

Animal cognition in a human-dominated world

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Introduction

In the USA, each year, up to one billion birds are estimated to die from colliding with windowpanes (Sabo et al. 2016). A further 573,000 are struck down by wind turbines, along with 888,000 bats (Smallwood 2013). Worldwide, unintended capture in fishing devices is recognized as the single most serious global threat to migratory, long-lived marine taxa including turtles, birds, mammals and sharks (Wallace et al. 2013). Estimates put the number of amphibians killed per year on Australian roads at 5 million (Seiler 2003). The likelihood of a green turtle erroneously ingesting plastic debris, often by mistaking them for food, rose from 30% in 1985 to almost 50% in 2012 (Schuyler et al. 2013). Human-induced rapid environmental change (HIREC, sensu Sih et al. 2011) is filling animals' environments with new threats which bear little or excessive similarity to those they have encountered in their evolutionary history (Dwernychuk and Boag 1972; Patten and Kelley 2010; Witherington 1997). As a consequence, many of the stimuli involved fall outside the adaptive processing space of animals' evolutionary perceptual, learning, memory and

decision-making systems, making individuals particularly vulnerable to their impact.

On the other hand, human-modified environments offer a myriad novel opportunities. Conversion of natural habitats to cities, the fastest form of planet wide environmental change currently (Angel et al. 2011), provides animals with overabundant year-round food resources, nesting opportunities and, according to some, seasonally dampened, more homogenous, predictable environmental conditions, along with protection from predators (Shochat et al. 2010). Under these conditions, the density of some avian populations has been found to be on average 30% higher in urban than in rural habitats and as much as 100-fold higher for some species (Møller et al. 2012). Large-scale land clearing to increase grazing opportunities for cattle, coupled with installation of permanent water holes, has created ideal ecological conditions for large grazing marsupials, such as the Australian eastern grey kangaroo (*Macropus eugenii*), whose Queensland populations exploded from 11 to 23 mio in just four years prior to the instigation of commercial harvesting in 2004 (Australian Government 2013). These and many other examples (Candolin and Wong 2012; Sol et al. 2013; Tuomainen and Candolin 2011; Wong and Candolin 2015) make it clear that for those animals with cognitive systems capable of handling these novel opportunities, HIREC offers opportunities that are not only extraordinarily abundant, but also fast increasing as a consequence of human population expansion.

There is now a general agreement that rates at which humans are transforming and modifying environments far exceed the rates of any form of historical evolutionary variation (Difffenbaugh and Field 2013; Levy et al. 2013). In many cases, genetic adaptation might be insufficient to allow animals to keep pace. This possibility has propelled phenotypic plasticity into centre stage as a mechanism of

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behavioural change. Hendry et al. (2008) undertook a meta-analysis of over 3000 rates of recent phenotypic change in 68 systems and found that rates of phenotypic change are greater in anthropogenic contexts than in natural contexts. Research to date has focused heavily on phenotypic plasticity in the context of reproduction, including competition and selection of mates, as well communication (for reviews, see Brown 2012; Ketterson et al. 2009; Lowry et al. 2013; Sol et al. 2013; Wong and Candolin 2015).

The cognitive processes that animals deploy to process and respond to their environment provide the central mechanisms underpinning 1. moment-to-moment behavioural responses (e.g. freezing in a response to a threat; exploring a novel opportunity) and 2. experience-dependent behavioural changes, or ‘learning’ (i.e. freezing in response to a previously unfamiliar predator following observation of an attack on a conspecific, avoiding a novel opportunity following an aversive experience) (Shettleworth 2010). Cognitive processes should therefore be an important target of investigation because they determine 1. whether animals are cognitively equipped to respond adaptively to the demands of anthropogenic environments, but also 2. whether animals are cognitively equipped to alter their behaviour within their lifetimes in order to respond *more* adaptively. Other reasons why cognition should be a target of study is that cognitive processes might be impaired by the conditions that prevail in anthropogenic environments (e.g. by pollution), and/or might be under positive or negative selection in anthropogenic environments depending on the ecological characteristics of those environments (e.g. their complexity, their variability) (Dridi and Lehmann 2016; Stephens 1991).

