The role of natural history in animal cognition

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Animals’ cognitive processes are shaped by the challenges they face in their environments over developmental and evolutionary time, but cognitive studies are often disconnected from these challenges. Here, we argue that a failure to ground research in natural history can inadvertently misdirect research efforts and make results difficult to interpret. We highlight these potential pitfalls using a series of case studies and consider how field research, ecologically informed lab studies and formal theory can offer potential solutions. Animal cognition research is entering an exciting new phase, with technological advances providing opportunities to tackle previously intractable questions, both in the lab and in the wild, while mathematical models are increasingly helping to strengthen the field’s theoretical foundations. Placing natural history at the centre of this work will be crucial to ensure that we capitalise on these advances to build a robust understanding of the proximate and ultimate basis of animal cognition.

Introduction

A central tenet of the field of animal cognition is that animals’ cognitive phenotypes are shaped by the challenges they encounter over the course of their lives and across generations through evolutionary time. Nevertheless, cognitive research often focuses on animals in contexts largely divorced from these challenges.

Gladly, this situation is changing. Inspired in large part by the work of the late Dorothy Cheney, who with Robert Seyfarth showed that it is possible to study animal cognition rigorously in the context in which it evolved, cognitive field research has burgeoned over the last couple of decades. Cheney and Seyfarth’s classic approach of using animals’ responses to playbacks of vocal signals as a window into their minds continues to yield new insights into the mechanisms and function of social knowledge and the origins of language [1]. At the same time, new experimental approaches and technologies to track and manipulate behaviour under field conditions are allowing us to tackle new topics, from contingent cooperation [2,3] and cultural transmission [4] to the action of selection on cognitive traits (e.g. [5,6]). Of course, studies in captivity remain vital: the fine-scale experimental control they provide is crucial to address certain questions (particularly concerning the details of cognitive mechanisms) and inform field-research paradigms. However, if they are to advance our knowledge of how cognition evolves, we argue that studies should be informed by a detailed understanding of the natural history of the study species, in the sense of what animals do during the course of their lives in the wild. Indeed, as we will discuss, a failure to consider natural history can generate findings that are difficult to interpret or cause us to overlook important issues and thus limit our understanding of cognitive evolution.

Replication, plasticity and natural history

Recent years have seen growing concerns surrounding the ‘replication crisis’ across many areas of science, including animal cognition. Potential solutions typically focus on increased openness, statistical rigour and collaboration between laboratories to boost sample sizes [7,8]. While these are clearly valuable, we feel they may miss two important issues. First, cognitive processes are often, by their very nature, highly plastic to cope with changing information-processing demands [9]. It is therefore not altogether surprising if studies using animals with different genetic backgrounds, rearing histories and experience with experiments yield differing results [10,11]. As science is an incremental process, apparently contradictory findings from different individual papers may be resolved as insights accumulate over time across the course of multiple studies [12]. However, if research paradigms lack ecological relevance, it may be difficult

* We dedicate this paper to the memory of Dorothy Cheney.

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Current Opinion in Behavioral Sciences 2022, 46:101154

This review comes from a themed issue on Cognition in the Wild
Edited by Alexandra Rosati, Zarim Machanda and Katie Slocombe

For complete overview of the section, please refer to the article collection, “Cognition in the Wild”

Available online 2nd June 2022
https://doi.org/10.1016/j.cobeha.2022.101154
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to identify general patterns or to establish whether any patterns that do emerge provide robust insights into cognitive evolution.

A second issue is that no matter how much we refine our statistics and boost our sample sizes, our science can only ever be as good as our theories. Unlike its sister field of behavioural ecology, which is largely grounded in formal, mathematical models based on the fundamental logic of natural selection [13], theories in animal cognition are commonly informal, verbal arguments. Moreover, animal cognition researchers are often concerned with unravelling the biological basis of cognitive traits in humans rather than understanding animals for their own sake. This, combined with incentive structures in academia [14], may generate a tendency to favour explanations based on ‘human-like’ mechanisms. The attempt to understand our own minds is certainly a crucial scientific endeavour, but if we are to make progress, our theories and experiments cannot be divorced from ecological contexts.

