Reproductive Science and Integrated Conservation

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INTRODUCTION AND OBJECTIVES

A distinguished student of human sexuality, John Money (1991), has commented that 'Reproduction is more respectable than sex. Reproductive biologists and sexologists seldom attend the same meetings or publish together in the same journals.' To some extent this bias against studies of behaviour, and especially studies of sexual behaviour, has also affected research on animal reproduction. However, the tide has begun to turn over the past two decades, and there are several reasons for this. Gamete biologists have begun to collaborate with behavioural scientists in order to explore the role played by 'sperm competition' and 'cryptic female choice' in the evolution of sexual behaviour and mating systems (Eberhard, 1985, 1996; Birkhead & Møller, 1992, 1998; Dixson, 1998). Stronger links have also been forged between behavioural biology and endocrinology; the emerging field of socioendocrinology seeks to understand relationships 'between social environment, hormones and behaviour, because they modulate the reproductive success of individuals' (Bercovitch & Ziegler, 1990). Finally, behavioural ecologists have taken a renewed interest in exploring the mating systems and mating tactics of a wide range of animals, especially because modern genetic techniques have made it possible to determine paternity and to measure the reproductive success of individuals in free-ranging populations (Davies, 1991; Martin *et al.*, 1992; Birkhead & Møller, 1992).

Multiple relationships between behaviour and reproduction are illustrated in a schematic fashion in Figure 2.1. From before birth until reproductive senescence, physiological and behavioural events are intertwined in a complex fashion which determines whether an individual will succeed, or fail, in its attempts to reproduce and pass on its genes to future generations.
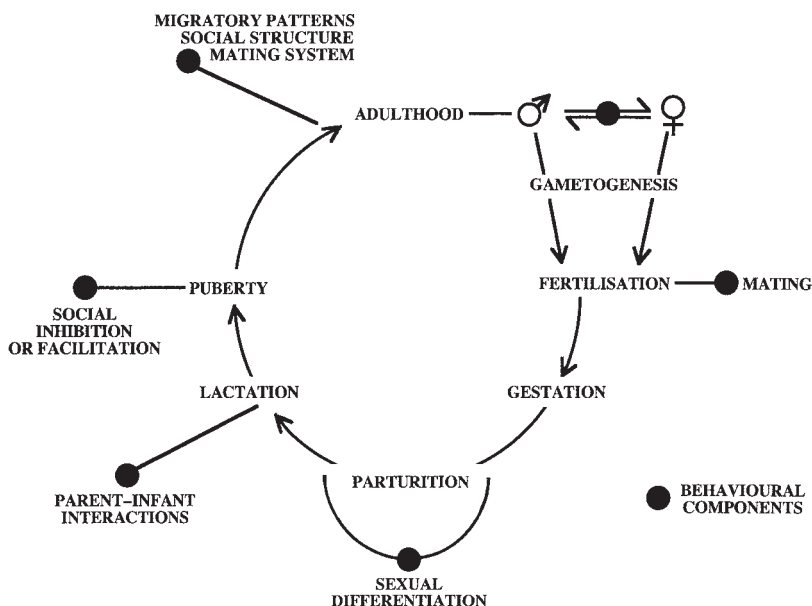
Figure 2.1 Relationships between behaviour and reproductive events during the lifetime of an individual.

Knowledge of behavioural biology therefore plays an integral role in efforts to conserve endangered species. Information on the social organisation, mating system, life history and seasonal patterns of reproduction of each species is required if we are to decide how populations can best be managed in the wild or how to implement captive breeding and reintroduction programmes.

This brief review will concentrate upon studies of captive populations of three endangered vertebrate species that have markedly different mating systems: the mandrill (*Mandrillus sphinx*), the Southern white rhinoceros (*Ceratotherium simum simum*) and the California condor (*Gymnogyps californianus*). In each case research on captive populations of these species has improved our understanding of their reproductive biology and has important implications for conservation of the animals in their natural habitats.

