

Universidade de São Paulo - Instituto de Biociências
Programa de Pós-Graduação em Zoologia

PhD project proposal

**The Evolution of self-domestication: a
comparative approach**



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Abstract

The animal domestication process most likely originated with humans selecting dog ancestors with less fearful responses towards themselves. Trying to understand the biological basis of animal domestication, Russian scientists experimentally selected silver foxes against defensive responses to humans. They found that the subsequent generations of selected individuals started showing similar characteristics present in domesticated animals. Hereafter, several studies found similar results in rats, minks, and chickens. Therefore, it has been suggested that these phenotypic patterns that resulted from domestication could also be widespread among different taxa in nature. A natural scenario in which the domestication pattern could appear is that of social tolerance. Indeed, bonobos, when compared to chimpanzees, show several phenotypic traits similar to those of domesticated animals. This process has been termed self-domestication and is a possible result of a selective regime in which low aggressiveness is favoured. In this context, this project aims to verify the plausibility of the self-domestication signature in a larger scale comparative framework using birds as a model system. The premise is that species with high complex behaviour would present high social tolerance, and therefore should present more domesticated phenotypic traits. To test this, I will use a phylogenetic analysis and, subsequently implement a meta-analysis to investigate correlations between social behaviour complexity and domesticated traits.

Introduction

The process of animal domestication by humans started roughly 15,000 years ago, at the end of the Palaeolithic Period, with the taming of dog ancestors [1;2] and the most likely trait selected in these individuals was a less defensive reaction towards humans [3]. Interestingly, animals of different evolutionary lineages when subjected to domestication, not only show differences when compared to wild close-related species or wild ancestors [4], but also display a wide set of common traits [5;6]. For instance, breeding becomes uncoupled from environmental stimuli, the key hormonal regulators of stress become attenuated, body and cranial proportions change, and colour patterns become distinctive [7;8].

A series of seminal experiments on silver foxes (*Vulpes vulpes*) have produced compelling evidence that selection strictly on low levels of defensive reactions to humans leads to the emergence of the complex domesticated phenotype [9;10]. Several morphological,

physiological and behavioural traits commonly observed in domesticated species developed as a correlated response of selection for tameness in the silver fox, such as depigmented fur spots, floppy-ears and less aggressiveness [9;10]. The consequence of these findings is that correlated selection responses are a driver of the emergence of the complex domesticated phenotypes observed across animals.

Whereas several experimental studies on the process of domestication have been carried out, most of them were conducted using mammalian species (*e.g.*, foxes [10], rats [11;12] and mink [13]). One valuable addition to these studies, has been the experimental selection for tameness carried out in the red junglefowl (*Gallus gallus* [14]). Angvall *et al.* [14] used the same protocol as the silver fox domestication experiment, in order to select and breed individuals only for tameness. The results of the red junglefowl study are interesting because they show that selection for tameness is genetically correlated with a suite of traits observed to emerge in domesticated mammals [15].

One of the proposed scenarios to explain the evolution of dogs starts before the domestication of wolves by humans. In this scenario, natural selection acts as a mechanism of 'self-domestication', that is, less aggressive and less fearful individuals gain a selective advantage because they are able to exploit a novel ecological opportunity [16]. Hare *et al.* [16] propose that this first stage of selection in the evolution of dogs from wolves should be seen as a model for self-domestication and can be understood as selection for reduced aggressiveness within a species. Then, they argue that the self-domestication hypothesis can operate in wild animals, in a similar fashion, as is observed among domesticated species. In their study, they consider that the empirical evidence from chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), arguing that the data support a scenario of self-domestication in the latter. A corollary, proposed by Hare *et al.* [16], is that self-domestication could be a widespread process responsible for shaping phenotypes across the evolutionary history of several animal lineages.

Objectives

In this study, we propose to test predictions of the self-domestication hypothesis using a comparative framework. We will test the predictions by adopting two approaches. The first approach will be to conduct a phylogenetic comparative analysis, and the second approach will be to implement a meta-analysis.

Our main innovation to understand whether the self-domestication hypothesis is a plausible process to explain the presence of the domesticated phenotypic signature in wild species, will be to conduct a phylogenetic comparative analysis using birds as a model system. The rationale is as follows. Birds present a wide range of variation in the types of social organization experienced by the individuals of a given species. Some species range from a lack of social pair bonds, such as lek mating systems, in which females seek males exclusively in order to copulate, and subsequently build nests and raise their young by themselves. On the other extreme of the social organization axis, some species present complex societies in which males and females exhibit long-term pair bonds and are part of cooperative groups that live together and conduct most activities as tight social units.

The premise of the self-domestication hypothesis is that individuals in species that live in complex social units and interact constantly are under selection for social tolerance and against aggressiveness. The corollary from this premise is that we should observe a pattern in which bird species with more complex social organization should display a greater range of traits associated with the domesticated phenotype.