In what follows, we present a series of case studies highlighting potential pitfalls in animal cognition research and how ecological perspectives grounded in natural history may offer some solutions.

Contingent cooperation

Cooperation may be cognitively demanding if individuals adjust their behaviour contingent on the responses of social partners. However, laboratory experiments on cooperation often bear little relation to the forms of cooperation that animals exhibit under natural conditions. Thus, if animals fail to cooperate in such tasks, it is difficult to determine whether they understood the nature of the task, and whether their failure indicates an absence of contingent cooperation in more ecologically relevant contexts [15,16]. In primates, for instance, field studies suggest that contingent cooperation is more likely to occur in the context of grooming or coalitionary support than foraging [17]. Nonetheless, the majority of experimental studies involve exchanges of food rewards, often with mixed findings [18]. Difficulties may also arise with the interpretation of positive findings. For example, elegant lab experiments show that Norway rats (Rattus norvegicus) preferentially allocate food to individuals who have helped them in the past and cooperate with both familiar and unfamiliar partners (e.g. [19,20]). While these studies indicate that the scope of reciprocal exchanges in animals may be wider than previously thought [15], their findings are difficult to interpret because relatively little is known about the behaviour of rats in the wild. In particular, it is unknown to what extent wild rats share food and, given that they are highly territorial, it is unclear whether interactions between unfamiliar individuals are likely to be cooperative or rather aggressive [21]. Thus, it is unclear whether the cooperative exchanges observed in lab tasks represent social strategies shaped by selection, or for instance, a by-product of learning reward contingencies during experiments (cf. [22]).

Another area that has attracted a great deal of attention is inequity aversion. Based on the premise that humans show a sense of ‘fairness’, numerous studies have tested whether animals of other species show an aversion to unequal outcomes in cooperative interactions, with mixed and highly contentious results (reviewed in Ref. [23]). The rationale for such studies is typically grounded in expectations of what humans do, rather than on the natural history of the study species themselves. Importantly, many of the species tested do not engage in food-related cooperation such as food-sharing or cooperative hunting in the wild [17], and so may not perceive experimental tests as cooperative situations. Moreover, evidence for inequity aversion typically comes from individuals rejecting food rewards or refusing to participate in tasks if they witnessed a conspecific obtaining a better reward for performing the same action (interpreted as refusing to work for unequal pay). Importantly, rejecting rewards increases rather than reduces inequity. This places individuals at a disadvantage relative to competitors [24], posing a challenge to the evolution of such responses as a strategy in cooperative interactions. Given that attention to relative pay-off distributions is common during social foraging, it is possible that what may look like a response to unfairness in fact reflects foraging decisions that are unrelated to cooperation [25,26].

To gain deeper insights into the cognitive demands of cooperation, it is important for studies to reflect the cooperative dilemmas that animals actually encounter. For example, a large body of research incorporating both lab and field studies has examined the decision-making strategies used by cleaner fish during interactions with clients. Among other findings, this work shows that cleaners can learn to over-ride their preferences to maximise cooperative rewards, manage their reputations by adjusting their behaviour in the presence of by-standers and strategically prioritise clients that are unlikely to stay if left unattended [27,28]. Similarly, experiments inspired by field observations have revealed partner-choice strategies underpinning reciprocal food-sharing by vampire bats (e.g. [29]) and predator mobbing by wild-pied flycatchers (e.g. [30]). Importantly, experiments designed around ecologically relevant challenges can sometimes challenge our intuitions. For instance, meerkats and cleaner fish are both obligate cooperators, yet the former do not donate food to others in lab experiments testing prosociality [31] and the latter show no aversion to inequity [32]. The use of paradigms to manipulate the trading of ecologically relevant commodities such as grooming and social tolerance (e.g. [2,3]) is likely to generate important insights.
Automated tracking technology also offers the possibility of large-scale manipulations of the benefits of social interactions under field conditions (c.f. [33]), allowing us to test whether and how individuals adjust their cooperative interactions to maximise rewards.

