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Innovativeness as an emergent property: a new alignment of comparative and experimental research on animal innovation

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Innovation and creativity are key defining features of human societies. As we face the global challenges of the twenty-first century, they are also facets upon which we must become increasingly reliant. But what makes *Homo sapiens* so innovative and where does our high innovation propensity come from? Comparative research on innovativeness in non-human animals allows us to peer back through evolutionary time and investigate the ecological factors that drove the evolution of innovativeness, whereas experimental research identifies and manipulates underpinning creative processes. In commenting on the present theme issue, I highlight the controversies that have typified this research field and show how a paradigmatic shift in our thinking about innovativeness will contribute to resolving these tensions. In the past decade, innovativeness has been considered by many as a trait, a direct product of cognition, and a direct target of selection. The evidence I review here suggests that innovativeness will be hereon viewed as one component, or even an emergent property of a larger array of traits, which have evolved to deal with environmental variation. I illustrate how research should capitalize on taxonomic diversity to unravel the full range of psychological processes that underpin innovativeness in non-human animals.

1. Introduction

The prime minister of Australia has recently called for more innovation, as have other governments around the planet. Innovation has become the motto of academic institutions worldwide. Central to human societies, innovation is perceived to be the saving grace of the human race as it faces the daunting challenges of climate change, rapidly diminishing planetary resources and exploding human populations [1,2].

Given the technological advances that spring to mind when thinking about innovation in humans, it might come as a surprise to some that there exists a vibrant field of research on innovation in non-human animals. The topic underwent a rapid expansion following the publication of Reader & Laland's [3] edited book *Animal Innovation* in 2003. The present theme issue is a tribute to the work that has been achieved.

What can research in non-human animals tell us about innovation and creativity? Are the mechanisms and drivers of innovation and creativity comparable to those in humans? Some researchers see them as qualitatively different, with human innovations calling on the ability to chain simple ideas into more complex ideas and to shift from convergent to divergent thinking [4,5]. Perhaps humans chain ideas, whereas non-human animals remain, broadly speaking, more limited to chaining motor actions [6]. It would not be the first suggestion that a motor strategy can be co-opted into a cognitive strategy. Hills [7] envisages that the 'molecular machinery' that initially evolved for the control of foraging and goal-directed behaviour was co-opted over evolutionary time to modulate the control of goal-directed cognition. 'What was once foraging in a physical space for tangible resources became, over evolutionary time, foraging in cognitive

space for information related to those resources' [7, p. 4]. In contrast, other researchers note substantial overlap between creative processes in humans and non-human animals and suggest the two fields of research can benefit from cross-pollination of ideas, concepts and methodologies [8].

In effect, research in non-human animals has dealt almost exclusively with innovation, leaving 'creativity' aside for the most part (but see [9,10]). Studying innovation in non-human animals provides many advantages, including the availability of a rich taxonomic diversity against which variation in innovation propensity can be mapped to probe the ecological drivers and evolutionary consequences of innovation. Non-human species also provide experimentally tractable systems in which underpinning creative processes can be manipulated to test their causal relation to innovation.

Two solid research traditions characterized by their distinct methodologies have emerged in the study of animal innovation. I present them briefly here, as an aim of this piece is to illustrate how the findings from these fields have tended to diverge, but also how the contributions to the present theme issue signal an era of new alignment. These methodologies differ first and foremost in the nature of the dependent variable by which innovativeness is operationalized. The first, comparative, methodology was initially applied to birds. It employs a species-level proxy of innovativeness, namely the number of anecdotes of novel feeding behaviours, referred to as *field innovation counts* or, when corrected for research effort and shared phylogeny, *innovation rates* (reviewed by [11]). This measure is obtained from surveying the ornithological literature and counting for each species the number of anecdotal reports of novel and unusual feeding behaviours in the wild [12,13]. The comparative approach was later extended to an analysis of behavioural innovations in primates, drawing upon both wild and captive observations [14–16]. The second methodology employs an individual or, more rarely, a species-level proxy of innovativeness, namely performance on novel problems, from manipulating objects to negotiating mazes to gain access to food or other desirable objects, such as offspring and nest decorations [17–27]. This measure of innovativeness is often referred to as *innovative problem-solving*.

