

Available online at www.sciencedirect.com



Biological Conservation 122 (2005) 431-439

BIOLOGICAL CONSERVATION

www.elsevier.com/locate/biocon

# Behavioural and morphological variation between captive populations of red junglefowl (*Gallus gallus*) – possible implications for conservation

Jennie Håkansson, Per Jensen \*

Department of Biology, IFM, Linköping University, SE-581 83 Linköping, Sweden Received 27 February 2004

#### Abstract

The escalating threats to ecosystems worldwide have lead to a need for efficient methods to breed animals in captivity and to prepare captive-born animals for release back to the wild. However, life in captivity may lead to modifications in the animal's behaviour mainly by genetic changes, including behavioural adaptations such as reduced predator responses. Such modifications may seriously affect survival after a reintroduction. The present study was a first screening of behavioural and morphological variation between different captive populations in standardized test situations using red junglefowl as a model species. The birds were tested in three different test situations in order to measure anti-predatory behaviour, social behaviour and exploratory behaviour. The results of this study clearly show that there are behavioural differences between the captive populations which potentially can be crucial for the animals in a reintroduction situation. However, the extent to which these differences are due to genetic changes caused by small breeding populations or adaptations to the different captive environments is not yet known, although morphological differences found suggest that genetic variation may cause some of the behavioural differences as well. The differences found imply that life in captivity can affect an animal's behaviour and even though the red junglefowl is merely used as a model here, this suggests that these aspects may be important to consider also in other species where reintroduction is a more central motive for keeping the animals in captivity.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Behaviour; Conservation; Captive breeding; Red junglefowl; Gallus gallus

## 1. Introduction

As threats to ecosystems increase worldwide, conservation of species has become a central concern. Along with the increasing numbers of endangered species, there is a need for efficient methods to breed animals in captivity and to prepare captive-born animals for release to the wild (Wallace, 2000). Today, conservation of threatened species is to a large extent carried out by zoos, where animals are kept in small populations under protected conditions. One major goal is to eventually reintroduce them into their natural habitats or an acceptable similar environment, in order to re-establish free-living populations to a previous range or to support the breeding in a declining population (Price, 1984; Campbell, 1980). However, captive environments differ significantly from wild ones and evolution does not stop just because animals are placed in enclosures (Kohane and Parsons, 1988; Carlstead, 1996; Spurway, 1955). Life in protected captivity affects the animals by genetic changes due to small breeding populations and this may lead to behavioural adaptations to the captive situation (Snyder et al., 1996; Price, 1984; Gosling and Sutherland, 2000; Allendorf, 1993). Genetic changes in small populations has for example been demonstrated experimentally

<sup>\*</sup> Corresponding author. Tel.: +46 13 281298; fax: +46 13 281399. *E-mail address:* perje@ifm.liu.se (P. Jensen).

<sup>0006-3207/\$ -</sup> see front matter @ 2004 Elsevier Ltd. All rights reserved. doi:10.1016/j.biocon.2004.09.004

in houseflies (*Musca domestica*) (Bryant et al., 1986) and in species released into a wild habitat, for example the common mynah (*Acridotheres tristis*) (Baker and Moeed, 1987), but its effect on behaviour has not yet been elucidated.

Maintaining genetic diversity in captive populations has often been emphasized as being the most critical element for the success of captive breeding programs but the true obstacles are usually behavioural, such as mate choice, social structure, predator avoidance behaviour and domestication (Snyder et al., 1996; Curio, 1996). An animal's behaviour is the outcome of interactions between the environment and the genotype and failure to produce an environment that is at least functionally equal to that of the wild is likely to result in modifications of frequencies and intensities of natural behavioural patterns (Shepherdson, 1994; Price and King, 1968; Hale, 1962). Therefore, the breeding and rearing of animals in a captive environment can result in changes that could reduce their ability to survive and reproduce in nature, partly as a result of natural selection in captivity. Consequently, the success of conservation programs will essentially depend on a comprehensive understanding of the role of the captive environment in the development of behaviour (Price, 1984).

Animals resulting from several generations of captive breeding are less likely to be successful after reintroduction into a wild environment than animals that are translocated or first generation captive-bred animals (Campbell, 1980). Causes of failure or problems in reintroduction of captive-bred animals vary from case to case but a common cause is behavioural deficiencies in released animals (e.g. Fleming and Gross, 1993; Kleiman, 1989; Shepherdson, 1994). This type of failure seems to be most frequent in species that learn most of their behavioural repertoires (Snyder et al., 1996), since a great deal of behaviours that are important to survival in the wild are learned by practice and this can not always take place in captivity (Brambell, 1977). Predator avoidance seems to be a critical matter for survival of reintroduced individuals into wild environments. After some generations of breeding and selection, Atlantic salmon (Salmo salar L.) show a reduced anti-predatory behaviour (Fleming and Einum, 1997; Einum and Fleming, 1997) and in a reintroduction situation, such behavioural modifications may have severe consequences. McPhee (2004) tested effects of captivity on predator response behaviours in oldfield mice (Peromyscus polionotus subgriseus), and found that the more generations a population had been in captivity, the less likely were the individuals to take cover after exposure to a predator. Furthermore, the social environment in captivity may deprive the young animal of specific stimulation necessary for the development of species-typical behaviour (Carlstead, 1996). Therefore, the composition