Consolation
Humans often invest time and effort in managing social relationships. For instance, we may offer unsolicited support — consolation — to social partners in distress. Other social animals may be expected to manage valuable relationships in a similar way, and accordingly, evidence for consolation has been reported in a number of captive primates, rodents and birds (reviewed in Ref. [34]). This evidence is often used to support arguments for the convergent evolution of empathetic concern across divergent taxa, but studies of consolation typically suffer from two key problems. The first is that in most studies, the putative ‘consoling individual’ also witnessed the stressor, making it impossible to distinguish between consolation and self-soothing. The second is that, as experimental studies have been restricted to work on captive animals, we do not understand whether and why consolation may be used under natural conditions.

To address these issues, Hooper and colleagues [35] investigated consolation in wild jackdaws, a corvid species that forms long-term, genetically monogamous pair bonds with highly interdependent fitness: precisely the context in which consolation is expected to occur. While their mate was absent, females in the nest were exposed to a mild stressor — a playback simulating the arrival of their mate was absent, females in the nest were exposed in a number of captive primates, rodents and birds (reviewed in Ref. [34]). This evidence is often used to support arguments for the convergent evolution of empathetic concern across divergent taxa, but studies of consolation typically suffer from two key problems. The first is that in most studies, the putative ‘consoling individual’ also witnessed the stressor, making it impossible to distinguish between consolation and self-soothing. The second is that, as experimental studies have been restricted to work on captive animals, we do not understand whether and why consolation may be used under natural conditions.

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Social learning
Traditionally, laboratory studies of social learning focused on identifying specialised processes such as imitation, thought to enable high-fidelity cultural transmission in humans [38]. These studies typically pit the mechanism of interest against a ‘killjoy’ [36] alternative such as local or stimulus enhancement. While such work has produced important insights, it tells us relatively little about how social learning is deployed under natural conditions or its ecological consequences.

Over the last couple of decades, social-learning research has become increasingly mindful of ecology. It is now clear that social learning operates across a wide range of taxa and is far more pervasive than we had once realised [39]. For instance, in our own work, we have found that social learning influences numerous aspects of wild meerkats’ foraging behaviour and even daily activity patterns (reviewed in Ref. [40]). Meanwhile, in cleaner fish, lab experiments have revealed that social learning can shape cooperative strategies and partner choice, overturning arguments that cultural influences on cooperation are restricted to humans [41]. Contrary to traditional lab approaches that pit one social-learning mechanism against another, it is also increasingly clear that multiple social and individual learning mechanisms can operate simultaneously [42,43] and that supposedly ‘simple’ mechanisms can be very powerful. For instance, foraging techniques can spread through populations via stimulus enhancement, and imitative is not necessary to generate stable cultural traditions [44]. Similarly, teaching does not require theory of mind, but may be underpinned by simple stimulus-response and associative learning processes [45,46]. As our understanding of the mechanisms of social learning and its role as a second inheritance system grows, field studies of its effects on survival and reproduction are vital to understand its evolutionary consequences [47], including the potential for gene-culture coevolution in natural populations [48].