STATE OF THE ART

1. The mandrill (*Mandrillus sphinx*): what is its mating system?

The mandrill remains an enigmatic species for primatologists. Despite the impressive number of field studies conducted on primates, very little is

known about the mandrill in the wild, or about the closely related drill (*M. leucophaeus*). Mandrills occur in Gabon, Congo, Rio Muni and in Cameroon, to the south of the Sanaga River. The drill is found to the north of the Sanaga, in Cameroon and Nigeria, and on the island of Bioko (Grubb, 1973). Both species are inhabitants of lowland rainforests, and both are threatened by deforestation and hunting. These are the largest monkeys in the world; an adult male mandrill weighs over 30 kilograms and is spectacularly adorned with red and blue 'sexual skin' on the face, rump and genitalia. In the wild, mandrill group sizes range from 15 to over 1000 individuals (Hoshino *et al.*, 1984; Rogers *et al.*, 1996; Setchell, 1999). Because mandrill groups are so difficult to locate and follow in the rainforests, most studies have focused upon the mandrill's diet and feeding ecology (e.g. Sabater-Pi, 1972; Lahm, 1986; Harrison, 1988). The social organisation of the mandrill is poorly understood but it has been reported that large groups fragment into smaller units, each containing one fully adult male per 20–50 members. These reports, coupled with the marked sexual dimorphism of this species and the male's striking secondary sexual adornments, have led to the assumption that social groups of mandrills are composed of numerous 'one-male units' and that the mating system is polygynous (e.g. Jouventin, 1975; Stammbach, 1987; Barton, 2000). Are mandrills polygynous and do they form one-male units ('harems') in the same way, for example, as the hamadryas baboon (Kummer, 1968) or the gelada (Dunbar & Dunbar, 1975)? Male mandrills are huge and brightly coloured, as are male hamadryas baboons and geladas, so have these traits evolved as a result of similar sexual selection pressures in all three species?

Studies of semi-free-ranging mandrill groups in Gabon have greatly expanded our knowledge of the behaviour and reproductive biology of this species. In 1983, 14 mandrills (8 females and 6 males) were released into a naturally rainforested enclosure (6 hectares) situated in a valley at the International Medical Research Centre, Franceville, Gabon. By 1991 the group contained more than 50 mandrills, all the descendants of the founding individuals. Studies conducted between 1989 and 1992 focused on social organisation and sexual behaviour. In 1996, 24 mandrills were moved to a second rainforested enclosure (3.5 ha) leaving 36 animals in the original group. Between 1996 and 1998 observations on both groups continued, in order to examine the physical and behavioural development of male mandrills, especially from puberty to adulthood. Because the mandrills were captured annually for a veterinary check, it was also possible to obtain somatic measurements, as well as blood samples for DNA fingerprinting and endocrine studies.

The picture that emerges from these studies is of a species that lives in 'female-bonded' social groups with a multimale–multifemale social organisation. A number of matrilines form the core of the social group; female relatives and their young offspring are frequently observed travelling together, foraging, grooming and associating during periods of rest and at sleeping sites. Females are philopatric, whereas male offspring emigrate from the natal group at 7–8 years of age. The enclosures were large enough to reveal this emigration process, as well as to quantify dominance relationships between adult males which remain in the social group, and those which lead a peripheral or 'solitary' existence. Intermale competition is intense in the mandrill, and alpha males have the brightest red sexual skin colouration. High rank is also associated with elevated plasma testosterone, larger relative testes size, and a more 'stocky' appearance due to fatting of the rump and flanks. By contrast, 'non-fatted' males exhibit muting of the secondary sexual adornments, lower testosterone levels and smaller relative testes size (Wickings & Dixson, 1992). In reality, 'fatted' and 'non-fatted' adult male mandrills are not completely distinct morphotypes; a continuous spectrum of possibilities exists between these two extremes (Setchell, 1999). Suppression of secondary sexual adornments is associated with lower rank, and/or a more peripheral/solitary social strategy in adult males. Removal of more dominant males from the enclosure resulted in pronounced changes in sexual skin reddening, elevations in plasma testosterone, increased testicular volume and higher group-association scores in a non-fatted male (Setchell & Dixson, 2002).

Although high-ranking males have the greatest mating success, and reproductive success as determined by paternity analyses (Dixson *et al.*, 1993), there are no 'one-male units' or 'harems' in semi-free-ranging mandrill groups. The mating system is multimale–multifemale under these conditions and females mate with a number of males. High-ranking males mate-guard *individual females* when they develop sexual skin swellings, during the annual mating season. This occurs during the driest period of the year, from June to October in Gabon. Most males are sexually active, however, and peripheral or solitary males may mate opportunistically with females. Females also present sexually to a variety of potential partners, although higher-ranking males do receive more of these sexual solicitations (Figure 2.2). This pattern of mating activity is quite unlike that which occurs in polygynous primate species, such as gorillas or hamadryas baboons, where the leader male of a one-male unit accounts for most, if not all, observed copulations (Harcourt *et al.*, 1980; Kummer, 1990). Because most female mandrills develop maximal sexual swellings and conceive during July and

