What is innovation? A review of definitions, approaches and key questions in human and nonhuman innovation

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Abstract

Innovation is core to cultural evolution and fundamental to the success of humans. Innovations allow us to adapt to and change habitats, solve novel problems, and survive and flourish in diverse environments. Innovation also appears to be pervasive across the animal kingdom, with adaptive importance within a wide range of species. As a result, the study of innovation has gained significant traction in recent years across diverse disciplines. Here, we discuss how innovation and its subcategories are defined, studied and its importance to both cultural and genetic evolution. We will discuss the difficulty of creating useful, operational definitions that can link disparate fields, and controversies in the study of innovation, such as the independence of innovation from processes such as exploration and creativity. Considering costs and benefits to innovation, we address how individual, social, and ecological influences shape innovative propensities. We finish by discussing how cross-disciplinary research is key to resolving controversies within the field.

Introduction

The global success of humans – as well as our numerous negative impacts on earth – rests substantially on our collective capacity to invent and acquire new skills, technologies, and artefacts. Such innovation allows us to solve novel problems, improve productivity and adapt to new and changing environments and are both diverse in scope and widespread across the animal kingdom. For humans, our vaccines mean global life expectancy continues to rise, our spacecraft have allowed us to reach uncharted territory in our solar system, and our increasingly digitised technology is means providing all children around the world access to high-quality educational resources is a realistic target over the next decade, Impressive examples in other animals include designing and using tools to open nuts or hard-shelled fruits by apes and monkeys, birds developing new migration routes in response to global temperature changes, or male whales increasing the complexity of their songs to attract females. From an evolutionary perspective, innovations are responsible for the remarkable diversity of life past and present, and there is increasing recognition that the propensity of many nonhuman animals to invent or adopt new behaviours within their lifetime can be fundamental to their success and may itself shape the course and tempo of genetic evolution. Thus, understanding innovation is crucial to numerous fields, with wide-ranging applications to human daily life, business, the creative arts, education, as well as to animal biology, welfare, and conservation (see chapters in the Applications section, this volume).

The substantial literature on the evolutionary origins and impacts of novel traits provides rich inspiration for research on behavioural innovation in humans and nonhuman animals (Moczek et al., 2011; Rafiqi et al., 2020; Sturmbauer, 1998; Szathmáry and Smith, 1995; West-Eberhard, 2005, 2003), though the focus of this chapter is non-genetic innovations. Key questions that have been addressed in both the human and nonhuman animal (henceforth 'animal') literatures include the factors that promote or inhibit innovation, innovation's underlying processes, the circumstances under which innovation is beneficial or harmful, and the consequences of innovation for individuals, groups, ecology, and for cultural and genetic evolution. Innovation has been documented in nonhuman animals ranging from bumblebees to whales, and from hyenas to chimpanzees, and across various domains, including foraging, migration, play, communication, and predator avoidance (Bateson, 2014; Caicoya et al., 2023; Gruber et al., 2019, 2015; Rawlings et al., 2014; Teitelbaum et al., 2016; Van Leeuwen et al., 2014). Innovation also holds significant adaptive importance for animals (i.e., organisms are more successful in their environments), allowing, for example, flexible adaptation to new or harsh environments, adjustment to anthropometric interference and more efficient foraging or improved navigational behaviours(Sol et al., 2002; Tebbich et al., 2016; Teitelbaum et al., 2016; see also Gruber, this volume).

Because of the widespread implications of innovation, researchers studying it now span a broad range of disciplines, including psychology, biology, archaeology, anthropology, sociology, industry, and economics, and there have been multiple reviews, theme issues, and books on innovation (e.g., Bandini and Harrison, 2020; Carr et al., 2016; Kaufman and Kaufman, 2015; O'Brien and Shennan, 2010; Perry et al., 2021; Rawlings and Legare, 2021; Rawlings, 2022; Reader et al., 2016a; Reader and Laland, 2003a; Utterback, 1974; Walsh et al., 2019). As a result of this breadth, there is growing debate on how innovation is defined, measured, and assessed across disciplines and animal species. A range of approaches are used including surveys, experiments, examining historical data, and long-term observations, while definitions differ in their diagnostic criteria. This diversity can be problematic, however, since different approaches provide different information and insights but can be difficult to compare directly to one another. How can one define innovation broadly enough to capture such diversity of novel behaviour, while not being so broad to capture a group of products and processes that may have little to do with each other? Relatedly, while some research programs have explicitly compared different animals, or animals and humans, using what is termed comparative approaches (e.g., Chappell et al., 2015; see also Wood et al., this volume), research programs are often field-specific, raising questions of whether insights can be usefully borrowed across fields (Rawlings et al., 2021).