Current trends in scientific activities suggest change is on the way, however. As cognition mutates from a field of study focused on general mechanisms in a handful of model laboratory species to one examining the role of cognition in real-life contexts (Healy and Rowe 2014), cognition is beginning to capture the fascination of biologists, and with it, the desire to study cognition in the real context of fast environmental change. Most telling of this growing trend is the observation that at the 2015 International Ethology Conference (IEC), one of the biggest scientific gatherings of behavioural biologists worldwide, the two largest symposiums were dedicated to *Avian Cognition* (organizers: Healy and Ten Cate) and *Human impact: Behavioural and cognitive responses to human-induced environmental change* (organizers: Arnold, Griffin, Fleming, Bateman, Bugnyar and Saaristo), respectively. The present collection of papers constitutes an important collection of new research findings and ideas within the field of animal cognition and HIREC, many of which were invited as a consequence of the 2015 IEC symposia.

The papers fall broadly into two categories, namely those that consider how cognition, and particularly

learning, can facilitate adaptation to HIREC, and those that explore how cognitive and personality traits can be altered or impaired as a consequence of HIREC. The collection illustrates that many different facets of cognition, including perceptual, learning, memory and decision-making processes (Shettleworth 2010), can be linked to HIREC. Of all behaviours studied in the context of HIREC, animal communication is undoubtedly one of the fields within which cognition has received the most attention (e.g. Gil and Brumm 2014). Here, Potvin’s (2016) contribution illustrates how cognitive processes can be impacted by environmental disturbances, but can also facilitate behavioural adjustments. Anthropogenic noise affects neural and endocrine systems, cognitive processes and signal characteristics in a wide range of taxa (birds, marine mammals, invertebrates and anurans), but learning can mediate increases in signal quality in noisy environments (Potvin 2016). Proppe et al. (2016) provide a very different perspective on the role of cognition in a human-dominated world by reviewing how learning principles can be applied to train animals to avoid stimuli that predict a detrimental outcome or to reduce fear of novel stimuli that could act as movement barriers like roads.

Coping style (Koolhaas et al. 2010) and personality (Réale et al. 2007; Sih et al. 2004) are facets of animal behaviour that are not generally considered cognitive per se, but are thought to influence or be influenced by, cognitive processing mechanisms (Carere and Maestripietri 2013; Griffin et al. 2015; Sih and Del Giudice 2012), justifying the inclusion of this topic in the present special issue. There is mixed evidence as to whether urban areas reliably contain more real and/or perceived threats than natural environments (Gering and Blair 1999; López-Flores et al. 2009; Odewald and Earns 2011). Nevertheless, many (but not all) urban animals show reduced fear responses to threatening stimuli, most notably approaching humans (e.g. Engelhardt and Weladji 2011; Lin et al. 2012; Møller 2008). Here, Ducatez et al. (2016) extend this body of work by undertaking a comparative analysis of several avian species on the Caribbean island of Barbados and showing that urban birds are overall bolder, less responsive to human disturbance and have shorter flight distances than their less urbanized conspecifics. Given the taxonomic prevalence of the capacity to learn in the context of predation (Griffin 2004; Lönnstedt et al. 2012), such differences might be acquired as a consequence of experience (Brown et al. 2013) (but see Carrete and Tella 2011; Sol et al. 2013 for other possible explanations). As suggested in a novel contribution by Bílá et al. (2016) the capacities to learn about novel predators and to respond to the alarm calls of other species through generalization or learning (Shriner 1999) might well assist animals in dealing with novel threats they encounter in urban areas.

The present issue also encompasses several new studies examining the behavioural flexibility, innovativeness and learning abilities of animals that have invaded urban areas successfully. The ability to take advantage of novel opportunities has been an important focus in the invasion biology literature interested in identifying the traits that predict invasiveness (e.g. Sol et al. 2005), but has received surprisingly little attention in the context of invasion of urban habitats. Here, in a rare field study of its kind, Preiszner et al. (2016) demonstrate that female great tits (*Parus major*) from urban populations are faster to solve a novel problem than individuals from rural populations, but this enhanced performance is not associated with higher breeding success. Higher problem solving might enhance survival to adulthood rather than reproductive success in urban areas (Preiszner et al. 2016). Federspiel et al. (2016) test a new prediction based on the hypothesis that some bird species encounter greater levels of food variability in urban than in rural areas. Their finding that urban common mynas (*Acridotheres tristis*) sample cue contingencies for longer than rural birds before learning them calls for further analyses of ecological factors that affect individual-level behaviour in urban areas. Bridging the gap between coping responses and the capacity to exploit novel opportunities, Ducatez et al. (2016) show that boldness is not related to innovativeness in birds from urbanized areas, however. These studies highlight the need for more extensive research to determine the relative balance between the capacity to cope with novel threats and that to exploit novel opportunities in colonization of urbanized environments.

