The Nature and Nurturing of Animal Minds

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Introduction

This chapter deals with ideas as old as Western philosophy itself. What is the nature of the mind, and how is it shaped? What is humanity's place in nature? In Aristotelian philosophy, nature was conceived as a linear, ladder-like progression of forms, from the lowly to the divine. During the Middle Ages, beautiful tableaus depicted this *scala naturae* as a glorious ladder of life with God and heavenly beings followed in descending order down the rungs by noblemen (not women) and commoners and then in turn by wild animals, domesticated animals, plants and minerals (Figure 1). Under this view, the human mind was uniquely endowed with the capacity for thought; a capacity that separates us from the rest of the animal kingdom and links us to the divine. Whereas animals were mere automata, Descartes (1637/1994) taught that humanity had a dual nature: a material body inhabited by a divine soul (residing in the pineal gland). Through this duality, we alone could reason and think.

Thus, our mental lives – our thoughts, emotions and virtues – were a God-given part of our nature. However, as the enlightenment dawned, a different view began to prevail, in which humans were increasingly seen as agents of their own destiny. In an essay published in 1690, the father of empiricism John Locke argued that the human mind was a blank slate (or *tabula rasa*), whose capacity for reason and knowledge was shaped by experience. Thus, the seeds of the nature-nurture debate were sown, but the debate concerned the human mind alone; the mere notion that other animals might have mental lives would have been laughable to most scholars at the time. Darwin's insights (1859; 1872) fundamentally overturned our conceptions of nature, revealing life not as a ladder, but as a branching tree, its tips inhabited by "endless forms most beautiful", each adapted physically, behaviourally and mentally to the specific challenges of its environment. Thus, by arguing that the intellectual difference between humans and other animals was one of degree and not of kind, Darwin revolutionised our conception of humanity’s place in nature and opened up the possibility of scientific investigation of animal minds.

Despite the triumphs of Darwinism, pre-Darwinian thinking regarding the minds of animals has continued to cloud the perceptions of the public and scientists alike. As recently as 1980, the eminent psychologist Arthur Jensen echoed the *scala naturae* view of life, claiming that intelligence increases progressively across “different levels of the phyletic scale—that is, earthworms, crabs, fishes, turtles, pigeons, rats, and monkeys” (Jensen, 1980, p. 177). While we now may scoff at Jensen’s naïveté, researchers often continue to rank animals’ cognitive performance based on the extent to which they match humans’ achievements. There also remains a residual assumption that animal behaviour is predominantly instinctive, or at most controlled by primitive learning processes, in contrast to the rational decision-making thought to underlie human behaviour. However, the history of the field of comparative cognition reads as a litany of the demise of supposedly uniquely human traits: tool manufacture, teaching, imitation, episodic memory, theory of mind and so on (Goodall 1986; Thornton & McAuliffe 2006; Whiten et al. 1996; Clayton & Dickinson 1998; Krupenye et al. 2016).

In this chapter we will probe the nature of the animal mind. We will begin by considering the evidence that cognition evolves and is shaped by genetic inheritance. We then turn our attention to the ways in which experiences throughout development shape animal minds. Finally, we consider the interplay between nature and nurture. Research in comparative cognition lags far behind other areas of biology in our understanding of gene by environment interactions, but recent developments offer some promise that we may at last begin to move away from asking whether geniuses are born or made.

Cognition Evolves

While psychologists commonly use rather restrictive and anthropocentric definitions of cognition, animal behaviour researchers tend to favour Shettleworth’s (2010) broader conception of cognition as all the neural processes involved in acquiring, processing, storing and using information to guide decisions. At its core, cognition involves neuronal processing to reduce informational uncertainty. This allows individuals to track statistical regularities in the environment and modify their behaviour in response to changing conditions. If the environment were either entirely stable and predictable, or completely unpredictable, there would be no benefit in in tracking environmental information to update one’s behaviour, and reflexive stimulus-response mechanisms would suffice. From this perspective, all animals may be considered cognitive, but natural selection shapes and constrains the manifestation of cognitive traits depending on the environmental problems individuals encounter in the same way as morphological, physiological and behavioural traits. However, in contrast to other biological traits, cognition is unobservable and can only be inferred through observation of behavioural or neural responses in carefully designed experiments. As a result of the difficulties in identifying and quantifying variation in cognitive traits, progress has lagged far behind other areas of biology, and methodological and conceptual debates continue to rage (Penn et al. 2008; Rowe & Healy 2014a; Thornton & Lukas 2012; Thornton et al. 2014).

Adaptive cognitive specialisations

The view of cognitive traits as being subject to natural selection may strike us now as obvious, but not so long ago it would have been seen by many psychologists as heretical. The behaviourist school of thought, exemplified by Skinner and Watson, effectively extended Locke's *tabula rasa* view of human behaviour to all animals. According to the behaviourists, all behaviour could be explained through universal processes of associative learning, whereby any previously neutral stimulus could become associated with positive or negative outcomes. Thus, behaviour was entirely moulded by experience. As a morbid illustration of the point, a hapless 9 month-old infant, Albert, was trained through Pavlovian conditioning to fear fluffy, white objects, a fear which later seemed to generalise to other similar stimuli, including Father Christmas's beard (Harris 1979). This view of universal, limitless learning was turned upside down by John Garcia's discovery that some associations are easier to learn than others. In a series of classic experiments, rats were exposed to ionising radiation to induce nausea after drinking water that was paired with either a novel flavour or an audio-visual stimulus ("tasty" water or "bright noisy water") (Garcia & Koelling 1966). While the rats readily learned to avoid the flavoured, "tasty" water, they did not appear to learn to avoid the "bright noisy" water. This conditioned taste aversion (also known as the "Garcia effect"), provides a beautiful illustration of how selection shapes cognition, favouring learning of biologically relevant information: while flavour is often a reliable cue of the palatability of food, noise and light are not. We now know that such biological constraints of learning are common, serving to limit learning of functionally irrelevant contingencies. A monkey seeing a conspecific appearing to respond in alarm to a snake or a bunch of flowers, for instance, will subsequently learn to fear the former but not the latter (Mineka & Cook 1988).

While some evolutionary influences on learning may be universal (after all, flowers are unlikely to launch a vicious attack on any creature), in many cases cognitive demands will differ depending on the species' ecological niche. Arguably, the most compelling examples of cognitive adaptations occur in food-caching birds, which store food during the autumn for later consumption in the winter. Storing food is of little use if you cannot remember where you stored it, so food-caching species typically have a larger hippocampus (the region of the brain associated with spatial memory) and are able to remember spatial locations for longer than non-cachers (Biegler et al. 2001; Krebs 1990).

Similar species differences in cognitive specialisations may be linked to variation in social ecology. In tests of transitive inference, for example, individuals must infer that if A beats B and B beats C, then A must beat C. Such an ability would be useful in a hierarchically structured society as a means for individuals to gauge their positions relative to other group members without having to fight every individual in the group. Accordingly, within the corvids (birds of the crow family), the highly social pinyon jay (*Gymnorhinus cyanocephalus*) outperforms the less social Western scrub jay (*Aphelocoma californica*) in transitive inference tasks (Bond et al. 2003). Similar cognitive differences related to socio-ecology have now been reported across a range of taxa, including fish, other birds and primates (Bshary et al. 2002; Maclean et al. 2008; Scheid & Bugnyar 2008).

