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Domestication Effects on Behaviour

Foraging, parent-offspring interactions and antipredation in pigs and fowl

Maria Andersson

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Abstract

The aim of this thesis was to study domestication effects on behaviour from a functional perspective. I have used the domestic pig versus the wild boar (*Sus scrofa*) and the domestic fowl versus the red jungle fowl (*Gallus gallus*) as experimental model animals. The foraging behaviour of pigs and fowl was studied in two environments where there was a difference in the energy acquired to move between the food sources. Both pigs and fowl responded to some qualitative predictions from optimal foraging theory, moreover the differences between the genotypes were concluded to be a result from a shift of behaviour optimum towards less costly strategies. Maternal behaviour, including nest-building behaviour, nursing behaviour, post-massage behaviour and mother-offspring interactions of pigs was studied in a semi-natural environment. Despite many generations of domestication, most aspects of maternal behaviour seem to be unaffected. However, the differences between genotypes that were found suggest that the domestic pigs are adapted to a domestic life and thereby more likely to invest more in current offspring. Anti-predatory behaviour of fowl was studied in two experiments. First the vigilance behaviour in two different group sizes and then the direct response to an airborne predator model. Results show that the anti-predatory behaviour is to a large extent unmodified during domestication. However, the differences between genotypes that were found are likely a result from the relaxation of natural selection factors, i.e. predator avoidance that follow with domestication. This thesis represents one of the first attempts to study functional effects of domestication. The results are mostly not conclusive but suggest that the approach can be very fruitful and helpful in providing a basis for future research.

Key words: domestication, behaviour, pigs (*Sus scrofa*), red jungle fowl (*Gallus gallus*), foraging, parent-offspring conflict, antipredation

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Now look at those pigs as they lie in the straw,
Said Dick to his father one day
They keep eating longer than I ever saw,
What nasty fat gluttons are they

I see they are feasting, his father replied,
They eat a great deal, I allow
But let us remember, before we deride,
Tis the nature, my dear of a sow

Jane Taylor, Original Poems for
Infant Minds, 1804

To my family

Contents

Appendix

Papers I-V

The thesis is based on the following papers, which will be referred to in the text by their Roman numerals I-V.

I Gustafsson, M., Jensen, P., de Jonge, F.H & Schuurman, T., 1999. Domestication effects on optimal foraging strategies in pigs. Applied Animal Behaviour Science 62, 305-317.

II Gustafsson, M., Jensen, P., de Jonge, F.H., Illmann, G. & Špinka, M., 1999. Maternal behaviour in domestic sows and crosses between domestic sows and wild boar. Applied Animal Behaviour Science 65, 29-42.

III Andersson, M., Jensen P., de Jonge F.H. & Schuurman, T., Domestication effects on post-massage behaviour in pigs (*Sus scrofa*). Submitted for publication.

IV Andersson, M., Nordin, E., & Jensen, P., 2000. Domestication effects on foraging strategies in fowl (*Gallus gallus*). Applied Animal Behaviour Science. In Press.

V Andersson, M., Jensen, P. & Lundberg, A., Domestication effects on anti-predatory behaviour in fowl (*Gallus gallus*). Submitted for publication.

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Introduction

Domestic animals are nowadays part of almost every person's life, in one way or another. And so it has been for as long as we can remember. Studies of domestication and domestic animals have interested people for a very long time and there is a large volume of literature on the subject. The domestic animal history during the latest 15 000 years is one of the greatest biological experiments with an enormous increase in rate and range of variability of the different domestic species. Domestic animals differ morphologically from their own ancestors much more than some different species do, and the history of evolution does not reveal any similar variability developed within such a short period of time (Belyaev, 1979). During the last 100 years there has been a dramatic change in the way we keep our domestic animals. Intensive husbandry and controlled routines have ruled out extensive systems with free-range conditions. Controversially, breeding has become more and more important in order to try to design animals to fit the intensive conditions of today's food production. However, we must bear in mind that the domestic animals still possess different behavioural needs that might not be considered in these intensive systems. It is therefore getting more and more important to increase our knowledge about the behaviour of our domestic animals in order to make environmental and housing conditions more suitable to fit their needs.

In Sweden, the animal welfare law from 1988 pointed out that animals used for food production must be "kept in a good environment that promotes their health and gives them opportunity to express their natural behaviour" (Djurskyddslagen, 1988:534). Both before and after 1988 a range of research concerning the natural behaviour of our domestic animals has been conducted (see e.g. Jensen, 1986; Stolba & Wood-Gush, 1989; Lidfors, 1994; Malm, 1995). To be able to give the animals the opportunity to express their natural behaviour we need to know what "natural" behaviour consists of and what needs the animals have. There are different ways to examine these aspects. One is to study the behaviour of the ancestors (see e.g. Collias & Collias, 1996) and another is to let the domestic animals out to roam freely and to study them in a semi-natural habitat (see e.g. Jensen, 1988), last but not least one can experimentally study the two different genotypes in the same type of environment and from this draw conclusions about the natural behaviour of the domestic animal (see e.g. Desforges & Wood-Gush, 1976). However, this assumes that the wild-type used is representative of the wild ancestor (Price, 1984). This assumption might not be true since many of the ancestors of our domestic animals are extinct (Isaac, 1970) and because selection pressure in the wild has affected the wild population to some extent (Price, 1997). In this thesis I have chosen to compare the behaviour of the wild boar (*Sus scrofa*) and the red jungle fowl (*Gallus gallus*) with the behaviour of the domestic pig and the domestic fowl. The wild boar and the red jungle fowl are comparable to the ancestors of pigs and fowl that were first domesticated. Rather than using the genuine wild animal, I have used crossings with domestic breeds, which has allowed me to better control for non-genetic influences on behaviour. This comparative approach generates hypotheses about the effects on behaviour but no information regarding the rate of behavioural change during domestication.

Definition of domestication and the domestic animal

Domestication has been defined in different ways by different authors, and they all agree that domestication involves a genetic modification of the animal in relation to the wild ancestor. Some authors (Price, 1984; Ruzzante, 1994) are of the opinion that the definition also should include non-genetic processes, i.e. ontogenetic adaptations to captivity, whereas others claim (Zeuner, 1963; Hale, 1969) that it should be limited only to the genetic process. Hale (1969) defined domestication as "that condition wherein breeding, care and feeding of animals are more or less controlled by man". According to Clutton-Brock (1989) a domestic animal is one that has been bred in captivity for purposes of economic profit to a human community that maintains complete mastery over its breeding, organisation of territory and food supply (Clutton-Brock, 1989). Hemmer (1990) defined domestic animals as "those animals kept and bred in and around human habitation to be used constantly to human advantage". There is a limit in all these definitions since they emphasise either a condition or a process that is dependent on human actions and not only the genetic changes that occur in the domestic population (Stricklin, 2000). There are other terms used in the context of domestication that need to be defined, i.e. a tame animal and a feral animal. Taming was probably a pathway to domestication in the initial stage but a tamed animal is not a domesticated one. The tame animal has learned by experience that humans are a source of food and shelter (Reed, 1980; Craig, 1981). For example, a tiger in a zoological garden can be a tame animal, but it may not have been domesticated. Feral animals on the other hand have been domesticated but are no longer cared for by the human population and are now free living and self perpetuating (Baker, 1981; Craig, 1981). For example the dingo in Australia and feral pigs in Australia, New Zealand and North America (Epstein & Bichard, 1984). As Ratner and Boice (1969) rightly pointed out, the terms domesticated, tame and feral reflect various stages of the different relations between humans, animal and the environment.