Although these research methodologies differ in the nature of their dependent variable, they are nevertheless comparable in the sense that they most often seek to establish the predictors of their respective measures of innovativeness using multiple regression analyses. The comparative approach gathers values of predictor variables from the literature, whereas the experimental method measures the values of predictor behaviours either within the context of the innovation test, or within an independent experimental context. As such, both approaches remain almost always correlational. **As I discuss later, experiments in which potentially causal ecological (e.g. environmental variability), contextual (e.g. social context) and psychological (e.g. neophilia) variables are manipulated to test their mediating role are scant.** This constitutes a major gap in the existing body of non-human animal innovation research.

The five contributions to this theme issue that focus on non-human animals fall nicely across this two-pronged tradition. Not only does the present set of studies exemplify these distinct approaches, but they also illustrate the breadth of questions that has been addressed since the late 1990s. Each makes a novel and significant additional contribution to our understanding of innovative behaviour in non-human animals. However, the present collection also typifies

the tensions that exist within research on innovation in non-human animals. In my view, these contradictions and controversies are the marker of a healthy and vibrant field of research motivated to push the knowledge boundaries of existing work.

Here, I focus first on one of the most debated issues to date, namely the question of whether innovation is a hallmark of intelligence in non-human animals. I then provide an overview of a few aspects of innovation research captured in the present theme issue, which in my opinion lie at the forefront of investigative efforts. My aim is to show how the field is moving towards a more integrated view of innovativeness, but also to suggest what research needs to be conducted to help achieve this integration progress more efficiently.

2. Proximate mechanisms of innovation

With proximate mechanisms of innovation, I refer to the individual-level psychological processes that underpin novel behaviours. These individual-level processes are distinct from the ecological drivers of innovation. For example, an environment where food is scarce might be an ecological driver of innovation, but greater attentional focus and/or increased motivation could be the psychological process(es) that mediate(s) the environment–innovation link. Broad-scale comparative research reveals associations between ecological variables and the occurrence of innovative behaviour at high taxonomic levels, telling us in which environments behavioural innovations are more common. However, this type of research cannot identify the psychological causes of innovative behaviour at the individual level and, most importantly, determine whether these processes differ across taxa.

(a) Is innovation a measure of intelligence?

The possibility that innovativeness is associated with 'greater' intelligence has been a strong driving theme of research on animal innovation over the last decade [11,14–16,28,29]. The causal involvement of cognition in innovation was initially invoked as an explanation for positive cross-taxon correlations between field-based innovation counts and the relative volume of multisensory integration brain areas in both birds and primates [12,13,16]. Several further sets of correlations with observational and experimental measures of cognition (e.g. learning) acted to consolidate the view that cognition mediated cross-taxon variation in innovative behaviour (reviewed by [11]). As a result, innovation counts have been referred to as 'a field-based quantitative measure of intelligence' [30, p. 143].

Reflecting on the extraordinary innovativeness and seemingly high levels of intelligence of our own species, the idea that intelligence and innovativeness might be linked causally is no doubt an intuitively attractive one. The data on innovation–brain relations have been criticized, however. Indeed, the conclusion relies fully upon the still controversial assumption that neural volumes provide a meaningful measure of information processing capacity ([31], but see [32]). The question of whether absolute brain size or brain size corrected for allometric relations with body size is most suited to measuring brain–performance relationships [32,33] and how to measure brain size reliably [34] are on-going debates in the literature. As outcomes will have fundamental ramifications for a large section of the non-human innovation literature, gathering

empirical evidence to resolve them, as Navarette *et al.* [35] do here, should be a priority research focus.