Variation across ecological niches may also drive species differences in the *sources* of information on which animals rely. Animals living in social groups may gather information either through their own interactions with the environment ("personal information") or by observing and interacting with others ("social information"). While personal information is likely to be more accurate, using social information can allow individuals to by-pass the costs of trial and error learning and effectively parasitize information from others, but at the risk that the information may be inaccurate, irrelevant or outdated. Consequently, one would predict that the costs of information-gathering will determine the extent to which individuals rely on personal versus social information (Boyd & Richerson 1985). In accordance with this prediction, three-spined sticklebacks (*Gasterosteus aculeatus*), which are armoured with robust defences, will ignore social information when assessing the relative quality of foraging patches. In contrast, the poorly defended and vulnerable nine-spined stickleback (*Pungitius*

pungitius) prefers to remain under cover, observing the foraging success of conspecifics before choosing a patch (Coolen et al. 2003). Whether this species difference reflects underlying differences in learning mechanisms or simply differential attention to social and non-social stimuli remains unclear (Heyes & Pearce 2015; Webster & Laland 2015). Either way, this example neatly illustrates how varying ecological pressures may drive species differences in information gathering.

Varying ecological pressures also have the potential to generate differences not only between species, but also within species. In an elegant series of experiments, Pravosudov and colleagues showed that in black-capped chickadees, *Poecile atricapilla,* climatic variation across the species' range is associated with cognitive differences between allopatric populations. In one study, chickadees were caught from two different populations: one in the harsh Arctic climate of Alaska, where food availability is limited and unpredictable and the other in the relatively benign environment of Colorado. When tested under identical lab conditions, the Alaskan birds cached more food, were more efficient in retrieving their caches and showed greater accuracy in one-trial spatial learning performance, but did not differ in non-spatial associative learning from their Colorado conspecifics (Pravosudov & Clayton 2002).

This result appears consistent with the suggestion that natural selection acting on heritable genetic variation has shaped spatial cognition in the two populations, allowing birds to survive in harsh Arctic climates by accurately retrieving the food they have cached for the barren winter months. However, as the birds were trapped as adults, it remains possible that population differences could be linked to developmental rather than genetic effects. To address this possibility, a subsequent study reared 10-day old chickadee chicks from the northern and southern extremes of their range (Alaska and Kansas, respectively) in a common garden environment. When subsequently tested as adults, the Alaskan birds outperformed those from Kansas in spatial memory tasks, and had substantially more neurons in the hippocampus (Roth et al. 2012; see Figure 2 a and b). Moreover, later work indicates that the two populations exhibit differential expression of genes, some of which are thought to be associated with hippocampal function (Pravosudov et al. 2013). While these results are consistent with the argument that neural and cognitive differences have evolved in response to local climatic conditions, it is important to note that maternal or other environmental effects prior to 10 days (when the chicks were caught from the wild) cannot be ruled out. It thus remains unclear whether differential gene expression results from genetic or epigenetic differences. Indeed, this work has also highlighted the potential importance of environmental effects, as both captive populations had lower overall hippocampal volumes than their wild counterparts (Roth et al. 2012; Figure 2c). The extent to which genetic and environmental effects interact to influence cognition remains very much an open question, which we shall return to later.

Heritability of cognitive traits

If selection is to act on cognitive traits, they must of course be heritable. A small number of studies have revealed the importance of specific genetic loci (e.g. for associative learning in *Drosophila* (Mery et al. 2007) and in human psychiatric disorders (Skuse et al. 1997)), but it is highly likely that most cognitive traits will be influenced by the expression of multiple different genes (Deary et al. 2009). Thus, research has tended to focus not on the identification of specific loci, but rather on estimating the heritability of cognitive or neuroanatomical traits. To date, the majority of work has focused on humans and other primates, with a small but growing body of evidence showing substantial heritability in general intelligence (positively co-varying performance across batteries of diverse cognitive tests), memory and even educational attainment (reviewed by Croston et al. 2015). In non-primates, a handful of studies provide some evidence for heritability in traits including avoidance conditioning and learning ability as well as avian song traits and their associated neural correlates (Croston et al. 2015). Through these studies, our understanding of how cognitive traits are inherited across generations is beginning to grow. However, it is important to note that as selection does not act on traits in isolation, heritability estimates of single traits may be of limited value. Moreover, the manifestation of an individual’s cognitive performance is likely to be influenced by a multitude of other variables including personality traits and life history strategies (Sih & Del Giudice 2012; Griffin et al. 2015; Thornton & Lukas 2012). Thus, to fully understand how selection acts on cognitive traits, future work must begin to consider the genetic covariance between a host of cognitive, behavioural and life history traits and their associated fitness outcomes (Thornton & Wilson 2015).

In recent years, studies have begun to reveal how artificial selection on heritable cognitive traits may generate associated responses in other traits. *Drosophila* lines selected for increased associative learning ability, for instance, show reduced longevity (Burger et al. 2008) and their larvae show reduced competitive ability (Mery & Kawecki 2003). In female guppies (*Poecilia reticulata*), selection for large brains appears to generate similar trade-offs, resulting in elevated performance in a numerical discrimination test (but see Healy & Rowe 2013), but also in reduced gut size (Kotrschal et al. 2013). A key priority for future research is to determine the heritability of cognitive traits in wild populations, and potential covariance between different traits.

Cognition develops

As we age, we acquire knowledge, skills and habits as a result of our interactions with the environment. But can environmental influences shape not just what we know, but the underlying processes through which we acquire and use our knowledge? A growing body of evidence indicates that cues and stressors in the physical and social environment may have profound influences on the development of cognitive processes. Research has typically focused on developmental influences early in life, as these are thought to have particularly pronounced effects. This is because young, inexperienced individuals are likely to have high levels of uncertainty as to the state of the world (Fawcett & Frankenhuis 2015; English et al. 2016). Nevertheless, it is important to remember that development is a continuous process, and may continue to shape the expression of cognitive traits throughout life. One particularly striking example of this is found in London taxi drivers, whose extensive experience of daily navigation through the city's maze of streets appears to be reflected in a larger posterior hippocampus than control subjects who do not drive taxis (Maguire et al. 2000). Moreover, in contrast to bus drivers, who drive fixed routes, taxi drivers' need to navigate unpredictable routes throughout the city also appears to be reflected in improved spatial cognitive performance such as better landmark recognition (Maguire et al. 2006).

Cognitive consequences of a poor start in life

Environmental conditions may have a variety of developmental effects on cognitive traits, ranging from the pathological to the adaptive. Neural tissue is extremely metabolically expensive to form and maintain (Aiello & Wheeler 1995), so the availability of resources, particularly during early life, may constrain neuroanatomical and cognitive development. Research into the effects of early nutritional stress on cognitive development was largely driven by attempts to understand the adaptive value of song learning in birds (Nowicki et al.

1998). Male song birds learn to sing by copying the songs of adult males in the vicinity, and females prefer males with elaborate songs (Catchpole & Slater 2003). Chicks that experience early nutritional stress cannot afford to invest as much in growing the brain nuclei underlying song learning (primarily the HVC) relative to their better-fed counterparts. Consequently, males that have had a poor start in life become poor singers and suffer reduced reproductive success (Spencer et al. 2005).