FEMALES' PRESENTATIONS
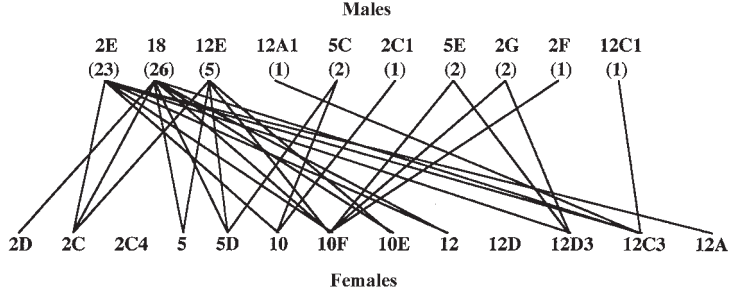
MALES' MOUNTS
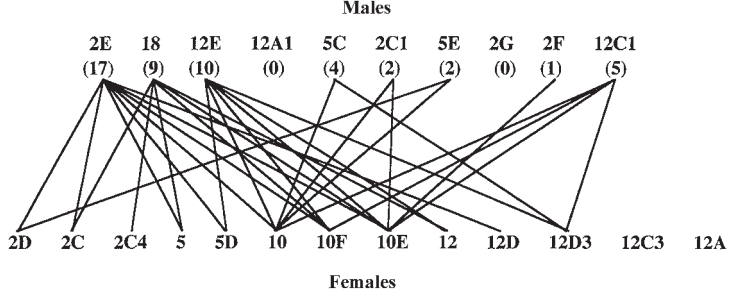
Figure 2.2 Webs of sexual relationships in a mandrill group. (Data are for the years 1996–98.) Males and females have code numbers and appear in order of social rank (the highest-ranking individual is on the left). Total sexual presentations received, and mounts by each male are given in parentheses, beneath his code number.

August, and because there are often several females fully tumescent at one time, even the alpha male is unable to mate-guard multiple partners during the peri-ovulatory period of their cycles (Dixson, 1998; Setchell, 1999). Under these circumstances, mate-guarding is a dynamic process; the male abandons one female as soon as her sexual skin swelling enters the 'breakdown' phase of detumescence and transfers his attentions to another partner (Figure 2.3). In baboons, ovulation is most likely to occur during the last few days of maximum sexual skin swelling (Wildt *et al.*, 1977); the same may be true in the mandrill, and this could account for the intense mate-guarding episodes which occur at this time.

Given the large social group sizes of mandrills, the dense nature of their rainforested habitat and the inability of males to mate-guard multiple females during conception periods, it seems highly unlikely that this species forms one-male units. Females are not passive in sexual contexts, and female
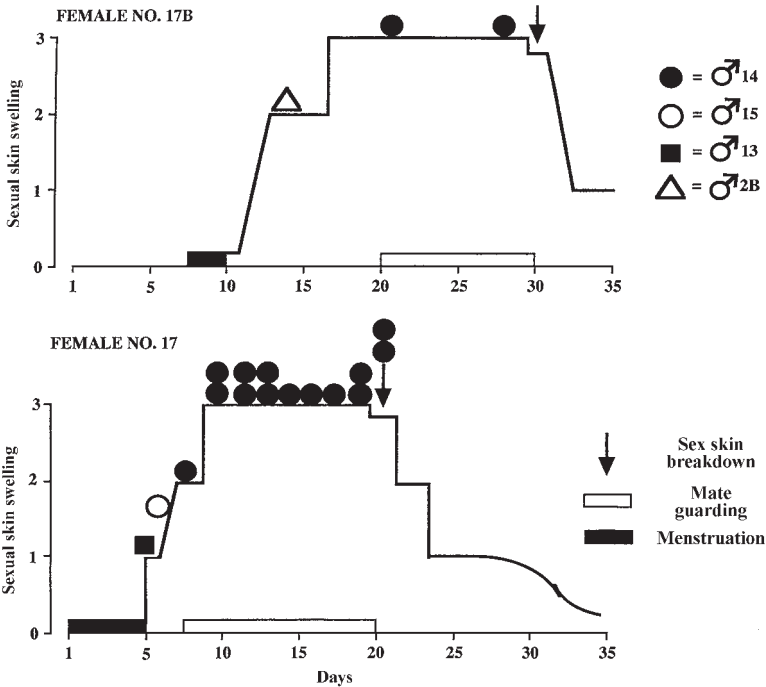
Figure 2.3 Mate guarding and copulation in mandrills. Data on sexual skin swelling are shown for two females (o = sex skin flat; 3 = fully tumescent). Data were collected in 1990, when Male 14 was the alpha male in the group. He accounts for all mate-guarding behaviour (open bars) and most copulations (dark circles) with both females. Three other males mate opportunistically, but at low frequencies and not when females are maximally swollen and likely to ovulate.