Permeating rapidly from high levels of analysis (taxon/species) down to individual levels of analysis, the idea that innovative individuals might be 'smarter' than non-innovative individuals is a hypothesis that has had a strong hold in the experimental innovation literature [21,24,35–37]. Cognition encompasses a large collection of abilities [38], each one of which can be thought of in terms of multiple attributes (e.g. how quickly information can be processed (speed), capacity available for storing information (space); [39]). In practice, within the context of animal innovation research, cognition has been experimentally operationalized, but also thereby reduced to one ability, namely associative learning, and almost exclusively to one of its attributes, speed. Most often, individual performance on innovation tasks (typically solving latencies and probabilities) has been correlated with, or modelled as a predictor or outcome of, individual performance on learning tasks (typically acquisition speed or errors) to investigate whether more innovative individuals are also those with a higher learning performance (reviewed by [40]). Positive correlations have been used in the broader literature to argue that individual-level innovativeness is a measure of individual variation in cognition [21,24,35–37].

The first difficulty with much of the existing research investigating whether high-performing learners are also more innovative is that studies rarely ensure that individuals differ consistently in their learning performance. Demonstrating consistent individual differences in a generalized learning ability is challenging because it requires measuring performance across multiple contexts [41]. The second difficulty is that some combinations of tasks and dependent variables do not allow one to distinguish between correlations attributable to innovators learning information more quickly (e.g. reaching a learning criterion faster over and above the number of opportunities they were given to learn; [41]) and correlations attributable to innovators encountering information at faster rates both during learning and during innovation (for example, because their task-directed motivation is higher and they make more non-rewarded physical contacts with both the learning and the innovation tasks; details in [42]). As a consequence, most of the purported reports of innovation–learning correlations at the individual level might well reflect correlations between innovation and personality traits and not between innovation and cognition [41,42]. One notable exception [43] has tested whether innovative problem-solving loads on to the same principal component as multiple measures of classical, operant, discriminative and reversal learning and quantifies the effects of task-directed persistence on problem-solving (pecks at task).

These limitations aside, it is also critically important to bear in mind the limits of inference. Correlational links do not mean that animals are more innovative *because* they are more intelligent. For example, innovative problem-solving in captivity was recently found to predict operant learning performance in the field [44]. This finding suggests that performance on innovative problem-solving tests in captivity provides a measure of individual variation in learning under field conditions [44]. However, the finding cannot be used to determine whether faster learning is a causal mechanism of innovative problem-solving or whether faster learning and innovative problem-solving share a common cause (e.g. motivation to access food). Therefore, the finding should not be used in the future to argue that individual variation

in problem-solving is a measure of cognitive performance or intelligence.

One approach to dealing with the correlational/causal dilemma might be to use experimental approaches [17,19, 20,45–48] in which it is possible to demonstrate involvement of specific cognitive processes in innovation propensity. A small collection of studies have shown that members of the highly innovative corvid family appear to be able to use causal reasoning to transfer knowledge acquired in a training context to a novel context and solve novel problems [20,45]. Unfortunately, when procedures stand up to the joys of developing explanations based on simple psychological processes for seemingly complex behaviour [49], these studies provide no indication as to whether innovations, or what proportion of innovations, in the wild rely on this type of process. In particular, one cannot help but note the discrepancy between the apparent complexity of certain experimental problem-solving tasks, and the apparent simplicity of many reported avian innovations. Even those classified as 'technical innovations', such as removing caps from milk bottles, catching insects on the wing, foraging for prey by artificial light or digging for prey in sand [12,13,50], bring to mind explanations based on exposure to, and motor variation in response to, novel stimuli rather than causal reasoning. It seems counterintuitive that any significant proportion of the now several thousands of reported innovations in birds could rely on causal inference. This is even more so because it is not entirely clear that this ability is present in non-human animals in the first place [49,51].

Perhaps what is needed in the field is to clear up the ambiguity as to what is meant by cognition. Throughout the comparative literature linking innovation to brain size, rarely are specific cognitive processes mentioned (but see [15,52]). However, numerous references to tool use and the problem-solving abilities of large-brained, seemingly intelligent corvids and primates can leave the reader with the impression that what is being discussed implicitly are higher-order inferential processing capacities [11,14,16,28,29,53]. I suggest that moving away from using general statements about cognition and replacing them with references to specific cognitive processes (e.g. associative learning, inhibition, habituation) would benefit the field and help future research identify more accurate predictions and tests [52].

