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Behavioural aspects of conservation breeding

Red junglefowl (*Gallus gallus*) as a case study

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Till morfar

Abstract

A number of endangered species are currently involved in conservation breeding programs worldwide. Conservation breeding deals with propagation of captive populations, often with the ultimate aim of releasing animals into the wild. However, an alarmingly high proportion of reintroductions have not been successful in establishing viable populations, possibly due to behavioural problems caused by genetic adaptation to captivity. The main aim of this thesis was to study behavioural aspects of conservation breeding and investigate whether, and how, maintenance of small populations in captivity cause behavioural modifications, which could affect the success of reintroductions. Throughout the project, the red junglefowl (*Gallus gallus*) was used as a case study, representing animals maintained in captive populations. A screening of behavioural variation revealed that captive populations differ in antipredator, social and exploratory behaviours, all of which are central components of life in the wild. A correlation was also found between genetic diversity and behavioural variation. This has not been reported before and may potentially have interesting implications for conservation breeding. When studying the behaviour of populations with different backgrounds being raised together as one group, the results suggested that fear-related behaviours may be more affected by long-term breeding in a certain captive environment than social and exploratory behaviours which seem to be more influenced by the immediate social or physical environment. A longitudinal study of antipredator behaviour in two populations across four generations revealed that the populations became more similar over time when maintained under identical conditions. This demonstrates that effects of a new environment can appear after only a few generations. Furthermore, daily behavioural routines in different captive environments as well as diurnal crowing rhythms in both wild and captive populations were studied in the species' natural region of distribution and the results suggest that such behavioural patterns are not affected by the captive environments to any notable extent. The present case study is one of the first attempts to, from a conservation perspective, study how captive environments can affect behaviour and the results imply that these aspects are important to take into consideration in conservation breeding programs.

— Sammanfattning (Swedish abstract) —

Ett stort antal utrotningshotade djurarter ingår idag i bevarandeprogram världen över. Små populationer hålls då i skyddade miljöer, exempelvis i djurparker, och i många fall är målet att återintroducera djur till naturen. Dessvärre är det vanligt att det uppstår problem när djur återintroduceras vilket kan bero på beteendemässiga anpassningar som uppkommit under tiden i fångenskap. Syftet med den här studien var därför att undersöka beteendemässiga aspekter på bevarandeavel och försöka ta reda på om och hur djur påverkas beteendemässigt av att hållas i skyddade fångenskapsmiljöer. I projektet användes röda djungelhöns (*Gallus gallus*) som en fallstudie. En granskning av beteendevariation mellan olika populationer av röda djungelhöns i fångenskap konstaterade skillnader i antipredatorbeteende, socialt beteende och födosöksbeteende. Vid en genetisk studie av samma populationer upptäcktes dessutom ett samband mellan genetisk diversitet och beteendevariation som potentiellt kan vara intressant ur ett bevarandeperspektiv. Socialt beteende, födosöksbeteende och olika aspekter av rädsla studerades vidare i populationer med olika bakgrund som fick växa upp tillsammans i en grupp. Resultaten visade att populationerna bara skilde sig åt i rädslbeteenden vilket antyder att denna typ av beteende i större utsträckning påverkas av långvarig avel i en viss fångenskapsmiljö medan socialt beteende och födosöksbeteende istället kan bero på den omedelbara sociala eller fysiska miljön. Antipredatorbeteende studerades också i en longitudinell studie av två populationer över fyra generationer och det visade sig att populationerna blev mer lika varandra ju längre tiden gick då de hölls under likadana miljöförhållanden. Det verkar alltså som om antipredatorbeteende kan förändras av avel i en viss miljö efter bara ett fåtal generationer. Utöver detta studerades även dagliga beteendemönster i olika djurparksmiljöer samt dygnsrytm av galanden hos både vilda populationer och djurparkspopulationer inom artens naturliga utbredningsområde. Resultaten tyder på att sådana beteendemönster inte påverkas nämnvärt av att djur hålls i fångenskap. Fallstudien som presenteras här är ett av de första försöken att, ur ett bevarandeperspektiv, studera hur fångenskapsmiljöer kan påverka djurs beteende och resultaten talar för att dessa aspekter är viktiga att ta hänsyn till vid planering av bevarandeavel.

List of papers

The thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I. Håkansson, J. and Jensen, P. 2005. Behavioural and morphological variation between captive populations of red junglefowl (*Gallus gallus*) – possible implications for conservation. *Biological Conservation* 122: 431-439.
- II. Håkansson, J., Kerje, S., Hailer, F., Andersson, L. and Jensen, P. Genetic diversity and its correlation with behavioural variance in captive populations of red junglefowl – possible implications for conservation. Accepted pending revision in *Zoo Biology*.
- III. Håkansson, J., Bratt, C. and Jensen, P. 2007. Behavioural differences between two captive populations of red jungle fowl (*Gallus gallus*) with different genetic background, raised under identical conditions. *Applied Animal Behaviour Science* 102: 24-38.
- IV. Håkansson, J. and Jensen, P. A longitudinal study of antipredator behaviour in four successive generations of two populations of captive red junglefowl. Submitted manuscript.
- V. Håkansson, J., Ahlander, S. and Jensen, P. Behavioural sex differences and diurnal crowing rhythms in red junglefowl (*Gallus gallus*) in Northern India. Submitted manuscript.