'mate-choice' doubtless occurs in mandrills. We have often seen females solicit copulations from certain males, while avoiding being mate-guarded by others. As the female is less than half the size of an adult male, she can, for example, take to the trees and more easily avoid her much larger partner than during terrestrial mate-guarding episodes. Kudo (1987) suggested that mandrills have a multimale–multifemale social structure, basing his arguments mainly upon studies of vocal communication in free-ranging groups. It seems likely that the mating system is also of a multimale–multifemale type in this species. Primates which have multimale–multifemale mating systems are characterised by possession of large testes in relation to adult male body weight (Harcourt *et al.*, 1981). Sperm competition has favoured the evolution of large relative testes sizes in such cases, because females mate with multiple partners. Males which can sustain higher sperm counts

in their ejaculates are more likely to sire offspring under these conditions. It is of interest, therefore, that male mandrills have large testes in relation to their body weight. Relative testes size in mandrills is comparable to that of many baboons and macaques, for example, and is much greater than occurs in polygynous primates such as the gelada or gorilla (Dixson, 1998).

Field studies of mandrills, such as those now in progress at the Lopé Reserve in Gabon may reveal, in time, the true nature of the social system and mating system. A working hypothesis is that this species has a multimale–multifemale system, and that the fragmentation of large groups may be for reasons of feeding ecology rather than representing 'one-male units' in the reproductive sense. Division of large social groups into smaller units probably occurs on a matrilineal basis, rather than because males have any direct control of female groupings. The 'solitary' males encountered in the wild may be maturing emigrants or fully adult individuals which spend varying periods separate from social groups. It is quite possible that such males are sexually active and contribute to the gene pool, however, since they may haunt the fringes of social groups, or actively immigrate into such groups during the annual mating season. The intense intermale competition and occurrence of social suppression of secondary sexual traits which occurs in semi-free-ranging mandrills, probably also occurs in the wild. Just as suppression of development of the 'cheek flanges' and other features occurs in subordinate male orang-utans in the wild, as well as in captivity (Kingsley, 1988; Maggioncalda *et al.*, 1999), we expect to find evidence of a spectrum of 'fatted' and 'non-fatted' males in free-ranging mandrill populations.

2. The white rhinoceros (*Ceratotherium simum*): is socioendocrinology important for reproduction?

The Southern white rhinoceros (*C. s. simum*) has returned from the brink of extinction, as a result of effective conservation of the population at Umfolozi and translocation of animals to other protected areas in southern Africa. More than 10,000 Southern white rhinoceros are thought to exist in the wild, whereas the closely related Northern subspecies (*C. s. cottoni*) survives only as a remnant population in the Garamba National Park, in the former Republic of Zaire (Emslie & Brooks, 1999).

Knowledge of the reproductive physiology of rhinoceros species is still very limited. As far as the white rhinoceros is concerned, there have been conflicting reports concerning the duration and endocrine characteristics of the ovarian cycle. All studies have involved the captive population of the white rhinoceros, however, and many females fail to reproduce in captivity.

Schwarzenberger *et al.* (1998) measured faecal pregnane excretion in 16 female southern white rhinoceros. Two females exhibited regular cycles of 10 weeks' duration, but most had cycles which varied in length from 4 to 10 weeks, or showed either limited luteal activity or none. Although Schwarzenberger and his colleagues suggest that longer (10-week) cycles are the norm for white rhinoceros, other studies support the view that shorter cycles may be more typical for this species (Hindle *et al.*, 1992; Radcliffe *et al.*, 1997; Patton *et al.*, 1999). The studies of Patton *et al.* included eight female rhinoceros at the Zoological Society of San Diego (Wild Animal Park) as well as five females housed in other collections. Measurements of faecal progesterone metabolites (allopregnane being the principal progesterone metabolite in the faeces of white rhinoceros) revealed two 'types' of oestrous cycles. Type I cycles averaged one month in duration (mean $\pm$ SEM $= 35.4 \pm 2.2$ days; $n = 10$). These appeared to be the most usual and normal type of cycle, by contrast to longer (Type II) cycles of approximately 2 months' duration (mean $= 65.9 \pm 2.4$ days; $n = 7$). Examples of both types of cycle are shown in Figure 2.4*a*, which also includes the faecal pregnane profile during pregnancy (Figure 2.4*b*). Pregnancy was detectable by 90 days after mating, as revealed by sustained elevations in faecal pregnane levels.