Origin of domestication

Already by 1859 Darwin published "On the Origin of Species" which was to a large extent based on observations of domestication effects on animals and plants. Somewhat later Darwin's cousin Francis Galton proposed a new theory about the beginning of domestication (Galton, 1883). He noted that nurturing tame wild animals was widespread among primitive people and he concluded that domestication must have arisen as a natural consequence of keeping pets. Later scientists (Zeuner, 1963; Clutton Brock, 1981) have supported this idea, especially regarding the domestication of dogs. However, nowadays pet-keeping is regarded as less important in the process of domestication. Before domestication began, humans were mainly hunting wild animals for their meat (Armitage, 1986). Later in the Neolithic age (started about 10 000 years ago) the agricultural period originated and humans began to settle. Archaeological findings from this period show that the number of different game animals decreased, which indicated a different relationship between humans and the animals. An increase in the number of specimens or bones from potentially domestic species as well as an increase in the age distribution (for example an increase in the number of individuals less than one year old) from the same species implies some cultural control (Perkins, 1964; Herre, 1989). These are findings that could indicate the beginning of domestication. However, it is difficult to draw the line when domestication really began, if for example the variation of specimens and bones is due to a natural change in the environment. A similar problem arises in studies of genetic comparisons between the domestic animal and its ancestor. It has been shown that genetic comparisons of the domestic and the wild ancestor reveal a much earlier date on when domestication really began (Vila et al., 1997; Giuffra et al., 2000). However, these results only show how long time it has taken for the domestic type to diverge from the ancestor genetically. They say nothing about the relationship between humans and the animal, it is rather more likely that the genetic changes started long before humans and animal began to live in close proximity.

The domestic pig

The European domestic pig is derived from the European wild boar (*Sus scrofa*) (Epstein & Bichard, 1984; Chen & Leibenguth, 1995) and was, according to archaeological records, domesticated in Asia 5000-11000 years ago (Zeuner, 1963; Reed, 1974). However, genetic comparisons reveal that the time since the domestic pig diverged from the wild boar is about 500 000 years ago and that domestication might have occurred independently in both Asia and Europe (Chen & Leibenguth, 1995; Giuffra et al., 2000). Archaeological records show that it is likely that pigs were already in the beginning used for food (Zeuner, 1963).

The domestic fowl

The red jungle fowl (*Gallus gallus*) has been considered to be the ancestor of all domestic fowl in the world (Kruijt, 1964; Crawford, 1990; Siegel et al., 1992; Fumihito et al., 1994). The larger size of the fowl and the numerous numbers of bones in archaeological findings are considered positive evidence for domestication of fowl in Asia about 6000-9000 years ago (Siegel, 1976; West & Zhou, 1988; Crawford, 1990). Fumihito et al. (1994) compared divergences in DNA sequences of 26 domestic breeds of fowl, 30 green jungle fowl individuals and 14 individuals of subspecies of red jungle fowl. The results showed that they could eliminate all but one single subspecies of red jungle fowl (*Gallus gallus gallus*) as the ancestor to all breeds of domestic fowl. These new findings also suggest that domestication took place more than 8000 years ago in Thailand and Vietnam. Archaeological and historical records suggest that the first use of domestic fowl was cultural in religion, arts and entertainment and that the fowl only later was used for food (Zeuner, 1963; Crawford, 1990).

The gradual process of domestication from an evolutionary perspective

The process of domestication is a contemporary and gradual procedure and is not a static state (Ratner & Boice, 1969; Bökönyi, 1989). For example there are efforts made nowadays to use the moose (*Alces alces*) and the eland (*Taurotragus oryx*) as well as fur bearing animals as domestic animals (Hemmer, 1976). This implies that all our domestic animals are domesticated to different degrees and that it is difficult to determine to which extent a population has become domesticated (Price, 1997). Figure 1 shows a schematic picture of the domestication degree of the giraffe, which is in the very beginning of the scale, the pig, which was domesticated for about 11 000 years ago and the dog, which was domesticated for about 14 000 years ago (according to archaeological records). Further, it suggests that domestication is an on-going process not limited to our ancestors in the past.

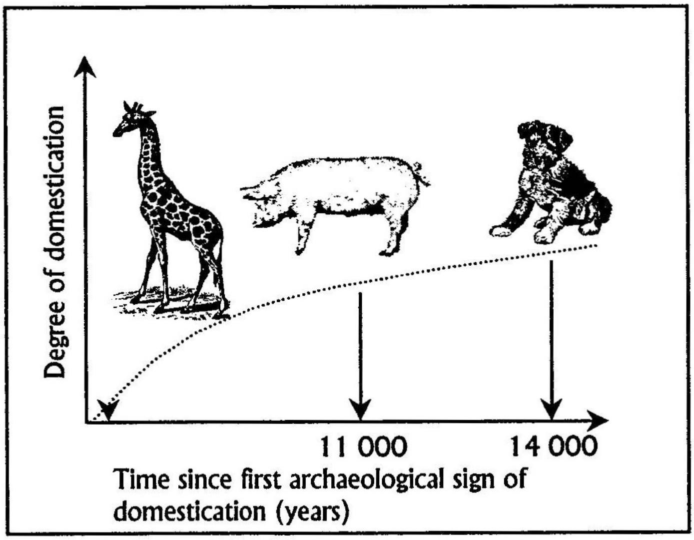

Figure 1. The domestic dog, the domestic pig and the giraffe on a gradual scale of the domestication process, where the dog is the first animal domesticated, pig is intermediate and the giraffe is in the very beginning of the scale.

Domestication can be regarded as a natural evolutionary process by which animals exploited a new ecological niche, and thus can be understood in terms of evolutionary theory (Rindos, 1980; Clutton-Brock, 1989; Trut, 1999). Fitness under domestication is determined to a large extent by whether the domestic animal is allowed to survive to maturity and reproduce (Craig, 1981). The purpose of this thesis was to put domestication in an evolutionary context and try to make some conclusions from a functional perspective. One of the first to refer to domestication as an evolutionary process was Budiansky (1992), who argued that domestication did not start because there was any particular need for humans to breed and control animals (Reed, 1980; Budiansky, 1992; Budiansky, 1994). Instead, animals with a suitable predisposition benefited from associating with humans, who in turn also benefited from these animals. There seems to be a paradox in that behavioural characteristics of the domestic animal are what makes domestication possible, like a lack of fear of humans, docility, high reproductive rate and juvenile characteristics. It would seem that at least some of these features somehow had to be in place before domestication started (Coppinger, 1983; Mason, 1984; Hart, 1985) and that the domestic animals probably could have been domesticated at any time before (Reed, 1980).

Domestication could be viewed as one example of a well-established, successful social symbiosis between two unrelated species, where two organisms interact resulting in benefits to both, and which positively affects their potential for survival and future reproductive success (Zeuner, 1963; Rindos, 1980; Coppinger, 1983; Budiansky, 1994). Other examples can be found among ants that keep and care for insects, from which they receive nutrients (Zeuner, 1963; Reed, 1980). Additionally there are numerous wild species that have gained advantage in associating with us, for example barn swallows, mice and rats (Budiansky, 1994).

In the evolutionary approach to behaviour the concept of trade-off is central. An animal will always make trade-offs between different behaviours and assess their different costs and benefits, because all behavioural traits have both positive and negative effects on the individual's reproductive success (Alcock, 1993). Initially I need to define the concept of "costly", in the context of behavioural strategies. From a strict evolutionary point of view, costs and benefits are ultimately measured in terms of Darwinian fitness (reproduction and the perpetuation of genes). The term costly refers to a fitness cost of a certain behaviour. It is difficult to directly measure fitness, therefore a number of indirect parameters have been used in order to measure fitness costs of a certain behaviour; such as energy expenditure, food intake or amount of body reserves (Krebs & Kacelnik, 1991; Lemon, 1991; Deerenberg & Overkamp, 1999). The most direct tool for examining the trade-offs in different situations is the use of optimality models from behavioural ecology (Cuthill & Houston, 1997).