The overarching aim of this chapter is to provide an overview of how innovation is defined and studied within the framework of cultural evolution. While much of this handbook discusses how innovations spread via social learning (see Wild & Hoppitt, this volume) and are altered during cultural evolution (cumulative cultural evolution, see Caldwell, this volume), here we focus specifically on innovation itself. In doing so, we will consider the difficulty of developing operational definitions and approaches that can usefully link disparate fields. We will also discuss controversies in the study of innovation, such as the independence of innovation from closely linked processes such as exploration and creativity. We will also address how individual, social, and environmental influences shape innovative propensities. The chapter concludes by discussing how continuing to foster cross-disciplinary research can assist in resolving controversies within the field.

What is innovation and how is it measured?

Fairly defining innovation is far from simple. Innovation can be judged on multiple characteristics such as relative novelty, potential utility, or whether adopted by others: characteristics that may not covary together and which themselves can be challenging to define and measure. For example, opinions may differ on the utility of an innovation, or its utility may not be clear for many years or may manifest in unexpected domains. That innovation is studied by multiple disciplines and in diverse animal species and populations presents additional theoretical challenges. For instance, diverse phenomena are often grouped under the umbrella term of innovation, leading to an assumption that there are commonalities in its causes or consequences, when it may be more useful to use distinct terms.

There is increasing recognition of concerns regarding how innovation is defined, and whether it is assessed the same way across species and studies (Bandini and Harrison, 2020; Carr et al., 2016; Perry et al., 2021; Reader et al., 2016b; Tebbich et al., 2016). Inconsistent use of definitions, or lack of clarity on how innovation has been assessed, makes it difficult to assess how innovation may differ across species and domains. As such, continued empirical research, which allows researchers to directly measure innovation and related behaviours, as well as the conditions which facilitate their expression, is vital for developing and modifying definitions.

At the broadest level, definitions of innovation can be parsed into product- and process-based definitions. Product-based definitions focus on innovation as a product or outcome, whereas process-based ones emphasise how the process of innovation leads to the occurrence of novel behaviour patterns. In an introduction to innovation in animals, Reader and Laland (2003b, pg 14) proposed two definitions to explicitly reflect this distinction, where an innovation *sensu* product is “a new or modified learned behaviour not previously found in the population”, and “innovation (*sensu* process) results in new or modified learned behaviour and introduces novel behavioural variants into a population’s repertoire”. These separate definitions allow researchers to divide the diagnostic criterion for innovation *sensu* product from how the behaviour itself was generated (i.e., the innovative process). Importantly, also, the specification that innovations are learned behaviours was intended to distinguish innovation from accidental behaviour, exploration, and unlearned (innate) behaviour.

Two related ongoing topics of debate are whether for a behaviour to qualify as an innovation, it should be novel to an individual or a population, and whether social transmission is required (see Bandini & Harrison, 2020). Regarding the former, some researchers classify an innovation as behaviour that is novel to an individual but that may exist in the broader population (Ramsey et al., 2007), whereas others focus on the novelty of the behaviour to the wider population (Reader and Laland, 2003b). Both definitions present different theoretical and methodological challenges and considerations. Measuring individual level innovation is comparatively simpler and is typically achieved by using problem solving paradigms, in which participants are presented with novel tasks to solve. Assays of problem solving - defined as generating solutions to problems in a goal directed manner - have become a key component of comparative research. As one example, the hook task, which requires individuals to fashion a hook shape from provided materials (such as piece of wire) to retrieve a reward, has now been administered to several animal species including great apes (Laumer et al., 2018), parrots (Laumer et al., 2017), crows (Rutz et al., 2016) and to children from multiple international populations (Frick et al., 2017; Gönül et al., 2018; Lew-Levy et al., 2021; Neldner et al., 2017; Nielsen et al., 2014). These studies have shown that most species find these types of problem-solving tasks extremely difficult, except for New Caledonian crows (*Corvus moneduloides*) who are frequent hook makers in the wild (see Wood et. al., this volume). Within and cross-species similarities and differences in performance has facilitated a vibrant body of research into the cognitive and contextual factors underpinning hook making in problem solving contexts (Beck et al., 2016; Laumer et al., 2018; Lew-Levy et al., 2020; Rawlings, 2022).