of captive populations, with respect to age, sex and experience is important to consider. The decrease in number of opportunities for social conditioning in captivity may influence thresholds for agonistic behaviours (Price, 1984). Swain and Riddell (1990), for example, found that hatchery stocks of juvenile coho salmon (*Oncorhynchus kisutch*) were more aggressive than hatchery-reared wild stocks of juvenile salmon.

The overall aim of this research project was to investigate whether maintenance of small populations in captivity cause behavioural modifications which hypothetically can affect an animal's survival and reproduction capacity after reintroduction. In order to investigate this, behavioural differences between captive populations were examined and the red jungle fowl (Gallus gallus) was used as a model species. The red jungle fowl is considered to be the ancestor of all modern poultry and domestication occurred about 8000 years ago (Yamashita et al., 1994; West and Zhou, 1989; Siegel et al., 1992). The species still exists in the wild in Southeast Asia (Collias and Collias, 1967; Collias and Saichuae, 1967; Nishida et al., 2000; Nishida et al., 1992) and is also kept in zoos all over the world. A relatively large amount of behavioural research has been conducted in the zoo populations (Collias and Collias, 1996; Collias et al., 1994; Dawkins, 1989), but the behaviour of wild-living birds has been very little studied, mainly because of their extreme shyness and inaccessible habitat (Collias and Collias, 1967). Previous research has shown that in fowl, relaxation of natural selection pressures and selection for specific production traits during domestication, cause a modification of the natural behaviour towards less energy demanding strategies (Andersson, 2000; Schütz, 2002). Since domestication is largely an adaptation process, it is possible that similar effects will occur in any captive environment, even if the motive is maintenance of the animals rather than domestication.

The aim of the present study was to perform a first screening of morphological and behavioural variation between captive populations of red junglefowl in standardized test situations. The birds were tested in three different test situations in order to measure anti-predatory behaviour, social behaviour and exploratory behaviour. We predicted that anti-predatory behaviour and exploratory behaviour would be less pronounced in populations with a long background of captivity and in populations with a captive environment which is greatly protected. In captivity, the fitness benefits of responding to predator attacks and search for food may be reduced simply because there are no predators and food is provided for by humans. The social tolerance may either increase or decrease depending on the competition situation in the captive environment.

## 2. Materials and methods

### 2.1. Observation sites

This study took place at four different sites; Copenhagen zoo, Ebeltoft zoo, Frösö zoo and Götala research station. Copenhagen zoo is one the oldest zoos in Europe, established in 1859, and is located near the city centre of Copenhagen, Denmark. Ebeltoft zoo opened in 1998 and is located in the Danish countryside on Jutland. Frösö zoo is a private zoo, founded in 1960 and located on the island Frösön, near Östersund, Sweden. Götala research station was established in 1996 and belongs to the Swedish University of Agricultural Sciences in Skara, Sweden. A few hundred red junglefowl and domestic fowl are kept at Götala for the purpose of research on domestication effects on behaviour.

## 2.2. Animals

The four populations of red junglefowl used in this study were kept under different captive conditions. Copenhagen zoo's population (Cop) was roaming freely over a total available area of seven hectares in the zoo. The zoo held about 15 birds and 12 (three males and nine females) of these were used in this study. Due to time restrictions three birds were not caught but with 80% of the population being tested this should still be representative for the entire population. These birds originate from a population brought into captivity in the beginning of the 1950's. The population in Ebeltoft zoo (Ebe) was a group of nine individuals (five males and four females) which roamed freely over an area of about two hectares and all these birds were used in the study. The origin of this population is uncertain, but it has been kept in the zoo since 1999. The Frösö zoo population (Fro) was kept in a large enclosure (about one hectare) together with other bird species. This population consisted of seven individuals (two males and five females) who were all used in the study. These birds derived from birds taken into captivity in 1993 and 1999. The population at Götala research station (Got) was kept indoors and under more crowded conditions (about 20 birds on  $3 \times 3$  m). 16 birds (seven males and nine females) were studied at Götala research station. These birds origin from birds taken into captivity in 1993 and were used to being handled by humans because of other research projects. The birds of the other three populations were rarely handled.