Unfortunately, no measurements of oestrogens or gonadotrophins are available for these females. However, nadirs in progesterone excretion coincided with mating resulting in conception, and this provides some indication of the likely timing of ovulation. The majority of cycles studied (59%) ranged from 29 to 44 days in length. Longer cycles involving extended luteal phases may have been related to a variety of factors including early embryonic loss or uterine pathology (Radcliffe *et al.*, 1997; Patton *et al.*, 1999). In addition, some females failed to show any luteal activity, as reflected by 'flat' profiles of faecal pregnane (Figure 2.4*c*). Interestingly, it was noted that social factors (removal or reintroduction of particular males) were correlated with loss (or resumption) of ovarian cyclicity, although these observations were anecdotal and have not been the subject of an experimental study.

Nutritional factors, as well as social stimuli, might affect reproduction of the white rhinoceros under natural conditions. In Zululand, South Africa, Owen-Smith (1975, 1988) recorded that although no restricted mating season occurs in this species, yet 'oestrus is apparently stimulated by a flush of green grass following a dry period'. The sexes are normally spatially separate; dominant males live in territories of approximately 2 km² in area whereas cows occupy larger ranges (10–12 km²) which may encompass the territories of six or seven males. Approximately one-third of adult males are non-territorial; they co-exist with territorial bulls, but do not show the
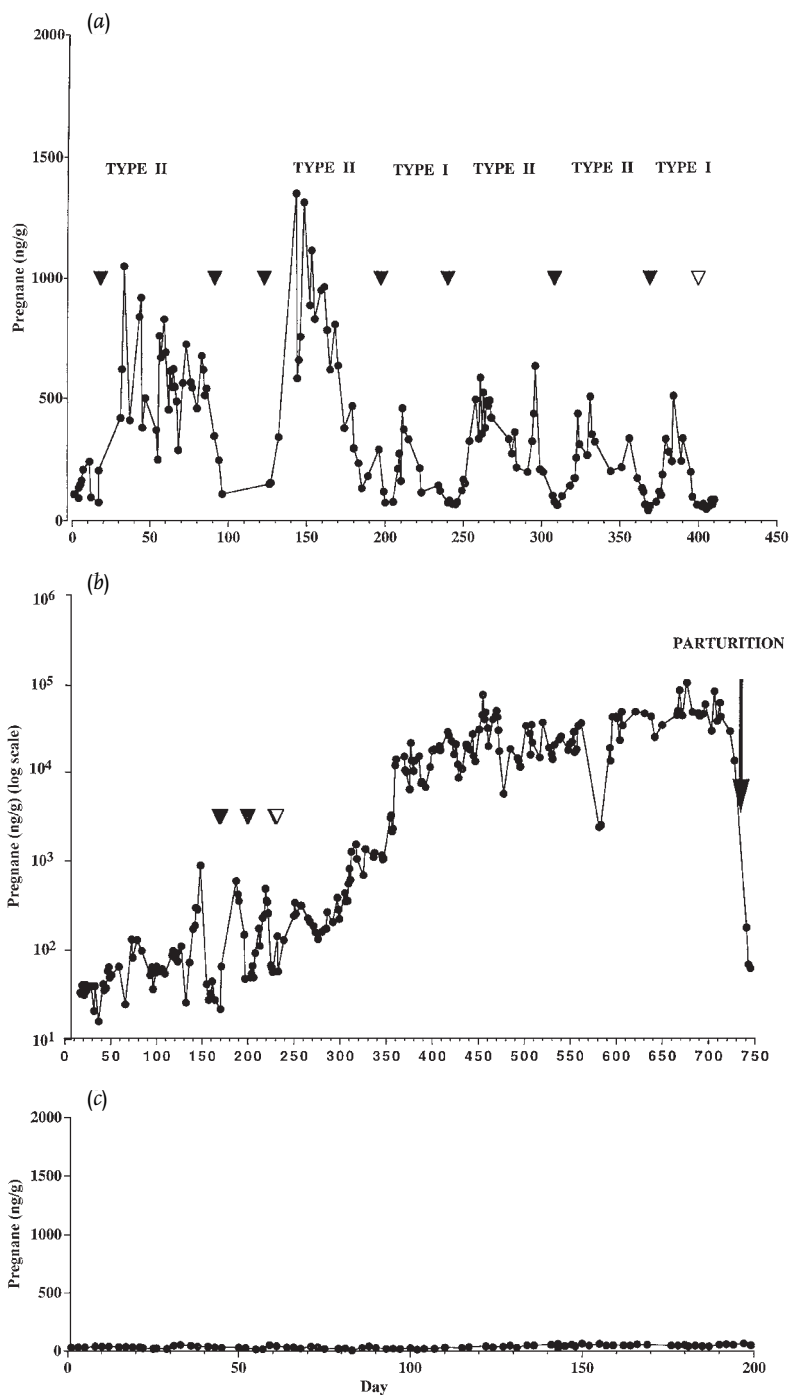
Figure 2.4 Faecal pregnane levels in female Southern white rhinoceros (*a*) during Type I and Type II ovarian cycles, (*b*) during pregnancy and (*c*) when no luteal activity was measurable. ▽, mounts; ▼, copulations.

