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Correlates of birth origin effects on the development of stereotypic behaviour in striped mice, *Rhabdomys*

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The behaviour and physiology of wild animals born in zoos, laboratories and breeding centres can differ substantially from that of their wild-caught (WC) conspecifics. For instance, captive-born (CB) animals are typically more prone to developing abnormal repetitive behaviours. In captive striped mice, *Rhabdomys*, we first confirmed that birth origin predicted the emergence of stereotypic behaviour (SB), with CB mice being most at risk. Second, to investigate correlates of this birth origin effect, we tested WC and CB striped mice in behavioural tasks to quantify fear/anxiety, activity and perseveration, and measured faecal corticosterone to assess physiological stress. WC mice proved more fearful and less active than CB animals, and had higher levels of faecal corticosterone metabolites. These effects, however, were unrelated to SB. WC mice were also less perseverative and more behaviourally flexible than CB animals, traits that covary with SB. Third, a retrospective analysis of laboratory records showed that SB incidence was significantly lower in adult-caught than juvenile-caught striped mice, with juvenile males being the most severely affected by early removal from the wild. In conclusion, our results indicate that adult, but not juvenile WC striped mice are typically protected against SB development in captivity, despite having poorer welfare than their CB conspecifics. They also reveal profound behavioural changes in CB mice, changes suggestive of altered forebrain function, a hypothesis now needing direct testing.

Wild animals are often bred in research laboratories, zoos and conservation centres. Several recent studies show that captive-born (CB) animals may differ behaviourally and physiologically from their wild counterparts, a potential problem when the aim of captive breeding is to conserve or study wild phenotypes. Some observed differences are unsurprising: CB animals may lack the experience to perform certain natural behaviour patterns competently (e.g. golden-lion tamarins, *Leontopithecus rosalia*: Kleiman et al. 1990; black-footed ferrets, *Mustela nigripes*: Biggins et al. 1999; bank voles, *Clethrionomys glareolus*: Mathews et al. 2005), and they are also typically less scared of humans than captive wild-caught (WC) conspecifics (e.g. black rhinoceros, *Diceros bicornis*: Carlstead et al. 1999; capybaras, *Hydrochoerus hydrochaeris*: Nogueira et al. 2004; starlings, *Sturnis vulgaris*: Feenders & Bateson 2011). Probably as a consequence of their reduced fear, CB animals also generally appear to have better welfare in captivity: for example, compared with WC conspecifics, CB pigtailed macaques, *Macaca nemestrina*, show reduced mortality after a stressor (Ha et al. 2000). Other differences between WC and CB animals, however, are somewhat counterintuitive: compared with captive WC conspecifics, the offspring of CB mongoose lemurs, *Lemur mongoz*, have greater mortality (Perry et al. 1992); female CB white rhinoceroses, *Ceratotherium simum simum*, often fail to conceive (Swaisgood et al. 2006); and zoo-housed CB Asian elephants, *Elephas maximus*, are likely to die prematurely (Clubb et al. 2008). These examples indicate that birth origin can have dramatic effects, both positive and/or negative, on the phenotypes of captive animals.

Birth origin also has a striking influence on the development of highly repetitive stereotypic behaviours (SBs) such as pacing or body rocking. Although SBs afflict at least 10 000 captive zoo animals worldwide (Mason et al. 2007), in eight of the 11 species studied to date they are rare or absent in WC individuals, and more common in conspecifics born in captivity (Mason 2006; Latham & Mason 2008). The hypothesized causes of SBs are two-fold. First, SBs may arise from poor adjustment to impoverished captive conditions, resulting in the sustained elicitation of highly motivated, but ultimately thwarted (i.e. frustrated), natural behaviour patterns (hereafter 'source behaviours'; frustrated motivation

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hypothesis). For example, bar chewing in laboratory mice, *Mus musculus*, derives from repeated attempts to escape (Nevison et al. 1999), whereas stereotypic digging in gerbils, *Meriones unguiculatus*, is triggered by the lack of a species-typical tunnel-shaped entrance to a nesting chamber (Wiedenmayer 1997). Second, SBs can arise secondarily to changes in areas of the forebrain, especially the neural pathways between the cortex and the basal ganglia, responsible for behavioural flexibility and for the inhibition of inappropriate and unsuccessful responses (abnormal behavioural control hypothesis; e.g. Garner 2006; Lewis et al. 2006; Graybiel 2008; Latham & Mason 2010). Thus in a number of species, a relationship has been found between individual levels of SB and increased 'perseveration' ('the continuation or recurrence of an…activity without the appropriate stimulus'; Sandson & Albert 1987, page 1736) and reduced behavioural flexibility (e.g. Garner & Mason 2002). Furthermore, treatments that induce SB (e.g. deprivation rearing or dosing with psychostimulants) correspondingly induce both perseveration and changes to these brain regions (e.g. Robbins et al. 1990; Lewis et al. 2006; Latham & Mason 2008). The likely causes of low/absent SB are therefore low motivational frustration, leading to the lack of repetition of source behaviours, and/or a well-functioning, species-typical forebrain that permits the ready inhibition of inappropriate behaviours. Both of these have been suggested to explain why SB is rarer in complex, naturalistic captive environments than it is in small barren cages (e.g. Latham & Mason 2010). However, a third reason has also been proposed to explain why some animals do not stereotype, even when they are kept in impoverished cages. Within these impoverished, SB-motivating environments, nonstereotypic individuals are generally atypically inactive (Meyer-Holzapfel 1968; Altman 1999), and also often seem to have poorer welfare than their stereotypic cagemates (Mason & Latham 2004). This suggests that in adverse captive conditions, inactivity is an alternative response to SB, perhaps because it represents hiding as a result of fear or excessive resting/sleeping secondary to 'apathy' (defined here as a lack of interest or motivation; Marin 1990).

