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Special Issue

Plastic animals in cages: behavioural flexibility and responses to captivity

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Billions of wild and semiwild animals live in captive conditions very different from their ancestral environments. Some of the potential challenges they face here, such as greater human proximity, constrained natural behaviours and altered climates, resemble those occurring during urbanization, translocation and other forms of human-induced rapid environmental change (HIREC) in the wild. These parallels between HIREC and captivity suggest that certain species could be in double jeopardy: struggling in both wild and captive environments. This raises new hypotheses for future research, including one tested in this paper: that a species' presence in captivity predicts its chances of establishment when translocated to novel natural habitats. Furthermore, understanding the mechanisms that predispose captive populations to thrive or fail can yield new insights into how animals respond to HIREC. For example, populations adjusting to captivity demonstrate rapid developmental effects. Within one generation, captive-reared animals may show beneficial phenotypic changes (e.g. smaller stress responses than F0s wild caught as adults), illustrating how adaptive developmental plasticity can help populations succeed. However, captive-reared animals also illustrate the risks of developing in evolutionarily new environments (being prone to reduced behavioural flexibility, and sometimes impaired reproduction), suggesting that disrupted ontogeny is one reason why HIREC can be harmful. Overall, analogies between captivity and HIREC are thus interesting and useful. However, captivity and HIREC do differ in some regards, captivity tending to be safer yet more monotonous; we therefore end by discussing how species-typical risk/protective factors, and the phenotypic changes induced in affected animals, may vary between the two.

Humans are profoundly affecting the natural world. Examples of 'human-induced rapid environmental change' (HIREC: Sih 2011; Sih et al. 2011) include deforestation, urbanization, climate change, introductions of novel predators or parasites, local extinctions of preferred food items and relocations to new sites (also see papers in this special issue by Sih 2013; Sol et al. 2013; Wingfield 2013; Slabbekoorn 2013). In response to such challenges, many populations or species move, decline or even become extinct; others, however, adapt, or even thrive and become invasive (e.g. Fisher & Owens 2004; Jeschke & Strayer 2006; Blackburn et al. 2009; Sih et al. 2011; Tuomainen & Candolin 2011; Van Dyck 2012; Sol et al. 2013): HIREC is reducing the number of species on the planet and modifying the phenotypes of populations that persist. This paper examines similarities between HIREC and the drastic changes to animals' lives caused by placing them in captivity. We argue that capturing and enclosing wild animals, and breeding them there, present them with threats, constraints and opportunities similar to those arising from certain forms of HIREC (particularly urbanization, translocation and ecotourism). Species that prosper in captivity thus may be particularly good at coping with these types of HIREC, and similar traits, including behavioural plasticity, the focus of this special issue, might help predict which animals fare well in both situations. Studying captive wild animals could also be a good way (albeit with caveats) to model and understand individual-level impacts of HIREC and the mechanisms involved when animals either adjust well or fail to cope.

First, we describe the diversity and scale of captive wild animal populations. Second, we compare the challenges and opportunities presented by HIREC and captivity, in three ways: (1) we review the potential parallels between captive life and HIREC; (2) we present evidence, including new analyses of translocation data, that wild species preadapted to thrive in response to HIREC also fare well in captivity; and (3) we discuss potentially important traits, including

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behavioural plasticity. In the paper's third and final section, we examine how F1 captive-bred animals differ from their wild-caught parents, in the context of the rapid phenotypic changes that have been observed in response to HIREC. Phenotypic changes evident within just one captive generation illustrate both adaptive developmental plasticity and disrupted ontogeny that compromises adult phenotypes. These cases thus highlight how developmental plasticity may help species cope with and adapt to HIREC, yet also how developmental vulnerability could cause populations to fail in new environments. However, one adverse developmental effect of captive rearing (reduced behavioural flexibility) flags a potential weakness in the analogy between HIREC and captivity: typically, HIREC does not involve understimulation or reduced opportunities to learn, while both may occur to varying degrees in captivity. In our Discussion, we therefore consider how phenotypic changes induced in affected animals (adaptive or harmful) and species-typical risk or protective factors may differ between captivity and HIREC.

Throughout, some related topics are mentioned only briefly; interested readers are directed to other papers. These topics include the welfare implications of captivity; the role of environmental enrichment and species differences in captive welfare; domestication; the evolution and mechanisms of developmental plasticity; individual differences in behavioural plasticity; plasticity in and HIREC's effects on nonbehavioural traits; the fates of captive-bred animals released into the wild; and HIREC's welfare and ethical implications. Note too that the focus is on vertebrates, primarily mammals and birds, because their responses to captivity have been relatively well documented.

WILD ANIMALS IN CAPTIVITY: DIVERSITY, PROVENANCE AND SCALE

Wild animals, by which we mean nondomesticated animals that come from naturally evolved species or subspecies and have extant free-living conspecifics, are currently kept in a variety of captive situations, from the large, naturalistic enclosures of the best zoos (where they might also be provided with 'enrichments': objects, structures and substrates designed to elicit exploration or enable highly motivated activities from their natural behavioural repertoires; e.g. Mason et al. 2001, 2007), through to densely stocked agricultural operations that greatly restrict natural behaviour. As we discuss below, some of these animals will have been caught directly from the wild ('F0s'); some are the first generation captive-bred offspring of wild-caught parents ('F1s'); and others are the products of multiple generations of captive breeding, perhaps well on their way to domestication (Fig. 1).