ritualised urine-spraying and dung-scattering behaviours typical of territorial males.

Owen-Smith's observations indicate that female white rhinoceros come into oestrus at 30-day intervals, similar to the 'Type I' cycle lengths recorded in captivity. Dominant bulls associate with cows which enter their territories, and they attempt to mate-guard females which are entering oestrus. Initially, the male grazes nearby; but if such an attachment persists it is indicative that the cow is coming into oestrus. If this is the case, then the bull may attempt to block the female's departure from his territory, he may herd her away from the territory boundary or actively chase her. A dominant bull will repeatedly approach a female, uttering a distinctive 'hic-throbbing' vocalisation and sniffing her urine. Such approaches may extend over 15–20 hours before copulation occurs; copulations last for 20–30 minutes and courtships finish 2–5 days after mating is complete. Subordinate bulls do not usually court females or form consortships.

The possibility that the courtship behaviour, or mere proximity of dominant bulls (or their olfactory signals), might affect hypothalamic–pituitary–gonadal activity in female white rhinoceros has not been studied and deserves attention. It is possible that social factors, as well as nutritional status, influence the onset of oestrus in this species. In captivity, it has repeatedly been observed that the greatest breeding successes occur in those collections where white rhinoceros are kept in large groups and/or in large enclosures (Rawlins, 1979; Lindemann, 1982; Killmar, 1997). Lindemann's analyses of captive breeding successes indicate that it is the presence of two or more males which improves breeding performance by females, rather than provision of a large enclosure *per se*. However, since interactions between bulls, as well as between the sexes during the courtship phase, often involve aggression, it is clearly advantageous if the animals have sufficient space to accommodate such behaviour. At present we have no information about the endocrine profiles of dominant and subordinate bulls. Measurement of faecal steroids, in captivity and under natural conditions, might reveal interesting socioendocrinological effects in bulls. Likewise, it may be that female cycles are influenced by exposure to males of varying social rank. The reproductive success of dominant and subordinate bulls has not been measured; however, since it is possible to extract DNA from rhino dung (O. Ryder, personal communication) it should be possible to conduct DNA typing studies of paternity in free-ranging populations. The mating system of the white rhinoceros may allow some degree of 'mate choice' by females as they move through the territories of dominant bulls and encounter their dung piles and urine marks. These olfactory cues may also be of importance

for captive animals, so that mate choice could also impact ovarian function under these conditions. All of these questions are open to inquiry by applying techniques developed for study of captive white rhinoceros to animals which can be followed individually, by use of radiotracking techniques, in their natural environment.

3. The California condor (*Gymnogyps californianus*): are captive pairs compatible?

Since the mid-1980s, when the last California condors were removed from the wild, captive breeding programmes at the San Diego Wild Animal Park, Los Angeles Zoo and World Center for Birds of Prey in Idaho, have succeeded in rescuing this species from extinction. From a founding population of 27 captive birds, there are now more than 180 condors, and over 50 have been returned to their natural habitat. California condors are sexually monomorphic, monogamous birds, which normally produce a single egg every two years. A replacement egg may be laid if the first egg is lost early in the season (January/February). Offspring are dependent upon their parents for at least one year, and reproductive maturity occurs at approximately 6 years of age (Koford, 1953; Snyder & Hamber, 1985).