For example, one might envisage that at a sufficiently coarse level of analysis, all novel behaviours involve some degree of generalization from existing knowledge [54]. The more an animal learns and therefore knows, the broader its generalization platform becomes. As a result, greater frequencies of associative learning and all its associated phenomena (e.g. contextual conditioning, second-order conditioning, etc.), greater amounts of stored knowledge, coupled with the resulting greater generalization potential, might be all that is needed to explain a large proportion of innovative behaviours [10]. For example, one could argue that a species that uses tools in the first place also has a greater knowledge base in the physical domain and broader skill set from which to invent new technical innovations through small behavioural variations. Hence, generalization might suffice to explain at least some novel behaviours involving tool use [10].

(b) Is neophilia a cause of innovation?

The motto 'necessity is the mother of innovation' has been another significant driving hypothesis for much of the work

on innovation in non-human animals [55]. According to this view, the innovative phenotype assists in coping with harsh and unpredictable environmental conditions. The hypothesis has received some support in studies comparing species, populations or cohorts tested at different time points that vary in their levels of need [55–57], but mixed support that individuals with the greatest need are the most innovative [40]. For example, manipulating food deprivation elicits a marked increase in the likelihood of innovative problem-solving [58], but classes of individuals assumed to have less access to resources do not always show higher innovativeness [57]. On the other hand, van Schaik *et al.* [59] describe wild orangutans as neophobic, reluctant innovators, but when innovations do arise, they do so accidentally or opportunistically, not by necessity and not by curiosity. The authors go on to suggest that the ‘curious’ innovator is only a recent evolutionary occurrence in the pathway to hominins.

This view contrasts with that of Tebbich *et al.* [60], who suggest that the propensity for exploration without the necessity for extrinsic reward plays a central role in discovering novel environmental opportunities in non-humans and call for more research on the topic. So what is the evidence that curiosity can underpin innovation in non-human animals (reviewed by [40])? Curiosity, the attraction to novelty in the absence of any extrinsic reinforcement, such as food, is typically referred to as neophilia in non-human animals [61]. Day *et al.* [62] found evidence for a positive relation between neophilia and innovativeness in primates, but Kendal *et al.* [63] did not. In passerine birds, measurements of neophilia and its association with innovation are, unfortunately, scarce, because the focus has been on fear of novelty (i.e. neophobia, but see [64]). A comparison of the highly innovative Darwin’s finches indicated that this family was no more neophilic than other Galapagos songbird species [18]. Attraction to novelty is far more commonly studied in psittaciforms (parrots) [65,66]. For example, New Zealand keas (*Nestor notabilis*) and Indonesian Goffin cockatoos (*Cacatua goffini*) show both high curiosity and high innovation propensity [17,66,67]. Corvids, another highly innovative family, are highly neophobic in some areas of their range, but willingly explore novel objects once they have overcome their fear [47,68,69].

These patterns suggest that neophilia has its place in the innovation toolkit of non-human animals, at least for some forms of innovation. Indeed, innovation encompasses two forms of innovations, namely the production of novel behaviours in old contexts and the application of old behaviours to novel contexts. Those innovations involving application of old or new behaviours to new contexts should be influenced by neophilia. For example, catching insects under a street light rather than under moonlight should only depend upon the motivation to approach a novel context (the unnatural light spectrum of a street lamp). By contrast, producing novel behaviours in old contexts might draw more heavily upon the tendency or ability to vary ones motor actions [26,58,70,71], and, as argued by Tebbich *et al.* [60], morphological features that increase the diversity of ways in which an organism can interact with its environment. Some species, such as keas and Goffin cockatoos, equipped with a high level of spontaneous attraction to novelty and multiple, exceedingly manipulative appendages (beak and feet), might excel at both forms of innovation outlined above and emerge as the most frequent innovators. Other species might display a high attraction to novelty but be less manipulative [70], or be highly manipulative, but more guarded in their

approach of novelty (e.g. corvids). Both these groups would emerge as less innovative because they are endowed with only a subset of the innovation toolkit.