## 2.3. General procedure

The study took place during May, June and July 2003. All birds were tested with identical testing methods. In order to minimize any external influences during the test, all tests took place inside a white plastic tent with  $3 \times 3$  m floor area and a height of 2.4 m. The tent was semi-transparent causing an even light condition and all tests were carried out during daylight hours. Different test arenas (described for each test below) were built inside the tent and consisted of solid plywood walls of 0.6 m in height (sections measuring  $0.8 \times 0.6$  m could be assembled to create different test arenas) and a roof made of plastic net. The floor consisted of a non-slippery carpet which was cleaned between each test.

The birds were caught with nets and spent at least one hour in a small pen  $(0.9 \times 0.9 \text{ m})$  outside the tent together with other birds before being tested. During all tests, there was at least one bird in the pen within hearing distance from the tent. Prior to the testing, the birds were marked individually with plastic leg bands of different colours. All birds were also photographed, weighed and measured (radius/ulna and tarsometatarsus) for morphological comparisons, before the behavioural tests. The birds were tested in three different test situations in the following order; anti-predatory behaviour test, social behaviour test and exploratory behaviour and sociality test. All behavioural observations were made by the same observer. Between the different tests, the birds were let to rest for at least one hour before being tested in the next one. The birds had access to feed and water at all times.

In tests involving two birds, a randomly chosen bird was sometimes used a third time as a stimulus and the data from this individual was then discarded. Tests involving two birds were interrupted if one of the following two criteria was fulfilled: Severe wounds including fast bleeding from comb or wattle; a seemingly long lasting fight that might lead to exhaustion or severe injuries of one or both birds involved. Three tests were interrupted – two social behaviour tests (Cop and Got) and one exploratory behaviour and sociality test (Cop).

## 2.3.1. Anti-predatory behaviour test

Modified anti-predatory behaviour would be critical for survival in the wild in a reintroduction situation. We therefore measured the anti-predatory reaction of the birds in a test where the birds were exposed to a standardized simulated predator attack. The birds were tested one at a time in a test arena measuring  $0.8 \times 1.6$ m. After five min of adaptation to the new environment, behavioural observations were carried out for five min. All behaviours were recorded with one-zero sampling with ten s intervals. Every ten s, the observer recorded whether or not the behaviour had occurred during the preceding interval. This was done irrespective of how often, or for how long the behaviour occurred during the interval (Martin and Bateson, 1993).

Two categories of behaviours were recorded: *Behaviours without agitation* 

- Exploring: walking or standing with attention downwards, head below the back
- Ground pecking: pecking at the floor
- Preening: trimming of plumage with the beak
- Feeding
- Drinking

## Agitated behaviours

- Crowing: loud vocalization of a male standing in an upright body position
- Vocalizing: every vocalization other than crowing
- Standing alert: standing with the neck stretched and eyes opened
- Walking alert: movement of legs, two or more steps with neck stretched
- Attempting to escape: jumping or attempts to fly away

After five min of observation, a hawk model with 0.75 m wingspan was presented over the arena for 1-2 s. The predator model was fixed on a stick hanging down from the ceiling and was secured at the wall and

hidden under a white cloth while not in use. The model was then released and caught when it had passed over the arena from one side to the other. The model was then hidden again. The bird's immediate response to the simulated predator attack was recorded according to a four level scale:

## 0 = no response at all

1 = the bird reacts by lifting the head once and then continues its previous behaviour

2 = the bird reacts by looking around for more than 3 s 3 = the bird reacts by trying to run or fly away

Immediately after the simulated predator attack, a second five min of behavioural observations, identical to the one preceding the attack, was carried out.

## 2.3.2. Social behaviour test

Modified social behaviour could affect an animal's reproduction and competition capacity after reintroduction. A test was therefore performed to measure the type and frequency of social interactions in a standardized situation. In this test, two birds were tested at a time

Table 1 The behaviours observed and the two categories in which they were divided