Bringing wild animals into captivity was typically a crucial early step in the classic domestication processes started tens of thousands of years ago (e.g. Price 1999; Driscoll et al. 2009), but it is a current practice as well. Zoos and public aquaria are obvious examples, housing over 2.6 million wild animals across about 10 000 species (ISIS 2012), with thousands more living in specialized conservation breeding centres. These figures are dwarfed by other enterprises, however. Hundreds of millions of wild animals are kept by private individuals (e.g. as pets): the number of 'exotic pets' in the U.K. alone is about 42 million (Warwick et al. 2012); while in the U.S., over 155 million fish and 16 million birds (albeit not all wild) are kept in human households, along with 13 million reptiles (Tweti 2008; American Pet Products Association 2011). Furthermore, billions of wild animals are commercially farmed for meat, musk, fur, leather and traditional medicines: turtles (over 3 billion on Chinese farms: CITES 2002); mink (ca. 50 million pelted annually; EFBA 2012); fish, crustaceans and molluscs (cultured in such vast numbers that individuals are not counted but weighed, totalling 56 million live-weight tonnes in 2009; FAO 2012); along with alligators, snakes, elk, foxes, tigers, bears and others (e.g. IUCN 2000). On smaller scales, wild animals are kept for human pleasure by circuses, falconries, entertainment-minded zoos, game bird and 'canned lion' hunting operations, put to work (e.g. Asian elephants, *Elephas maximus*, used for logging: Clubb et al. 2009; Mar et al. 2012; pigtailed macaques, *Macaca nemestrina*, used for coconut-harvesting: Bertrand 1967; see also IUCN 2000), and used in research. Research on wild species primarily involves a few, widely used 'model species' (e.g. *Xenopus* toads; rhesus monkeys, *Macaca mulatta*), but myriad other wild taxa are brought into laboratories as well (e.g. Hubrecht & Kirkwood 2010).

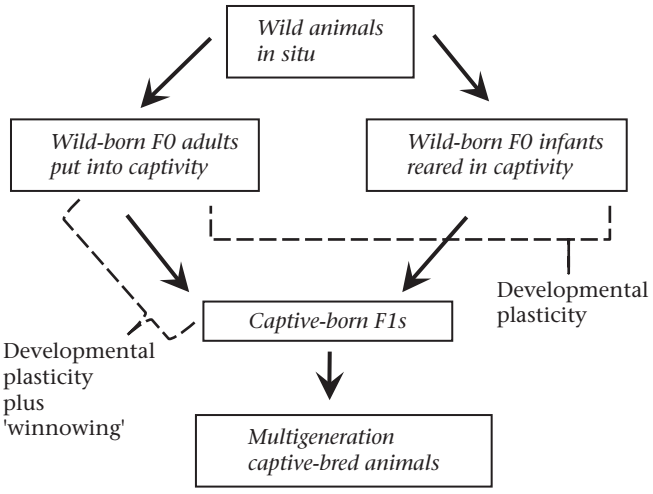

Figure 1. Stages involved as animals are moved from the wild to captivity.

Captive populations are thus vast, and in some instances captive individuals even represent a substantial proportion of a species' global population. This is true, for example, for tigers, *Panthera tigris* (the thousands kept by private individuals in the U.S. alone outnumber those in the wild; Nyhus et al. 2003), chelonians such as golden coin turtles, *Cuora trifasciata* (whose critically endangered wild populations are tiny compared to the vast numbers farmed: CITES 2002; Rhodin et al. 2011), Asian elephants (ca. 16 000 work in Asia, for instance in timber camps and temples, compared with the 40–50 000 living wild; Sukumar 2006), and certain highly threatened species where most individuals live in breeding centres (e.g. Spix's macaws, *Cyanopsitta spixii*, California condors, *Gymnogyps californianus*, and black-footed ferrets, *Mustela nigripes*). Furthermore, captive populations have marked impacts on the free-living or total population sizes of some wild species: positively or negatively, depending on their growth rates and the extent to which positive growth reflects captive breeding versus the harvesting of free-living wild subjects (e.g. Zhou & Jhiang 2004; Sukumar 2006; Haitao et al. 2007; Clubb et al. 2009).

As well as varying in size and purpose, populations of wild animals thus vary in provenance. At one extreme are populations that have been captive bred for tens of generations, such as those farmed for fur or used as standard research models in biomedical science. American mink, *Neovison vison*, for instance, have been farmed for about a century; these animals retain features of their free-living counterparts (e.g. Mason et al. 2001), but their phenotypes have also changed: a case of contemporary domestication (Joergensen 1985). In other cases, the taking of animals from the wild has essentially ceased, but so recently that many extant subjects are F1 or even F0. For instance, zoos were commonly supplied with wild-caught individuals well into the 1960s and 1970s (e.g. Durrell 1971, 1972). A database collated by one of us (J.K.) on zoo Carnivora consequently showed that, of 873 animals of known birth origin that