How birth origin influences the development of SBs is unknown. However, the hypothesized reasons for low SB performance suggest that this birth origin-induced variation is mediated by experience-dependent changes in (1) forebrain structure and function (affecting abilities to inhibit inappropriate behaviours); (2) motivational systems (affecting the degree to which natural behaviours are frustrated and/or animals are fearful or apathetic); and/or (3) the extent of animals' fearfulness or apathy (affecting the level of hiding behaviour and inactivity). This gap in our knowledge reflects the type of previous investigation into CB–WC differences in SB. Previous reports have been either serendipitous findings from studies in which the main focus was not SB, or have comprised findings from the retrospective analysis of multizoo data of animals spread over numerous sites (Mason 2006). As a result, none have allowed investigation into the precursors or correlates of the influence of birth origin on SB in a way that could shed light on underlying mechanisms. In this study, using the striped mouse *Rhabdomys*, we had the unique opportunity to compare WC and CB conspecifics kept as study subjects in the same laboratory. These small, diurnal murid rodents are abundant in many southern African habitats (Skinner & Chimimba 2005); they are not endangered, they offer the typical advantages of a rodent species (e.g. small body size, successful reproduction in captivity and short generation times; Schradin & Pillay 2003) and, because they are diurnal (Schradin 2006), are easy to observe and are not prone to sleep disruption when tested during the day. The striped mouse is a particularly good model for studying birth origin effects on SB as about half of all CB striped mice reared in standard cages develop locomotor SBs (Schwaibold & Pillay 2001; Jones et al. 2008, 2010a, b). This incidence of SB is also similar to that reported in a number of zoo species (e.g. brown bears, *Ursus arctos*, 48%; clouded leopards, *Neofelis nebulosa*, 49%; reviewed in Mason et al. 2007), as is the proportion of time that stereotypic striped mice engage in SBs (about 50% of active time in striped mice [Nel 2003] compared with 48% in lions, *Leo panthera*, and 52% in spectacled bears, *Tremarctos ornatus* [reviewed in Clubb & Mason 2007]). The current study comprised three experiments in which we assessed whether WC striped mice are less stereotypic than CB animals (experiment 1), explored correlates of birth origin and SBs as preliminary investigations into potential mechanisms (experiment 2), and analysed historical data to identify any constraints on the protective effects of being WC (experiment 3).

GENERAL METHODS

All wild striped mice were trapped using PVC live traps (290 × 60 mm and 70 mm high) which were covered with grass for insulation, and set for 4 consecutive days. Traps were baited with half a handful of a mixture of oats, raisins, salt, peanut butter and vegetable oil, and contained water-moistened cotton wool for hydration and dry cotton wool for bedding. Traps were checked both early morning and late afternoon, immediately after the peak activity of *Rhabdomys*, ensuring that caught individuals were unlikely to spend more than 2 h in the traps. No trap deaths were recorded. Following capture, individuals were transferred into holding cages (200 × 150 mm and 150 mm high, containing wood shavings for bedding, a handful of hay for nesting material, and provisioned with mouse cubes and water bottles), and then transported by road to the University of the Witwatersrand. Thereafter, adults were housed individually (except during breeding) as wild grassland striped mice are naturally solitary living (Schradin & Pillay 2005), and the tendency to fight often precludes the caging of same-sex groups after weaning age (M. Jones, personal observations). Striped mice used in these studies were ultimately euthanized using either an overdose of an inhalant anaesthetic (Isoflurane or Halothane) or via carbon dioxide asphyxiation. Approval for all studies was provided by the University of the Witwatersrand's Animal Ethics Screening Committee.

EXPERIMENT 1: WC VERSUS CB MICE

In this first experiment, we compared the incidence of SB in a cohort of WC striped mice to a randomly chosen subsample of their first-generation CB offspring. Because previous work in striped mice has suggested that SB is genetically based, and also may be selected for over generations in captivity (Jones et al. 2010b), we used only F1 CB individuals to maximize the genetic similarity between WC and CB animals (so allowing us to distinguish between environmental and genetic effects). We predicted that WC striped mice would be less likely to develop SBs than their CB offspring.

Methods

Study subjects

WC striped mice (males: $N = 11$; females: $N = 15$; all adults at the time of capture) were trapped in a grassland locality (Honeydew; Gauteng; 27°55′S, 26°4′E) between July 2006 and May 2007 as part of ongoing studies into SB in captive wild animals. The comparison group of CB striped mice was a randomly selected group of the F1 offspring bred from 15 different WC breeding pairs (males: $N = 36$; females: $N = 34$) for use in other behavioural studies.