Under what environmental conditions should one expect to find heightened neophilia and therefore innovations involving the application of old or new behaviours to new contexts? Neophilia is first and foremost an information-gathering exercise with costs and benefits. Van Schaik *et al.* [59] suggest, as have others, that safe environments allow the evolution of neophilia by reducing its costs. However, neophilia calls upon learning and memory processes [52,72], supported by a neural machinery that is no doubt costly [73]. Therefore, benefits likely outweigh costs only in environments where resources change (and thereby produce novel opportunities) at rates faster than the lifetime of the individual [64,74]. In the light of the discussion above on indirect links between cognition and innovation, it is noteworthy that this evolutionary setting is analogous to that proposed for learning [75].

For those species that live in environments that fluctuate at slower rates, for example across generations but less so within generations, one would expect neophilia (and therefore innovations requiring approach of novel contexts) to show the same sensitive period as some learning phenomena (e.g. song learning). Neophilia should be high in juveniles and show a declining trajectory with age as the environment becomes more familiar and behavioural repertoires (e.g. diet) become established. This is exactly the trend seen in the human personality analogue of neophilia, openness to experience, which increases from early adolescence until some time in the 20s, and then gradually declines [76]. One would also expect maternal influences and early ontogenetic social and individual experience to contribute to setting baseline response levels and speeds of habituation to novelty. Such developmental programming of novelty responses could explain why van Schaik *et al.*’s [59] captive orangutans and many other captive primates and birds are so much more neophilic and innovative than their wild counterparts (for a review, see [77]). In other words, neophilia-driven innovation propensity is itself a plastic strategy. The theory of neoteny (the retention by adults of traits previously seen only in the young) would offer us an evolutionary mechanism for adult neophilia to evolve from an ancestor with juvenile neophilia in conditions where an organism finds itself faced with increasing rates of environmental variability and therefore an increasingly lifelong need to approach novelty.

Different forms of innovation (novel context versus novel behavioural sequence) and potential developmental changes in neophilia interact to potentially mask relations between neophilia and innovation. For example, if neophilia declines with age, young individuals might display more innovations in novel contexts and adults more innovations involving novel behavioural sequences in familiar contexts [26,27]. Without distinguishing between different forms of innovations, analyses might reveal no evidence of a relation between neophilia and innovation, because low neophilia adults are just as innovative overall as high neophilia juveniles.

(c) Future research directions into proximate mechanisms of innovation

(i) Move towards establishing the role of psychological processes I concur wholeheartedly with Quinn *et al.* [57]. If we are serious about establishing individual-level causal

mechanisms of innovation, then research methods need to transition from correlational approaches towards more incisive experimental paradigms. In species where individuals are well accustomed to humans, some experiments might be feasible in the wild.

Social psychologists have a long and strong tradition of measuring and manipulating process variables to establish causal chains and make sense of divergent findings [78]. We can learn from them. For example, correlational research might establish that individuals who approach novelty produce innovations involving *old* behaviours applied to novel contexts more frequently. To establish that neophilia mediates innovation, the next step would involve manipulating neophilia and showing that changes in neophilia are associated with changes in innovativeness. This might be achieved by allowing an experimental group of animals to obtain food repeatedly in novel environments but not familiar environments (i.e. novelty is learnt as a signal for food in a rule-based learning task) and showing that this manipulation increases approach of novel contexts and novel-context innovations.