Captive birds have been paired to maximise outbreeding, an important goal because deleterious genes may affect reproduction in such a small founding population (e.g. chondrodystrophy syndrome in condors; Ralls *et al.*, 2000). 'Mate choice' by the birds themselves has not, therefore, been a factor in the captive breeding programme. In most instances eggs have been removed in order to stimulate production of a second or third egg by the captive birds. Eggs thus removed have been artificially incubated and chicks have been hand-reared. However, since 1994 captive breeding facilities have attempted to allow condor pairs to retain their second or third egg of the season. Thus it has been possible to obtain quantitative data on incubation and chick rearing for comparison with the very limited information on parental behaviour in wild condors (Snyder & Snyder, 2000).

Eight breeding pairs are housed at the Zoological Society of San Diego, and videotaped records of parental behaviour are available for these birds throughout the incubation period and for the first 50 days post-hatching. From 1994 to 1999 the pairs had incubated their own eggs ($n = 9$), the eggs of Andean condors ($n = 4$) or dummy eggs ($n = 3$) which were supplied in order to provide them with additional experience. The incubation period for the eight viable California condor eggs was 55–60 days (mean $\pm$ SEM = 57.5 ± 0.55 days). On average, both sexes spent the same percentage of time

AGGRESSION DURING INCUBATION

AGGRESSION DURING CHICK REARING
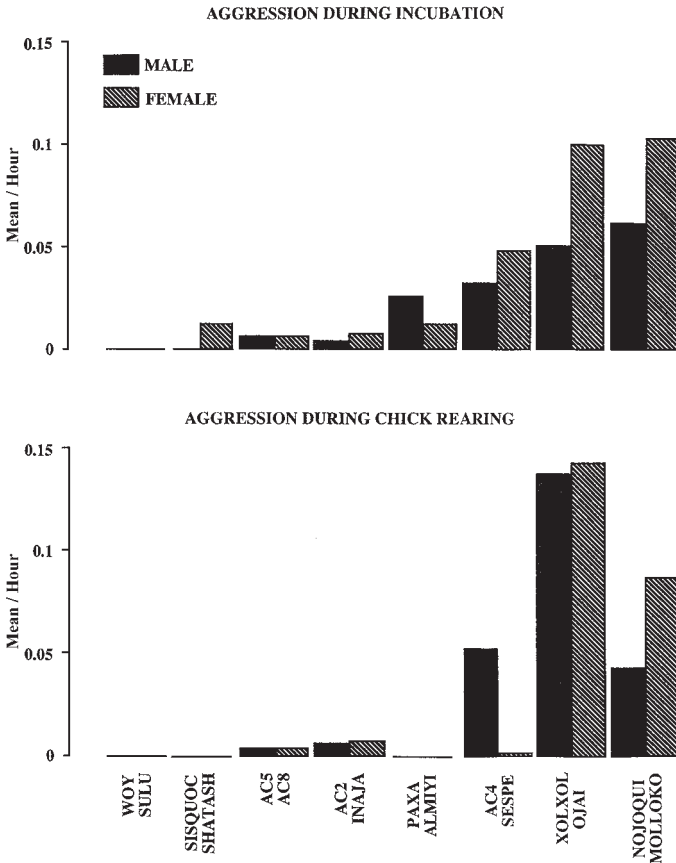
Figure 2.5 Mean rate of aggression during incubation and the first 30 days following hatch for eight pairs of captive California condors.

incubating the egg (males 44.4%; females 43.5%) and they manipulated it at similar frequencies (males 0.87/hour; females 0.91/hour). A significantly greater proportion of male (-17.71 ± 6.43 SEM) than female (-4.86 ± 1.01 SEM) nest-box entries occurred when the nest box was already occupied ($z - 2.24$, $P < 0.03$). Females had a higher rate of aggression (-0.036 ± 0.016 SEM) than the males (-0.022 ± 0.025 SEM) when in joint occupied nest boxes ($z = -1.69$, $P < 0.10$). Aggression included head-posture threats, displacing the partner, lunging, chasing and striking with wing, foot or beak. These events typically occurred as one bird attempted to re-place its partner in incubating the egg. Four of the eight pairs had higher

combined rates of aggressive behaviour in the nest box, indicating that they were less compatible as mates than the remaining four pairs.