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Introduction

Conservation breeding and reintroduction as a conservation tool

The earth is presently undergoing an era of unprecedented number of species extinctions (Lawton and May 1995). Current and predicted future extinction rates are much higher than the estimated natural levels and most extinctions appear to be caused by human activity (e.g. Magin et al. 1994, Frankham et al. 2002). As threats to ecosystems continue to increase worldwide, conservation of species has become a central concern. One field of conservation, conservation breeding or *ex situ* conservation, is dealing with captive populations and may aid conservation through education, fundraising and research as well as breeding for release into the wild (Hutchins et al. 1995). Conservation breeding should not be seen as an alternative to, but rather a complement to *in situ* conservation; the protection of wildlife habitats. However, conservation breeding is sometimes the only hope for species near extinction in the wild. Some of the last wild individuals of seriously threatened species may then be taken into captivity in order to increase their population size until conditions are suitable for re-establishment of free-living populations. For example, the last few wild Californian condors (*Gymnogyps californianus*) were taken into captivity during the 1980's. They were incorporated into an intensive breeding program with the aim of release and today there is a wild population of more than 100 birds (Kaplan 2002, WAZA 2007). In other cases, the breeding program may not be initiated until the species is already extinct in the wild. For example, a coordinated conservation breeding program was set up with 12 captive individuals when the Przewalski's horse (*Equus przewalskii*) had become extinct in the wild. The program has been running since 1979 and has resulted in successful reintroductions as well as a vital population of over 1500 individuals kept in captivity worldwide (WAZA 2007).

Conservation breeding with the aim of reintroduction is today a widespread technique used to restock or re-establish populations of species that have undergone extensive declines. However, animal collections in individual zoos are generally too small to be of much value for long-term conservation and consequently, international or regional breeding programs are required to form viable populations. A reintroduction involves the release of individuals into a suitable habitat in the hope that they will survive, reproduce and lead to a self-sustaining wild population (Griffith et al. 1989).

This has been achieved for a number of species, such as the European bison (*Bison bonasus*), the Scimitar-horned oryx (*Oryx dammah*) and the Red wolf (*Canis rufus*), whereas for others, such as the Hawaiian goose (*Branta sandvicensis*), reintroduction has failed. An alarmingly high proportion of reintroductions have not been successful in establishing viable populations (Griffith et al. 1989, Kleiman 1989, Beck et al. 1994, Wolf et al. 1996). In many species, predation is the major factor reducing survival after release (Short et al. 1992, van Heezik et al. 1999). However, the reasons for either success or failure of reintroductions are variable and often unknown (Wolf et al. 1996), and, as a consequence, understanding the factors contributing to the outcome of a reintroduction is essential in order to improve conservation breeding as an effective conservation tool (Curio 1996, Wolf et al. 1998, Fischer and Linder Mayer 2000).

Genetic diversity vs. genetic adaptation

There are basically two types of harmful genetic changes which can occur during conservation breeding and management in captivity: loss of genetic diversity and genetic adaptation. Until recently, the majority of discussions in conservation biology have focused on how to monitor and preserve genetic variability within species with the assumption that higher variation enhances a population's viability over time (Avisé et al. 1995). Genetic variability is randomly reduced by inbreeding and genetic drift in relatively closed small populations. Inbreeding increases homozygosity which may result in a lowering of fitness because of expression of deleterious genes previously masked by dominant alleles, while genetic drift causes certain genes to become fixed in a population as a result of their relative abundance in the small founding population. Alleles that are passed on from one generation to the next may only represent a small sample of the allelic variation in the parental generation. Furthermore, by chance alone, some alleles may not be passed on to the offspring generation at all while others may increase or decrease in frequency.

The behavioural difficulties experienced in the reintroduction of captive-bred animals have been suggested to, at least partly, result from adaptations to captivity (Frankham 1995, Frankham et al. 2000). Ever since Darwin (1868) described selection for tameness and general adaptations to captivity in captive populations, the potential for genetic adaptation to captivity has been recognized. Rapid genetic adaptation to captivity has, for example, been documented in *Drosophila* (Frankham and Loebel 1992) and the rat

(*Rattus norvegicus*; King 1939). However, despite the awareness of potential undesirable consequences of adaptation to captivity, there is still a lack of experimental evidence (Gilligan and Frankham 2003). Consequently, while maintaining genetic diversity per se is often emphasized as critical to the success of conservation breeding programs (e.g. Foose and Ballou 1988, Allendorf 1993) behavioural effects caused by genetic adaptation, are not taken into consideration to any great extent (Snyder et al. 1996, Frankham et al. 2002).

Captivity vs. the wild

The phenotype of an organism is determined by the interaction between its genotype and the environment in which it develops but exactly how this interaction occurs is not instantly recognizable (Pigliucci 2001). The behaviour of a wild animal is the product of many generations of natural selection and adaptation to specific environmental conditions. However, captive-bred animals may experience environmental conditions considerably different from that in the wild (Price 1999, Waples 1999). Compared with a wild environment, captivity may be perceived as a stressful environment in many different ways, such as unnatural sounds, light conditions, odours, substrates, restricted space and foraging opportunities and abnormal social groups (reviewed by Morgan and Tromborg 2007). Perhaps one of the most distinctive elements of a captive environment is close contact with humans which is a feature that can be expected to produce behavioural characteristics not found in a wild-reared animal. Furthermore, captive environments may be considerably less complex than the dynamic wild environments.

Evidently, despite comprehensive genetic management, populations gradually become more adapted to captivity (Beissinger 1997). Hence, animals born and reared in captivity may be behaviourally distinct from those born and reared in the wild and the extent of this difference will depend on the degree of environmental difference between captivity and the wild as well as the phenotypic plasticity of the species (Moltz 1965).

Huntingford (2004) suggested the following explanations to behavioural differences between wild and cultured animals; different previous experience, selection of behavioural phenotypes that increase survival rate and inheritance of selected behavioural characteristics through several generations. Considering the plasticity of phenotype traits like behaviour or

morphology depending on the presence or absence of predators, one could expect that some responses could be attenuated in animals reared in captivity (Brokordt et al. 2006). However, the main behavioural differences between captive and wild populations are quantitative rather than qualitative as they are the result of changes in intensity or frequency of behaviours rather than addition or elimination of behaviours in the behavioural repertoire of an animal (Kretchmer and Fox 1975, Price 1999). Furthermore, they may be caused by genetic changes in the population or by learned alteration of a behaviour occurring during the animal's lifetime (Hale 1969, Price 1984).