Given the relative rarity of innovations, particularly in nonhuman animals (van Schaik et al., 2016), measuring innovative propensities through experimentally induced problem-solving challenges circumvents difficulties of documenting naturally occurring innovations. Problem solving has been suggested to share similar cognitive processes to innovation and thus to be a suitable method for studying innovation (Griffin and Guez, 2014). Problem solving tasks also allow comparisons of performance across species, as noted with the hook task and with other similar tasks (Caicoya et al., 2023; Ebel et al., 2019; Jacobson et al., 2023; Mendes et al., 2007; Tennie et al., 2009). There are, however, understandable concerns about the ecological validity of these types of paradigms within and between species (Lew-Levy et al., 2020; Reader et al., 2016b), and some researchers have taken to experimentally reconstructing 'natural' behaviours as problem solving challenges. Examples include nut cracking and algae scooping in chimpanzees (Bandini and Tennie, 2017; Neadle et al., 2020) and breaking down large food pellets in sixbar wrasse, *Thalassoma hardwicke* (Paśko, 2010). Important questions stemming from these types of problem solving paradigms include assessing the extent to which innovative behaviour is repeatable across tasks and domains: are the same individuals more innovative than others on a variety of tests (Johnson-Ulrich et al., 2020; Rawlings et al., 2022)? Likewise, research is needed to document whether predictors of innovation are consistent, both within and between species (Griffin and Guez, 2014; Sims and Reader, 2021).

Conversely, surveys and observations are used to measure innovation at the population level. In humans, researchers analyse innovations - as measured by questionnaires, patents, awards or rates of employment in creative industries - at the level of businesses, cities or countries (Bettencourt et al., 2007; Bettencourt and Lobo, 2016; Broekel et al., 2023; Cirera and Muzi, 2020; Soumitra et al., 2018). Documenting counts of innovations in populations of animals has also been a constructive enterprise (Lefebvre et al., 2004, 1997; Reader et al., 2011; Reader and Laland, 2001; Robbins et al., 2016; van Schaik et al., 2016), allowing comparisons of innovation rates and investigation of social and environmental factors impacting innovation (see below). Population-based approaches also provide a measure of innovation variety within a population, species, or other groups.

However, population-level assays of innovation also present their own difficulties. Deciding what is novel to a population is not straightforward, innovation counts may be skewed by anthropogenic interference, and results can be distorted by population sizes, research effort, or researcher bias - which should be accounted for (for discussions, see Bandini and

Harrison, 2020; Byrne and Bates, 2011; Lefebvre et al., 2004; Morand-Ferron et al., 2015; Reader and MacDonald, 2003; Sol et al., 2002). As such, population and individual approaches may be better suited to different contexts. In animal research, for instance, in wild or semi-wild settings, population approaches may be logistically easier than experiments. Conversely, in captivity, individual approaches are more feasible and experimental manipulations allow fine grained assessment of predictors of innovation.

Several researchers have proposed further delineating innovation into sub-categories, beyond product and process-based ones. Doing so allows a more granular examination of species differences as well as the circumstances and cognitive attributes underpinning different forms of innovation. For example, innovations can arise through chance events, accident or copying errors. These types of innovations have been termed cognitively simple (Whiten and Schaik, 2007), weak (Ramsey et al., 2007), low level (Carr et al., 2016), type II (Burkart et al., 2009) or passive (Rendell et al., 2007), and are argued not to result from requiring a solution to a problem, but due to the specific context facilitating incidental innovations. For some (Burkart et al., 2017, 2009) these types of innovations are also facilitated by social learning (i.e. learning from others; see Wild & Hoppitt, this volume). Innovations that reflect goal-directed, deliberate efforts to solve a problem have been termed cognitively complex, invention, high level, type I, or active. These are suggested to be rarer, to reflect the cognitive capacities of the innovator and are typically problem induced. However, care is needed when determining which category an innovation belongs to. Concluding whether an animal innovation was goal-directed is not simple, and researchers must be able to objectively attribute a given behaviour to sub-categories across animal species (Reader et al., 2016b). One possible alternative approach is to examine the magnitude of innovation, but again broadly-applicable definitions can be difficult to establish (Arbilly and Laland, 2017).