Later work has shown that the negative effects of poor developmental conditions are not restricted to song learning, but may influence a range of cognitive traits including spatial memory and associative learning across taxa (Buchanan et al. 2013). For instance, in Western scrub-jays, a food-caching corvid species, experimental food deprivation in early life led to substantially impaired performance in spatial memory tasks relative to control birds. These impairments were reflected in reduced hippocampal volume and neuron numbers (Pravosudov et al. 2005). Cognitive development may be influenced not only by how much you eat, but also by what you eat. Seabirds, for example, thrive on a diet of lipid-rich fish. In a study of red-legged kittiwakes (*Rissa brevirostris*), chicks reared on lipid-poor diets showed important impairments in an associative colour discrimination task, taking substantially longer than control birds to learn that food could be found only in either black or white dishes. This reduced ability to use visual cues to learn about the locations of food has been argued to play an important role in recent, sharp population declines in seabirds as result of human-induced changes in the availability of lipid-rich fish (Kitaysky et al. 2006).

Although nutritional deprivation can have major negative effects on the development of cognitive function, in social species early-life exposure to social interactions may be no less important for later cognitive function. Familiar, but happily rare, examples of “feral” human children, who have managed to survive outside society, highlight the severe linguistic and cognitive impairments that can result from a life devoid of social interaction (Newton 2002). Better studied are tragic cases of large-scale institutional abuse. Children that suffered severe socio-emotional deprivation in Romanian orphanages, for instance, often showed impairments in brain function and socio-cognitive ability (Nelson 2007; Chugani et al. 2001). Similar effects of social deprivation have been reported in other primates and in rodents (Würbel 2001; Winslow et al. 2003). Nevertheless, in many, if not all of these cases, it is difficult to disentangle the specific effects of social deprivation from nutritional effects and other stressors induced by impoverished rearing conditions.

Cognitive silver spoons

Thus far we have painted a gloomy picture of reduced cognitive function resulting from a poor start in life. One flip side of this picture is that benign conditions may induce the so-called "silver-spoon" effect: those individuals lucky enough to be raised in times of plenty may reap cognitive rewards. The majority of research on cognitive silver spoons to date has focused on humans. For example, growing up in bilingual environments has been shown to be associated with a range of positive outcomes, including not only linguistic abilities but also cognitive traits such as enhanced working memory, attentional control and abstract thinking (Adesope et al. 2010). In recent years, whole "brain training" industries have sprung up, claiming to harness the effects of a plethora of interventions including nutritional supplements, yoga, massage and dance to promote infants' cognitive development. While most of these claims lack any clear scientific basis, there is some evidence that musical training in childhood can enhance cognitive function (Moreno et al. 2011; Schlaug et al. 2005).

In non-human animals, research has tended to focus on the negative cognitive effects of deprivation, but there is some evidence for silver spoon effects. For instance, in passerine birds, parents provision their young with large numbers of spiders early in life. Spiders are particularly high in the amino acid taurine, which is thought to be vital for normal brain growth and development in mammals (Aerts & van Assche 2002). In blue tits (*Cyanistes caeruleus*), experimental supplementation of taurine has been shown to be associated with improved ability to learn to remove an obstacle to uncover hidden seed and to subsequently remember the location of the food (Arnold et al. 2007). Similar positive cognitive effects have also been associated with numerous and varied social interactions. In captive rhesus macaques (*Macaca mulatta*), for example, individuals that had been living in larger social groups had increased grey matter and increased neural connectivity in some brain regions than those from small groups (Sallet et al. 2011). Whether these neuroanatomical differences are associated with particular benefits for cognitive function remains to be investigated. However, recent work indicates that early life social conditions can have substantial impacts on cognitive development, with knock-on consequences for reproductive success. In Western Australia, Australian magpies (Cracticus tibicen dorsalis) live in stable groups. Using a battery of cognitive tasks, Ashton et al (2018) showed that individuals that grow up in larger social groups show elevated cognitive performance and females that perform well in tasks have elevated reproductive success. Thus, social factors may influence the development of cognitive abilities, which in turn affect fitness.

Adaptive developmental plasticity in cognition?

An important question that is receiving increasing attention from evolutionary biologists is whether developmental responses to environmental conditions early in life may be adaptive, effectively preparing animals for circumstances they will encounter later. Adaptive developmental plasticity occurs if there has been selection for the expression of a particular phenotype conditional on having experienced particular developmental inputs (Nettle & Bateson 2015). If environments show temporal auto-correlation, such that conditions in early life are likely to be predictive of those encountered later, then cues encountered during early development may help to shape phenotypes so as to maximise later gains (Buchanan et al. 2013; Fawcett et al. 2014; Monaghan 2008). Although such adaptive phenotypic plasticity has attracted a great deal of attention, a recent meta-analysis of examples in plants and animals suggests that the evidence is weak at best (Uller et al. 2013). Nevertheless, there are some tantalising suggestions that the means by which animals gather information may be shaped by early developmental experiences. In particular, evidence for such developmental effects is beginning to accumulate in the field of animal social learning, although in virtually all cases it remains to be established whether this phenotypic plasticity is actually adaptive.

There is extensive evidence that animals across a wide range of taxa are able to learn socially by observing and interacting with others (Hoppitt & Laland 2013). Social learning can provide substantial benefits by allowing individuals to bypass the costs associated with learning through individual experience. However, learning from others is not always beneficial: individuals that copy others blindly are liable to acquire outdated or irrelevant information. Theoretical models show that the solution to this problem is to use "social learning strategies", that is, rules that determine when, how and from whom to learn (Boyd & Richerson 1985; Hoppitt & Laland 2013). Such strategies, have been documented in taxa from insects to birds and humans (Laland 2004; Heyes 2016), and are generally assumed to have evolved through natural selection. The possibility that social learning strategies are moulded by experience has received relatively little attention until recently.

In birds, mothers are able to modify the yolk composition of their eggs. For example, mothers exposed to unpredictable food availability may deposit increased levels of the avian stress hormone corticosterone (CORT) into their eggs (Henriksen et al. 2011). These changes in CORT levels can be mimicked experimentally by injecting the hormone directly into the eggs. Adult Japanese quail (*Coturnix japonica*) that had been exposed to experimentally elevated CORT in the egg were more likely to copy the choices of conspecific demonstrators trained to feed from one of two novel food sources. In contrast, chicks exposed to unpredictable food availability in early life were more inclined to choose the container that demonstrators did not feed from (Boogert et al. 2013). These results suggest that the nature and timing of developmental stressors may influence later information-gathering strategies. They are also consistent with theoretical and empirical evidence that individuals are more likely to use social information when uncertain (Laland 2004; Rafacz & Templeton 2003), as elevated egg CORT levels may be associated with maternal uncertainty about environmental conditions. The chicks exposed to unpredictable food on the other hand may have chosen the unpopular food container so as to avoid food competition. Further work is needed to determine whether these effects necessarily provide fitness benefits.

Similar experiments suggest that early life conditions may modify information-gathering strategies in highly gregarious animals such as colonial song-birds. While unmanipulated juvenile zebra finches (*Taeniopygia guttata*) preferentially copied their parents to solve a novel foraging task, their CORT-fed siblings copied only unrelated adults (Farine et al. 2015). Similar patterns were observed when juvenile males learned their songs, with controls learning from their fathers while CORT-fed birds were less inclined to do so (Boogert et al, unpublished data). Together, these findings raise the possibility that stressed juveniles use the fact that they are stressed as a cue that their parents have made poor choices in life and are therefore not to be copied. However, the alternative explanation, that the parents of stressed chicks are less tolerant (and so more difficult to copy) cannot yet be excluded.