Category	Behaviours included (e.g., Kruijt, 1964; Guhl, 1962; Wood-Gush, 1989)				
Aggressive behaviours	<i>Still threat.</i> Bird stands in a stiff upright position <0.25 m from another bird. Head positioned above the receiver's head. <i>Threat when moving.</i> Bird walks with high steps and stretched neck around another bird which is standing or walking, at <0.5 m distance.				
	<i>Threat with wing lifting.</i> Bird stands in an upright position and lifts its wings once in front of another bird at <0.5 m distance.				
	<i>Threat with wing flapping.</i> Bird stands in an upright position and flaps its wings more than once in front of another bird at $<0.5$ m distance.				
	Threat with waltzing display. Male circles around another male at $<0.5$ m distance, with the outer wing dropped towards the ground.				
	<ul> <li>Threat with ground scratch display. Male scratches and pecks on the ground in front of another male at &lt;0.5 m distance.</li> <li>Threat to attack. Bird changes its body posture in order to approach or attempt to peck another bird so that the receiver immediately retreats with fast steps, running, jumping or flying away. The head is kept above the receiver's head.</li> <li>Attack. Bird runs, jumps or flies when approaching another bird in order to give one or more aggressive pecks. The head is kept above the receiver's head.</li> <li>Chase. Bird follows another bird. Both birds are running, jumping or flying.</li> <li>Aggressive peck. Bird gives a fast peck, directed to an anterior part of another bird's body.</li> </ul>				
Courtship behaviours	<i>Crouch.</i> Female lies down with bent legs and head protruding or held downwards. <i>Circling.</i> Male walks with high steps around a female at <0.25 m distance. The neck is stretched and the male watches the female intensively.				
	Rear approach. Male approaches a female from behind. The neck is stretched and neck feathers are lifted. Walizing display when courting. Male circles around a female at <0.5 m distance, with the outer wing dropped towards the ground.				
	<i>Wing lifting when courting.</i> Male stands in an upright position and lifts the wings once in front of a female at <0.5 m distance.				
	Wing flapping when courting. Male stands in an upright position and flaps the wings more than once in front of a female at $< 0.5$ m distance.				
	<i>Tail wagging display when courting.</i> Male lowers the tail and moves it rapidly from side to side in front of a female at <0.5 m distance, right before or after one or more of the other courtship behaviours.				
	<i>Crouch-scratching.</i> Male crouches on the ground and scratches at substrate with feet in front of a female at <0.5 m distance.				
	<i>Tidbitting.</i> Male scratches and pecks on the ground in front of a female at <0.5 m distance. May also make a clucking sound.				
	Mating. Bird is involved in copulation.				

in an arena measuring  $1.6 \times 1.6$  m. After five min of adaptation to the new environment, behavioural observations were carried out using continuous recording (Martin and Bateson, 1993). Each occurrence of a particular behaviour (Table 1) and which individual performed it was recorded continuously. The birds were tested once with a randomly chosen individual of the opposite sex and once with a randomly chosen individual of the same sex. Each pair of birds was observed for five min × six with a 30 s break after each five min session. This way, each individual was observed for a total of 60 min.

### 2.3.3. Exploratory behaviour and sociality test

Animals reintroduced into the wild are dependent on well-adapted exploration strategies in order to find food in a new and variable environment. The purpose of this test was to study the birds' exploration strategies in a social setting. Two birds were tested at a time in an "L-shaped" arena (Fig. 1). The arena was divided with black marking tape into five zones. Food containers with familiar and unfamiliar food were randomly put in the two zones of each arm before each test. A water container was put in the central zone.

All birds were tested once with a randomly chosen individual of the opposite sex and once with a randomly chosen individual of the same sex. After two min of adaptation, direct observations were carried out for five min  $\times$  six, using instantaneous sampling. The location of each bird was recorded every 10 s, starting with the same bird each time. After each five min session, there was a



Fig. 1. The test arena for the exploratory behaviour and sociality test, which was divided into five zones. Food containers with familiar and unfamiliar food were randomly placed in the two zones in each arm.

30 s break. The total observation time was 60 min for each bird.

This way, we recorded both exploration and sociality at the same time. The birds could choose to be in a zone with familiar or unfamiliar food and also in the same zone as the other bird or further away. Location in the same zone or opposite arm was regarded as a measure of sociality.

#### 2.4. Data treatment and analyses

All analyses were performed on individual level. Since data were found not to be normally distributed, nonparametric Kruskal–Wallis tests were used for all analyses. In addition to this, a Mann–Whitney U test was used for analyzing the number of aggressive behaviour observed in the social behaviour test. All deviations from mean values are given as standard error of the mean (SE).

## 2.5. Ethical note

The study was approved by the local Ethical Committee of The Swedish National Board for Laboratory Animals. The Committee evaluates the welfare of the animals in relation to the purpose of the study and the possibilities for the problem to be solved without the use of experimental animals, and ascertains that the experiment is not an unnecessary repetition of previous experiments.

### 3. Results

#### 3.1. Anti-predatory behaviour test

Following the exposure to the predator model, there was a tendency for a difference between the populations in percent of birds in each response category  $(H_{3, 42} = 7.05, p = 0.070)$  (Fig. 2). The median values for the response levels were 2 (Cop), 1 (Ebe), 2 (Fro) and 1 (Got).

There were significant differences between the populations in frequency of agitated behaviours both before  $(H_{3, 42} = 16.08, p = 0.001)$  and after  $(H_{3, 42} = 12.42, p = 0.006)$  the predator model exposure (Fig. 3(a)). The birds' reaction on the predator model, measured as the frequency of agitated behaviours before minus after the exposure, differed significantly between the populations  $(H_{3, 42} = 9.94, p = 0.019)$ .