Innovation and related processes

Identifying individual characteristics that shape innovative propensities has gathered significant momentum over recent years. Published reviews have noted that numerous psychological processes and personality traits may be implicated in innovation, including neophilia, neophobia, exploration, stimulus generalisation, motor diversity, inhibitory control, persistence, motivation, risk-taking, individual (asocial) learning, curiosity, insight, creativity, causal reasoning, behavioural and cognitive flexibility, analogical reasoning, divergent thinking, conservatism, functional fixedness and the endowment effect (Audet and Lefebvre, 2017; Carr et al., 2016; Griffin and Guez, 2014; Rawlings and Legare, 2021; Reader et al., 2016b; Reader and Laland, 2003a). A recurring debate revolves around the independence of innovation from such processes: namely, asking whether they are derived processes that underpin innovation, or whether innovation is a by-product of processes that have evolved or developed for other reasons (Griffin and Guez, 2014; Reader, 2015; Reader et al., 2016b). While comparative evidence suggests that innovative propensities evolve together with several cognitive traits (Burkart et al., 2017), the value of distinguishing them is that doing so allows investigation into the psychological underpinnings of innovation within and across species. To illustrate this, we will discuss exploration and other related personality traits, as well as creativity, in more depth.

Exploration refers to any information-gathering activity, and as with some treatments of innovation, has been divided into extrinsic exploration (activity directed toward an overt goal, such as feeding) and intrinsic exploration (activity not motivated by an immediate overt goal; Berlyne, 1960; Archer and Birke, 1983; Reader, 2015). Exploration can thus result in discovery, trial and error learning and innovation (Reader, 2015). Exploration allows individuals to acquire information about the environment and test new ways of doing things, which in turn can foster new knowledge and skills. An individual exploring an object will learn about its affordances and potentially different (and more effective) uses for it. Recent developmental work has shown that young children who explored more of the provided materials when attempting to solve the hook task described above were more likely to succeed than those who were less exploratory (Evans et al., 2021). Although studies of animals show mixed findings regarding the relationship between exploration and innovation, exploration determines the likelihood that animals will approach novel resources and contexts around which an innovations may occur (Griffin and Guez, 2014).

In addition to exploration, investigation of how other personality traits predict innovation has become a particularly active research area - though as with innovation itself, researchers should be mindful of inconsistencies in definitions and measurement of personality traits when drawing comparative conclusions (Carter et al., 2013). In animal research, traits such as boldness, risk-taking, and neophilia are especially strong predictors of innovation across diverse species (Amici et al., 2019; Barrett et al., 2022; Caicoya et al., 2023; Griffin and Guez, 2014; Reader and Laland, 2003a; Wat et al., 2020). It is thought that individuals who are bolder are more likely to take risks and those who have an affinity for novelty are those who are more likely to encounter and interact with novel situations, paving the way for innovation (Amici et al., 2019; Caicoya et al. 2023). In human children and adults, where questionnaires are typically used to measure personality, the trait ‘openness to experience’ is consistently associated with innovation across diverse domains, including self-report measures of innovative skills, problem solving, divergent thinking and innovation measures in business settings (Ali, 2019; Baer and Oldham, 2006; Laursen and Salter, 2006; Rawlings et al., 2017, 2022). Openness to experience encompasses being inquisitive, curious, exploratory, and inventive - characteristics that intuitively map on to innovativeness.

Creativity is often used interchangeably with innovation. Nevertheless, in the human literature there is a key difference which makes the distinction valuable. Typical definitions of creativity are that it is the *generation* of novel and valuable ideas, whereas innovation requires the *implementation* of these ideas (Dahlman et al., 2013; Rawlings et al., 2022; Runco, 1992). Thus, creativity can be considered a precursor to human innovation (Carr et al., 2016; Simonton, 2003). In humans, creativity and innovation are strongly correlated at individual and population levels (Rawlings et al., 2022; Sarooghi et al., 2015). Given the difficulty of measuring animal thoughts, however, making a formal distinction between creativity and innovation is much more challenging in nonhuman research. Definitions of animal creativity are scarce (Griffin and Guez, 2014), and creativity and innovation are often treated as the same construct (Kaufman and Kaufman, 2015, 2014; Kuczaj, 2017), making direct comparisons between animal and human creativity difficult (Shevlin, 2020).

Innovation in groups

A constant among definitions is that innovation (*sensu* process) involves the generation of a novel behaviour, which is not *purely* the result of social learning (Bandini and Harrison, 2020; Carr et al., 2016; Reader and Laland, 2003b). That is, an innovation must involve some form of individual (also termed 'asocial') learning for the producer to generate a new behaviour, rather than simply the adoption of an innovation displayed by another individual. For example, the development of a new tool or navigational route requires the implementation of a new design, application, or the discovery of a new way of getting from A to B. Of increasing interest, however, is the delineation of the role social learning (learning through observation or interaction with others) plays in the process of innovation. Some definitions have treated innovation as a largely asocial process, devoid of the influence of social information (Ramsey et al., 2007). However, recent theoretical and empirical work has argued that innovations are often products of social information, where individuals modify observed behaviours, rather than inventing them ‘from scratch’ *solely* through asocial learning (Carr et al., 2016; Hopper, 2016; Muthukrishna and Henrich, 2016; Rawlings and Legare, 2021; Rawlings et al., 2022). That is, improvements in cultural traits typically stem from tweaks to existing ones, rather than developing completely new behaviours (Miu et al., 2018). Others have argued that rates of individual innovation may be quite high, and thus social learning may facilitate, but not be essential for certain, behaviour patterns (Tennie et al., 2020).

