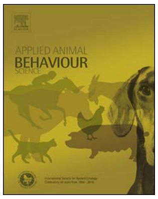
ARTICLE IN PRESS

Applied Animal Behaviour Science xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim



Is evolution of domestication driven by tameness? A selective review with focus on chickens

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ARTICLE INFO

Keywords:
Genetics
Epigenetics
Domestication
Red junglefowl

ABSTRACT

Domestication of animals offers unique possibilities to study evolutionary changes caused by similar selection pressures across a range of species. Animals from separate genera tend to develop a suite of phenotypic alterations referred to as "the domesticated phenotype". This involves changes in appearance, including loss of pigmentation, and alterations in body size and proportions. Furthermore, effects on reproduction and behaviour are typical. It is hypothesized that this recurring phenotype may be secondary effects of the increased tameness that is an inevitable first step in the domestication of any species. We first provide a general overview of observations and experiments from different species and then review in more detail a project attempting to recreate the initial domestication of chickens. Starting from an outbred population of Red Junglefowl, ancestors of all modern chickens, divergent lines were selected based on scores in a standardized fear-of-human test applied to all birds at 12 weeks of age. Up to the eighth selected generation, observations have been made on correlated effects of this selection on various phenotypes. The fear score had a significant heritability and was genetically correlated to several other behavioural traits. Furthermore, low-fear birds were larger at hatch, grew faster, laid larger eggs, had a modified metabolism and increased feed efficiency, had modified social behaviour and reduced brain size. Selection affected gene expression and DNA-methylation in the brains, but the genetic and epigenetic effects were not specifically associated with stress pathways. Further research should be focused on unraveling the genetic and epigenetic mechanisms underlying the correlated side-effects of reduced fear of humans.

1. Introduction

When Charles Darwin published what was later called the theory of evolution, he devoted the first chapter of his book to domestication. The reason was of course simple: at that time (1859), no proper theory of inheritance and genetics was known, and the fact that species can gradually change due to selection and develop into new varieties was not self-evident to his readers. But domestication served as an important proof-of-concept. If human-imposed selection can result in the rich variety of forms seen, for example, in domesticated pigeons, dogs and garden plants, why could natural selection not achieve the same effects on natural populations?

Hence, domestication as a field of study has a rich and important tradition in biology, and to this day it can serve as a model to explore evolutionary mechanisms and functions. Animal domestication has been defined as the modifications in a population caused by human selection (Price, 2002). It is a genetic process that ranges over generations, and can therefore be considered a special case of evolution where humans drive the process. But the selection imposed by people is only one factor in domestication. Natural selection continues to act on domestic populations, and sexual selection can also have a very high impact (Jensen and Wright, 2013). Furthermore, genetic drift, as well as correlated genetic responses can exert large effects.

Understanding evolution is an important reason for studying domestication, but there are other lessons to be learnt as well. For example, modern selection of farm animals have on average more than doubled their production capacities, while at the same time a range of health problems have become wide-spread as unintended side-effects (Rauw and Kanis, 1998). By examining the mechanisms in domestication we may gain important knowledge necessary to develop breeding programs that do not induce poor animal welfare as side effects.

Domestic animals from widely different species tend to develop a suite of similar phenotypic changes, often referred to as the domesticated phenotype (Jensen, 2014; Price, 2002). This includes, for example, changes in size, pigmentation, body proportions, reproduction and social behaviour. Similar developments happens in species that have been domesticated at different historical time periods and in different parts of the world. For example, the dog was the first

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http://dx.doi.org/10.1016/j.applanim.2017.09.006
Received 30 May 2017; Received in revised form 5 September 2017; Accepted 8 September 2017

Please cite this article as: Agnvall, B., Applied Animal Behaviour Science (2017), http://dx.doi.org/10.1016/j.applanim.2017.09.006