Domestication

The success of future conservation breeding will most likely depend on a comprehensive understanding of the domestication process and its effects on animals, as well as knowledge of behavioural development in captive environments. Domestication is defined by Price (1984) as the “process by which a population of animals becomes adapted to man and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation”. The process of domestication can proceed rapidly (Moyle 1969, Swain and Riddell 1990), it is difficult to reverse (Lyles and May 1987, Derrickson and Snyder 1992) and, occasionally, it can be quite strong (Belyaev 1979). Even if the intention is to avoid it, some degree of domestication is inevitable when breeding animals in captivity (Allendorf 1993, Snyder et al. 1996). In Pacific salmonids, for example, there is evidence that, although there is no deliberate plan for artificial selection, conditions in captivity inadvertently select for behavioural and morphological traits that are not optimal in the wild (e.g. Reisenbichler and McIntyre 1977, Fleming and Gross 1989, Swain and Riddell 1990, Fleming and Gross 1992, 1993). Furthermore, when investigating captivity effects on predator response in populations of Oldfield mice (*Peromyscus polionotus subgriseus*), McPhee (2004) found that the more generations a population had been in captivity, the less likely were the individuals to take cover in response to being exposed to a predator. Such captivity-induced modifications of behaviour could seriously diminish the chances of survival after reintroduction and, hence, management should be designed to reduce the effects of adaptation to the captive environment.

According to Price and King (1968) and Price (1984), there are three major selective mechanisms which influence the gene frequencies of captive populations; artificial selection, natural selection in captivity and relaxed natural selection.

Artificial selection is selection for biological traits desired by humans. This is presumably avoided during conservation breeding. However, there is a risk that individuals that are easy to handle and cope well with the captive situation are preferred simply because of maintenance issues. Individuals exhibiting either extreme fear or extreme aggression towards humans may be removed from a breeding pool because they are too difficult to manage.

Natural selection in captivity is usually initiated early in the domestication process as individuals differ in their ability to cope with a captive environment. This selection acts primarily to eliminate those individuals that are biologically and/or psychologically incapable of producing offspring in captivity. Hence, without human interference, individuals possessing the phenotypes which are best able to cope with captive conditions will have the highest reproductive success.

The *relaxed natural selection* is a natural consequence of environmental conditions in captivity. It occurs when captive conditions allow or favour certain behavioural traits which would have been selected against under wild conditions. As animals are provided with food and shelter, certain behaviours that are vital for survival in nature lose much of their adaptive significance. Predators and parasites are usually absent or controlled and carnivores are no longer selected for their ability to catch prey. Hand-rearing of weak or rejected juveniles also preserves genes in the captive populations which might have been eliminated in the wild.

There are a number of characteristics which can be referred to as being typical for a domesticated phenotype. For example, domestic animals often differ extensively from their wild ancestors in colour and hair growth. Wild animals have protective colouring and their hair growth is adapted for thermal regulation while domestic animals may have a great variety of colours as well as shorter, longer or curlier hair (Belyaev 1969). Generally, some traits become more frequent or more conspicuous during domestication while others become less frequent or less conspicuous but it

also varies between species. Body size, for example, has increased for some species (e.g. rabbit and most horse breeds) while it has decreased for others (e.g. sheep and cattle). A behavioural trait that is seen in essentially all domestic animals is reduced responsiveness or sensitivity to environmental change (Price 1999). This is, for example, reflected in their response to new environments, unfamiliar conspecifics or novel objects. Furthermore, domestication typically selects for behavioural traits such as docility, low aggression, and better ability to cope with crowding stress (Kretchmer and Fox 1975).

Antipredator behaviour in captivity

Predation is suggested to be a key factor limiting the initial success of reintroduction efforts (Short et al. 1992, Beck et al. 1994, Miller et al. 1994, Wolf et al. 1996, Fischer and Lindenmayer 2000), as mortality of animals raised in captivity is typically very high shortly after release (Griffith et al. 1989). Antipredator behaviour is expected to be under particularly strong selection (Abrams 2000) and hence, natural selection acts to favour stronger antipredator behaviour in habitats with higher risk of predation (Riechert and Hedrick 1990, Chivers et al. 2001). Animals raised in captivity generally tend to differ behaviourally from those in the wild, particularly in fear-related behaviours such as predator avoidance (Kleiman 1989, McLean et al. 1996, 1999, Griffin et al. 2000, Johnsson et al. 2001, Griffin and Evans 2003). Differences in antipredator behaviour between different populations have been found in, for example, insects (Lewkiewicz and Zuk 2004), spiders (Riechert and Hedrick 1990), amphibians (Chivers et al. 2001), fish (Giles and Huntingford 1984) and mammals (Oda and Masataka 1996). As an example, inspection behaviour in guppies responds to selective pressures associated with predator regimes as individuals from high predation populations inspecting more frequently than guppies from populations with low predation pressure (Dugatkin and Alfieri 1992, Reznick et al. 2001).