There were also significant differences between the populations in percent of observations with behaviours without agitation both before ( $H_{3, 42} = 8.05$ , p = 0.045) and after ( $H_{3, 42} = 10.88$ , p = 0.012) the simulated predator attack (Fig. 3(b)). However, the birds' reaction on the predator model, measured as the frequency of



Fig. 2. Percent of birds in each of the four levels of response to a simulated predator attack (0: no response; 3: most intensive response).



Fig. 3. Percent of observations  $(\pm SE)$  of agitated behaviours (a) and behaviours without agitation (b) before and after the simulated predator attack.

behaviours without agitation before minus after the exposure, did not differ significantly.

## 3.2. Social behaviour test

Although we found some numerical differences, no significant overall difference was found between the populations in number of observations of aggressive behaviour in the social behaviour test (Fig. 4a) ( $H_{3, 41} = 6.23$ , p = 0.101). However, when comparing only the two extreme populations (Got and Cop), a Mann–Whitney U test showed a significant difference (U = 49.50, p = 0.049).



Fig. 4. Mean number  $(\pm SE)$  of aggressive (a) and courtship (b) behaviours observed during a 60 min observation period in the social behaviour test.

There was also a significant difference between the populations in number of courtship behaviours observed  $(H_{3, 41} = 16.33, p = 0.001)$  (Fig. 4b).

## 3.3. Exploratory behaviour and sociality test

There was a significant difference between the populations in percent of observations a bird was located in the same zone as the other bird in the pair ( $H_{3, 39} = 14.12$ , p = 0.003) (Fig. 5). There was also a significant difference in percent of observations the birds spent the opposite arms ( $H_{3, 39} = 10.58$ , p = 0.014).



Fig. 5. Percent of observations  $(\pm SE)$  when the two birds were in the same zone and in opposite arms of the arena in the exploratory behaviour and sociality test.

There was a significant difference between the populations in mean number of zone changes observed during the exploratory behaviour and sociality test  $(H_{3,39} =$ 14.32, *p* = 0.003) (Fig. 6).

There were also significant differences between the populations in percent of observations spent in zones with unfamiliar feed ( $H_{3, 39} = 8.59$ , p = 0.035) and familiar feed  $(H_{3, 39} = 12.06, p = 0.007)$  (Fig. 7).



Fig. 6. Mean number (±SE) of zone changes observed in the exploratory behaviour and sociality test.



Fig. 7. Percent of observations ( the exploratory behaviour and se

Table 2

#### Mean values from the morpholo lefowl

unfamiliar feed±SE) in zones with unfamiliar feed in bociality test.gical measurements (±SE) of males and females in the four captive populations of red jungle Mean weight (kg)Mean weight (kg)Mean length (mm)Mean size (c				
<b>unfamiliar feed</b> ±SE) in zones with unfamiliar feed in between the locations and the lack of in the birds' genetic background make speculate about this matter at this tim morphological differences found sug- may be genetic differences between gical measurements (±SE) of males and females in the four captive populations of red jungle	Mean weight (kg) Mean ler	Mean length (mm)		
<b>unfamiliar feed</b> ±SE) in zones with unfamiliar feed in between the locations and the lack of in the birds' genetic background make speculate about this matter at this tir morphological differences found su may be genetic differences between	gical measurements (±SE) of males and	d females in the four captive popula	ations of red jung	
ments is still uncertain. The environments	unfamiliar feed tSE) in zones with unfamiliar feed in ociality test.	ments is still uncertain. between the locations an the birds' genetic back speculate about this ma morphological difference may be genetic differen	The environment of the lack of in ground make tter at this tir wes found sug nees between	

Population	Sex	Mean weight (kg)	Mean length (mm)		Mean size (cm <sup>2</sup> )	
			Radius/ulna	Tarsometatarsus	Comb	Wattle
Сор	М	$1.09 \pm 0.01$	79.14 ± 1.45	$87.93 \pm 2.97$	$19.32 \pm 1.87$	$9.00 \pm 0.75$
Ebe	Μ	$1.00 \pm 0.04$	$75.92 \pm 1.49$	$85.61 \pm 2.09$	$18.58 \pm 3.69$	$9.40 \pm 1.93$
Fro	М	$0.90 \pm 0.20$	$75.79 \pm 0.48$	$81.14 \pm 1.54$	$7.03 \pm 0.68$	$5.04 \pm 0.44$
Got	Μ	$1.20 \pm 0.04$	$85.08 \pm 1.29$	$94.14 \pm 1.60$	$25.53 \pm 2.02$	$10.36 \pm 1.23$
Cop	F	$0.88 \pm 0.05$	$70.48 \pm 0.76$	$71.68 \pm 1.07$	$2.61 \pm 0.23$	$1.67 \pm 0.22$
Ebe	F	$0.74 \pm 0.04$	$67.26 \pm 2.17$	$71.14 \pm 1.58$	$3.39 \pm 0.52$	$2.24 \pm 0.36$
Fro	F	$0.62 \pm 0.05$	$67.97 \pm 1.91$	$71.73 \pm 2.36$	$1.14 \pm 0.32$	$0.70 \pm 0.22$
Got	F	$0.90 \pm 0.03$	$74.34\pm0.70$	$77.81 \pm 0.86$	$4.55\pm0.84$	$2.36\pm0.35$