For innovations involving performance of a *new* behaviour in a novel context, the relation between neophilia and innovation might be indirect via an intervening variable. One possibility is that more neophilic individuals might be more variable in their foraging actions. For example, neophilic individuals might vary their solving action spontaneously over the course of repeat testing on a given innovation task. This would be apparent if individuals were tested on an innovative problem-solving task that can be solved in a variety of ways. They might be more inclined to express different solving techniques even if they already know one way to solve it [47]. Although such variability might be interpreted as a failure to learn, avoiding a behaviour becoming rapidly fixed might provide benefits in terms of setting the stage for future innovations [79]. Such spontaneous exploration of alternative task contingencies has been reported in keas [17], Goffin cockatoos [66] and in New Caledonian crows (the famous Betty solved a rake-box task correctly prior to failing it systematically) and has been proposed to reflect systematic exploration of causal relations [80]. This might be true and certainly merits further investigation, but it is also possible that such spontaneous variation (with or without exploration of causal relations) occurs in other innovative species too. There is emerging evidence that some species show consistent individual differences in variability in other behavioural traits, such as activity [81], and that response variability can be learnt [82–84], suggesting that the raw material for the evolution of enhanced motor variability and its genetic assimilation exists.

If neophilia, motor variability and innovation form a causal chain, then increasing neophilia should increase motor variability, which in turn should increase the occurrence of novel behaviours in new contexts. But manipulating intervening variables experimentally is not the only means to explore causal chains. Statistical methods such as mediational analyses and structural equation modelling are commonly used in human psychology research but much more rarely in the animal innovation literature [85]. Pharmacological interventions might also be possible. Identifying causal variables informs future efforts to identify neural and hormonal mechanisms and locate candidate genes. If in contrast, future experimental research reveals inconsistent relationships between neophilia and innovativeness, then this is indicative of moderation of the neophilia–innovation relationship by a

(several) third variable(s). Age, sex, social context and innovation context (old/new) are potential moderator candidates. Much research has investigated the direct effects of these traits on innovation, but not whether they moderate the neophilia–innovation relation. Identifying moderator variables is particularly informative about variation in empirical findings across different circumstances.

(ii) Obtaining multiple measures and assessing individual consistency in innovativeness

It is well accepted that no one test (e.g. classical conditioning) can provide a reliable measure of interindividual variation in general intelligence ('g') [86]. In the same way, can we expect that one experimental measure of innovation can provide a meaningful measure of individual variation in innovativeness? Quinn *et al.*'s [57] contribution to this themed issue makes clear that innovative problem-solving is affected by a large number of environmental influences. As pointed out by the authors, task- and situation-specific factors likely also come into play. Some sources of variation can be accounted for by incorporating measures of motivation (e.g. persistence [21,25,40,58,87]), but others are likely to be more difficult to quantify (e.g. whether the required solving technique is a common or rare motor action in the individual's foraging repertoire).

For these reasons, transitioning towards a more holistic appraisal of what it means to be an innovative individual might be a fruitful research avenue, particularly if innovativeness is an emergent property as proposed by Sol *et al.* [88] (see below). Innovation propensity could be measured across a variety of contexts (e.g. with versus without food rewards; alone versus in groups; novel food versus novel foraging technique; novel foraging versus novel nesting technique). Cross-task consistency in performance might be due to inherent attributes of the individual but might also arise from learning [27]. Therefore, innovation tests should take care to employ a variety of quite different tasks (e.g. requiring different foraging techniques). Different facets of innovation could also be measured, including neophilia, motor diversity and more generally, intraindividual behavioural variability. Data reduction methods could then be employed to produce a composite score of innovativeness, as is commonly done for individual differences in cognition [43,86]. Several studies to date have assessed correlations across more than one innovation task and this is a step in the right direction [36,70,87,89,90].

3. Innovation and the flexible stem hypothesis

Lefebvre *et al.* [91] provide the first test of the flexible stem hypothesis, which postulates that phenotypic plasticity is an ancient feature of some phylogenetic lineages [92]. The authors present an analysis of a new avian innovation dataset from the Neotropical region. The dataset includes the superfamily Emberizoidea, to which the highly innovative Darwin's finches belong. Under the flexible stem hypothesis, the frequencies of innovations should be high in the nested clades leading to the Darwin's finches. Analyses on innovation counts provide initial support for the hypothesis, but once innovation frequencies are corrected for phylogeny and research effort, the authors find more limited evidence for the prediction, with high innovations only at the superfamily and family levels, but not at the subfamily level. The authors argue that their survey, which comes from

lower-impact regional ornithology journals, may underestimate innovation rates in Darwin's finches because their innovations may be reported in high-impact journals increasing research effort but not innovation counts. This seems a reasonable hypothesis because research on Galapagos ecosystems is typically highly charismatic.