Reintroduced individuals have usually been raised in captive environments without any risk of predation and are hence unfamiliar with the natural environment (Wolf et al. 1996) and this inexperience could increase their short-term vulnerability to predators after release (Beck et al. 1991, Short et al. 1992, Miller et al. 1994, Curio 1996). Antipredator behaviour must be expressed properly the very first time it is required, i.e. when a predator is first encountered. However, many animals can improve their responses with experience (Griffin et al. 2000). Furthermore, some species possess innate

predator avoidance capabilities, while others may require some experience in order to respond behaviourally to predation risk and thereby reduce the likelihood of being killed (Curio 1993). Expression of antipredator behaviour as adults is influenced by past experience with predator-like stimuli in several different species (e.g. marsupials, McLean et al. 1996; birds, McLean et al. 1999; and fish, Huntingford et al. 1994). Therefore, conservation breeding programs should be designed to condition animals to respond in appropriate ways to the challenges of a wild environment. In some cases, pre-release training has been used to enhance antipredator skills and hence, increase the likelihood of survival after release (Maloney and McLean 1995, McLean et al. 1996, 1999, Griffin et al. 2000). Results of pre-release antipredator training are encouraging for those attempting to develop techniques to help captive-bred individuals of endangered species survive encounters with potential predators after release (Griffin et al. 2001). However, as suggested by Rabin (2003), behavioural management would be more effective if it occurred regularly during the time in captivity rather than being disregarded until the time just prior to reintroduction.

Social behaviour in captivity

A major component of an animal's environment is the presence of other members of the same species and this may differ considerably between a natural habitat and a captive environment. In the wild, animals can retreat from, or avoid, agonistic encounters but in captivity such strategies may be impossible to employ due to space restriction and crowding (e.g. Price 1984). Furthermore, mate choice is often absent in intensively managed populations and hence, reproduction occurs without the need to attract mates or compete with rivals.

The nature of social groups in captivity may be a critical factor for the well-being of captive animals of social species and furthermore, it may have crucial effects when animals are released. For example, evidence from studies of captive-bred and wild stocks of fish suggests that agonistic behaviour may increase during domestication (Moyle 1969, Swain and Riddell 1990, Kelley et al. 2006). Hence, competition in captivity may favour the most aggressive and territorial individuals at the expense of the less aggressive ones. A shift in social behaviour, for example towards more aggressiveness, could have crucial effects on the outcome of reintroduction as this behaviour may not be optimal in the wild.

Exploratory behaviour in captivity

No single aspect of maintenance in captivity is more dependent on field observations than the question of foraging behaviour (Eisenberg and Kleiman 1977). Many animals spend a large portion of their daily activity budget exploring their environment in search for food. In captivity, however, food is usually provided by keepers and found without much effort. As a result of the altered selection pressure, domestication may result in a modification of exploratory behaviour towards less energy demanding strategies (Schütz et al. 2001). Sometimes, the challenge of replicating a natural diet may be almost impossible which may create difficulties during conservation breeding as well as after reintroduction. It has been shown that, for example, wild and hatchery fish differ in feeding efficiency; wild fish ate more, attacked quicker and were more efficient in consuming novel prey (Sundström and Johnson 2001).

Behavioural conservation

Management techniques resulting in healthy young are generally all that are needed for keeping animals in captivity, however, if the intention is to release the offspring of captive animals behavioural considerations ought to become a priority. In order to maintain behaviour as it evolved in the wild, selection must be minimized in conservation breeding populations and animals must be kept in an environment providing appropriate stimuli for eliciting wild behaviour in order to minimize genetic adaptations (Carlstead 1996). For each species involved in conservation breeding, this requires thorough knowledge of behaviours in the wild as well as consideration of the environmental influences on the development of those behaviours. The potential benefits of behavioural studies in the area of conservation breeding have been discussed by several authors (e.g. Curio 1996, Sutherland 1998) but relatively few have been conducted. Mathews et al. (2005) suggests that behavioural experiments could help explain why reintroductions fail and how to improve conservation breeding techniques, by focusing on fundamental questions relating to evolutionary fitness.

Red junglefowl as a case study

There are four species of junglefowl known to the modern ornithology: Ceylon junglefowl *Gallus lafayettei*, green junglefowl *G. varius*, grey (or Sonnerat's) junglefowl *G. sonnerati* and red junglefowl *G. gallus*. The red junglefowl is considered to be the ancestor of all poultry and domestication occurred about 8000 years ago (West and Zhou 1989, Siegel et al. 1992, Yamashita et al. 1994, Niu et al. 2002). Small populations of red junglefowl are kept in zoos and bird collections all over the world and the species can still be found in the wild in Southeast Asia (Delacour 1951, Collias and Saichuae 1967, Crawford 1990, Kaul et al. 2004). Morphological variation in red junglefowl is connected to their geographic distribution and is especially marked in males (Crawford 1990). This has led to the designation of five different subspecies: Cochin-Chinese red junglefowl *G. g. gallus*, Burmese red junglefowl *G. g. spadiceus*, Tonkinese red junglefowl *G. g. jabouillei*, Indian red junglefowl *G. g. murghi* and Javan red junglefowl *G. g. bankiva* (Delacour 1951; Fig 1). However, the standards for how to separate the subspecies are still under discussion (e.g. Niu 2002). Furthermore, although the red junglefowl is generally not considered to be of major conservation concern, the “purity” (i.e. degree of hybridization with its domesticated form) of both captive and free-roaming populations has been questioned (Peterson and Brisbin 1998, Brisbin et al. 2002, Corder 2004, Kaul et al. 2004). However, these suspicions are based on morphological and preliminary molecular studies of captive birds and museum specimens and hence, there is a need for more extensive and systematic genetic comparisons between wild, captive and hybridized birds.

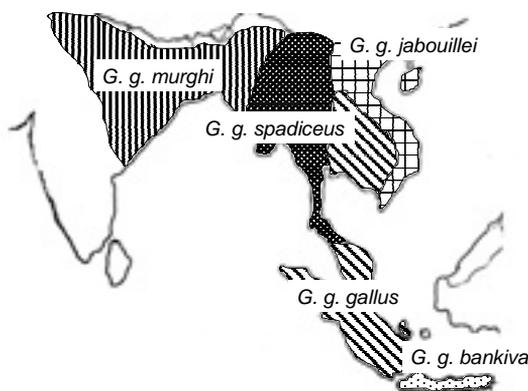


Figure 1. Distribution of five subspecies of red junglefowl in Southeast Asia (After Nishida et al. 1992).

