925 taxa of mammals, birds, and reptiles may be managed with gene pool preservation in mind (see also the article by Ralls and Ballou on page 19 of this issue). Which species should be the focus of concern and which may be neglected? Furthermore, should the focus of *ex situ* conservation effort be directed at populations, subspecies, or species?

The consideration of these issues was the subject of a recent conference of zoo biologists and systematists concerned with the establishment of species' survival programs (SSPs) of the American Association of Zoological Parks and Aquariums (AAZPA). The focus of the meeting, held in July 1985 at the Zoological Society of Philadelphia, was on the subspecies problem. How much space is required for tigers, for example, in zoos is actually a dual problem of how many *individuals* must be held in order to achieve a self-sustaining captive population that only incurs acceptable losses of genetic variation over a sustained period of time (200 years is a current goal) as well as how many of the five extant tiger *subspecies* should be conserved. Thus, the 'subspecies problem' is considerably more than taxonomic esoterica.

The tiger example is by no means unique. Of the 37 taxa that are designated for SSP programs, at least 16 are listed as trinomials. The black rhino of Africa (Fig. 1) has been divided into seven extant subspecies[2]. A recent status review prepared by the African Elephant and Rhino Specialist Group of IUCN suggested that the three northernmost black rhino subspecies have been nearly eliminated[3]. The Somali black rhino (*Diceros bicornis brucii*) is thought to survive with a population of 90 or fewer individuals.

Zoo biologists are now faced with the task of identifying which subspecies actually represent populations possessing genetic attributes significant for present and future generations of the species in question. The folklore of mammalogy is replete with humorous anecdotes such as two subspecies being named from individuals that were littermates. Yet, other taxa that have been considered by some authorities to be conspecific, for example the barking deer or muntjacs of India and China, produce sterile hybrids. Out of a sense of frustration with the limitations of current mammalian taxonomy in determining which named subspecies actually represent significant adaptive variation, those assembled at the Philadelphia conference willingly discarded the concept that all subspecies are equal. Rather, it emerged that zoos ought properly to address the conservation of evolutionarily significant units

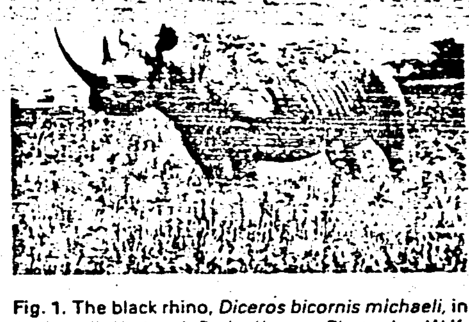

Fig. 1. The black rhino, *Diceros bicornis michaeli*, in Amboseli National Park, Kenya. Photo by W.K. Lindsay.

Oliver Ryder is at the Center for Reproduction of Endangered Species, Zoological Society of San Diego, CA 92112, USA.

(ESUs) within species. (No one present really liked the idea of creating a new jargon term. An alternative suggestion was to call such populations 'ESPs', standing for evolutionarily significant populations.)

Identification of ESUs within a species was recognized as a difficult task, requiring the use of natural history information, morphometrics, range and distribution data, as well as protein electrophoresis, cytogenetic analysis, and restriction mapping of nuclear and mitochondrial DNA. The recognition of inevitable uncertainty in the classification of potentially significant populations led to a recommendation that concordance between sets of data derived by differing techniques be a criterion for identifying ESUs. Thus, when geographic distribution data indicate the existence of discrete populations within the range of a species, an estimate of genetic distance, for example, should be made to determine whether the populations have ESU status.

In the past zoos seldom knew the exact location of capture of animals they imported. Data concerning geographic origin of individuals destined to be genetic migrants into captive breeding programs is obviously important, especially where ESUs may be involved, and should be recorded meticulously.

Some ESUs may be in jeopardy of extinction through inbreeding and the inevitable stochastic events that affect small populations. Under what circumstances is the mixing of threatened populations with populations of other related forms justified? The participants at the Philadelphia meeting concluded that mixing was appropriate when the extinction of the small population would jeopardise the higher taxon.

Decisions with important conservation implications increasingly require more understanding of the systematics of populations, subspecies and species than is currently available. Zoo biologists recognize that additional systematic research is needed to ensure that captive management programs can preserve gene pools as they exist in nature. Expertise in diverse areas of vertebrate biology, genetics and ecology is required for zoos to meet these formidable challenges. Although the most current expression of these concerns may now be voiced by zoo biologists, the implications of their concerns reach into other conservation-oriented disciplines such as wildlife management and the management of national parks and nature preserves.

References

1 Conway, W.G. *International Zoo Yearbook*, 25: (in press)
2 Groves, C.P. (1967) *Z. Saugetierkd.* 32, 267–276
3 Western D., and Vigne, L. (1985) *Swara*, 8 (2), 10–13