The distinction between asocially- and socially-mediated innovations is important because each may differentially contribute to cultural evolution (Kandler and Laland, 2009). Novel inventions that are transmitted facilitate diversification of cultural technology, whereas cumulative technological progression is contingent upon the modification of current technology (Muthukrishna and Henrich, 2016; see Caldwell, this volume). Recent work with human children has also shown that children engage in innovation by modification of observed behaviour more readily than innovation by invention (Rawlings et al., 2022), the two types of innovation have different developmental trajectories (Carr et al., 2015), and are associated with different personality traits (Rawlings et al., 2022). Conversely, other work has shown that chimpanzees (*Pan troglodytes*) are conservative to established behaviours and find innovation by modification challenging (Davis et al., 2016; Harrison and Whiten, 2018; Manrique and Call, 2011), particularly compared to children (Davis et al., 2022). Whether this phenomenon is widespread in animals remains an open question, however (e.g., Lehner et al., 2011).

Debate also surrounds whether novel behaviours must be socially transmitted to qualify as innovations. Several authors include the transmission of an innovation as a definitional criterion or stipulate that the innovation must become part of a populations' repertoire (Mesoudi, 2009a; Perry et al., 2021; Rawlings and Legare, 2021; Tebbich et al., 2016). The transmission of an innovation is an indicator of its value, and is key to cultural evolution by facilitating the generation of new traditions and the improvement of existing cultural traits (Legare and Nielsen, 2015, see Caldwell, this volume). While social learning is key to maintaining behaviour patterns within populations, innovations introduce new information into a population, which, if subsequently culturally transmitted, leads to cultural change at the population level (Muthukrishna and Henrich, 2016; Rawlings et al., 2021; Caldwell, this volume). Others, however, indicate that the transmission of innovations is not required (Kummer and Goodall, 1985), or that without it, the innovation should be classified as lower level (Carr et al., 2015). One pertinent issue is that the types of problem solving experiments described above, wherein participants are individually tested, do not measure transmission and thus if transmission is required, they can only capture part of the innovation process (Rawlings and Legare, 2021). This has led some researchers to term the creation of novel behaviours that are not transmitted inventions, and ones that are, innovations (McGuigan et al., 2017; Mesoudi, 2009; Perry et al., 2021; Rogers and Adhikarya, 1979).

Theoretical and empirical work also highlights the need to balance innovation and social learning for cumulative cultural evolution (the process in which knowledge and skills improve over time through cycles of innovation and their subsequent transmission). An over focus on innovation can be a non-optimal learning strategy, and can hinder the process of cumulative culture, because improved cultural traits will not spread or will be lost (J. Kendal et al., 2009; R. Kendal et al., 2009; Miu et al., 2018; Toelch et al., 2011). Heyes (1993, 1994) has also suggested that specific mechanisms may act to insulate culturally acquired innovations from change, and that decoupling informational from behavioural transmission may be particularly relevant to explaining human cumulative cultural evolution. Thus, while both innovation and social learning are vital to cultural evolution, other processes may also be important to the process.

Individual differences in sociality and exposure to social cues are also known to impact innovativeness. In adults and children, being central in one's social network (i.e., having many and several close contacts) is linked with innovation, both in industry settings (Baer et al., 2015; Kratzer et al., 2016) and in tool use based puzzlebox solving (Rawlings, 2018). Similar results have been reported with animals, with network centrality predicting problem solving success in three bird (*Paridae*) species (Aplin et al., 2012), 13 ungulate species (Caicoya et al., 2023), and squirrel monkeys, *Saimiri sciureus* (Claidière et al., 2013). This is hypothesised to be because having many connections increases exposure to more diverse information, which individuals can subsequently use to foster innovation (Baer et al., 2015; Franke & Shah, 2003). Similarly, cues providing information on peer performance can increase the tendency to use innovations (Toelch et al., 2011). Alternatively, less integration into social networks may also allow individuals to overcome neophobia when resources are unevenly distributed across groups (Caicoya et al., 2023).