Another perhaps more provocative possibility is that the Coeribinae, including the Darwin's finches, are not, at face value, as innovative in the foraging context relative to research effort as some of the other subfamilies within the Thraupidae, such as the Thraupinae (fig. 2b in Lefebvre *et al.* [91]). This is despite the Coeribinae showing high phenotypic variation in morphology and high diversification rates [93]. There is increasing evidence both in the present theme issue and elsewhere for a close link between diet generalism and foraging innovations [94], potentially mediated by more evenly distributed motor foraging repertoires [42]. Although Darwin's finches are considered diet generalists, diversification of their beak morphology points to diet specialization at the species level. Dietary specialization would predict that Darwin's finches should have lower levels of innovations than would be expected relative to research effort. Clearly, more study is needed in the closely related, apparently highly innovative Thraupinae [91]. One should also bear in mind that the conclusions of comparative analyses, especially those that drill down to low taxonomic levels, are vulnerable to changes in phylogenetic classifications and yield very small numbers of innovations, reducing the power to identify patterns.

The flexible stem hypothesis is central to our understanding of how innovation propensity evolves. It should also apply to the human lineage. If variation in innovativeness were to be sought at the superfamily level, a flexible stem should be apparent at the level of the hominoid superfamily (lesser (gibbons) and great (gorillas, bonobos, orangutans, chimpanzees, humans) apes). This hominoid flexible stem would presumably have had at its disposal the same innovation toolkit as the Emberizoidea flexible stem, including curiosity. Hence, this collection of primates should be more innovative relative to other primates unless diet specialization has acted to constrain innovations, as suggested for the Darwin's finches above (innovation rates are lower than expected in gibbons [14]).

According to this logic, it is not curiosity that got added to the human innovation toolkit in recent times, but some other source of innovation capacity. Some authors view the creative processes underpinning innovation in humans as fundamentally different from those involved in non-human animals. These include (i) chaining, the ability to combine simple ideas into complex ones and (ii) contextual focus, the ability to shift from a convergent to a divergent thinking when the fitness of one's current actions is low [4,5,54]. Another possibility is the intellectual capacity for ratchet evolution where the knowledge of each generation builds upon knowledge transferred from the previous generation. Cross-generational transfer of knowledge, particularly without the need for direct contact between knowledgeable and naive, would have been facilitated by the evolutionary emergence of symbolic encoding of knowledge (via language and writing). Any of these processes, or others discussed by Sterelny [95] in the present theme issue, might have been added to the innovation toolkit of a recent descendant of a humanoid flexible stem.

4. Is innovation selected upon directly or is it part of a collection of traits selected to deal with environmental variability?

After leading the way in linking variation in innovation propensity to variation in ecological conditions and evolutionary diversification rates, Sol *et al.* [88] pioneer a new research area linking innovation to variation in life history. In the present analysis, Sol *et al.* [88] test the prediction that innovation propensity is a co-opted product of a collection of traits that allow an organism to cope with environmental change rather than a direct target of selection. As also seen in Navarrete *et al.*'s contribution [96], there is a welcome effort to transition from correlational analyses to identifying the most likely causal scenarios. Relative brain size exerts a common causal effect on innovation propensity and lifespan, which like Navarrete *et al.*'s [96] present finding of a direct relationship between technical innovations and brain size, point to a causal rather than to correlational relationship between brain size and innovativeness. Sol *et al.* [88] go on to replicate previous work showing that both habitat and diet generalism are also predictors of higher innovation rates [94,97].