#### 3.4. Morphological comparisons

There were significant differences between the populations in weight (males  $H_{3, 16} = 8.90$ , p = 0.031, females  $H_{3, 26} = 12.48$ , p = 0.006), radius/ulna length (males  $H_{3, 16} = 11.85$ , p = 0.008, females  $H_{3, 26} = 13.26$ , p =0.004) and tarsometatarsus length (males  $H_{3, 16} = 10.33$ , p = 0.016, females  $H_{3, 26} = 12.63$ , p = 0.006). There were also significant differences between the populations in comb size (males  $H_{3, 16} = 8.40$ , p = 0.04, females  $H_{3,26} = 13.37$ , p = 0.004) and in female wattle size  $(H_{3, 26} = 11.53, p = 0.009)$ . However, no significant difference was found in male wattle size (Table 2).

#### 4. Discussion

The results show that there are clear behavioural differences between the captive populations of red junglefowl included in this study. Some of these differences are relevant from a reintroduction perspective. For example, anti-predatory behaviour, sexual behaviour and exploration all differed between the populations, and these appear to be crucial aspects of reintroduction success (Curio, 1996; Carlstead, 1996; Snyder et al., 1996). In this study, it was not possible to compare wild-caught birds to captive-bred ones or to do an experimental reintroduction of the birds. However, the differences found between the populations imply that life in captivity can have an influence on behaviour, possibly due to altered selection pressures. Hence, even though we only used red junglefowl as a model, the results suggest that these aspects may be important to consider also in other species, where reintroduction is a more central motive for keeping the animals in captivity.

The extent to which these differences are due to genetic change or adaptations to the different captive environmental variations nformation about it impossible to ne. However, the ggest that there the populations.

All animals were sexually mature, so the variation probably reflects developmental differences between the populations. For example, Got females had longer radius/ ulna and tarsometatarsus and bigger combs and wattles than Cop birds, despite having approximately the same weight. Hence, genetic variation could perhaps have caused some of the differences in behaviour as well. Further research is needed in this area and this project will continue to investigate such issues.

Differences in anti-predatory behaviour between red junglefowl and domestic fowl and between wild and farmed Atlantic salmon have been suggested to be a result of relaxed natural selection in captivity (Fleming and Einum, 1997; Andersson, 2000). A similar suggestion may well be suitable here. Animals in captivity are influenced by relaxed natural selection e.g. due to protection against predators (Price and King, 1968). This can be viewed as an early step in domestication. Zoo animals, for example, are not adapted to an environment where a predator attack is likely to occur and as a result, their anti-predatory behaviour may well be modified. The degree of modification may be due to time spent in captivity or the level of protection in the captive environment. McPhee (2004) found that the more generations a population of oldfield mice had been in captivity, the less likely the individuals were to take cover after exposure to a predator. This correlation was not possible to investigate in this study due to a lack of background information of the populations. However, in accordance with the results of McPhee (2004), the youngest (least number of years in captivity) population (Fro) reacted strongest on the simulated predator attack. This population also showed most agitated behaviours and hardly any behaviours without agitation during the entire anti-predator behaviour test. As predicted, the most protected population (Got) showed the most behaviours without agitation and least agitated behaviours. Furthermore, more than 30% of the Gotbirds did not react at all on the simulated predator model (reaction response 0).