During incubation, none of the real eggs was damaged or destroyed by the pairs during agonistic interactions in the nest box. The same cannot be said during the chick-rearing phase. From 1991 to 2001, 20 chicks (13 California condor and 7 Andean condor chicks) were left with the eight pairs for rearing. While all the behavioural data have yet to be completely analysed, records show that all four of the pairs not characterised by aggression in the nest-box were successful in rearing all of their chicks ($n = 8$). However, the less compatible pairs identified during the incubation phase failed to rear 33.3% (4/12) of their chicks successfully (Figure 2.5).

The indications from these data are that despite lack of active choice, some of the captive pairs are sufficiently compatible to successfully incubate and rear their own offspring. However, the aggressiveness that occurs between partners as they change place to incubate or brood is a cause for concern. Such behaviour was noted in the wild condors (Snyder & Snyder, 2000) but at that time so few condors were left that patterns of mate choice were constrained and probably not normal. The behavioural analyses on captive birds presented here are far from complete. We wish to analyse the dynamics and outcome of male and female displays, which may have some significance during 'dominance' interactions, that may be related to agonistic interactions in the nest box. The *relationships* between members of a pair are more likely to be revealed by such analyses than by examining frequencies of individual display or aggressive behaviour.

SUMMARY AND CONCLUSIONS

The three species considered here represent variations on the theme of how to manage declining populations. In the case of the mandrill, a viable population of this magnificent primate still exists, especially in the north of Gabon. There is no room for complacency, however, as threats from logging and the bushmeat trade are on the increase. The drill (*M. leucophaeus*) has already been greatly affected by these problems in Cameroon and Nigeria; it is probably the most endangered primate species in Africa. Because so little is known about the social organisation and reproduction of mandrills and drills, the information summarised here on semi-free-ranging mandrill groups is of some interest. For far too long, mandrills and drills have been characterised in the published literature as polygynous primates in which large social groups are made up of one-male units. In reality the social organisation of the mandrill is likely to be multimale–multifemale, and the

same is true of its mating system. Lone males occur, and they are likely to interact with social groups, especially during the annual mating season. Fragmentation of mandrill groups may occur for reasons of feeding ecology; large groups represent a huge biomass, and it may be difficult for the animals to find sufficient food throughout the year. Another possibility is that fragmentation of mandrill, or drill, groups may occur because of hunting pressures and deforestation. On Mt Kupe in Cameroon, for example, drill groups are smaller and more labile than they were 10 years ago; many monkeys have been taken by hunters throughout this period (C. Wild, personal communication).

Because mandrills and drills are semi-terrestrial and can move large distances through the rainforest, it has so far proved impossible to follow them and study their behaviour in any detail. Radiotracking studies may succeed in resolving this problem, and the information derived from studies of captive groups will be valuable in interpreting what occurs under natural conditions. In designing conservation programmes for both these species, data on population biology, social organisation and reproduction will be crucial. A useful start has been made in gathering some of this information.

The example of the white rhinoceros has been cited here because this species came very close to extinction. Protection of the animals, and their habitat, in the Umfolozi–Hluhluwe reserves has allowed their numbers to increase, and animals have been translocated to other reserves, as well as being placed in zoological gardens. Studies of captive rhinoceros have facilitated the development of non-invasive techniques to monitor their reproductive endocrinology. These techniques can now be applied to free-ranging white rhinoceros (as for the black rhinoceros; Garnier *et al.*, 1998), and they hold the promise of new insights concerning the mating systems of these fascinating animals. Important questions concern the socioendocrinology of the white rhinoceros, possible differences between dominant and subordinate bulls and effects of social stimuli upon ovarian function in females. Rhinoceros dung is a source not only of sex steroids, but also of DNA. Genetic studies may allow us to identify individuals in the wild and to measure their biological relatedness and reproductive success.

At the far end of the spectrum for declining populations is the California condor; only resorting to removal of the last individuals from the wild saved this species from extinction, and a reintroduction programme is still in its early stages. Reintroduction of the California condor to the wild is a difficult process. There are environmental challenges, such as lead and other pollutants. There are also behavioural problems. Some condors are inclined to approach human settlements and to be less fearful of human beings than

normal. Of course, it is very difficult to define 'normal' behaviour for a species which could not be adequately studied in the wild before its population had been drastically reduced (Snyder & Snyder, 2000). In these circumstances we do not know, for example, whether hand-rearing techniques for captive condor chicks affect their later behaviour as adults. It is good news that in 2002 several pairs of released condors have succeeded in hatching eggs and caring for their chicks. Behavioural studies have a vital role to play in management of the captive and reintroduced populations of California condors. A huge, and costly, effort will be required over the next two decades to restore the California condor to the wild.

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