Male and female red junglefowl show strong sexual dimorphism (Fig. 2) and they typically live in territorial groups containing one dominant male, several females and their offspring. The two sexes form separate social hierarchies and have different roles in the flock; the female taking care of the chicks while the male protects the territory and competes for females (Wood-Gush 1989). Younger males are subordinate to the dominant male and are typically excluded from the flock when they mature.



Figure 2. Sexual dimorphism is an obvious characteristic in female and male red junglefowl (Photos: J. Håkansson).

Wild red junglefowl are subject to hunting in their natural habitat (often mixed forests nearby to sparsely cultivated areas; Fig. 3) and extremely cautious and difficult to observe for any length of time (Collias and Collias 1967, 1996). Hence, very few studies have been conducted on the natural behaviour of red junglefowl in the wild. Most research has instead been carried out in American and European zoo settings or at research stations with birds originating from zoos or from game bird breeders. Zoo populations of red junglefowl are generally not subject to any controlled breeding programs and hence, they are isolated from each other which suggests a high risk of inbreeding. The origin of the populations is often uncertain and it is possible that the founder birds were collected in close vicinity to villages which increases the risk of intercross with domestic fowl. Furthermore, in many cases, Western zoo populations tend to descend from birds caught in the wild a long time ago. Hence, it may be expected that captive populations of red junglefowl within their natural distribution have not been kept in captivity for as long as the ones elsewhere.



Figure 3. The natural habitat of red junglefowl in Northern India; mixed forests adjacent to scattered cultivated areas (Photo: J. Håkansson).

Red junglefowl has been used for a number of years in research concerning the effects of domestication on the behaviour of fowl as well as the genetic basis for it (e.g. Andersson et al. 2001, Schütz and Jensen 2001, Lindqvist et al. 2002, Väisänen et al. 2005). This research has shown that relaxation of natural selection pressures and selection for specific production traits during domestication cause modifications of natural behaviour towards less energy demanding strategies. This is genetically controlled by loci which seem to have effects on growth or egg production and behaviour simultaneously (Schütz et al. 2004). Since domestication is an evolutionary process based on a shift in selective pressures and behaviour is regarded to be among the first traits to undergo adaptive changes (Kohane and Parsons 1988, Ruzzante and Doyle 1993, Price 1999), similar effects will possibly occur in any captive situation even if the motive is maintenance for conservation rather than domestication. Therefore, in the present thesis, the red junglefowl is used as a case study for studying the effects of captive environments on behaviour from a conservation perspective.

Aim of thesis

The general aim of this thesis was to study behavioural aspects of conservation breeding and investigate whether, and how, maintenance of small populations in captivity cause behavioural modifications, which could affect the success of reintroductions. Throughout the project, the red junglefowl was used as a case study, representing animals maintained in captive populations.

To explore whether or not captive populations of red junglefowl differ in behaviours essential for a life in the wild, the aim of **Paper I** was to investigate behavioural variation between populations of red junglefowl maintained in different captive environments. In **Paper II**, the aim was to examine the genetic relationships between the populations and investigate possible correlations between genetic diversity and the results of **Paper I**. The aim of **Paper III** was to study the behaviour of two populations with different backgrounds when they were raised under identical conditions. Antipredator behaviour was studied in **Paper IV** in two populations over four generations with the aim to investigate how a protected captive environment affected the antipredator response over generations. As all birds studied in **Papers I-IV** had been kept in European zoos for numerous generations and as the purity of captive populations of red junglefowl has been questioned, the aim of **Paper V** was to describe daily behavioural routines and diurnal crowing rhythms of red junglefowl in their natural area of distribution.

Summary of papers

Paper I

The study presented in Paper I was a first screening of behavioural variation between captive populations. Four populations of red junglefowl, kept under different captive conditions and differing in number of years of maintenance in captivity, were studied in standardized test situations. The birds were tested in three different tests in order to measure antipredator behaviour, social behaviour and exploratory behaviour.

The results showed that there were behavioural differences between the captive populations in antipredator behaviour, social behaviour and exploratory behaviour, which potentially could all be crucial for animals in a reintroduction situation. However, the extent to which these differences were due to genetic changes caused by small breeding populations or adaptations based on the individual birds' experiences in the different environments was not yet known, although morphological differences suggested that genetic differentiation may cause some of the behavioural differences as well.

Paper II

The genetic diversity of the populations studied in Paper I was examined by using microsatellite markers distributed throughout the chicken genome. The genetic diversity of each population was also compared to the behavioural differences found in Paper I and possible correlations were considered.

The results showed that, as could be expected from the small population sizes, the studied populations had low genetic diversity. Furthermore, the populations were highly genetically differentiated which could, at least partly, explain the behavioural differences found in Paper I. Interestingly, the genetic variation within each population was correlated to rank of behavioural variation which may suggest that genetic diversity affects behavioural variance.

Paper III

Eggs were collected from two populations, one of which was maintained in a semi-natural environment while the other was kept under more protected conditions, and chicks were hatched and raised together in one group. The birds were tested in several different behavioural tests in order to study exploratory behaviour, social behaviour and several aspects of fear-related behaviours; fear of humans, antipredator response, tonic immobility, handling as well as behaviour in complex and novel environments.

The study revealed that the populations differed in several ways in fear-related behaviours but not in exploratory or social behaviours. Generally, the population originating from the semi-natural environment showed more intense fear behaviours than the other. This suggests that fear-related behaviours depend more on the genetic background of animals than exploratory and social behaviours which may be more influenced by the immediate physical or social environment.