The different selection processes that are involved in domestication

Natural selection acting in the wild situation could also influence the selection pressure under domestication (Craig, 1981), for example concerning reproductive success and breeding success (Price, 1999). However, there are basically three factors involved in the process of domestication that differentiate domestication from the selection processes acting in the wild: 1) Relaxation of natural selection factors which means that behaviour important for the survival in the wild loses its significance and fitness in captivity such as food and shelter seeking and predator avoidance (Price, 1984; Zohary et al.,1998; Price, 1999); 2) Artificial selection for specific traits and against undesirable ones, for example increased growth and large litters; 3) Unintentional selection of traits correlated either functionally or genetically to the selected ones (Jackson & Diamond, 1995). However the different selection processes could act at the same time or at different times depending on conditions (Trut, 1999). In the domestic environment, there are two other types of phenomena that also affect the genetics of domestic animals, i.e. inbreeding and genetic drift. Inbreeding can be difficult to avoid in a small captive population and may result in a reduction of genetic variability. Genetic drift (certain alleles may be fixed or lost in the gene pool) is also common in small isolated populations and may also result in a reduction of the genetic variability of the domestic animals (Verspoor, 1988; Price, 1997). Inbreeding and genetic drift produce random changes in the gene frequencies whereas the process of selection is directional.

In the beginning of domestication when humans and domestic animals lived in loose coexistence (Serpell, 1986), the relaxation of natural selection factors might have been most significant. In this first stage animal species had loose ties to their wild ancestors and interbreeding was still common. Darwin suggested that domestic animals were modified through unconscious selection long before humans selected for specific traits (Darwin, 1868) and it is probable that this unconscious selection is partly made up by the relaxation of natural selection factors acting in the wild. The natural selection factors that are most likely to be relaxed during this period are mainly predation and food shortage. Humans provided shelter and food as well as a protective environment against predators. In this thesis I have focused on this process and its implications on the behaviour of our domestic animals.

A model for adaptation during domestication

We may assume that the domestic animals and the wild ancestors differ in the benefits they gain from a certain behavioural response due to food and shelter provided during domestication. Figure 2 shows a simple model of the costs and benefits of different behavioural responses. The intensity of different behavioural responses that can be selected for is shown on the x-axis, arranged along the axis according to increasing costs, and the costs and benefits of the responses are shown on the y-axis. In the model, I assume that the slope of the benefit curve decreases with increasingly costly responses. The benefit of a certain response is assumed to be higher for wild animals than for the domestic animals, for which food and shelter already are provided. The cost of a certain response is assumed to be equal. The optimal response intensity for the domestic animal would then be lower than the optimal response intensity for the wild animal. In other words, domestication will favour the strategy that maximises the net benefits and in this case the strategy with a lower optimum (the less costly strategy) will be selected for. This hypothesis forms the theoretical background in this thesis and has been used in a similar context by Johnstone (1997). It is an important aspect that this process occurs irrespective of any directed selection for specific traits, and therefore represents a passive evolutionary adaptation to a life in domestication.

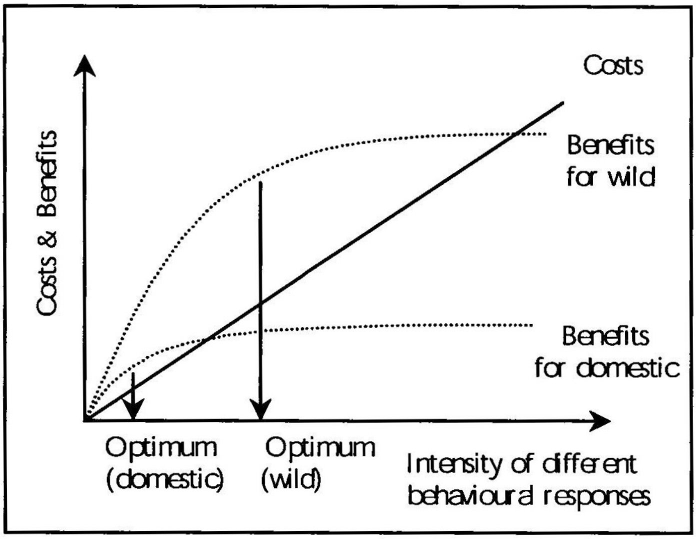

Figure 2. On the x-axis is a number of different behavioural responses with increasing intensities that can be selected for. During the process of relaxation of natural selection, the selection will favour the strategy that maximises the net benefits. Since the benefits for a certain response is lower for the domestic animal, the strategy with a lower optimum will be selected for during domestication.

Welfare and fitness

There is a large distinction between the fitness of an animal and its welfare. Fitness is solely measured in terms of Darwinian evolution, whereas welfare is a concept of ethics and what we think is important to the animal. The definition of fitness concerns the individuals' lifetime reproductive success and should include the progeny produced over the whole life of the animal as well as the fate of the progeny (Beilharz et al., 1993). The definition of welfare of an animal is continuously discussed and suggested by Broom to be "its state as regards its attempts to cope with its environment" (Broom, 1986). Adaptations in behaviour are traded-off by selection against the reproductive success of the individual. While the animal might experience bad welfare, the trade-offs of different strategies are part of the mechanisms of natural selection acting on the individuals' lifetime reproductive success (Barnard & Hurst, 1996). The parameters used to measure fitness and welfare could however overlap for example behaviour, health, reproduction and production. Finally, I would like to stress one point clearly. To say that the domestication process is an evolutionary process and its effect on behaviour is functional is not at all to say that mistreatment of domestic animals does not occur or to deny the fact that farm animal practices today raise serious questions about animal welfare.

Behavioural theories - a tool in understanding the process of domestication

In this thesis I have used concepts from the following theories in order to predict and interpret the results of my experiments.

Optimal foraging theory

Optimal foraging models predict that selection will favour the strategy which maximises the difference between the costs and the benefits of searching and ingesting food (Krebs & Kacelnik, 1991). In a patchy environment, the Marginal Value Theorem predicts that an animal should stay and forage for a longer time when there is a large distance to the next food source and as well adapt their foraging to the food intake per time unit in the patch and consequently leave a food source when the intake rate has fallen under a certain level (Stephens & Krebs, 1986). Optimal foraging models rely on the assumption that there is a close link between net energy intake and fitness.

Parent-offspring conflict theory

Natural selection can act differently on the genes expressed in the parent and in the young. Since the parent is equally related to each offspring, it is selected to give equal share of the resources to all its young. Each sibling on the other hand is selected to attempt to take a larger share of the resources compared to its siblings. However there is a limit since they share genes to some extent with the siblings as well. The parent-offspring conflict is predicted to occur over all allocations of resources from parents to young, including the duration of the parental care period (Trivers, 1974; Godfray, 1995).

Theory of honest begging

Young animals and especially young chicks beg with different intensities which have been shown to vary with the need of the individual chick (Price & Ydenberg, 1995; Price et al., 1996). The parent is also suggested to use the level of begging as an accurate indicator of the chick's condition and to respond to it accordingly (Stamps et al., 1989; Godfray, 1991; Redondo & Castro, 1992; Cotton et al., 1996). When the signal from the young is costly, it has been shown that an evolutionary stable system of honest begging can evolve. For example, this is the case when there is a conflict between the offspring and the caring parents (Harper, 1986).

Antipredation

Different behaviours have evolved to help animals escape from predators. Animals live in social groups and show a wide variety in anti-predatory behaviour, for example foraging in places with low predation, using cover and being vigilant (Rasa, 1989; Walters, 1990). There will always be a trade-off between looking for predators and other activities such as foraging, which means that if an individual spend time on vigilance, it will loose time and energy that could have been used for feeding (McNamara & Houston, 1992).

Changes during domestication

Behavioural biologists and particularly comparative researchers into physiology have interpreted changes between domestic and wild animal such as shortening of muzzles and extremities and a lack of fear of humans, in terms of degeneracy rather than adaptations to the domestic habitat (Zeuner, 1963; Hale, 1969; Ratner & Boice, 1969; Boice, 1972; Hemmer, 1990; Budiansky, 1994). Domestic animal behaviour has also been regarded as artificial with little relation to the natural behaviour of their ancestors. However, with the evolutionary approach domestic animals can be considered as adapted to survive and reproduce in the domestic habitats provided by humans (Ratner & Boice, 1969; Coppinger, 1983; Clutton-Brock, 1992) and it is not logical to look upon the domestic animal as unfit or degenerated because it is not adapted to a wild environment (Boice, 1973).