Collective intelligence, resulting from our sophisticated social networks, may also be a driver of humans' unusual innovativeness. Muthukrishna and Henrich (2016) argue that our complex social networks act as shared brainpower, allowing us to produce the ever-increasingly sophisticated innovations that characterise our species. This claim is supported by multiple studies demonstrating demography has a strong influence on innovation (for a review, see Derex and Mesoudi, 2020). Population size and connectedness is positively linked with innovation among business firms (Aktamov and Zhao, 2014), cities (Bettencourt et al., 2007; Broekel et al., 2023) and even oceanic islands (Kline and Boyd, 2010). Greater population size and optimal within-group connectivity levels (some research indicates that too much connectivity can limit discovery of novel solutions; Derex and Boyd, 2016; Lazer and Friedman, 2007), provides more knowledge and skill diversity and prevents deterioration of innovations over time. In the same way, human migration facilitates innovation because individuals bring skills and knowledge from previous populations to new ones (Creanza et al., 2017; see Creanza, this volume).

Costs and benefits of innovation

Innovation can provide considerable benefits for both humans and animals. Humans inhabit all of earth's continents, and since 1900, the global human life expectancy has more than doubled (Roser et al., 2019). The advent and development of biomedicine, formal education, sanitization and food and water treatment has had a marked impact on our longevity. Vaccines alone save an estimated five million lives every year (Vanderslott et al., 2013). The development of elaborate food processing techniques have allowed horticultural societies to consume otherwise-poisonous foods, providing access to new resources (Beck, 1992; Henrich et al., 2010; Wilson & Dufour, 2002). Since the 1950s years, the proportion of children globally attending primary school has risen from around 50% to 92% (Imchen and Ndem, 2020). Likewise, ecology-specific hunting techniques have allowed indigenous populations to survive and flourish across the globe (Henrich, 2015). These accomplishments are a result of our propensity for innovation.

Many animals benefit by adjusting to or creating novelty in their environments, and ecological variability is widely assumed to be a selective force promoting innovation (Gruber et al., 2019; Kalan et al., 2020; see Gruber, this volume). For instance, bird species who are successful invaders of new environments have greater innovation rates in their origin site than unsuccessful species (Sol et al., 2002) and ecological variation is also a driver of chimpanzee behavioural diversity (Kalan et al., 2020). Multiple studies in birds and mammals have examined links within species between individual problem solving performance and various components of adaptive success (or 'fitness'), such as competitive ability, body condition, parental behaviour, mating, survival and offspring number (reviewed and critiqued in Audet, 2020; Boogert et al., 2018; Morand-Ferron et al., 2016, also see Cauchard et al., 2017; Johnson-Ulrich et al., 2019; Preiszner et al., 2015). However, as noted in the aforementioned reviews, some caution is needed in interpreting such results, with the generalizability of problem-solving performance a particular concern.

One specific, and increasingly important, way that innovation confers benefits toi animals is by facilitating adaptation of anthropogenic change (see Gruber, this volume). Human presence introduces novel predators, provides new sources of food, impacts navigation routes and increases noise levels (Barrett et al., 2019), and behavioural flexibility allows animals to circumvent these types of human-induced problems. For instance, whooping cranes (*Grus americana*) altered migration routes to establish new winter breeding grounds in response to increased temperatures and reduced food availability stemming from human presence (Teitelbaum et al., 2016). Indeed, animals spanning birds (Sol et al., 2013), lizards (Putman et al., 2019), mice (Mazza and Guenther, 2021), chimpanzees (Gruber et al., 2019) and numerous other species (for a review, see Barrett et al., 2019 and Gruber, this volume) have been documented to show impressive flexibility to adapt to human induced rapid environmental change. Flexibility is also associated with lower extinction rates in birds (Ducatez et al., 2020). However, note that innovation is not always positively affected by humans - chimpanzee behavioural diversity has been shown to decrease in areas of high human impact (Gruber et al., 2019; Kühl et al., 2019). Human impacts on innovative propensities, for example via impacts on social contacts that influence innovation, may differ between species, a consideration for conservation planning (see Greggor, this volume).