Paper IV

The study reported in Paper IV was a longitudinal study of antipredator behaviour in four successive generations of two populations. During generation 1, the populations were kept under different captive conditions; one was kept in a semi-natural environment while the other was kept under more protected conditions. From generation 2 and onwards, the populations were kept under identical conditions. In each generation, predator responses were measured in a standardized simulation test and all tests were conducted by the same observer.

The results showed that the two populations became more similar in their antipredator behaviour in successive generations. In all generations, the population which was originally kept in a semi-natural environment was more agitated during the tests than the other population, although they became more similar over time. The study suggests that modifications of behaviour can occur after only a few generations in a new environment, even though there is no intended directed selection.

Paper V

Daily routines and crowing fluctuations of red junglefowl were studied in their natural area of distribution, Northern India. Time budgets were studied in four different captive populations and the study of crowing fluctuations involved two captive populations and two wild ones.

The time budget study revealed that the birds spent most of their day foraging and that females spent more time foraging than males. Males, on the other hand, spent more time performing comfort behaviours and walking/running than females. Furthermore, male time budgets differed more between populations than female time budgets, possibly suggesting that males are more affected by the social or physical environment than females. Regarding diurnal crowing fluctuation, no qualitative differences were found between wild and captive birds. Most crowing calls were heard around dawn with a second peak around sunrise and all populations showed high agreement regarding time of first crowing call in the morning and last crowing call in the evening. This suggests that crowing behaviour is stable across different environmental conditions.

Discussion

Antipredator behaviour and other fear-related behaviours

Mortality of animals raised in captivity is typically very high shortly after release (Griffith et al. 1989) and, in many species, predation is the principal factor reducing the survival (Short et al. 1992, van Heezik et al. 1999). Hence, information about how antipredator behaviour is affected by captive environments is essential in order to increase the efficiency of conservation breeding programs.

Animals maintained in captive environments are not adapted to situations in which a predator attack is likely to occur and, as a result, their antipredator behaviour may be modified. The degree of modification may depend on the amount of time spent in captivity or the level of protection in the captive environment. In captivity it may not be favourable to be alert and cautious. The most alert animals may even be too stressed by the contact with humans, a potential predator, to be able to reproduce in captivity. Hence, their genes may be lost in the captive population. There may also be costs associated with antipredator behaviours as the time animals would spend being cautious may be better spent competing for resources in the captive environment.

In Paper I, the population which had been kept for the least number of years in captivity reacted strongest to the simulated predator attack while the population living under most protected conditions were least agitated by the simulated predator attack. This is in accordance with the findings by McPhee (2004) who found that the more generations a population of Oldfield mice had been in captivity, the less likely were the individuals to take cover after exposure to a simulated predator. Differences in antipredator behaviour between red junglefowl and domestic fowl (Andersson 2000) as well as between wild and farmed Atlantic salmon (Einum and Fleming 1997, Fleming and Einum 1997, Johnsson et al. 2001) and brown trout (*Salmo trutta*; Johnsson et al. 1996) have been suggested to be a result of relaxed natural selection in captivity. A similar suggestion may well be suitable for the findings in Paper I as the populations were kept under conditions differing in their level of protection from predation and thus, differing in their selection pressures.

Relaxed natural selection may be an explanation also in Paper III. The populations descend from birds living under different selection pressures and this may have caused genetic-based modifications of antipredator responses as well as other fear-related behaviours. The two populations studied in Paper III differed, for example, in response to the simulated predator attack as well as response to human hand approach even though they had been raised in the same environment. When animals are kept in close contact with humans, the selection pressure may change from favouring human avoidance towards accepting daily encounters with the keepers. Nogueira et al. (2004) found that captive-born capybaras (*Hydrochoerus hydrochaeris*) were more docile in the presence of humans while wild-caught individuals showed flight responses. Similarly, in Paper III, the population originally kept under semi-natural conditions (from here on called “the semi-natural population”) was more nervous in the fear-for-humans test than the population derived from birds living in a more protected environment with daily contact with humans (from here on called “the protected population”). In most tests, reported in Paper III, the semi-natural population was more alert or agitated than the protected one. This was also the case in Paper IV, where four generations of the two populations was studied with focus on antipredator behaviour. The semi-natural population was more agitated than the protected one in all generations, both before and after the simulated predator attack. However, the populations became more similar in their antipredator behaviour over time. The semi-natural population generally decreased in agitation index while no clear pattern could be seen in the protected population. Interestingly, no birds from the protected population scored category 3 (strongest response) in generation 1, whereas during the subsequent generations about 20-30% of the protected population birds reacted according to the strongest response category. A possible explanation may be that the protected birds were influenced by the semi-natural birds, which, in general, seemed to be more wary and alert in the home pen and during handling as well as during testing. Furthermore, prenatal stress may have had an unknown effect on the behaviour of the subsequent generations as the social environment can be an effective stressor and can be crucial for the development of the offspring as well (reviewed by Kaiser and Sachser 2005).

The population differences found in Papers I and III are suggested to be a result of genetic adaptations to the different captive environment. Therefore, in Paper IV, the expectation was that since the protected population had been kept at the research station for many years, they would not change their

behaviour over generations. The semi-natural population, on the other hand, was expected to become more and more similar to the protected population as they were transferred into a new, more protected captive environment. However, evidently, the antipredator behaviour of both populations differed over generations, suggesting that behavioural modifications can occur in captivity even though there is no intended directed selection. The results are probably best explained by a combination of genetic drift, social influence and some unintentional selection of stress coping. As suggested by Belyaev and Borodin (1982), environmental differences between captive and wild environments may lead to a selection for stress resistance during the first few generations in captivity. This may be what was causing the semi-natural population to become less agitated and more similar to the protected population.