Genetics

Nature has a store of various forms hidden as recessive mutations in every natural population of wild animals. It is this accumulated mutation pool that is exploited by humans in breeding. The differentiation of wild species during domestication originates in the utilisation of mutations developed during their evolutionary history. In small populations with restricted freedom to breed, random-in-breeding and occasions of genetic drift, genetic variability might decrease (Verspooor, 1988; Agnèse et al., 1995, Price, 1997), with the consequence that possible mutations will have a great impact on the gene pool. However, some studies have shown that genetic drift does not always reduce the genetic variation (Connor, 1975). Homozygous individuals that could develop will survive in conditions controlled by humans and many of them become objects of artificial selection, whereas they would have been eliminated in nature by natural selection (Belyaev, 1969; Herre, 1989).

Morphology

A first look at our domestic animals reveals a striking fact. The individuals generally differ more from each other than the wild individuals do (Darwin, 1859). In nearly all large domestic mammals there has been a reduction in size of bones and a change in the shape of the horns (Clutton-Brock, 1992). Furthermore, domestic animals also usually possess smaller brains compared to their ancestors (Hemmer, 1990). Coat colour and changes in fur thickness are also characteristics that are affected by domestication (Clutton-Brock, 1992). One of the best known general characteristics of domestication is neoteny. It is the retention of juvenile characters and behaviour into the adult domestic animal and may in part result from selection for individuals that are docile and easy to handle (Hemmer, 1990). As mentioned before, it is probable that these characteristics were in place before domestication occurred and it could explain why domestic animals share a surprising similarity of traits even though they represent different species (Coppinger, 1983).

Behaviour

Behavioural traits are controlled by complex genetic systems whereas morphological traits often are controlled by few genes (Krebs & Davies, 1991; Plomin, et al., 1997). Therefore, it is not likely that a certain allele may have a large impact on the development of certain behavioural characteristics, as could happen concerning morphological traits. Studies have shown that there are no losses or additions of behaviours from the species' repertoires or from the basic structures of the behaviour of our domestic animals (Künzl & Sachser, 1999; Price, 1999). The behavioural changes occurring during domestication are instead mostly quantitative rather than qualitative and are due to threshold changes to responses to stimuli (Kruijt, 1964; Desforges & Wood-Gush, 1976; Price, 1984; Price, 1999). Most domestic animals can reproduce at almost any season of the year and molt little or not at all in contrast to their wild ancestors (Belyaev, 1979). Most domestic animals are less aggressive than their ancestors, they reach sexual maturity earlier and have a wider range of adaptability and behavioural plasticity (Boice, 1973).

Examples of experimental studies on behavioural changes during domestication

Rats and mice

The burrow behaviour of domestic rats and the wild Norway rat (*Rattus norvegicus*) was studied in a semi-natural environment and no differences were found between the two types of animals (Boice, 1977). Some studies have tried to replicate the domestication process. Connor (1975) for example bred ten generations of wild house mice (*Mus musculus* L.) and then subjected them to different behavioural tests. The results revealed few behavioural differences between the wild and the ten generation bred mice. However, there was an effect of inbreeding, which strongly reduced inter-male aggression.

Fish

There has been concern in aqua-culture research that artificial selection for growth indirectly will select for more aggressive fish compared to the wild conspecific. However, in an experimental study it was shown that growth rate selection favoured a decrease in both aggressive and submissive behaviour in hybrid Tilapia (*Oreochromis mossambicus/hornorum*) (Robinson & Doyle, 1990). It was also argued on a basis of game-theoretic analysis, that artificial selection for rapid growth instead indirectly selected for tameness and not aggression (Doyle & Talbot, 1986).

Fleming and Einum (1997) studied aggression and antipredation in farmed and wild juvenile salmon (*Salmo salar*). The farmed salmon were more aggressive than the wild salmon in an environment typical of aqua-cultural facilities. The wild salmon dominated in pair-wise contests in a stream-like environment but not in an environment typical of aqua-culture facilities. Farmed salmon were also more risk-prone since they reappeared from cover sooner after a simulated predator attack than the wild salmon.The authors argue that the results are generated by intentional or unintentional selection during the seven generations and not of inbreeding or genetic drift. The authors suggested that the results from the anti-predatory experiment were due to a relaxation of selection against predator-vulnerable phenotypes.

Fowl

Schütz and Jensen (in Press) studied the foraging behaviour of different breeds of fowl representing different degrees of domestication. They showed that the breed subjected to artificial selection for production used a less demanding foraging strategy. These birds obtained a higher proportion of food from a site that did not require effort, compared to breeds not subjected to any selection for production traits. They conclude that the selection for increased production will result in a modified behavioural strategy where the selected breed is devoting more energy to production traits.

Foxes

D.K Belyaev was the first to explicitly start an experimental study on selection during domestication and its effects on behaviour. His experimental set-up is widely known and started in 1959 with a large selection on domestic behaviour in silver foxes (*Vulpes vulpes*). Belyaev defined domestic behaviour (tamability) as; "not to be afraid of man, to obey him and to reproduce in the captive environment provided by man" (Belyaev, 1979). About 15-20 % of the animals were selected at every occasion, which resulted in 500 females, 150 males and 2000 young to be studied in detail in comparison with the foxes that had not undergone selection for domestic behaviour. The pups from the domestic foxes opened their eyes sooner after birth and responded earlier to sound. They also prolonged their sensitive period of socialisation to about 60 days compared to about 40 days in the unselected foxes (Belyaev et al., 1985). The foxes showed an active and positive reaction to human contact and there was an increase in extra-seasonal oestrus activity as well as extra-seasonal mating. The time of molting was also longer in the tame foxes.

The model species used in this study

The domestic pig and the European wild boar represent the first species used as experimental animals in this thesis and the domestic hen and the red jungle fowl represent the second. The domestic pig and the wild boar still belong to the same species and therefore are able to reproduce, as do the domestic hen and the red jungle fowl.

The natural behaviour of pigs

The natural behaviour of the wild boar has been studied by Gundlach (1968), Graves (1984), Boitani et al. (1994) and Horrell (1997) and the domestic pig in a semi-natural environment by Stolba and Wood-Gush (1989), Jensen (1986; 1988; 1995) and by Jensen and co-workers (1989; 1991; 1993). One to several sows form stable groups together with their offspring. The adult males live alone on larger home ranges than the females and associate with the females only during oestrous. The home ranges vary with resource abundance and density (Boitani et al., 1994). They live in forest areas often close to dense cover. The wild boar is diurnal, however the activity pattern depends to a large extent on the weather. Pigs are omnivorous and can live on a wide variety of foods. The pigs reach sexual maturity at about 18 months of age and are fully grown at about five years (Epstein & Bichard, 1984). The gestation period is about 113 days. The pregnant sow leaves the group about 24 hours before farrowing. She builds a nest where she gives birth to up to nine piglets. The domestic sow can give birth to up to 15 piglets. After a period of about two weeks she will take her piglets back to the group. A suckling includes different distinct phases; a pre-massage period of one to three minutes when the piglets are massaging their own udder segment, a short period (about ten seconds) of slow sucking, a short period of intensive sucking (15-20 sec) during which the milk is ejected and finely a post-massage period of up to 15 minutes, when the piglets again massage their own udder segment (Fraser, 1980).

The natural behaviour of fowl

The natural behaviour of the red jungle fowl has been studied by Collias and Saichuae (1967) in Thailand and in India by Collias and Collias (1967, 1996) and of the feral domestic hen by (McBride et al., 1969). The red jungle fowl are polygynous and show strong sexual dimorphism. They form small groups of about 6 to 30 adult individuals of males and females, their offspring and juveniles. One large cockerel guards the group, which seldom moves more than 50 m from its home territory (McBride et al., 1969; Morejohn, 1973; Collias & Collias, 1996). The hens leave the group to nest and incubate their eggs. By the time the broods are being raised it is common to see cockerels alone or in groups of only males (Collias & Collias, 1967). Broody hens with chicks behave in much the same way as dominant males; they control movements of the group, draw attention to food, maintain vigilance for intruders and are protective. The red jungle fowl hen lays about eight to ten eggs per clutch and one clutch per season

(Nishida et al., 1990; Nishida et al., 1992). After incubation of 21 days, all eggs hatch within about 15 hours (Meijer & Siemers, 1993).