While there is mounting evidence that social learning strategies may be influenced by stress, they may also be shaped through learning from previous experiences: that is, social learning strategies may themselves be learned (Heyes 2016; Mesoudi et al. 2016). Human populations, for instance, show cultural differences in patterns of social learning. In computer-based experiments, people from mainland China showed a higher tendency to copy others than did people from Hong Kong, the UK and Chinese immigrants in the UK. This difference was attributed to cultural differences in social norms between collectivist and individualist societies (Mesoudi et al. 2015). There is also evidence from other species that associative learning processes shaped by past experience may help to determine social learning strategies. In a study of house sparrows (*Passer domesticus*), chicks were assigned to two experimental groups: in one, a parent model (a stuffed female adult conspecific) visited locations containing food while in the other treatment group the model visited unprofitable locations. After five days of training in which they followed the parent model, chicks in the former group were significantly more likely to join others when searching for food as compared to chicks in the unhelpful-mother-model group, suggesting that past experience shapes reliance on social information (Katsnelson et al. 2008). Similarly, in fringe-lipped bats (*Trachops cirrhosis*), a tendency to use the social learning rule "copy others when dissatisfied" can be explained through learned associations from previous interactions with food sources in the presence or absence of conspecifics (see Heyes' (2016) interpretation of experiments by Jones et al. 2013).

The potential for adaptive phenotypic plasticity in response to information acquired during development may also help to explain some of the more puzzling aspects of human and non-human psychology, including the prevalence of patterns of behaviour that appear to violate economically rational expectations (Fawcett et al. 2014). For instance, economically rational decisions ought to be based on accurate estimates of the current value of alternative options, but both human and non-human animals commonly exhibit distinct "optimistic" or "pessimistic" biases, judging outcomes as better or worse than they really are. Recent theoretical work suggests that such cognitive or emotional biases may generate important benefits and have evolved under natural selection (Fawcett et al. 2014; Nettle & Bateson 2012). Animals in poor environments should be risk-averse, seeking to avoid the negative consequences of poor decisions that can edge them closer to death, so they may benefit from "playing it safe" and from interpreting ambiguous stimuli unfavourably. If an animal experiences poor environmental conditions, and environmental quality remains stable over time, this could induce long-term pessimistic biases. For instance, in an elegant experiment, honeybees (*Apis mellifera*) were trained that one odour was associated with sucrose rewards, inducing them to extend their mouthparts, while another was associated with bitter-tasting quinine, inducing them to withhold their mouthparts. Some bees were then shaken vigorously to simulate a vicious attack by a nest-predator. When subsequently presented with novel odours that were intermediate in composition between the previously trained positive and negative stimuli, shaken bees were substantially more likely to withhold their mouthparts compared to the controls (Bateson et al. 2011). These results suggest that negative experiences in bees can induce pessimistic emotion-induced biasing of information processing analogous to that seen in humans. Similar results have been reported in a number of bird and mammal species (reviewed in Bateson 2016). Conversely, several studies have shown that environmental enrichment may be linked to optimistic over-estimates of the outcomes of ambiguous stimuli (Bateson 2016). To date, no study has yet documented the occurrence of such cognitive biases in wild animals, so their potential adaptive value remains to be confirmed.

While it is becoming increasingly clear that cognitive traits are shaped by developmental processes, we still know little about whether this developmental plasticity is necessarily adaptive. Even less is known about the means by which an individual's genetic endowments interact with its developmental experiences to influence the expression of its cognitive traits. We turn our attention to this mysterious issue in the next section.

Cognitive reaction norms: mind-moulding Gene x Environment interactions

Thus far we have presented evidence that cognitive traits are shaped by both genetic inheritance and developmental factors, but how do nature and nurture intertwine? Evolutionary biologists working on other traits, including physiology, morphology and behaviour, are increasingly exploring this issue. For example, phenotypic "reaction norms" are used to depict how the phenotypic consequences of a given genotype are altered by particular environmental conditions (Figure 3c). However, in a recent review, Buchanan et al highlighted the fact that not a single study has yet addressed how such reaction norms may underlie the expression of cognitive traits in non-human animals (Buchanan et al. 2013). To our knowledge, this remains the case today. The core of the problem for researchers is that individual variation in cognitive traits is not directly observable, and thus extremely difficult to quantify. Research in comparative cognition has therefore focussed primarily on detecting the existence of particular cognitive traits in the first place, rather than probing whether and why these traits may vary within species (Thornton & Lukas 2012). Nevertheless, there is a growing consensus that, if we are to understand how cognitive traits evolve, we must move to the individual level of analysis to determine how gene-environment interactions give rise to the phenotypes that are exposed to natural selection (Rowe & Healy 2014b; Thornton et al. 2014; Morand-Ferron, Cole, et al. 2015).

The mystery of (the lack of) cognitive resilience

It is commonly assumed (but seldom tested), that elevated cognitive performance provides fitness benefits. For example, a food-caching bird that can accurately remember the location of its caches ought to be more likely to survive the winter than a more forgetful peer. A major outstanding question, therefore, is why, if cognitive traits are so important, they appear to be so sensitive to developmental stressors. For example, as we considered in the previous section, early-life food deprivation in Western scrub jays resulted in reduced hippocampal volume and spatial memory (Pravosudov et al. 2005). Given this species' reliance on food caching, why has selection not acted to constrain plasticity, thus safeguarding the neuro-cognitive traits that individuals rely upon for survival? A similar argument holds for bird song, which, although a critical component of reproductive success, seems particularly vulnerable to impairments resulting from developmental stressors (Buchanan et al. 2013). One possibility is that these apparent negative effects are artefacts of experimental conditions. First, it is possible that the levels of environmental perturbation imposed in experiments would reduce the probability of survival in the wild to such an extent that the effects on cognition are irrelevant, so selection could not drive cognitive resilience. Alternatively, as there are no studies of the long-term effects of these developmental stressors, it is possible that animals are able to compensate or bounce back under benign conditions later in life.

If it is confirmed that early-life stresses produce long-lasting cognitive impairments in wild animals, one potential explanation might be that cognitive processes must, by their nature, be plastic to cope with varying informational demands. However, this may generate a double-edged sword, as this need for plasticity renders cognition particularly vulnerable to perturbation. In seasonally breeding songbirds, for example, the size of the song control nuclei (HVC and RA) increases during the breeding season and declines afterwards when courtship and territorial song are no longer needed (Catchpole & Slater 2003). Here neuronal plasticity allows individual to invest in song production when required, but this very plasticity may render the song system vulnerable to stresses. To examine the possibility that variation in the benefits of plasticity may generate differences in developmental resilience between species or populations, one valuable approach may be to compare reaction norms in animals that are more or less reliant on a particular cognitive function (e.g. bird species or populations varying in their reliance on cached food in winter). Similarly, it would be interesting to compare reaction norms within populations for traits that differ in their assumed importance for fitness.

Practice makes perfect: genetic quality and cognitive silver spoons

As we have seen, just as poor environmental conditions may impair cognitive development, good conditions may promote cognitive performance. One as yet unexplored possibility is that, under the right conditions, individuals may be able to drive their own cognitive development. Young animals often spend time and energy in behaviour that appears to have no current benefit. Meerkat pups (*Suricata suricatta*), for example, spend a great deal of time digging ineffectually in the sand, but very rarely find prey on their own, and are reliant on adults to feed them (Figure 3a). Pups that are in good body condition tend to spend more time digging and less time begging for food than pups in poor condition (Figure 3b), and show elevated foraging efficiency later in life (Thornton 2008). Given extensive evidence that prior experience in cognitive tasks boosts later cognitive performance (Thornton & Lukas 2012), it is possible that such practice-make-perfect effects could allow individuals to promote their own cognitive development. Indeed, this may help to explain the adaptive function of play, which is observed at higher frequencies in individuals in good condition (Sharpe et al. 2002) and may help to facilitate brain and cognitive development (Ferchmin & Eterovic 1982). Here, the interplay between genetic quality and current condition may be critical. For any given level of environmental quality, individuals of higher genetic quality may be expected to invest more in practising to improve their cognitive performance. For individuals of high genetic quality in benign conditions, this could generate strong positive feedback loops whereby early-life silver spoon conditions are amplified, resulting in particularly ”clever” individuals (Figure 3c).