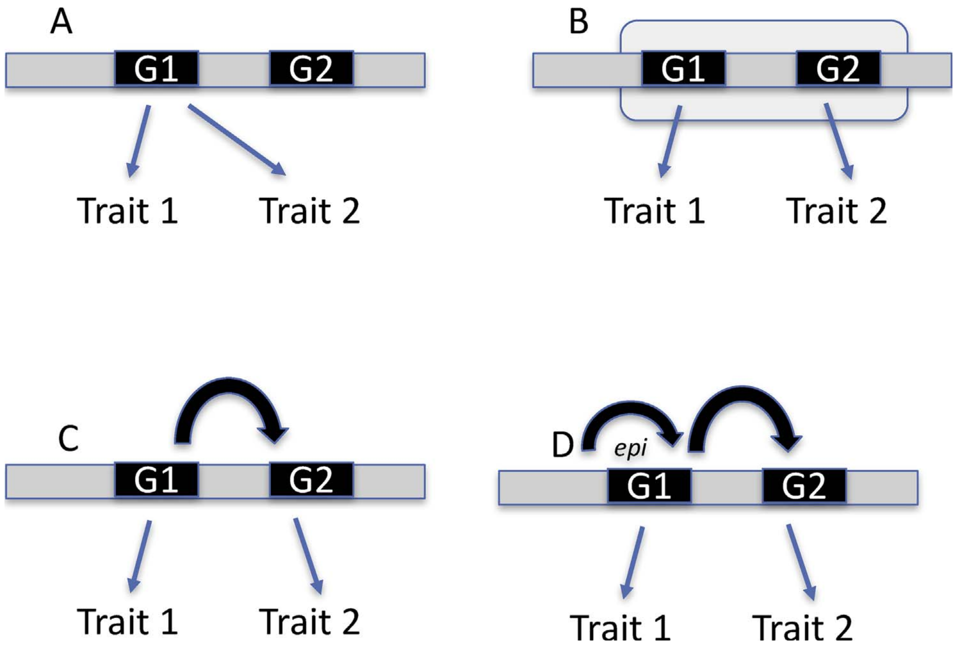

Fig. 1. Schematic outline of four possible genetic mechanisms that may cause correlated selection responses in two seemingly unrelated traits. The figure shows a schematic part of a chromosome with two separate genes, G1 and G2. (A) Pleiotropy, in which the genotype of G1 affects the phenotype of both traits simultaneously. (B) Linkage, in which G1 and G2 are linked due to close physical co-localisation, and hence inherited as a unit. (C) Epistasis, in which the effects of G2 on trait 2 depends on the genotype on G1. (D) Epigenetics, in which G1 is epigenetically modified (for example by DNA-methylation) and thereby affects the expression of both G1 and G2.

domesticated species, originating in south-east Asia some 15000 years ago (Ding et al., 2011), and the rabbit is a late addition domesticated about 1400 years ago in southern Europe (Carneiro et al., 2014). In spite of the large differences in time and geographical origin, in both species we find a radiant development of breeds with changes in behaviour, size, pigmentation, as well as skull and ear shapes.

All domestication events show individual differences and peculiarities, but they also share important aspects. Whereas it was long believed that humans have been actively choosing and enforcing domestication on species that they preferred, archeological and genetic data have shown that a period of "proto-domestication" or "pre-domestication cultivation" preceded actual domestication for most domesticated species (Larson et al., 2014). This means that there has been extensive co-evolution between man and animal, and shared traits in different domesticates could be a result of similar natural selection pressures occurring even before humans applied active selection for preferred traits.

Domestication therefore offers a powerful model for studies of evolution. One may view the process as a gigantic biological experiment, where humans have imposed similar selection pressures on replicated populations of different species at different time periods. With the modern biological tool-box, we can now harvest the results of this unintentional experiment (Andersson and Georges, 2004).

2. Tameness as a driver?

Considering the possible common aspects of animal domestication, one trait has been recurrently suggested to be of main importance. Successful domestication of any species must have relied on the animals showing drastically reduced fear of humans. Individuals showing excessive fear and stress reactions in the proximity of humans would have been unlikely to reproduce and thrive in captivity. The Russian geneticist Belyaev expressed it this way: "What do I mean by domesticated behavior? The main criterion here is the ability of animals to have direct contact with man, not to be afraid of man, to obey him, and to reproduce under the conditions created by him (…). It is obvious that selection for behavior has been unconsciously carried out by man since the earliest stages of animal domestication." (Belyaev, 1979).

Could tameness in fact drive the development of other aspects of the domesticated phenotype? Based on this assumption, Belyaev, together with his colleague Lyudmila Trut, selected farmed silver foxes for reduced fear over many generations and measured the occurrence of correlated traits in the selected population (Trut et al., 2009). They found a rapid increase of domesticated phenotypes in the tame animals. For example, the frequency of de-pigmented animals increased, as well as foxes with changes in skull shape, body proportions, and ontogenetic development.

Similar experiments have since been carried out on a few other, unrelated species. For example, the Russian group also selected wild-caught rats for high or low degree of defensive aggression towards humans (Albert et al., 2008; 2012), and Danish scientists have performed similar experiments on farmed mink (Malmkvist and Hansen, 2001). In general, increased tameness appears associated with a range of correlated phenotypic effects.

It therefore remains a plausible possibility that tameness is the driving factor underlying the development of domesticated phenotypes in widely separate species. Belyaev speculated that this could be caused by various hormones that are affected by reduced fear of humans, and simultaneously regulate gene function and developmental patterns (Belyaev, 1979).

3. Possible genetic mechanisms in domestication

A number of genetic mechanisms could tentatively cause the changes associated with domestication. The first and most straightforward would be that humans independently in different species selected novel mutations occurring randomly in the tame populations. This would mean that similar types of mutations would have to occur in all species, something Belyaev considered highly unlikely (Belyaev, 1979). He suggested that rather a few central genes might be responsible for a cascade of effects leading to the domesticated phenotype. However, independent and repeated selection of random mutations have been suggested to underlie pigment changes in domesticated pigs (Rubin et al., 2012).

Effects of few genes on many phenotypes could be caused by other mechanisms as well: pleiotropy, epistasis, linkage and epigenetics would all be possible (Fig. 1). Pleiotropy is the term used when variation in one single gene causes changes in several unrelated phenotypes. For example, a mutation in the gene *PMEL17* causes loss of pigmentation in chickens, and at the same time reduces the risk of being exposed to feather-pecking (Keeling et al., 2004). Possibly, genes related to tameness could exert pleiotropic effects on domestication phenotypes in a