The results also show some differences in social behaviour between the populations. The social environment in captivity generally differs from the wild situation and this may modify the animals' social behaviour. Competition is an important aspect of social behaviour and the more the animals have to compete for resources, the more aggressive they are likely to be. Swain and Riddell (1990) found that hatchery stocks of juvenile coho salmon were more aggressive than hatchery-reared wild stocks of juvenile salmon. In our case, the population that showed most aggressive behaviours (Got) was also the one that differed from the other ones regarding the captive conditions. Got was the only population that was kept indoors under crowded conditions and it is possible that there were more competition for resources than in the other more freely kept populations. These findings are also in accordance

with Price (1984) who stated that a decrease in number of opportunities for social conditioning may influence thresholds for agonistic behaviours. Furthermore, the results from the exploratory behaviour and sociality test reveal some differences in time spent in close contact (same zone) and more or less out of sight (opposite arms). For example, birds in Fro spent more than twice as much time in the same zone than birds in Cop which was more likely to spend time in opposite arms compared to the other populations. Differences in social environment between captivity and a wild environment may also induce modification in sexual behaviours. For example, in mammals, rearing by the mother provides the young animal with explicit stimulus essential for the normal development of social interactions and sexual behaviour (Carlstead, 1996). The present study shows significant differences in sexual behaviour and such modifications could be critical in a reintroduction situation.

This study also shows that there are differences in exploratory behaviour between the populations. In nature, a large amount of an animal's time and energy is spent in acquiring food and water (Price and King, 1968). However, in captivity this is usually no longer necessary since man provides all such resources. If animals are going to be reintroduced, it is important for them to have an exploratory behaviour suitable for the natural environment. It has been shown that domestication can influence exploration behaviours towards less energy demanding strategies. In a comparison of foraging behaviours in red junglefowl and White Leghorn, it was found that the former preferred to obtain novel food instead of feeding from a familiar, freely available food source which was preferred by the latter breed (Schütz et al., 2001). In the present study, birds in Ebe spent almost twice as much time in a zone with unfamiliar food than birds in Cop. The populations also differed in number of zone changes which can be seen as a way of exploring the new test environment and possibly search for food.

The conclusion of this study is that there are morphological and behavioural differences between captive populations of red junglefowl. These differences are of a kind which hypothetically could be crucial in a reintroduction situation. This implies that life in captivity can affect an animal's behaviour and although a model species was used, we suggest that it is important to consider such differences in any species bred for reintroduction. However, it is also important to point out that the environmental variation may have influenced the results to an unknown degree.

### Acknowledgements

We thank Flemming Nielsen (Copenhagen zoo), Jesper Stagegaard (Ebeltoft zoo), Åke Netterström (Frösö zoo), Alf Blomqvist (Götala research station) and all other staff at the zoos for providing research facilities and technical assistance. We are also grateful for excellent technical assistance from Nadine Smits, Edwin Jousma and Gisela Håkansson. This work was financed by FORMAS, the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning.

## References

- Allendorf, F.W., 1993. Delay of adaptation to captive breeding by equalizing family size. Conservation Biology 7, 416–419.
- Andersson, M., 2000. Domestication effects on behaviour. Foraging, parent-offspring interactions and antipredation in pigs and fowl. Doctoral thesis. Acta Universitatis Agriculturae Sueciae, Veterinaria 86, Uppsala, Sweden.
- Baker, A.J., Moeed, A., 1987. Rapid genetic differentiation and founder effect in colonizing populations of common mynas (*Acridotheres tristis*). Evolution 41, 525–538.
- Brambell, M.R., 1977. Reintroduction. International Zoo Yearbook 17, 112–116.
- Bryant, E.H., McCommas, S.A., Combs, L.M., 1986. The effect of an experimental bottleneck upon quantitative genetic variation in the housefly. Genetics 114, 1191–1211.
- Campbell, S., 1980. Is reintroduction a realistic goal?. In: Soulé, M.E., Wilcox, B.A. (Eds.), Conservation Biology: An Evolutionaryecological Perspective. Sinauer Associates, Sunderland, pp. 263–269.
- Carlstead, K., 1996. Effects of captivity on the behavior of wild mammals. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity. The University of Chicago Press, Chicago, pp. 317–332.
- Collias, N.E., Collias, E.C., 1967. A field study of the Red Jungle Fowl in North-Central India. The Condor 69, 360–386.
- Collias, N.E., Collias, E.C., 1996. Social organization of a red junglefowl, *Gallus gallus*, population related to evolution theory. Animal Behaviour 51, 1337–1354.
- Collias, N.E., Collias, E.C., Jennrich, R.I., 1994. Dominant red junglefowl (*Gallus gallus*) hens in an unconfined flock rear the most young over their lifetime. The Auk 111, 863–872.
- Collias, N.E., Saichuae, P., 1967. Ecology of the red jungle fowl in Thailand and Malaya with reference to the origin of domestication. Natural History Bulletin of the Siam Society 22, 189–209.
- Curio, E., 1996. Conservation needs ethology. Trends in Ecology and Evolution 11, 260–263.
- Dawkins, M.S., 1989. Time budgets in red junglefowl as a baseline for the assessment of welfare in domestic fowl. Applied Animal Behaviour Science 24, 77–80.
- Einum, S., Fleming, I.A., 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology 50, 634–651.
- Fleming, I.A., Einum, S., 1997. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES Journal of Marine Science 54, 1051–1063.
- Fleming, I.A., Gross, M.R., 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecological Applications 3, 230–245.
- Gosling, L.M., Sutherland, W.J. (Eds.), 2000. Behaviour and Conservation. Cambridge University Press, Cambridge.
- Guhl, A.M., 1962. The behaviour of chickens. In: Hafez, E.S.E. (Ed.), The Behaviour of Domestic Animals. Baillère, Tindall & Cox, London, pp. 491–530.
- Hale, E.B., 1962. Domestication and the evolution of behaviour. In: Hafez, E.S.E. (Ed.), The Behaviour of Domestic Animals. Baillère, Tindall & Cox, London, pp. 21–53.