Cultural and epigenetic inheritance of cognitive traits?

When biologists think of inheritance, they typically think of genetic inheritance. However, there is now abundant evidence that behavioural traits may be inherited culturally, as a result of social learning between generations. Examples of this in nature include song-learning in passerine birds (Fehér et al. 2009; Catchpole & Slater 2003), as well as daily activity budgets in meerkats (Thornton et al. 2010) and food preferences and foraging techniques in a range of vertebrates (Galef & Giraldeau 2001; Thornton & Clutton-Brock 2011; Slagsvold & Wiebe 2007; Aplin et al. 2015; Allen et al. 2013). These behavioural traits are the *products* of cognition (specifically social learning), but it remains to be seen whether cognitive *processes* themselves can be similarly culturally inherited: in other words, might individuals socially learn how to learn and think? There is some evidence to suggest that this may be the case in humans, where, for example, people in regions with a cultural history of collectivism tend to show higher levels of holistic thinking than people from regions with a history of individualism (Talhelm et al. 2014; see also Mesoudi et al. 2016). There is also the potential for cognitive traits to be passed on through the generations through epigenetic inheritance. A recent example is found in Japanese quail, where mothers exposed in the egg to experimentally elevated CORT levels showed changes in stress physiology, neurotransmitter expression and reduced neophobia, facilitating the discovery of food in a novel environment. Remarkably, the same stress-coping physiological, neurological and behavioural phenotypes were observed in the offspring of these mothers, who themselves had not been exposed experimentally to CORT (Zimmer et al. 2017). Some researchers have recently claimed that such examples of non-genetic trait inheritance call for a dramatic extension of the Modern Synthesis in evolutionary biology (Laland et al. 2015). Although many feel that such claims are overblown (see debates in Laland et al. 2014), understanding the interplay between genetic and non-genetic inheritance is a clear priority for future research.

G x E and Methodological Issues in Comparative Cognition

Acknowledging the potential interplay between genetic and environmental factors in shaping cognition has fundamental implications for the way in which cognitive research is conducted and interpreted. In the field of comparative cognition, the results of comparisons between species are typically interpreted as genetically controlled traits shaped by natural selection. These comparisons are then used, either implicitly or explicitly, to rank species according to their supposed similarity to humans. However, such comparisons typically confound genetic differences with developmental effects related to factors such as age, rearing conditions and prior experimental experience. For instance, a large body of research focuses on comparisons between human children and apes, but invariably uses adult apes. This age confound, combined with radical differences in the physical and social rearing conditions of the test subjects, renders any meaningful interpretation of the results very difficult. Moreover, such comparisons tend to ignore the variation that exists within species. For example, enculturated apes that have been raised from a young age in human environments, typically outperform conspecifics across a range of cognitive tasks (Lyn et al. 2010; Thornton & Lukas 2012). These tasks often require apes to interact with, or learn from, human demonstrators. This suggests that performance on these tasks is more reflective of developmental conditions than of genetically endowed adaptive cognitive abilities.

Comparing animals to humans may also carry the assumption that the trait in question is universal and adaptive in humans. For example, mirror self-recognition is used as a test of self-awareness in animals. A small and select number of species are thought to have the "capacity" to recognize themselves in mirrors, but often on the basis of a very small proportion of test subjects actually passing the test (Thornton & Lukas 2012). Exacerbating this issue, the development of mirror self-recognition appears to be far from universal in our own species: while children from Western societies display self-oriented behaviours in front of a mirror from 1.5 to 2 years old, children in a host of non-Western societies do not display these behaviours until much later (Broesch et al. 2011). This raises the question what the underlying trait is that mirror self-recognition tests actually capture. Rather than focussing on crude differences between species irrespective of developmental effects, on the assumption that these species differences have adaptive meaning, a more valuable approach would be to address what drives variation in the developmental trajectory of attentional, learning or reasoning processes that determine performance on the test. Theoretical models are beginning to consider how seemingly complex cognitive traits such as Theory of Mind, which are often assumed to have arisen *de novo* as distinct cognitive modules, may instead be shaped gradually through the co-evolution of information acquisition (e.g. the particular environmental stimuli an animal attends to) and processing (e.g. learning) (Goldstein et al. 2010; Lotem & Halpern 2012; van der Vaart et al. 2012). Comparative empirical studies considering both animals' evolutionary history and developmental influences are now critical to test theoretical predictions.

Conclusion

Perhaps the clearest theme that has emerged throughout this chapter is the current lack of understanding of how nature and nurture combine to shape cognition. Although this may sound rather gloomy, we see it instead as an exciting challenge. The evolution of cognition remains one of the most mysterious aspects of biology. The fact that neuro-cognitive traits are strikingly plastic makes them extremely difficult to quantify, but also extremely interesting. Understanding cognitive reaction norms is not only of fundamental scientific importance, but also of immense potential practical value, with applications ranging from the treatment of human psychiatric disorders to improving the welfare of captive animals. As animals' cognitive responses to stimuli in their environment may have dramatic consequences for individual fitness and population dynamics, understanding these cognitive processes is also critical in a world dominated by human-induced environmental change (Greggor et al. 2014). The tools we need, ranging from advances in molecular genetics and automated behavioural testing to the more humble but no less important workhorses of field biology such as cross-fostering, exist to tackle this challenge head on.

References

Adesope, O.O., Lavin, T., Thompson, T., & Ungerleider, C., 2010. A Systematic Review and Meta-Analysis of the Cognitive Correlates of Bilingualism. *Review of Educational Research*, 80, 207–245.

Aerts, L. & van Assche, F.A., 2002. Taurine and taurine-deficiency in the perinatal period. *Journal of Perinatal Medicine*, 30, 281–286.

Aiello, L.C. & Wheeler, P., 1995. The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology*, 36, 199–221.

Allen, J. et al., 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, 340, 485–488.

Aplin, L.M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C., 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518, 538–541.

Arnold, K.E., Ramsay, S. L., Donaldson, C., & Adam, A., 2007. Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. *Proceedings of the Royal Society B*, 274, 2563–2569.

Ashton, B.J., Ridley, A.R., Edwards, E.K & Thornton, A. (2018) Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature* 554, 364–367

Bateson, M., Desire, S., Gartside, S. E., & Wright, G. A., 2011. Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology*, 21, 1070–1073.

Bateson, M., 2016. Optimistic and pessimistic biases: a primer for behavioural ecologists. *Current Opinion in Behavioral Sciences*, 12, 115–121.

Biegler, R., McGregor, A., Krebs, J. R., & Healy, S. D., 2001. A larger hippocampus is associated with longer-lasting spatial memory. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 6941–6944.

Bond, A.B., Kamil, A.C. & Balda, R.P., 2003. Social complexity and transitive inference in corvids. *Animal Behaviour*, 65, 479–487.

Boogert, N.J., Zimmer, C. & Spencer, K.A., 2013. Pre- and post-natal stress have opposing effects on social information use. *Biology Letters*, 9, 20121088.