Social behaviour

The social environment in captivity generally differs from that in the wild and this may have an effect on the development of social behaviours in captive populations. For example, the social environment in captivity may deprive a young animal of specific stimulation essential for the development of a certain species-typical behaviour such as how to behave in social interactions (Carlstead 1996). A modified social behaviour could seriously affect an animal's reproduction and competition capacity after reintroduction. An issue which is not often discussed in conservation breeding contexts is the risk of the intense genetic management leading to offspring with low "social fitness". Females and males are paired based on the best match to avoid inbreeding and loss of genetic diversity, perhaps in combination with the minimum need of transportation between zoos. Hence, females may be "forced" to mate with males which they would not have preferred in the wild and this could then result in offspring with non-preferable characteristics. Furthermore, as food and other resources are usually provided by humans, selection for competition skills may be drastically different in a captive environment.

In Paper I, the populations differed slightly in social behaviour and the population showing the most aggressive behaviours (the protected population) was the one differing the most from the other ones regarding captive conditions. The protected population was kept indoors at Götala research station and under more crowded conditions than the other three

populations and it is possible that there was more competition for resources than in the other, more freely kept, populations.

The birds studied in Paper III were derived from the two populations differing the most in social behaviours in Paper I; the semi-natural population and the protected one. Interestingly, no differences were found between the populations in social behaviours when they were raised together in one group. This suggests that social behaviour may be more influenced by the immediate social environment than by genetic adaptation to a specific captive condition. However, while certain social behaviours may change rapidly when animals are released to natural environments, others may develop gradually over several years (Tear and Ables 1999). Therefore, only long-term monitoring will give insight into how social behaviour may affect the outcome of reintroductions.

Exploratory behaviour

Animals released into the wild are dependent on adaptive exploration strategies in order to find food in a new and variable environment. In nature, a large amount of an animal's time and energy is spent acquiring food and water (Price and King 1968). However, domestication may influence exploratory behaviour towards less energy demanding strategies (Schütz et al. 2001). In captivity, the animals are usually provided with food and do not have to search for it. In the wild, on the other hand, many animals spend a large portion of their day exploring their environment in search for food. It is possible that changing feeding routines during maintenance, for example by varying feeding sites, feeding times, preparation and presentation of food, could prepare the animals for a life in the wild. The presentation of food may also have a profound effect on the animals' health in captivity. For example, animals which normally kill their prey in isolation from the rest of the group may be stressed when forced to eat in close proximity to other individuals. Some species may also need pre-release training in order to learn specific skills needed for life in a particular wild environment. Captivity may not prepare animals for the necessity to adopt an energy conserving strategy in order to survive potentially hard times with poor food supply. Association with wild animals which are familiar with environmental condition may allow released animals to learn survival skills (Britt and Iambana 2003). Furthermore, some species may require supplemental food when transited to the wild but this does not appear to be necessary in all cases (e.g. Tweed et al. 2003).

Significant differences were found in exploratory behaviour between the four populations studied in Paper I. The populations differed in, for example, movement between food sources, which can be seen as a way of exploring the new environment. As the two populations studied in Paper III did not differ much in exploratory behaviour when studied in their original captive environment (Paper I), it may not be a surprise that they did not differ when raised together in an identical environment either. It would have been very interesting to see if animals with clearly different exploration strategies in their original captive environment would still differ in exploratory behaviour when raised together. This would be an interesting proposal for future studies in order to broaden the knowledge about how exploratory behaviour may be affected by captive environments.

Time budget and crowing fluctuation

In order to make conservation breeding programs efficient as a conservation tool, there is a need for thorough understanding of the species' daily routine and how captive environments may influence it. The captive environments could then be designed in way to let the animals live as "natural" as possible. Comparisons between wild and captive animals of a certain species could be useful in this matter. The study of crowing fluctuation reported in Paper V was an attempt to investigate the routines of wild and captive red junglefowl in their natural area of distribution. Time budget, on the other hand, was not possible to study in the wild but instead several captive populations were compared to investigate the effect of the captive environments.

The captive populations studied in Paper V spent most of their day engaged in foraging activities which is in conformity with the behaviour of their wild conspecifics (Collias and Collias 1967) and free-living hens (Dawkins 1989). Furthermore, no differences were found in diurnal crowing rhythm between wild and captive birds. Most crowing calls were heard around dawn, followed by a smaller peak at sunrise which is also in accordance with the crowing patterns found by Collias and Collias (1967). Crowing has been suggested to have several different functions such as reinforcing general territorial relations, helping to keep flocks separated and strengthening dominance relations between males within multi-male flocks (Collias and Collias 1967, Leonard and Horn 1995). Thus, it seems that territory and dominance proclamation are natural parts of the life of a male red junglefowl also in captivity. The similarity of both time budgets and crowing routines in wild and captive birds, suggests that behavioural routines are relatively

constant across different environmental conditions and not affected by captivity.

General discussion of key results

Behavioural consideration is an exceptionally important component of conservation breeding with the aim of reintroduction (Lyles and May 1987, Kleiman 1989, Snyder et al. 1996). The work presented in this thesis has focused on how maintenance of animals in captive environments may affect their behaviour and the possible implications of this for conservation. As antipredator behaviour appears to be a particularly important aspect of reintroduction (Curio 1996, Carlstead 1996, Snyder et al. 1996), this has been the focus of several studies presented here.

The behavioural differences found in Paper I, III and IV imply that life in a captive environment can influence an animal's behaviour in a way that could be crucial in a reintroduction situation. Since modified antipredator behaviour, possibly as a result of genetic adaptation, plays a central role in the outcome of a reintroduction, this has been the main focus of this thesis and the differences found were also most pronounced in antipredator behaviours. When studying populations in different captive environments, differences were also found in social and exploratory behaviours (Paper I). Interestingly, no differences were found in social or exploratory behaviours in birds from different environments, when they were raised under identical conditions (Paper III), suggesting that these types of behaviours may be more dependent on the immediate social or physical environment than on genetic adaptation to a specific environment.