However, innovation is not universally beneficial and deviating from established behaviour may carry risks. Although there is far less research examining the costs of innovation compared to its benefits, a body of research has documented some of its disadvantages. Innovation is a risky strategy when compared to copying what others do (R. Kendal et al., 2009). For example, in business settings, too much focus on innovation brings significant financial risks, and in conditions that favour maintaining the current state of affairs may lead to business failure (Arundel & Huber, 2013; Cole & Matsumiya, 2007; Greve, 2003). In business startups, which are particularly vulnerable to non-survival, innovativeness has been shown to be positively correlated with failure (Hyytinen et al., 2015). In primates, rodents and birds, innovation is associated with increased disease risk, ostensibly because innovation and environmental exploration leads to greater exposure to pathogens (Garamszegi et al., 2007; McCabe et al., 2015; Soler et al., 2012). However, innovative birds also show enhanced immunocompetence, suggesting a trade-off (Audet et al., 2016). Exploration and innovation may also confer costs by increasing risk of exposure to predators, injury or ingestion of poisonous substrates, or by diverting attention from vigilant behaviour, and these costs may be particularly significant in human-impacted environments (Jacquin et al., 2017; R. Kendal et al., 2009; van Schaik et al., 2016). This field and the findings described above are important, and we encourage future research to further determine the costs of innovation and indeed what underpins these costs. Likewise, understanding motivators underpinning exploration versus exploitation strategies, and the costs/benefit trade-offs associated with each, is a vibrant, multi-disciplinary field, including how the environment shapes innovative propensities across species – a topic to which we now turn.

Necessity, opportunity, and spare time hypotheses

Considerations of the costs and benefits of innovation relative to other behaviour have led to various hypothesis about how local ecological and social conditions can influence innovative propensities in animals. Similar considerations have been proposed for humans, with a common question being the circumstances under which constrained resources facilitate or hamper different types of innovation (Acar et al., 2019; Simonton, 2003). Resource availability is known to impact innovation, and several competing theories have been examined. First, the 'necessity' hypothesis advocates that innovation is more likely when resources are scarce, and as such, innovations increase productivity or foraging efficiency (Fox et al., 1999; Laland & Reader 1999). As Rutz and St Clair (2012) emphasise, most relevant here is the profitability of innovation relative to alternative behaviours. Second, the 'opportunity' hypothesis proposes that exposure to certain resources or environmental conditions (e.g., encountering fruits in the presence of tool materials) facilitates innovation (Fox et al., 1999; Koops et al., 2013). Finally, the 'spare time' hypothesis (Kummer and Goodall, 1985) contends that innovation is facilitated by a lack of distractions or environmental stressors, in line with the idea that slack resources such as time or capital can promote human innovation (Troilo et al., 2014).

All three hypotheses have some support, though none has universal support and it has been suggested some may operate together (Grund et al., 2019). In line with the necessity hypothesis, primate innovation has been documented during periods of food shortages or habit degradation (Reader and Laland, 2001), and increased problem solving has been reported in chimpanzees who have travelled further, when presumably energy levels are lower than those who had travelled less (Grund et al., 2019). Juvenile great tits are more innovative in winters when over-winter fledgling-survival was low (Quinn et al., 2016), with similar results found across birds broadly (Sol et al., 2005a) - findings that also highlight some methodological issues with short term studies. Food deprived guppies (*Poecilia reticulata*) are also more likely to solve novel foraging tasks than non-deprived fish (Laland and Reader, 1999). Subordinate or smaller animals, who typically have less access to resources than dominant individuals, have also been shown to be more innovative in chimpanzees (Reader and Laland, 2001), great tits (Cole and Quinn, 2012), meerkats, *Suricata suricatta* (Thornton and Samson, 2012), guppies (Laland and Reader, 1999) and black-capped chickadees, *Poecile atricapillus* (Prasher et al., 2019). However, some research fails to support the necessity hypothesis, suggesting other mechanisms, such as opportunity, may also contribute to innovation (Benson-Amram and Holekamp, 2012; Koops et al., 2013; Sanz and Morgan, 2013). For instance, wild chimpanzees of the Nimba Mountains (Guinea) and Goualougo Triangle (Republic of the Congo) showed no change in tool use foraging during periods of food shortage (Koops et al., 2013; Sanz and Morgan, 2013). Koops et al. (2014) also found that resource availability had no impact on tool use in capuchins, chimpanzees, or orangutans, but that encounter rates with resources did. It is likely that opportunity, shaped by prospects of interacting with appropriate resources in spatiotemporally favourable circumstances, supports innovation in addition to necessity resulting from resource shortage (Grund et al., 2019).

The spare-time hypothesis may apply particularly to captive animals, where a lack of predation threat and food provisioning can allow abundant time for exploration and to develop skills such as tool use (Benson-Amram et al., 2013; Rawlings et al., 2021; van Schaik et al., 2016). This hypothesis is used to explain findings of high innovation rates in young group members, who are thought to have more time and energy to devote to exploration and innovation (Benson-Amram and Holekamp, 2012). However, again, evidence for this hypothesis is mixed, with other studies finding no support (Amici et al., 2020; Kendal et al., 2005).