Boyd, R. & Richerson, P.J., 1985. *Culture and the evolutionary process*, Chicago: University of Chicago Press.

Broesch, T., Callaghan, T., Henrich, J., Murphy, C., & Rochat, P., 2011. Cultural variations in children's self-recognition. *Journal of Cross-Cultural Psychology*, 42, 1018–1029.

Bshary, R., Wickler, W. & Fricke, H., 2002. Fish cognition: a primate's eye view. *Animal Cognition*, 5, 1–13.

Buchanan, K.L., Grindstaff, J.L. & Pravosudov, V. V, 2013. Condition dependence, developmental plasticity, and cognition: implications for ecology and evolution. *Trends in Ecology & Evolution*, 28, 290–296.

Burger, J.M.S., Kolss, M., Pont, J., & Kawecki, T. J., 2008. Learning ability and longevity: A symmetrical evolutionary trade-off in *Drosophila*. *Evolution*, 62, 1294–1304.

Catchpole, C.K. & Slater, P.J.B., 2003. *Bird song: biological themes and variations*, Cambridge: Cambridge University Press.

Chugani, H.T., Behen, M. E., Muzik, O., Juhász, C., Nagy, F., & Chugani, D. C., 2001. Local brain functional activity following early deprivation: a study of post-institutionalized Romanian orphans. *NeuroImage*, 14, 1290–1301.

Clayton, N.S. & Dickinson, A, 1998. Episodic-like memory during cache recovery by scrub jays. *Nature*, 395, 272–274.

Coolen, I., van Bergen, Y., Day, R. L., & Laland, K. N., 2003. Species difference in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society B*, 270, 2413–2419.

Croston, R. et al., 2015. Heritability and the evolution of cognitive traits. *Behavioral Ecology*, 26, 1447-1459.

Darwin, C., 1859. *On the origin of species by means of natural selection*, London: John Murray.

Darwin, C., 1872. *The expression of the emotions in man and animals*, London: John Murray.

Deary, I.J., Johnson, W. & Houlihan, L.M., 2009. Genetic foundations of human intelligence. *Human genetics*, 126, 215–32.

Descartes, R., 1994. *Discourse on the method* G. (Ed and T. Heffeman, ed., Notre Dame, IN: University of Notre Dame Press (Original work published 1637).

English, S., Fawcett, T. W., Higginson, A. D., Trimmer, P. C., & Uller, T., 2016. Adaptive use of information during growth can explain long-term effects of early life experiences. *American Naturalist*, 187, 620–632.

Farine, D.R., Spencer, K.A. & Boogert, N.J., 2015. Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, 25, 2184–2188.

Fawcett, T.W. et al., 2014. The evolution of decision rules in complex environments. *Trends in Cognitive Sciences*, 18, 153–161.

Fawcett, T.W. & Frankenhuis, W.E., 2015. Adaptive explanations for sensitive windows in development. *Frontiers in Zoology*, 12, S3.

Fehér, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. , 2009. De novo establishment of wild-type song culture in the zebra finch. *Nature*, 459, 564–568.

Ferchmin, P.A. & Eterovic, V.A., 1982. Play stimulated by environmental complexity alters brain and improves learning-abilities in rodents, primates, and possibly humans. *Behavioral and Brain Sciences*, 5, 164.

Firth, J.A., Voelkl, B., Farine, D. R., & Sheldon, B. C., 2015. Experimental evidence that social relationships determine individual foraging behavior. *Current Biology*, 25, 3138–

3143.

Galef, B.G. & Giraldeau, L.A., 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, 61, 3–15.

Garcia, J. & Koelling, R.A., 1966. Relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123–124.

Goldstein, M.H., Waterfall, H. R., Lotem, A., Halpern, J. Y., Schwade, J. A, Onnis, L., & Edelman, S., 2010. General cognitive principles for learning structure in time and space. *Trends in cognitive sciences*, 14, 249–258.

Goodall, J., 1986. *The chimpanzees of Gombe: patterns of behaviour*, Cambridge, MA: Belknap Press.

Greggor, A.L., Clayton, N. S., Phalan, B., & Thornton, A., 2014. Comparative cognition for conservationists. *Trends in Ecology and Evolution*, 29, 489–495.

Griffin, A., Healy, S.D. & Guillette, L.M., 2015. Cognition and personality: An analysis of an emerging field. *Trends in Ecology & Evolution*, 30, 207-214.

Harris, B., 1979. Whatever happened to little Albert? *American Psychologist*, 34, 151–160.

Healy, S.D. & Rowe, C., 2013. Costs and benefits of evolving a larger brain: Doubts over the evidence that large brains lead to better cognition. *Animal Behaviour*, 86, e1–e3.

Henriksen, R., Rettenbacher, S. & Groothuis, T.G.G., 2011. Prenatal stress in birds: Pathways, effects, function and perspectives. *Neuroscience and Biobehavioral Reviews*, 35, 1484–1501.

Heyes, C., 2016. Who Knows? Metacognitive Social Learning Strategies. *Trends in Cognitive Sciences*, 20, 204–213.

Heyes, C. & Pearce, J.M., 2015. Not-so-social learning strategies. *Proceedings of the Royal Society B*, 282, 20141709.

Hoppitt, W. & Laland, K.N., 2013. *Social learning: an introduction to mechanisms, methods and models*, Princeton, NJ: Princeton University Press.

Jensen, A.R., 1980. *Bias in mental testing*, New York, NY: The Free Press.

Jones, P.L., Ryan, M. J., Flores, V., & Page, R. A., 2013. When to approach novel prey cues?

Social learning strategies in frog-eating bats. *Proceedings of the Royal Society B*, 280, 20132330.

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A., 2008. Early experience affects producer-scrounger foraging tendencies in the house sparrow. *Animal Behaviour*, 75, 1465–1472.

Kitaysky, A.S., Kitaiskaia, E. V, Piatt, J. F., & Wingfield, J. C., 2006. A mechanistic link between chick diet and decline in seabirds? *Proceedings of the Royal Society B*, 273, 445–450.

Kotrschal, A. et al., 2013. Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Current Biology*, 23, 168–171.

Krebs, J.R., 1990. Food-storing birds: adaptive specialization in brain and behaviour? *Philosophical transactions of the Royal Society B*, 329, 153–60.

Krupenye, C. et al., 2016. Great apes anticipate that other individuals will act according to false beliefs. *Science*, 354, 110–114.

Laland, K. et al., 2014. Does evolutionary theory need a rethink? *Nature*, 514, 161–164.

Laland, K.N., 2004. Social learning strategies. *Learning & Behavior*, 32, 4–14.

Laland, K.N. et al., 2015. The extended evolutionary synthesis: its structure, assumptions and predictions. *Proc. R. Soc. B*, 282, 20151019.

Locke, J., 1690. *An essay concerning human understanding*, *London:* Bassett.

Lotem, A. & Halpern, J.Y., 2012. Coevolution of learning and data-acquisition mechanisms: a model for cognitive evolution. *Philosophical transactions of the Royal Society B*, 367, 2686–2694.

Lyn, H., Russell, J.L. & Hopkins, W.D., 2010. The impact of environment on the comprehension of declarative communication in apes. *Psychological Science*, 21, 360–365.

Maclean, E.L., Merritt, D.J. & Brannon, E.M., 2008. Social complexity predicts transitive reasoning in prosimian primates. *Animal behaviour*, 76, 479–486.

Maguire, E.A., Woollett, K. & Spiers, H.J., 2006. London taxi drivers and bus drivers: A Structural MRI and neuropsychological analysis. *Hippocampus*, 16, 1091–1101.