Aims of the thesis

Functional effects of domestication on different behavioural strategies are studied in this thesis. This was accomplished by using the domestic pig versus the wild boar and the domestic fowl versus the red jungle fowl as experimental model animals. The aim was first to try to use models from behavioural ecology when predicting and studying the differences in behaviour between the domestic animal and the wild ancestor and to study the relaxation of natural selection and what effects it could have on behaviour. Second, the aim was to see whether domestic animals still possess capacities to adapt to environmental changes, since the domestic animals have been regarded as artificial with degenerative behaviour patterns.

- In Paper I, I studied the foraging behaviour of domestic pigs and wild boar crossings. The aim was to investigate whether domestic pigs still are able to behave in an adaptive fashion in an optimal foraging situation, and how domestication may have affected foraging strategies.

- In Paper II, I studied the maternal behaviour of domestic pigs and wild boar crossings. The aim was to investigate the sows' different abilities to care for offspring and if this ability was affected by domestication.

- In Paper III, I studied the post-massage behaviour of domestic pigs and wild boar crossings. The aim was to study the domestication effects on the post-massage behaviour in pigs and to see whether the pigs responded to a reduction in milk intake.

- In Paper IV, I studied the foraging behaviour of domestic fowl and red jungle fowl crossings. The aim was to investigate whether domestic fowl still are able to behave in an adaptive fashion in an optimal foraging situation, and how domestication may have affected foraging strategies.

- In Paper V, I studied the anti-predatory behaviour of domestic fowl and red jungle fowl crossings. The aim was to investigate what effect domestication might have had on anti-predatory vigilance and response to a predator.

Summary of Material and Methods

Animals and management

The first three studies (Papers I-III) were carried out at the Wageningen University of Agricultural Sciences in the Netherlands, where Dr Francien de Jonge had developed an experimental set-up comparing domestic pigs and wild boar crosses. She started with eight domestic sows (Holland landrace), half of which were artificially inseminated with domestic boar (Great Yorkshire), and the other half were naturally mated with wild boar. Offspring were then domestic pigs ("domestic"; Holland landrace x Great Yorkshire) and wild boar crosses ("wild-type"; 50 % wild boar). This set-up made it possible to control effects of the mothers, since all were domestic sows. All offspring, i.e. the experimental pigs, were born, housed and raised in an outdoor enclosure with farrowing huts (9 m^2), where straw was provided in one half and the other half was used as dunging area. A 30 cm barrier kept all piglets inside the hut (described earlier in de Jonge, 1996). This meant that all experimental pigs had been subjected to the same environment and conditions since birth.

The fourth and fifth studies (Papers IV-V) were carried out at Tovetorp research station (belonging to Stockholm University) and Götala research station in Skara, Sweden. A set-up of domestic fowl and red jungle fowl crosses were bred for experimental purposes at Tovetorp . Five domestic fowl of the Swedish Bantam breed were mated with domestic cockerels of the Swedish Bantam breed and five were mated with red jungle fowl cockerels. Eggs were then collected from these two groups. Half of the offspring were then domestic chicks ("domestic"; Swedish Bantam) and half were red jungle fowl crosses ("wild-type"; Swedish Bantam X red jungle fowl). All chicks were hatched and raised together with Swedish Bantam mothers in four outdoor pens with woodshavings, nest-boxes and perches. Food and water was provided *ad lib.* Half of each clutch was domestic chicks and the other half wild-type chicks. The mothers were removed when the chicks were 14 weeks old. The fowl were kept in these pens from 14 weeks to the start of the experiments.

Paper I: Eight female domestic pigs, nine months old, were together with eight wild-type pigs used in this study. Since weaning (9.5 - 11 weeks of age) domestic pigs and wild-type pigs had been kept in pairs indoors in standard commercial pens (4.2 m^2). Domestic pigs were kept separated from wild-type pigs. The light was turned on at 0730 hours and off at 2130 hours. Each pig was provided with 1 kg standard commercial feed twice a day and had free access to water.

Paper II: Seven domestic sows were together with seven wild-type sows used in this study. In January/February all experimental sows were inseminated with Great Yorkshire sperm. Hence, the offspring of the experimental animals were either pure domestic pig or 25 % wild boar. During the summer, all sows farrowed in huts (9 m^2), where straw was provided in one half and the other half was used as dunging area. A 30 cm barrier kept all piglets inside the hut. Two days before farrowing, sows were locked into the farrowing pens. All sows were fed 3 kg commercial concentrate twice daily in separate feeding crates in the outdoor pasture, in order to allow the experimenter to carry out essential manipulations in the farrowing pens (weighing and numbering of the piglets, etc.). Water was provided *ad lib.*

Paper III: Eight domestic piglets and twelve wild-type piglets were used in this study. The mothers were all domestic sows. Piglets were between seven and ten days of age at the start of the experiment. The environment was the same as described in Paper II.

Paper IV: Fourteen domestic fowl were together with 16 wild-type fowl used in this study. The fowl had free access to food and water. The fowl were held in four pens with a flock of hens and cockerels, of both wild-type fowl and domestic fowl. All fowl were identified by foot rings.

Paper V: In the first experiment 16 domestic fowl and 16 wild-type fowl were used and in the second experiment there were 14 domestic fowl and 16 wild-type fowl. The fowl had free access to food and water. Every pen contained a flock of hens and cockerels, of both wild-type fowl and domestic fowl. All fowl were identified by foot rings.

Methods and behavioural observations

Paper I: The foraging behaviour of the pigs in a maze was recorded for 30 minutes. A maze consisting of six patches where the pigs foraged from a bucket with holes was used in this study. In every second session barriers were introduced between patches in order to increase the costs of travelling between patches. Each session was video-recorded and direct observations were also made. Feeding behaviour patterns were recorded on a one-zero basis once a minute by means of direct observations. A pig was scored to be feeding when it ingested at least one food pellet. In addition, the cumulative number of patches visited was recorded as well as the cumulative number of barriers passed. From the video recordings, frequencies of visits to each patch and time spent in each patch were observed.

Paper II: Nest-building behaviour was recorded with the Psion hand-held computer and the Observer software (Noldus Information Technology) during 15 minutes every third hour for each sow (following Jensen et al., 1993). Observations started one hour after injection of $PGF_{2\alpha}$ (on day 112 of gestation) and continued until the first piglet was born. Between 4 and 7 days after parturition suckling behaviour was observed directly during four hours for each sow with a litter. Each sow with a litter was observed once for four hours. This observation schedule was repeated from day 8 to 11. From day 12 to 22 sampling sessions were similar, but were extended by activity measures and measures of proximity between sow and piglets in the open enclosure.

Paper III: The post-massage behaviour was observed after milk ejection for 15 minutes. The piglets were subjected to two different treatments during the three sucklings before the observed sucklings. First, the no-milk treatment when the piglets were withheld from the udder during milk ejection. Second, the control treatment when piglets could suckle normally, however they were gently hand-held during 5 s after the suckling to control for handling. Each minute the number of performed massage movements was recorded. If the sow or the piglet terminated the suckling this was noted as well as the behaviours; sucking, persistence in seeking udder and movements away from udder.

Paper IV: The foraging behaviour of the fowl was observed in a runway cage with the Psion hand-held computer and the Observer software (Noldus Information Technology) for 15 minutes. Food was provided in two patches in the cage. Every second session the travel distance between the food patches was increased in order to increase the costs in reaching the patches. Movements into or out of a patch were noted. The duration and frequency of patch visits was also recorded.

