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Research Paper

Effects of captivity on house mice behaviour in a novel environment: Implications for conservation practices

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ABSTRACT

Captive breeding programmes offer a method for preventing the extinction of threatened species, but often have difficulty establishing self-sustaining populations and generating individuals for release. This difficulty can arise because the behaviour of captive-reared animals differs from wild animals. Whilst the effect of captivity on animal behaviour has been widely reported, few studies have explicitly compared differences between captive-reared and wild-caught animals. Even fewer have examined behavioural types (a composition of behavioural traits) displayed in novel environments, which is particularly relevant for determining reintroduction success. Further, the transgenerational effects on behavioural type, and potential differences between sexes in response to captivity, remain almost completely unknown. Using house mouse (*Mus musculus*) as a model for small mammals, we tested whether behavioural types displayed in a novel environment differed between captive-reared and wild-caught animals. In addition, it was tested whether behavioural types were subject to transgenerational effects in captivity, and whether there were sex-specific differences in behavioural types. We used an open field test to simulate a novel environment. Captive-reared mice were found to differ in their boldness and activity behavioural type compared to their wild-caught mice ($p < 0.001$). There was marginal evidence for transgenerational effects on behavioural type in captivity, but three behavioural traits displayed a shift away from wild behaviours (% Time active: $p < 0.001$; % Time mobile: $p = 0.004$; Centre: maximum speed: $p = 0.004$). Furthermore, behavioural types of individuals in captivity did not differ depending on sex (F_0: $p = 0.161$; F_1: $p = 0.665$), however behavioural type did differ between wild-caught females and males ($p = 0.015$). These findings suggest that captivity can result in behavioural changes and loss of sex-specific behaviours. In addition, phenotypic plasticity may have a significant influence on behavioural type. This knowledge may be critical for developing methods to improve small mammal reintroduction programmes.

1. Introduction

Captive breeding programmes (hereafter CBPs) are increasingly relied upon as an important conservation tool for threatened species management (Conde et al., 2011). Captive breeding programmes provide a controlled environment for the rearing, maintenance and preservation of many species challenged by key threatening processes in the wild (Thomas et al., 2004; Bryant et al., 1999). However, captive populations often produce behavioural phenotypes that differ from wild populations (Snyder et al., 1996). These behavioural changes may lead to captive individuals having reduced survivorship compared with their wild conspecifics, as well as reduced reproductive success following reintroduction (Johnson et al., 2014; Anthony and Blumstein, 2000; Philippart, 1995). It is understood that the captive environment induces changes to the behavioural phenotype, but identifying specific mechanisms that cause such changes can be challenging, largely due to a multitude of abiotic and biotic differences between captive and natural environments. For instance, differences in behavioural phenotypes between captive-reared and wild individuals have been associated with environmental enrichment, habitat complexity and social learning environment (*see* Shier and Owings, 2006; Bremner-Harrison et al., 2004; Geiser and Ferguson, 2001; Carducci and Jakob, 2000).

While the effects of the captive environment on behaviour have been widely reported (Snyder et al., 1996), few studies have quantified the particular composition of behavioural traits that an individual expresses (hereafter referred to as behavioural type;

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Bell, 2007) in comparison to a control group of wild animals. Using an 'adaptive baseline' provides the ability to demonstrate and track the effects of captivity. That is, the scale of behavioural plasticity, the direction of change, and the specific behavioural traits that change (Jarvie et al., 2015; Mathews et al., 2005). For example, in a study comparing the behaviour of captive-bred versus wild-caught bank voles (*Clethrionomys glareolus*) it was found that captive-bred individuals displayed some wild-caught nest building and burrowing behaviours. However, captive-bred individuals were unable to utilise key food resources, and were less dominant in their interactions with conspecifics than wild-caught individuals. As a consequence, the captive-bred individuals were determined unsuitable for release (Mathews et al., 2005). Of note, few studies have attempted to investigate behavioural types that may impact the fitness of individuals following reintroduction (Moseby et al., 2014; Smith and Blumstein, 2008; McDougall et al., 2006).