Maguire, E. a et al., 2000. Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America*, 97, 4398–403.

Mery, F. et al., 2007. Natural polymorphism affecting learning and memory in Drosophila. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 13051–13055.

Mery, F. & Kawecki, T.J., 2003. A fitness cost of learning ability in Drosophila melanogaster. *Proceedings of the Royal Society B*, 270, 2465–2469.

Mesoudi, A., Chang, L., Murray, K., & Lu, H. J.,, 2015. Higher frequency of social learning in China than in the West shows cultural variation in the dynamics of cultural evolution. *Proceedings of the Royal Society B*, 282, 20142209.

Mesoudi, A. Chang, L., Dall, S. R. X., & Thornton, A., 2016. The evolution of individual and cultural variation in social learning. *Trends in Ecology and Evolution*, 31, 215–225.

Mineka, S. & Cook, M., 1988. Social learning and the acquisition of snake fear in monkeys. In T. R. Zentall & B. G. Galef, eds. *Social learning: psychological and biological perspectives*. Hillsdale, NJ: Erlbaum, 51–73.

Monaghan, P., 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B*, 363, 1635–1645.

Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L., 2015. Taking the operant paradigm into the field: associative learning in wild great tits. *Plos One*, 10, e0133821.

Morand-Ferron, J., Cole, E.F. & Quinn, J.L., 2015. Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological Reviews*, 91, 367–389.

Moreno, S. et al., 2011. Short-term music training enhances verbal intelligence and executive function. *Psychological Science*, 22, 1425–1433.

Nelson, C. A, 2007. A neurobiological perspective on early human deprivation. *Child Development Perspectives*, 1, 13–18.

Nettle, D. & Bateson, M., 2012. The evolutionary origins of mood and its disorders. *Current*

Biology, 22, R712–R721.

Nettle, D. & Bateson, M 2015 Adaptive developmental plasticity: what is it, how can we recognize it and when can it evolve? *Proceedings of the Royal Society B*, 282, 20151005.

Newton, M., 2002. *Savage girls and wild boys: a history of feral children*, London: Faber & Faber.

Nowicki, S., Peters, S. & Podos, J., 1998. Song learning, early nutrition and sexual selection in songbirds. *American Zoologist*, 38, 179–190.

Penn, D.C., Holyoak, K.J. & Povinelli, D.J., 2008. Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, 31, 109-30-178.

Pravosudov, V. V. et al., 2013. Differential hippocampal gene expression is associated with climate-related natural variation in memory and the hippocampus in food-caching chickadees. *Molecular Ecology*, 22, 397–408.

Pravosudov, V. V. & Clayton, N.S., 2002. A test of the adaptive specialization hypothesis: Population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience*, 116, 515–522.

Pravosudov, V. V, Lavenex, P. & Omanska, A., 2005. Nutritional deficits during early development affect hippocampal structure and spatial memory later in life. *Behavioral neuroscience*, 119, 1368–1374.

Rafacz, M. & Templeton, J.J., 2003. Environmental Unpredictability and the Value of Social Information for Foraging Starlings. *Ethology*, 109, 951–960.

Roth, T.C. et al., 2012. Variation in memory and the hippocampus across populations from different climates: a common garden approach. *Proceedings of the Royal Society B*, 279, 402–410.

Rowe, C. & Healy, S.D., 2014a. Measuring cognition will be difficult but worth it: a response to comments on Rowe and Healy. *Behavioral Ecology*, 25, 1298–1298.

Rowe, C. & Healy, S.D., 2014b. Measuring variation in cognition. *Behavioral Ecology*, 25, 1287–1292.

Sallet, J., Mars, M. P., Noonan, J. L., Andersson, J. X., O’Reilly, S., Jbabdi, P.L., Croxson, M., Jenkinson, K. L., Miller & Rushworth, M.F.S. et al., 2011. Social network size affects neural circuits in macaques. *Science*, 334, 697–700.

Scheid, C. & Bugnyar, T., 2008. Short-term observational spatial memory in jackdaws (*Corvus monedula*) and ravens (*Corvus corax*). *Animal Cognition*, 11, 691–698.

Schlaug, G., Norton, A., Overy, K., & Winner, E., 2005. Effects of music training on the child’s brain and cognitive development. *Annals of the New York Academy of Sciences*, 1060, 219–230.

Sharpe, L.L., Clutton-Brock, T., Brotherton, P. N. M., Cameron, E. Z., & Cherry, M. I., 2002. Experimental provisioning increases play in free-ranging meerkats. *Animal Behaviour*, 64, 113–121.

Shettleworth, S.J., 2010. *Cognition, evolution and behaviour, 2nd Edition*, Oxford: Oxford University Press.

Sih, A. & Del Giudice, M., 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B,* 367, 2762–2772.

Skuse, D.H., James, R. S., Bishop, D. V, Coppin, B., Dalton, P., Aamodt-Leeper, G., Bacarese-Hamilton, M., Creswell, C., McGurk, R., Jacobs, P. A., 1997. Evidence from Turner’s syndrome of an imprinted X-linked locus affecting cognitive function. *Nature*, 387, 705–708.

Slagsvold, T. & Wiebe, K.L., 2007. Learning the ecological niche. *Proceedings of the Royal Society B*, 274, 19–23.

Spencer, K.A., Wimpenny, J. H., Buchanan, K. L., Lovell, P. G., Goldsmith, A. R., & Catchpole, C. K., 2005. Developmental stress affects the attractiveness of male song and female choice in the zebra finch (*Taeniopygia guttata*). *Behavioral Ecology and Sociobiology*, 58, 423–428.

Talhelm, T., Zhang, X., Oishi, S., Shimin, C., Duan, D., Lan, X., & Kitayama, S., 2014. Large-scale psychological differences within China explained by rice versus wheat agriculture. *Science*, 344, 603–638.

Thornton, A., 2008. Early body condition, time budgets and the acquisition of foraging skills in meerkats. *Animal Behaviour*, 75, 951–962.

Thornton, A. & Clutton-Brock, T., 2011. Social learning and the development of individual and group behaviour in mammal societies. *Philosophical transactions of the Royal Society B*, 366, 978–987.

Thornton, A., Isden, J. & Madden, J.R., 2014. Toward wild psychometrics: linking individual cognitive differences to fitness. *Behavioral Ecology*, 25, 1299–1301.

Thornton, A. & Lukas, D., 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B*, 367, 2773–2783.

Thornton, A. & McAuliffe, K., 2006. Teaching in wild meerkats. *Science*, 313, 227–229.

Thornton, A., Samson, J. & Clutton-Brock, T., 2010. Multi-generational persistence of traditions in neighbouring meerkat groups. *Proceedings of the Royal Society B*, 277, 3623–3629.

Thornton, A. & Wilson, A.J., 2015. In search of the Darwinian Holy Trinity in cognitive evolution: A comment on Croston et al. *Behavioral Ecology*, 26, 1460–1461.

Uller, T., Nakagawa, S. & English, S., 2013. Weak evidence for anticipatory parental effects in plants and animals. *Journal of Evolutionary Biology*, 26, 2161–2170.

van der Vaart, E., Verbrugge, R. & Hemelrijk, C.K., 2012. Corvid re-caching without “theory of mind”: a model. *PLoS ONE*, 7, e32904.

Webster, M.M. & Laland, K.N., 2015. Public information use by foraging ninespine sticklebacks: Social learning or an unlearned social influence on travel direction? *Behaviour*, 152, 1569–1584.