The second objective of this project is to implement a meta-analysis to quantify and synthesize empirical data already available in the literature. We will evaluate what is the magnitude of the effect size when comparing traits between a domesticated species and its closest relative (or control group; in case of experimental studies such as the silver fox study). By estimating these effect sizes, we will be able to investigate whether some types of traits that are correlated to tameness (the variable that is selected during the domestication process) respond to a larger or smaller degree when compared amongst themselves. For instance, several studies quantify morphological and developmental traits in the domesticated lines, when compared to the wild ancestor. We want to address whether these different life-history traits respond differently to selection for tameness across the different model species for which data is available.

Justification

The biological basis of domestication became better understood with the silver fox studies. The experimental selection of individuals against defensive behaviour towards humans leads to the emergence of domesticated characteristics also present in dogs, such as depigmented fur spots and floppy-ears [10;11]. Additionally, similar experimental domestication patterns

were demonstrated in other animals (see examples above), including chickens [15]. All these findings suggest wild animals that undergo specific natural selection regimes that prioritize social tolerance instead of aggressive behaviour should exhibit traits observed in the domesticated phenotype (defined as the **self-domestication hypothesis** by Hare *et al.* [16]). The self-domestication hypothesis has never been tested in a large-scale phylogenetic comparative context. Consequently, we currently do not know how widespread the process of self-domestication is in wild animals. Thus, it is of utmost interest to investigate whether animals that are under selection against aggression and towards social tolerance exhibit similar phenotypes as domesticated animals. Additionally, testing the self-domestication hypothesis in a wide evolutionary context would allow us to better understand how distinct traits can differ across several closely related species when attempting to explain behavioural evolution.

In this context, the development of this project will allow me to delve even deeper into theoretical evolutionary subjects of behavioural ecology. Moreover, under Dr. Santos' supervision I will learn the required phylogenetic and meta-analytic techniques to complete this project. In addition, this study will enrich my previous education in experimental design for studies in animal cognition and behavioural ecology. Furthermore, the knowledge acquired during my PhD will contribute to a differentiated background of a professional exposed to an integrative approach that combine concepts in Ecology, Evolution and Animal Behaviour.

Material and Methods

Data collection will involve two different aspects. Firstly, for the phylogenetic comparative analysis of the relationship between social complexity and the level of domestication among bird species, we will collect data from databases that are already accessible. We will restrict our phylogenetic analyses to the order Passeriformes, because these birds have similar life-history and also because of logistical reasons. We will use the phylogeny from Jetz *et al.* [17] in order to account for phylogenetic relatedness in our analyses. These data are freely available from birdtree.org. To quantify the social complexity of the species involved we will use data available *Handbook of the Birds of the World Alive* [18], an online database that contains data on all extant bird species. Initially, we will concentrate our analyses of the effect of social complexity on the response variable plumage coloration. As discussed above (see Introduction and Objectives), pigmentation is one of the traits to present correlated response

to selection for tameness among domesticated species. Thus, our first analysis will quantify what happens to bird plumage coloration, from a macroevolutionary perspective, when social complexity changes across species. We will use phylogenetic generalised least squares methods to analyze these data [19].

Secondly, for the meta-analytic investigation, we will collect empirical data that is already published in the primary literature. For this part of the project, we will focus on studies that quantify different life-history traits in domesticated species (or domesticated experimental groups), and the correlated data available for the closest related non-domesticated relative (or the control group in case of experimental studies). We will quantify effect sizes using standardized formulas [20]. These effect size metrics will represent the magnitude of the difference between the domesticated and the wild species for each of the life-history traits available. We will use multilevel meta-regression models [21] in order to estimate the overall effect sizes to investigate whether certain life-history traits present greater or smaller responses to selection for tameness.

Work Plan and Project Feasibility

This PhD project was designed to be carried out within 48 months. During my first year, I will undertake the required credits for graduation and will gather all data and literature about social complexity of bird species. These are readily achievable because there are completed databases online and reviews that compile information about the social behaviour of birds. In the next two years, I will analyse the data using computational tools in the laboratory and attend to scientific meetings. During the final year, I intend to write the respective manuscripts and finish the dissertation. Finally, this project is achievable without the need for much financial support, because Dr. Santos' lab already has the necessary resources.

	Annual quarter															
	1°	2°	3°	4°	5°	6°	7°	8°	9°	10°	11°	12°	13°	14°	15°	16°
PhD programme subjects	■	■	■	■												
Literature and data collecting	■	■	■	■												
Phylogenetic analysis					■	■	■	■	■	■	■	■				
Meta-analysis				■	■	■	■	■	■	■	■	■				
Manuscript writing								■	■	■	■	■	■	■	■	■
Thesis writing	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Qualification exam						■	■									
Scientific meetings attendance						■	■			■	■			■	■	

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