Migratory avian species might be particularly vulnerable to HIREC according to a new contribution by Mettke-Hofmann (2016). Contrasting the high behavioural canalization of some species with the apparent cognitive flexibility of others, Mettke-Hofmann (2016) provides new evidence that migrating species show a low propensity to explore and are avoidant of environmental change, whereas nomadic species are more proactive, less neophobic and more sensitive to environmental cues. Migratory species might hence lack the flexibility to adapt to the increased uncertainty and variability of the environment associated with climate change, whereas cognitive abilities of nomadic and resident species might help buffer them against the negative impacts of environmental change. The impact of HIREC on short- and long-distance navigation is clearly a research area of future growth.

Along with animal communication, chemical pollution and temperature changes are perhaps the fields of research where cognitive processes have received the greatest amount of attention (Zala and Penn 2004). Within these fields, the focus has been on impairment of cognition, however, rather than on cognition as a mediator of

behavioural adjustment. The present special issue contributes four new studies, which advance existing research by considering interactions between cognition and personality. First, Philips et al. (2016) show that dietary lead contamination does not affect learning abilities in the cabbage white butterfly (*Pieris rapae*), but raises activity levels, which could, in turn, reduce energy stores and increase predation. Second, Jacquin et al. (2016) show that Trinidadian guppies (*Poecilia reticulata*) exposed to short- and long-term oil pollution show decreased levels of exploration, but no change in activity or shoaling, suggesting, just like Philips et al. (2016), that information sampling (exploration) and personality might be differentially affected. Illustrating potential effects of climate change on animal cognition, our final two studies are examples of research on the effects of changing temperature in reptiles and amphibians, taxonomic groups that have received only minimal attention in this regard. Whereas Siviter et al. (2016) focus on the effects of incubation temperature on reptile personality, Amiel et al. (2016) suggest that increased incubation temperatures may directly modify brain structures and related learning abilities in scincid lizards (*Bassiana duperreyi*). These studies highlight the need to design long-term studies in which temperature is gradually stepped up across generations in levels that mimic predicted temperature rises. This approach will allow researchers to study how plastic and evolutionary mechanisms will interact to produce behavioural change in response to gradual climate-induced temperature rise.

In future studies of cognition and urbanization in particular, it will be important to distinguish between how cognition can facilitate transition from one environment to another, from how cognition might facilitate long-term persistence and expansion (Evans et al. 2010). Drawing upon concepts familiar to the invasion biologist, the capacity to learn might be important during the early stages of colonization and establishment, but less so during expansion (Sol et al. 2013). Whether or not learning is relevant to the later stages of invasion will depend upon the temporal and spatial variability, complexity and levels of resource competition of urban areas (Dridi and Lehmann 2016; Smolla et al. 2015; Stephens 1991). Unfortunately, we know little about these environmental variables at scales that can be linked to the behaviour of individuals (Shochat et al. 2006). It will also be important to consider whether learning facilitates or inhibits genetic adaptation to changing environments (Brown 2012). While learning might reduce the likelihood of genetic change because it provides a mechanism by which organisms move closer to a novel adaptive peak (Price et al. 2003), behavioural innovations coupled with cultural transmission can accelerate evolutionary change (Nicolakakis et al. 2003; Wyles

et al. 1983). Rapidly changing environments create exciting natural experiments in which such interactions between plastic and evolutionary responses can be examined in real time. But more importantly, such interactions have important implications for management. Will training wildlife to respond to novel threats slow or accelerate evolutionary change (Griffin et al. 2000; O'Donnell et al. 2010; Proppe et al. 2016)? Modelling of scenarios that combine learning and genetic adaptation will be an important tool in future wildlife management research and one in which behavioural biologists versed in cognition need to play a prominent role.

We would like to thank the organizers of *Behaviour 2015* for hosting the Human Impact symposium, as well as all the presenters who helped put together a fascinating series of talks, several of whom have contributed to this special issue. We also thank the many individuals and authors who have further assisted in reviewing the manuscripts. Finally, we are grateful to Ken Cheng and the journal *Animal Cognition* for entrusting us with the responsibility of putting together the first special issue for this journal. We thank the many staff, as well as chief editor, Stephen Lea, for their generous help on many occasions. Basic learning research has shown that animals can flexibly process information depending on many circumstances (Urceley and Miller 2010). Exploring these capacities in more depth, as is the case in fundamental research in animal cognition, will enable us to understand how equipped animals are to deal with HIREC. Hence, we predict a rich future of interaction between fundamental research in cognition and applied HIREC-related research. We hope that the 11 featured articles will provide a catalyst for further advancement in the field of cognition and HIREC in the years to come.

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