It is possible that the behavioural differences found in Paper I were a result of the environmental differences. However, in Paper III and IV, when the environment was identical for all birds, several behavioural differences were still seen which further suggest that the differences in antipredator behaviour are caused by genetic adaptations to the different environments. Hence, these findings underline the importance of taking genetic adaptation to captivity into consideration when planning conservation breeding programs.

Furthermore, because of the similarity of crowing routines in wild and captive populations and of time budgets in different captive populations (Paper V), such routines seem to be stable across different environmental conditions and not affected by captive environments as, for example,

antipredator behaviour appear to be (Paper I, III and IV). This is in accordance with the fact that antipredator behaviour is expected to be under particularly strong selection pressure (Abrams 2000). However, as shown in Paper IV, modifications of antipredator behaviour may occur after only a few generations in a new environment. This may be a consequence of a selection for stress resistance during the first few generations in a protected captive environment, as is the case in early domestication (Belyaev and Borodin 1982).

A note on genetic diversity and behavioural variation

An interesting correlation between genetic diversity and behavioural variation ranks was found in Paper II. The populations with the lowest genetic diversity also showed low behavioural variation. To my knowledge, such correlation has not been reported before and since genetic diversity is a critical aspect of conservation breeding, further investigation of its influence on behaviour would be of interest. Furthermore, McPhee (2004) suggested that increased behavioural variation may be translated into decreased survivorship after reintroduction. This may seem contradictory to my result as long-term maintenance in captivity usually leads to decreased genetic diversity. Nevertheless, this correlation may potentially have crucial implications for conservation breeding and the results are preliminary and need to be followed up by more studies. In this study we used microsatellite markers for investigating genetic diversity, however, in future studies it would be interesting to connect genetic diversity in markers to genes relevant for behaviours of interest for conservation breeding success.

The future of conservation breeding

Since behaviour is a consequence of interactions between genetic and environmental factors both of these must be considered when planning for conservation breeding if the goal is to reintroduce animals which are fit for a life in the wild. As mentioned earlier, past discussions of conservation breeding have mostly concerned genetic diversity and have generally disregarded environmental issues, however, these may be equally important for long-term conservation. Failure to present captive environments which are, at least functionally, equivalent to that of the wild will inevitably result in the loss of certain patterns of natural behaviour (Shepherdson 1994). Therefore, and as suggested by, for example, Frankham et al. (1986) and Stamps and Swaisgood (2007), captive populations should be maintained

under conditions that are as similar to the wild environment as possible. An example of this is the successful conservation breeding program for the endangered Lord Howe Island woodhen (*Gallirallus sylvestris*), for which the captive population was maintained close to the release site. If consideration is given to both genetic diversity and behavioural issues such as effects of captivity, conservation breeding will most certainly be an even more effective tool for conservation than it is today. Thus, it would be better to involve behavioural biologists at the beginning of a conservation breeding program than to wait until a problem emerges (Blumstein and Fernández-Juricic 2004). The success of conservation breeding programs will essentially depend on a comprehensive understanding of the role of the captive environment in the development of behaviour. However, one must never forget that in order for a reintroduced animal to have a chance to survive in the wild, conservation breeding must always be complemented with habitat preservation and elimination of the threats causing the animals to become endangered in the first place.

The use of red junglefowl as a case study

In this exploratory work of behavioural aspects on conservation breeding, the red junglefowl was used as a case study representing animals maintained in captivity. At first sight, it may seem ambiguous to attempt to generalize from the results of a case study, when the success or failure of conservation breeding naturally differs greatly between species. Nevertheless, if conservation breeding is going to progress as an efficient conservation tool, more research is needed from the perspective of how captive environments affects behaviour over generations and how this may affect reintroduction results.

It may be argued that the European populations included in this study are not “pure” red junglefowl due to introgression of domestic fowl. If so, the differences in Paper I, II and III could possibly depend on different degrees of hybridization. Nevertheless, the results reported in Paper IV highlight the importance of taking genetic adaptation to captivity seriously into consideration in conservation breeding as the two populations became more similar after only a few generations in the same environment.

Different species will of course differ in how they are affected by a captive environment. A thorough understanding of each species in need of conservation breeding is a necessity in order to provide rearing conditions

which maximize survival after reintroduction. Several aspects must be taken into consideration, such as degree of sociality and imprinting. However, studies of fundamental concepts, such as domestication effects during maintenance in captivity, may provide general information applicable to any species. Furthermore, case studies of non-threatened animals can result in promising proposals of how general processes work without interfering with exclusive and vulnerable populations of rare species. If several different species are studied in this way, it may lead to more and more accurate generalizations in the future. Hence, it is my anticipation that this case study will offer one small piece to the puzzle of conservation breeding.

Conclusions

The main conclusion of this thesis is that behaviour of animals can be affected by captive environments in a way that may influence their survival chances after reintroduction to the wild. Furthermore, long-term breeding in a certain captive environment seem to affect fear-related behaviours, such as antipredator behaviour, through genetic adaptation, while the immediate social or physical environment is suggested to influence social and exploratory behaviours. However, effects of a new environment on antipredator behaviour can evidently appear after only a few generations. Behavioural routines such as time budget and crowing fluctuation, on the other hand, do not seem to be affected by captivity to any notable extent. As antipredator behaviour is a crucial aspect of reintroduction, knowledge about how it is affected by captive environments in species involved in conservation breeding programs is essential in order to plan efficient programs in suitable captive environments.

The present thesis is one of the first attempts to study how captive environments may affect behaviour from a conservation perspective. Although only one species was used as a case study, the results suggest that the aspects discussed are important to consider also in species for which conservation breeding is a more central motive for maintaining the animals in captivity.

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