Paper V: Two different experiments were included in this study. First a study on vigilance behaviour where all fowl were subjected to two different group sizes (3 and 9). The vigilance duration and frequencies were recorded. The second experiment studied the response to an airborne predator model of an eagle owl. The response to the simulated predator attack was recorded on a three level basis. The time required before the fowl returned to feed and the time to the first peck at the floor was also recorded.

Statistics

We used Anderson-Darling Normality test to test the normal distribution. If criteria of normal distribution were met we used; Student's t-test and Analyses of Variance, with a repeated design where appropriate. Otherwise non-parametric tests were used; Kruskal Wallis, Mann Whitney Rank Sum test and Wilcoxon Signed Rank test. The analyses were made with Minitab (12.21, 1998) and Sigma stat (2.0, 1995) software packages. All variations are given as standard errors (SE).

Summary of Results

Foraging strategies in pigs (Paper I)

For both domestic pigs and wild-type pigs the average time spent in each patch decreased with successive visits to the same patch. However, there was no significant difference between the breeds in the distribution of visits to different patches. Domestic pigs spent significantly more time on average in each food patch compared to the wild-type pigs ($p<0.05$). Both breeds spent a longer average time in the patches when the maze contained barriers ($p<0.01$). The total time spent in patches during the entire test tended to be shorter in wild-type pigs ($p<0.1$). The domestic pigs on average passed fewer barriers per test than the wild-type pigs ($p<0.05$). Both breeds visited fewer patches when there were barriers present than when there were no barriers ($p<0.001$). Domestic pigs tended to perform more feeding behaviour than wild-type pigs ($p<0.1$). There was also a tendency that feeding behaviour was affected by treatment ($p<0.1$), so that less feeding behaviour was performed when the maze contained barriers. The amount of ingested feed per patch was reduced in both breeds when the maze contained barriers ($p<0.05$). Total amount of ingested feed was significantly lower when there were barriers present ($p<0.05$). Weight was not a major factor in affecting the results. The breed of the pig mainly affected the number of passed barriers and both breed and treatment mainly affected the time spent in each patch.

Maternal behaviour in pigs (Paper II)

The average number of hours from injection to first piglet born was longer in the wild-type sows than domestic (wild-type: 26.4 hours ± 1.8; domestic: 19.0 hours ± 1.6, $p<0.05$). There were no differences between the genotypes in the frequencies of nest-building behaviours; pawing, carrying/arranging, walking/standing or nosing/biting/rooting. Average proportion of sucklings that were non-nutritive was similar in both genotypes in the first week (wild-type=11.3 %, ± 5 %, domestic=10.8 % ± 4 %) and in the second (wild-type=26.7 % ± 7 %, domestic=14.4 % ± 5 %. The number of nutritive sucklings was reduced in the second week of observation for both wild-type and domestic sows ($p<0.05$), however there was no significant difference between the genotypes. The inter-suckling interval in the first week of observation was similar in the wild-type sows and in the domestic sows, whereas in the second week of observation the inter-suckling intervals tended to be longer for domestic sows ($p=0.1$), but not in wild-type sows. The pre-massage time tended to be shorter in the second week of observation for both wild-type and domestic sows ($p=0.059$), but there was no difference between the genotypes. Domestic sows allowed the piglets to post-massage for a longer time than wild-type sows in the first week of observation ($p<0.05$) and tended to do the same the second week of ($p=0.1$). There was no significant difference in the percentage of sucklings initiated by the sow, either between weeks or between the genotypes. Both wild-type sows and domestic sows tended to terminate more nutritive sucklings in the second week of observation compared to the first week (p=0.064) and wild-type sows terminated a higher proportion of sucklings than domestic sows in both weeks (p=0.01). Wild-type sows tended to leave the farrowing huts more frequently than the domestic sows in the second week of observation (p<0.1). However, there were no differences between genotypes in the first week. In the study of mother-young interactions out in the field the time spent lying tended to be longer for domestic sows compared to the wild-type sows (p=0.073). Time spent in locomotion was longer for the wild-type sows compared to the domestic sows (p=0.011). The frequency of nose-contacts between the sow and her piglets was higher in the wild-type sows compared to the domestic sows (p=0.001).

Post-massage behaviour in pigs (Paper III)

The interval between the sucklings was 54.5 minutes (SE=2.0) for domestic piglets and 51.1 minutes (SE=2.3) (n.s) for wild-type piglets The number of massage movements per minute after milk ejection was significantly reduced over time after milk ejection (p<0.001), and the number of massage movements tended to be higher for domestic piglets after milk ejection (p=0.066), than for wild-type piglets. However there was no effect of treatment on the number of performed massage movements. When we considered only those sucklings where the sow did not interrupt the post-massage the pattern was the same. The different behaviours: sucking, "persistence" and "away from udder" were all reduced in frequency over time after milk ejection (p<0.05), however there were no differences between genotypes or treatments.

Foraging strategies in fowl (Paper IV)

Wild-type fowl had more total patch visits than the domestic fowl in the short distance tests (p<0.05). When patches were further apart there were no significant differences in number of patch visits between the genotypes. The wild-type fowl also had more patch visits when the distance was short compared to the long distance tests (p<0.05). The difference between short and long distance test was not significant in domestic fowl. The average patch visit time was significantly shorter for the wild-type fowl than for the domestic fowl for short distance tests (p<0.05) and the same tendency was found when patches were further apart (p=0.064). Wild-type fowl stayed longer in each patch when the distance between patches was long compared to when it was short (p=0.001), in the domestic fowl the difference was not significant. Average time spent in each patch decreased with successive visits to the same patch for both breeds and for both short and long distance tests (p<0.05).

Antipredation in fowl (Paper V)

In the first experiment on vigilance behaviour there were no differences in the vigilance duration between the genotypes. However, the vigilance duration was affected by group size within breed ($p=0.005$), due to a longer vigilance duration within the larger group compared to the smaller group in domestic fowl. There were no differences in the vigilance frequency between the genotypes. However, there was a tendency of a difference in vigilance frequency for group size within breed ($p=0.055$), due to a higher vigilance frequency in the smaller group compared to the larger group in domestic fowl. In the second experiment the wild-type fowl tended to respond more to the simulated predator attack than the domestic fowl did ($p=0.062$). There was no difference in the anti-predatory response between the sexes. There were no differences in the duration to first peck after predator or the duration to first peck in feed.

General discussion

The experimental design in the different studies in this thesis was developed to reduce environmental factors that could affect the results. First, both pigs and fowl of the two different genotypes were born and raised by the same types of mothers i.e. domestic mothers. Thereby possible effects caused by different genotype mothers are minimised. Since learning to some extent has been shown to affect different behavioural repertoires this strengthens the results of the experiments. Second, they were also cross-fostered on the mothers so that the litters and clutches were made up of half wild-type animals and half domestic animals. Third, all animals were subjected to the same type of environment during the early development and during the different experiments. All these aspects minimise the possibility that other than genetic differences affected our results. The experimental design of letting all animals be subjected to the different treatments also make the results stronger since the within individual variation is to a large extent controlled for.

The results could have been clearer if we would have used pure (wild boar, red jungle fowl) wild animals instead of hybrids. However, it is likely that the hybrids would represent an intermediate type. It was also clear that it was difficult to differentiate effects from relaxation of natural selection from effects on artificial selection, in particular in the studies of pigs.

Domestication effects on foraging strategies (Paper I, IV)

All pigs and fowl responded to the experimental foraging set-up according to some predictions obtained from optimal foraging theory; they moved between patches throughout the tests, they stayed shorter time on successive visits in each patch and thereby adapted their foraging pattern to the depletion of the food sources. This is a pattern predicted by optimal foraging theory in a situation where the animal periodically must check its options to be able to maximise the long-term rate of energy intake (Stephens & Krebs, 1986). It would then pay off to leave a depleted patch before it is completely empty and search for a not yet depleted patch. Both types of pigs responded to the induced costs of travelling and adapted their moving pattern between the patches. However, in the study of fowl it was only the wild-type fowl that adapted their foraging behaviour according to the increased costs of travelling. The domestic fowl did not adapt their foraging pattern to the same extent. Feed intake did not differ between treatments or between genotypes for either pigs or fowl.