Testing behaviour in a novel environment (e.g. open field test) is a commonly used tool for determining behavioural types, such as activity or boldness (Yuen et al., 2015; Rosemberg et al., 2011). Consequently, measuring behavioural types in a novel environment, and quantifying any changes resulting from maintenance in captivity may provide a valuable approach for increasing the success of captive-breeding and reintroduction programmes. Indeed, behavioural characterisation has been used as a criterion for selecting animals for reintroduction (Bremner-Harrison et al., 2004; Mathews et al., 2005). Specifically, boldness and activity relate to the tendency of an individual to take risks and explore novel environments (Coleman and Wilson, 1998). In addition, boldness has been used to predict the probability that individuals survive and reproduce following reintroduction (Herborn et al., 2010; Wilson and Godin, 2009). If changes in these behavioural types occur in captivity, the probability of an individual's survival and reproductive success might decline, and in turn, impact the likelihood that the reintroduction programme is successful. Based on optimality theory, an optimal level of boldness and activity would be expected for any given species in any given environment, with extremes on the axes of variation (shy-bold; inactive-active) being costly and selected against (Herborn et al., 2010). Boldness and activity can affect performance and fitness, and by determining these behavioural types, this information may be used to determine an individual's suitability for release (Mathews et al., 2005). Further, knowledge of behavioural changes occurring in captivity may be used to develop strategies to alleviate problems associated with domestication (Mason et al., 2013), or the effect of captivity on behaviours considered important for reintroduction success (McDougall et al., 2006).

How directional selection and phenotypic plasticity alter behavioural traits in the captive environment is only beginning to be investigated (Evans et al., 2014; Nelson et al., 2013). Developmental plasticity in behaviour allows individuals to alter their behavioural traits to suit their captive environment. In contrast, transgenerational effects in the captive environment influence the behavioural traits passed from parents onto offspring (Evans et al., 2014). Due to changes in the strengths and targets of selection in captivity, and the heritable nature of behavioural traits, a shift in behaviour that increases fitness in the captive environment can be expected (McPhee, 2004). Therefore, one might expect behaviour to shift away from the wild behavioural phenotype with each subsequent generation in captivity. Indeed, there is a growing body of evidence for transgenerational behavioural changes occurring in captivity. Previous research has shown that animals maintained in captivity for multiple generations usually display a consistent directional shift in behaviour away from the wild phenotype. Furthermore, these transgenerational behavioural changes have been shown to increase fitness within the captive environment (Johnson et al., 2014; Mason et al., 2013; Christie et al., 2012; McPhee, 2004). Commonly reported transgenerational behavioural changes include loss of anti-predator responses and reduced exploratory behaviour (Håkansson and Jensen, 2008). For example, refuge-seeking behaviour of oldfield mice (*Peromyscus polionotus subgriseus*) decreased in frequency with an increasing number of generations maintained in captivity (McPhee, 2004).

The way behavioural traits change in captivity, and the direction of transgenerational effects, could depend on a multitude of factors, but one of the most important is likely to be sex. It is well established that behavioural types can differ between the sexes due to sexual selection favouring different trait values in each sex (Fresneau et al., 2014; Schuett et al., 2010). In general, it is expected that intra- and inter-sexual selection (male-male competition and female mate choice) will favour bolder and aggressive males and shy and discriminant females (Kokko, 2005). However, such effects might be species- or taxon-specific. For example, a study investigating the effect of reproductive tactics on behavioural syndromes (i.e. personality) in African striped mice (*Rhabdomys pumilio*) found consistent sex-based differences in activity, boldness, exploration and aggression (Yuen et al., 2015). Given that sexual selection in behavioural types is evident across various taxa, captive-based research stands to benefit enormously from exploring the effects of captivity on the strengths and targets of sexual selection, and resultant behavioural differences between the sexes. A small number of behavioural studies on captive populations have examined the effects of captivity and sex on behaviour (*see* Benson-Amram et al., 2013; Herborn et al., 2010; Mathews et al., 2005; Bremner-Harrison et al., 2004). Of these studies, only one examined the interaction between rearing environment and sex on behaviour, therefore more studies are required.

The overall aim of this study was to investigate whether behaviour in captive-reared and wild-caught animals differ using house mice (*Mus musculus*) as a model species. To address this overall aim, we had three specific aims i) to compare behavioural types displayed by captive-reared and wild-caught individuals in a novel environment; ii) to determine whether behavioural types are subject to transgenerational effects in the captive environment; and iii) to examine the behavioural types displayed by each sex. The respective predictions for these aims were i) the captive-reared animals would display differing trait values for boldness and activity behavioural types compared to wild-caught individuals, with; ii) the behavioural type would be subject to transgenerational effects in the captive rearing environment, with captive-reared individuals displaying behavioural types that do not significantly differ from their captive-reared parents, but do significantly differ from wild-caught individuals; and iii) the behavioural types would differ depending on sex. Further, the behavioural type displayed by each sex will be consistent across captive-reared and wild-caught individuals, with captive-reared animals displaying differing trait values for boldness and activity behavioural types regardless of sex.

2. Methods

2.1. Ethical note

This study was conducted under University of Wollongong Animal Ethics Approval AE13/17.

2.2. Study species

The house mouse (*M. musculus*) is a small rodent species widespread throughout the world. The species has a short generation time, has an iteroparous reproductive strategy, displays clear sex roles, polygamous mating strategies and can be easily maintained in captivity. For these reasons, it is being increasingly used