Innovation and genetic evolution

Comparative studies in birds and primates have investigated the evolution of innovative propensities, finding correlations with brain component volume measures and with other behavioural measures such as rates of tool use and laboratory learning performance (Lefebvre et al., 2004; Reader et al., 2011; Navarrete et al., 2016; Overington et al., 2009). Thus, the propensity to innovate appears to evolve together with a suite of traits. Only one study has examined neuromolecular correlations of innovation with a comparative approach, finding differences in the expression of glutamate receptors between an innovative and a non-innovative finch species (Audet et al., 2018). More work is required to expand and establish the generality of these findings (Audet, 2020).

Innovations have long been proposed to impact genetic evolution (West-Eberhard, 2003; Wyles et al., 1983). Innovations allow for rapid responses to the environment and can accelerate, slow or alter the course of genetic evolution by altering selection on genetic variation (Duckworth, 2008; Huey et al., 2003; Whitehead et al., 2019). Gene-culture coevolution describes how behaviour is a product of both genetic and cultural evolution (see Laland et al., this volume). Perhaps the most prominent example in humans is how the advent and cultural transmission of dairy farming has facilitated a genetic change in dairy-farming populations to produce the enzyme lactase, allowing digestion of milk in adults (Beja-Pereira et al., 2003). Similarly, the invention of various agricultural practices is thought to have selected for genes enhancing metabolism of products such as alcohol and other difficult to digest foods (Laland et al., 2001; Smith, 2007). Beyond agriculture, several populations living in high altitudes (made possible through innovation) such as inhabitants of Tibet or the Andes have evolved respiratory systems adapted for high altitude living (Julian and Moore, 2019). Killer whales (*Orcinus orca*) have been suggested to provide a similar animal example, with dietary traditions linked to genes involved in digestion (Foote et al., 2016; Whitehead et al., 2019). In birds, taxa who are innovative exhibit greater evolutionary diversification than less innovative taxa (Nicolakakis et al., 2003; Sol et al., 2005b), while work in primates finds some support for a similar pattern, but only at older diversification events, perhaps due to increased extinction resistance rather than increased speciation in innovative primate taxa (Creighton et al., 2021).

Concluding remarks and future directions

In this chapter we have argued that innovation holds considerable importance to humans and nonhuman animals alike, but that, owing to its broad interest, discrepancies remain in how it is defined and measured. Differences in definitional opinions include whether innovations require social transmission, the inclusion of social information and whether the behaviour should be novel to the individual or population. Differences in how it is measured include experimentally induced problem-solving tasks, literature or other surveys, long-term observations, or short-term opportunistic observations. Researchers from different disciplines tend to focus on different questions. Psychologists often investigate cognitive and contextual factors predicting innovation, while biologists often emphasize the adaptive function of innovation. Anthropologists have traditionally asked questions of the cultural influences on innovation and researchers from industry focus on organizational level factors facilitating or inhibiting innovation and its implications for business success.

Recent years has seen increasing collaborations which have proven to be extremely fruitful in helping to resolve some of the ongoing debates, which are starting to pose new questions. For example, collaborations between anthropologists and psychologists have seen innovation tasks presented to children from over a dozen populations across the globe (see Rawlings & Legare, 2021). In turn, this has stimulated important questions regarding construct validity of this approach and whether culturally relevant tasks should be developed rather than ones designed and validated in Western populations (Burger et al., 2022; Lew-Levy et al., 2021; Rawlings, 2022; see Stengelin et al., this volume and Mace & Zhang, this volume for further discussion of cross-cultural research). Likewise, industry researchers have investigated how personality impacts workplace innovation, with results overlapping with those stemming from experiments with children (Baer and Oldham, 2006; Rawlings et al., 2022). Mathematical modelers, who have a rich history of innovation research, working alongside biologists have helped simulate the conditions in which innovations are established and maintained in animal populations (Kopps and Sherwin, 2012).

Continued collaborations of this kind are crucial to developing our understanding of the function, development, and processes of innovation, as well as to applying this knowledge.

There is still much to learn about the causes and consequences of innovation, and its ontogeny across different species. Cross-disciplinary research is also critical to resolving controversies. While recent years have undoubtedly seen progress, engaging in discussion with researchers in other fields will continue to help bridge gaps in the terminology, definitions, and methodology used. These steps are fundamental to continuing to move work forward and progress our understanding of innovation.

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