- Kleiman, D.G., 1989. Reintroduction of captive mammals for conservation. BioScience 39, 152–161.
- Kohane, M.J., Parsons, P.A., 1988. Domestication: evolutionary change under stress. Evolutionary Biology 23, 31–48.
- Kruijt, J.P., 1964. Ontogeny of social behaviour in Burmese red junglefowl (*Gallus gallus spadiceus*) Bonnaterre. Behaviour, Supplement 12, 1–201.
- Martin, P., Bateson, P., 1993. Measuring Behaviour. An Introductory Guide. Cambridge University Press, Cambridge.
- McPhee, M.E., 2004. Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. Biological Conservation 115, 71–77.
- Nishida, T., Hayashi, Y., Shotake, T., Maeda, Y., Yamamoto, Y., Kurosawa, Y., Douge, K., Hongo, A., 1992. Morphological identification and ecology of the red jungle fowl in Nepal. Animal Science and Technology (Jpn) 63, 256–269.
- Nishida, T., Rerkamnuaychoke, W., Tung, D.G., Saignaleus, S., Okamoto, S., Kawamoto, Y., Kimura, J., Kawabe, K., Tsunekawa, N., Otaka, H., Hayashi, Y., 2000. Morphological identification and ecology of the red jungle fowl in Thailand, Laos and Vietnam. Animal Science Journal 71, 470–480.
- Price, E.O., 1984. Behavioral aspects of animal domestication. The quarterly review of biology 59, 1–32.
- Price, E.O., King, J.A., 1968. Domestication and adaptation. In: Hafez, E.S.E. (Ed.), Adaptation of Domestic Animals. Lea & Feibiger, Philadelphia, pp. 34–45.
- Schütz, K., 2002. Trade-off in resource allocation between behaviour and production in fowl. Phenotypic studies and QTL-analyses in red junglefowl, White Leghorn and their F<sub>2</sub>-progeny. Doctoral thesis. Acta Universitatis Agriculturae Sueciae, Veterinaria 115, Uppsala, Sweden.
- Schütz, K.E., Forkman, B., Jensen, P., 2001. Domestication effects on foraging strategy, social behaviour and different fear responses: a comparison between the red junglefowl (*Gallus gallus*) and a modern layer strain. Applied Animal Behaviour Science 74, 1–14.
- Shepherdson, D., 1994. The role of environmental enrichment in the captive breeding and reintroduction of endangered species. In: Olney, P.J.S., Mace, G.M., Feistner, A.T.C. (Eds.), Creative Conservation: Interactive Management of Wild and Captive Animals. Chapman & Hall, London, pp. 167–177.
- Siegel, P.B., Haberfeld, A., Mukherjee, T.K., Stallard, L.C., Marks, H.L., Anthony, N.B., Dunnington, E.A., 1992. Jungle fowl – domestic fowl relationships: a use of DNA fingerprinting. World's Poultry Science Journal 48, 147–155.
- Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D., Miller, B., 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10, 338–348.
- Spurway, H., 1955. The causes of domestication: an attempt to integrate some ideas of Konrad Lorenz with evolution theory. Journal of Genetics 53, 325–362.
- Swain, D.P., Riddell, B.E., 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 47, 566–571.
- Wallace, M.P., 2000. Retaining natural behaviour in captivity for reintroduction programmes. In: Gosling, L.M., Sutherland, W.J. (Eds.), Behaviour and Conservation. Cambridge University Press, Cambridge, pp. 300–314.
- West, B., Zhou, B.-X., 1989. Did chickens go north? New evidence for domestication. World's Poultry Science Journal 45, 205–218.
- Wood-Gush, D.G.M., 1989. The Behaviour of the Domestic Fowl. D.G.M. Wood-Gush and Nimrod Press Ltd., Alton.
- Yamashita, H., Okamoto, S., Maeda, Y., Hashiguchi, T., 1994. Genetic relationships among domestic and jungle fowls revealed by DNA fingerprinting analysis. Japanese Poultry Science 31, 335– 344.