There were some differences between the genotypes. Both wild-type pigs and wild-type fowl stayed shorter time on average in patches and moved more between them compared to the domestic pigs and fowl. Therefore in total they spent more energy on moving while receiving the same amount of food which suggests that they were using a behavioural strategy that is more costly than the strategy used by the domestic animals, with the assumption that it demands more energy to move between patches than to stay in a patch and forage. Under natural conditions, energy demanding foraging behaviour is likely to pay off by an increased total food intake. This indicates that the wild-type pigs and wild-type fowl showed a decision strategy adapted to a situation where the net benefit of more costly foraging is greater than in a domestic situation.

The manipulation of travelling costs by inserting barriers for the pigs and increasing travel distance for the fowl, was assumed to affect the cost/benefit ratio in the same way for both genotypes. However, this was possibly not the case in the experiments with the pigs since there was a difference in weight between the genotypes. Some facts however contradict this. The wild-type pigs were generally smaller than the domestic pigs, which means that the barriers were relatively higher for the wild-type pigs, which may have increased the perceived costs of the wild-type pigs relative to the domestic pigs. Furthermore, the fact that the domestic pigs stayed longer in each patch even when there were no barriers present again suggests that differences in behaviour patterns may be attributed to strategy differences caused by domestication. The fowl on the other hand are likely to experience similar costs since there were no significant size differences between the two. However, we have no data on factors such as metabolic rate, muscle strength, etc, for any of the breeds, which could have affected the feeding motivation during the tests.

Domestication effects on parent-offspring interactions (Papers II, III)

These experiments on nest-building behaviour, suckling and post-massage behaviour as well as mother-young interactions demonstrate large similarities between the wild-type pigs and the domestic pigs and indicate that these particular behaviour patterns are consistent through domestication as has also been shown in a similar experiment by Spinka et al. (in Press). It could be interpreted that these patterns are quite resistant to modifications due to relaxed natural selection, artificial selection for production traits and unintentional selection. The similarities were most striking in the studies of nest-building behaviour and suckling behaviour. There were no differences in the different behavioural features that were involved in the nest-building behaviour or in the general suckling patterns. The lifetime reproductive costs of nest-building are likely to have been very low since it is not a very frequently used behaviour, which may have reduced the selection pressures to remove or change this behaviour. The results from the suckling behaviour support the study of wild boar by Horrell (1997). Both genotypes of sows terminated more sucklings, decreased the number of nutritive sucklings and increased the inter-suckling interval the second week of the study compared to the first week. This fits well into the parent-offspring conflict theory (Trivers, 1974), according to which the mother is trying to make it harder and harder for the young to suckle. This has earlier been reported in studies of domestic pigs in semi-natural environments (Jensen, 1988;

Jensen & Recén, 1989; Jensen et al., 1991). However, there were some differences in the maternal behaviour that were significant. Wild-type sows terminated more sucklings, stayed in the recumbent suckling position for shorter time after milk ejection and tended to leave their piglets more frequently. Domestic sows were less active and it appeared as if they had less nose-contact with their piglets.

It is likely that the wild-type sows may be genetically adapted to a situation where it is more beneficial to save resources for future offspring and reduce the care for the present, considering the lifetime reproductive success. There is a trade-off between investing in current reproduction and future reproduction. The current reproduction uses up energy and body reserves and may also endanger the survival of the parent, since it will be more vulnerable during the caring period (Krebs & Davies, 1991). The domestic sows may rather be adapted to a situation where food and protection is provided and where they do not benefit to the same extent from saving resources for future offspring, since reproduction is controlled for by humans. Instead the domestic sows might be better off investing more in the present offspring.

The differences between the two genotypes in the experiment on post-massage behaviour are hard to explain. The domestic piglets responded to a decrease in milk intake by increasing massage intensity however the opposite was found in the wild-type piglets. Since earlier studies have shown an increase in post-massage after sucklings without milk ejection (Algers & Jensen, 1985; Spinka & Algers, 1995; Jensen et al., 1998) this study contradicts these results. However, the experimental set-up of three treatment sucklings and three observed sucklings could have influenced the results. During the three treatment sucklings the piglets did not receive any milk and during the three observed sucklings the piglets could suckle normally. Since it could be that there is a higher risk of short time fluctuations in the milk production in the wild, then it would possibly be more adaptive for the wild-type piglets to save energy instead of investing in massage. Another possibility could be that the wild-type piglets reacted to the decrease in milk intake already during the treatment sucklings, where their behaviour was not recorded. Other explanations are also based on the type of experimental set-up that was used. Since all mothers were domestic and consequently likely to give more milk per teat than a wild sow, it could imply that the wild-type piglets were relatively well nourished compared to the domestic piglets. The prediction that wild-type piglets would respond more vigorously to a decrease in milk flow was not supported by the data.

Domestication effects on anti-predatory behaviour (Paper V)

The results suggested that the anti-predatory behaviour is to a large extent unaffected by domestication but also that the genotypes might be adapted to different environments where different strategies are optimal. The two genotypes used similar vigilance behaviour and changed their behaviour between foraging and being vigilant according to hypotheses from theories of vigilance. They also responded to a direct approach of a predator model in the same manner.

The present experiment shows that the wild-type fowl did not change their vigilance duration according to group size, which supports the earlier study of Roberts (1995), where individuals changed the inter-scan levels but not the duration of vigilance bouts. In the large group size, the domestic fowl spent more time vigilant compared to when the group size was smaller. The vigilance frequency on the other hand, was higher in the smaller group than in the larger group for domestic fowl. The total duration of vigilance bouts (vigilance duration x vigilance frequency) during the whole tests were not different between group sizes or between genotypes, which consequently suggested that the different genotypes are using different vigilance strategies and accordingly get the same results. The longer duration of vigilance bouts in the large group for domestic fowl could be a result of social influences, which also has been argued in earlier studies (Lima, 1990). The results could also be an indication of the domestic fowl being adapted to a situation where food is abundant, and therefore they can afford to attribute more time to vigilance instead of feeding. The wild-type fowl responded somewhat stronger to the simulated predator attack, which suggests that they are adapted to an environment where predator attacks occasionally occur. In the domestic environment, fowl have been protected against predators, which might have resulted in a relaxed natural selection of the anti-predatory response, as has also previously been suggested in an experiment with salmon (Fleming & Einum, 1997).

Synthesis

The results of this thesis support other studies which show large similarities in the behaviour of domestic animals and their ancestors, for example different behaviours in ducks (Desforges & Wood-Gush, 1975; 1976), aggression and schooling in fish (Ruzzante, 1994) and life-history adaptation in salmon and sea trout (Peterson, et al., 1996). However, the results also support previous studies, which show that behavioural differences between wild and domestic breeds exist, although mainly in quantity or intensity (Hale, 1969; Boice, 1977). It is clear that studies of domestication effects on behaviour from a functional perspective can be a fruitful approach. The animals behaved partly as predicted from the optimal foraging theory, from the parent-offspring conflict theory and from theories on antipredation, though differences were found in the quantitative responses.

The differences in foraging strategies and in the anti-predatory behaviour in fowl are most likely a result of relaxed natural selection pressure from food shortage and predatory avoidance. The domestic fowl used in my studies had not been subjected to any directed selection for production or growth, as judged by physical appearance, body weights and egg weights. The experiments with pigs also indicate that effects on foraging strategies are mainly from relaxation of food shortage. When humans provide food and protection for animals, energy demanding behaviours for finding or using food resources may not pay off. These are behaviours therefore likely to be passively selected against during domestication, with the result that in comparisons between the wild-type animal and the domestic animal, the wild-type animals are found to use more demanding and costly strategies. As was previously suggested from the graphic model (Figure 2), the lower benefits of a behavioural response in the domestic situation consequently move the optimum of a behavioural response towards a lower intensity.