Whiten, A. et al., 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110, 3–14.

Winslow, J.T., Noble, P. L., Lyons, C. K., Sterk, S. M., & Insel, T. R., 2003. Rearing effects on cerebrospinal fluid oxytocin concentration and social buffering in rhesus monkeys. *Neuropsychopharmacology*, 28, 910–918.

Würbel, H., 2001. Ideal homes? Housing effects on rodent brain and behaviour. *Trends in* *neurosciences*, 24, 207–11.

Zimmer, C., Larriva, M., Boogert, N. J., & Spencer, K. A., 2017. Transgenerational transmission of a stress-coping phenotype programmed by early-life stress in the Japanese quail. *Scientific Reports*, 7, 46125.

Figure legends:

Figure 1. The Great Chain of Being, reproduced from the Retorica Christiana by Didacus Valdes in 1579. Similar conceptions of a ladder-like progression of intellectual abilities continue to dog the study and public perception of animal cognition.

Figure 2. (a) Black-capped chickadees from Alaska (black circles) were faster and more accurate in an associative spatial learning task than conspecifics from Kansas (white circles) raised in the same common-garden environment. The horizontal line indicates the number of attempts to locate the food expected by chance. (b) Alaskan birds had more hippocampal neurons (relative to total number of brain neurons) than those from Kansas, regardless of whether they were raised in a common-garden environment or in their natural environments in the wild. This finding is suggestive of genetically-controlled differences between the populations. However, environmental effects are also important (c) as wild birds from both populations showed greater hippocampal volumes than their counterparts raised in captivity. Figures reproduced with permission from Roth et al. (2012). Photo of black-capped chickadee reproduced under GNU Free Documentation License.

Figure 3. (a) A meerkat pup digging in the sand, and failing to find any food [Photo credit: Alex Thornton]. (b) Meerkat pups in good body condition spend less time begging to adults for food (solid lines) and more time practising foraging (dashed lines) than those in poor condition [Reproduced with permission from Thornton (2008)]. (c) A hypothesised reaction norm illustrating how individuals may drive their own cognitive development. If high-quality individuals in good environmental conditions can afford to invest time and effort in practising for the future, this may boost their future cognitive performance.

Figure 1

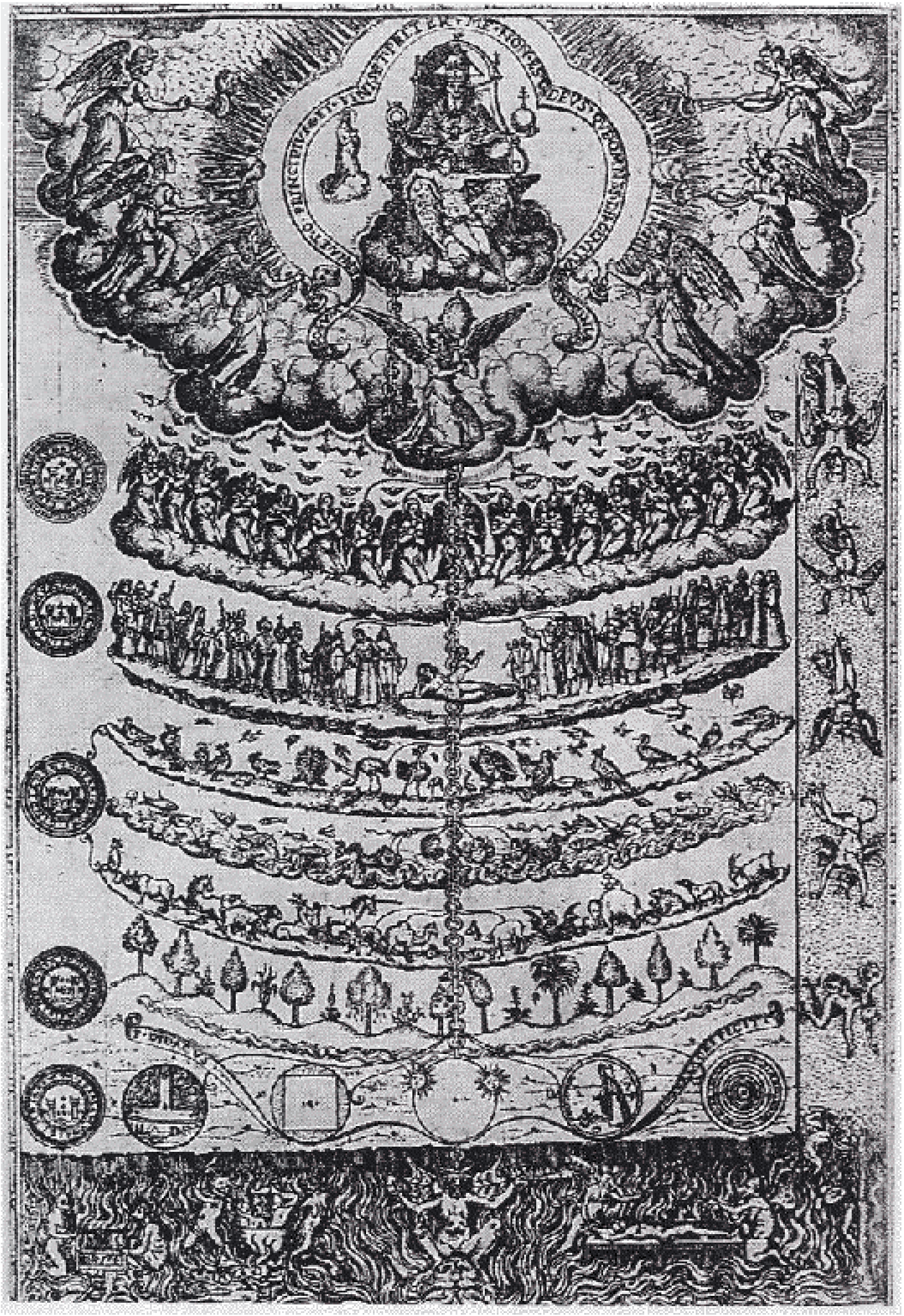

Figure 2

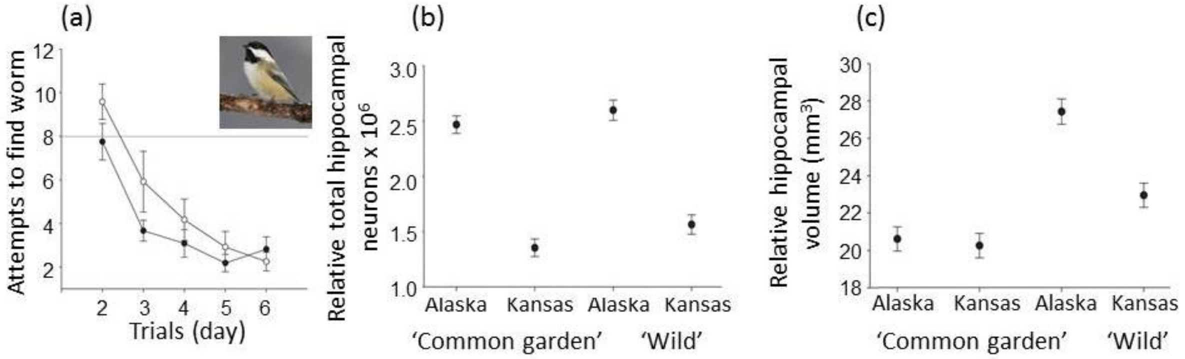

Figure 3