The most startling aspect of this conclusion is how well it fits with the conclusions of Navarrete *et al.* [96], who suggest that innovations are part of a suite of co-evolving traits, including ecological generalism. It also fits well with Quinn *et al.*'s [57] conclusion that innovativeness has a weak if any evolutionary potential. Together, these studies herald a new working paradigm, one in which innovativeness is not a direct target of selection. Instead, innovativeness is an emergent property of an adaptive generalist system. From another point of view, however, it feels like we have come full circle from Lefebvre *et al.*'s 1997 original suggestion [12] that an opportunist-generalist lifestyle might favour the evolution of innovativeness. This original framework seems to have been overshadowed by a heavy focus on understanding the relationship between innovation and intelligence.

The transition is welcome. It is in line with the finding from the broad-scale comparative literature that innovation covaries with a suite of social, technical and ecological abilities in primates [14]. It also reconciles comparative research at high taxonomic levels with individual-level experimental research, which has consistently viewed innovativeness as part of a larger array of traits (i.e. as one component of a behavioural syndrome), such as boldness and risk-taking ([23,98,99], and [57]). The transition towards viewing innovation as one of a suite of traits also provides support for a recent proximate model of innovation in birds [42]. The model links diet generalism to innovation via motor diversity and proposes that the association between cognition (i.e. brain size) and innovativeness is not causal. Rather, it arises as a consequence of correlated evolution, because both cognition and diet generalism evolve in response to environmental variability [42].

(a) Future directions in determining the ecological correlates of innovativeness

Understanding the ecological conditions that drive the evolution of innovativeness is essential. However, rather than using proxies of environmental variables, *assumed* to reflect specific environmental conditions, future research should aim to employ measured ecological variables. In one example,

innovations are considered to assist in coping with novel environments based on the finding that establishment of birds in areas outside their geographical range is associated with higher innovation counts [100]. However, the novelty of the recipient environment is assumed, not measured. In fact, many invasive birds are pre-adapted to man-made environments (from which they are transported and to which they are introduced) meaning recipient environments share many similarities with source environments.

To test the prediction that innovations are associated with harsh and changing conditions, one could examine the overlap between species range and climate variability documented in large meteorological databases. To the best of my knowledge, this kind of analysis has been undertaken for primates but not birds [15]. It might also be possible to measure variation in innovativeness experimentally in populations undergoing different rates of urbanization obtained from historical satellite imaging records. Finally, in some animals, most likely captive systems, it should be possible to manipulate environmental variability temporarily or during development and quantify associated changes in innovativeness at the individual/population level. For example, food availability could be made variable in both space and time [101]. Enrichment protocols and early stress paradigms could be applied [102,103].

5. General conclusions

The contributions to this themed issue signal to me a fundamental shift in our thinking about innovativeness. In the past decade, the implicit and explicit working paradigm has been that innovativeness is a trait, innovativeness is a direct product of cognition, and innovativeness is under direct selection. However, the evidence I have reviewed here

indicates that innovativeness will no longer be considered a trait, but rather one component, or even an emergent property, of a larger array of traits that have evolved to cope with environmental variation. These traits probably include first and foremost neophilia, motor flexibility, learning (and probably inhibition [27,52]) and morphological features that increase the diversity of ways in which an individual can interact with its physical surroundings. This transition re-aligns the outlook of experimental, individual-level and comparative, cross-taxon-level research.

I have identified existing research gaps to be in establishing causal relationships between psychological process variables and innovativeness, measuring innovativeness across multiple contexts, obtaining direct measurements of environmental variability and demonstrating that living in variable environments makes animals more innovative. It has become clear that innovative behaviour arises from a combination of psychological mechanisms. Tebbich *et al.* [60] propose that different mechanisms operate at different stages of the innovation process. Taxa might reach different stages because they differ in the range of creative processes in their toolkit, or in their relative reliance on different creative processes. Quantifying this taxonomic richness will require undertaking experimental research in a diverse range of species. The next frontier will be to determine whether particular combinations of (particular) psychological mechanisms lead to exponential, rather than linear, increases in innovativeness, as appears to have been the case in humans.

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