The present thesis represents one of the first attempts to study functional effects of domestication by concentrating on differences in behavioural strategies rather than differences in behavioural frequencies. The results are mostly not conclusive, but the studies suggest that the approach can be very fruitful and provide a better understanding of how animals are affected during domestication. The main contribution of the studies may therefore be to provide a basis for future research.

Possible objections

It could be argued that the use of a wild-type animal of 50 % wild and 50 % domestic origin could have made the results unclear. However, in the experiments the assumption was that the behavioural strategy of the wild-type animal resembles that of the wild ancestor. In fact, it is most likely and has also been shown experimentally that a hybrid animal would represent an intermediate type of behavioural strategy (Price & Loomis, 1973; Alcock, 1993). Any effect I have found is therefore likely to be even stronger if comparing with the pure wild form.

To demonstrate effects from relaxation of natural selection factors, one must be able to differentiate effects from artificial selection, which evidently could be difficult. However, in a study by Schütz and Jensen (in Press), it was shown that selection for increased production also has caused a modification in behavioural strategies as well as a decrease in energy demanding behaviour in fowl. In this thesis the first part consists of experiments on wild-type pigs in comparison with domestic pigs. It is obvious that the domestic pigs have been subjected to artificial selection during domestication, judging by their appearance. However, in the experiments with fowl the artificial selection is unlikely to have a great impact since these fowl were very similar in both appearance and weight (except the subjects in paper V).

It may also be that domestication has led to selection for tamer fowl, which are less affected by handling and exposure to tests such as these included in the thesis. The results in the thesis could then be caused by increased stress in the wild-type fowl in the different test situations. However, there were no signs of such effects in any of the experiments, on the contrary the animals behaved very similarly. As already mentioned, all animals of the two genotypes were subjected to identical conditions and were also used to human handling throughout the experiments, therefore effects from increased stress are unlikely to play a major role. However, all these possible objections call for some caution in the conclusions of the study.

Future prospects

An interesting observation in Paper I was that the interval between injection of $PGF_{2\alpha}$ and onset of parturition was almost 8 hours longer in the wild-type sows compared to the domestic sows. This indicates differences in physiological responsiveness to parturition related hormonal changes. This may be an interesting finding to follow up in future research, since such an effect has never been reported earlier. Both genotypes of pigs also had a similar proportion of non-nutritive sucklings, which supports suggestions of Jensen et al. (1991) and Illmann et al. (Illmann et al., 1998), that non-nutritive sucklings probably constitute a part of the normal behavioural repertoire of pigs. However, their function would be interesting to study since their presence remain unclear (Illmann et al., 1998).

It is difficult to design experiments to study domestication effects on the domestic animals that live today; often the ancestor is extinct and if not it has undergone selection pressures that cannot be controlled for since the beginning of domestication. It would be really interesting to start a long time selection experiment as D.K Belyaev and co-workers have done in Russia, where all other factors than genetic are controlled. However, unlike earlier selection experiments, such studies should focus on behavioural strategies. By using models such as those in this thesis, it would be possible to predict the strategy differences that would occur under specific selection pressures.

Conclusions

In this thesis it has been shown that models and cost/benefit analyses from behavioural ecology can be successfully used to study changes in behavioural strategies due to domestication.

The thesis also stresses the fact that despite many generations of artificial selection domestic animals still possess basic capacities for behavioural adaptation. It is also concluded that there is a remarkable resemblance between the wild conspecific and the domestic animals. However, the differences shown are suggested to be a result of relaxation of natural selection factors, which most likely have resulted in a use of less energy demanding strategies.

- In Paper I, I conclude that domestic pigs still are able to respond in an adaptive manner in an optimal foraging situation and that domestication might have shifted behaviour optima towards less costly behavioural strategies.

- In Paper II, I conclude that most maternal behaviour aspects are unaffected by domestication. However some differences might suggest that since domestic sows are adapted to a life under human protection, they are more likely to invest more in the current offspring.

- In Paper III, I conclude that post-massage behaviour is to some extent unaffected by domestication. However the pigs did not respond to our prediction that they would increase post-massage behaviour according to a reduction in milk intake. The results also indicated that further research in this area is needed.

- In Paper IV, I conclude that domestic fowl still are able to respond in an adaptive manner in an optimal foraging situation and that domestication might have shifted behaviour optima towards less costly behavioural strategies.

- In Paper V, I conclude that the anti-predatory behaviour is to a large extent unaffected by domestication, but differences between genotypes are likely to be an effect of the relaxed natural selection pressure accompanying domestication.

The present thesis represents one of the first attempts to study functional effects of domestication by concentrating on differences in behavioural strategies rather than differences in behavioural frequencies. The results are mostly not conclusive, but the studies suggest that the approach can be very fruitful and provide a better understanding of how animals are affected during domestication. The main contribution of the studies may therefore be to provide a basis for future research.

Svensk sammanfattning

Den här avhandlingen innefattar fem olika delexperiment där domesticeringens effekt på beteendet har studerats. Domesticeringen är den process som alla våra husdjur har gått igenom på deras väg från vild förfader till den domesticerade form vi ser idag, t.ex. från vildsvinet till tamgrisen och från den röda djungelhönan till tamhönan. Det är främst tre processer som påverkat den här utvecklingen. 1) En reducering/relaxering av de selektionsfaktorer som verkar i det vilda, 2) en artificiell selektion på t.ex. hög tillväxt eller hög mjölkproduktion, 3) en omedveten selektion som beror på att vissa egenskaper är kopplade till varann, t.ex. benskörhet kopplat till avel på hög tillväxt. I de experiment som jag har gjort har jag koncentrerat mig på de beteendeeffekter som kan bero på den första processen. I det första experimentet (Paper I) studerades födosöksbeteendet hos vildsvinskorsning och tamgris med syftet att se om tamgrisen fortfarande kan anpassa sitt födosöksbeteende till olika födosöksmiljöer samt studera hur domesticeringen har påverkat detta beteende. I det andra experimentet (Paper II) studerades modersbeteendet hos vildsvinskorsning och tamgris med syftet att studera suggornas olika modersegenskaper och hur domesticeringen påverkat dessa beteenden. I det tredje experimentet (Paper III) studerades eftermassagebeteeendet (en fas i digivningen) hos vildsvinskorsning och tamgris med syftet att se om griskultingarna anpassade sitt eftermassagebeteende till en minskning i mjölkintag och hur domesticeringen har påverkat detta beteende. I det fjärde experimentet (Paper IV) studerades födosöksbeteendet hos djungelhönskorsning och tamhöna med syftet att se om tamhönan fortfarande kan anpassa sitt födosöksbeteende till olika födosöksmiljöer samt studera hur domesticeringen har påverkat detta beteende. I det femte experimentet (Paper V) studerades vaksamhetsbeteendet och hur djungelhönskorsning och tamhöna reagerade på en rovfågelmodell, med syftet att studera domesticeringens effekt. Från resultaten dras följande slutsatser: 1) både tamgrisen och tamhönan kan fortfarande anpassa sitt födosöksbeteende till olika situationer, men det förefaller som om domesticeringen har påverkat djuren så att de nu visar färre kostsamma beteenden (energikrävande beteenden), 2) modersbeteendet är till stora delar helt oförändrat, men vissa skillnader tyder på att tamsuggan är anpassad till en miljö där hon investerar mer i nutida kull än i framtida, 3) eftermassagebeteendet är till viss del oförändrat, men våra resultat tyder på att mer forskning på detta område är nödvändig, 4) vaksamhetsbeteendet och reaktionen av en rovfågelmodell är till största delen oförändrat, men resultaten tyder på att de skillnader som hittats är en följd av den reducering av selektionsfaktorer som sker under domesticeringen. Slutligen, den här avhandlingen representerar ett av de första försöken till att studera funktionella effekter av domesticeringen. Resultaten är inte helt entydiga men gör tydligt att denna väg kan vara gynnsam och kan ge en bättre förståelse för hur djurens beteende påverkats av domesticeringen.

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