More than most areas of animal cognition, social-learning research has benefitted from an extensive, formal theoretical framework (reviewed by Ref. [38]). For example, experiments have tested theoretical predictions about the relative value of personal versus social information and the role of conformity [4,49]. This work has been facilitated by advances in automated tracking methods and analytical techniques that allow us to detect social learning and examine the influences of ecological parameters such as social network structure and dispersal in the wild [4,50]. At the same time, laboratory studies highlight how even minor changes in task structure can determine whether and how information spreads [51,52].
alter social foraging dynamics and lead to contrasting group-level outcomes — promoting either conformity and uniformity, or negative frequency-dependent learning [53]. Insights from such controlled experiments may help us to understand when traditions emerge under field conditions and why they persist or collapse. Empirical research will also benefit from the development of further theory, grounded in natural history. In particular, it is known that animals rely on social-learning strategies to determine when and how to use social information [54], but we lack a predictive framework regarding which strategies should be favoured under which socioecological contexts. Such a framework, in tandem with further field research into the fitness consequences of learning from others, will further advance our understanding of the ecological role of social learning and aid efforts to harness it in the development of effective conservation strategies [55].

**Individual cognitive variation**

Cognitive experiments often reveal substantial variation in the performance of different individuals. Traditionally, this has been treated as mere noise, but explicitly considering the causes and consequences of individual variation in ecological context can provide important insights into how cognition develops and evolves. It is increasingly recognised that a powerful approach to understanding cognitive evolution is to focus on the three fundamental tenets of Darwinian natural selection: individual variation, heritability and differential success. In line with this view, researchers have begun to explicitly quantify individual variation in cognition, incorporating approaches from human psychometrics and animal-personality research [56]. Artificial selection experiments under laboratory conditions have provided vital evidence that individual cognitive phenotypes and the neural structures that underpin them are heritable and can respond to selection (e.g. [57]). However, explicit consideration of natural history is crucial to furthering our understanding as differences in the socioecological conditions individuals and populations face in their natural environments may modify the cognitive challenges they face. Accordingly, to establish how naturally occurring developmental factors and selection pressures shape cognition, field researchers are increasingly developing robust methods to quantify individual cognitive variation and its consequences in wild populations [56].

For example, work on mountain chickadees, a species that relies heavily on food-caching, used automated RFID-enabled feeders to quantify spatial memory, finding that higher-performing individuals are more likely to survive the winter [6]. This, alongside evidence that variation in performance has a genetic basis [58], provides strong evidence that the ecological challenge of food-caching may drive adaptive specialisations for spatial memory. However, selection may not act on cognitive traits in isolation, but as part of a suite of domain-general cognitive mechanisms enabling appropriate responses to environmental variation across contexts. For instance, cooperatively breeding Australian magpies that grow up in larger groups perform better than those from small groups across a range of cognitive tasks and high-performing females show elevated reproductive success [5]. These findings provide important support for the argument that the challenges of social life may drive cognitive evolution [59]. In the future, ecologically grounded psychometric approaches will be vital to further our understanding of how cognitive phenotypes are shaped by interactions between developmental and genetic influences and the conditions under which elevated cognitive performance may or may not be favoured by selection [56].

**Collective behaviour**

The study of collective behaviour has traditionally been dominated by laboratory experiments and theoretical models derived from particle physics. These have produced remarkable insights, showing that by following simple interaction rules, individuals can coordinate their movements and generate sophisticated group-level outcomes, transcending their individual cognitive limitations. However, these approaches are necessarily limited in their ability to capture the heterogeneity intrinsic to natural ecological and social environments [60]. As a result, we risk overlooking the possibility that stereotyped, simple rules of interaction may not always suffice.

Under natural conditions, engaging in collective behaviour in the wild sometimes entails substantial risks, so individuals may need to make strategic decisions as to when to join in. For example, playbacks of recruitment calls show that jackdaws use individual vocal recognition and numerical assessments to make decisions to join potentially risky collective antipredator mobbing events [61]. Variation across time and contexts may also require plasticity in behaviour in the wild that may not be evident under traditional modelling and experimental approaches. Technological advances in tracking technology are now allowing us capture the detailed movements of free-living animals and so quantify this plasticity. Among other insights, this has revealed important roles for learning and culture in the development of effective collective behaviour [62,63] and plastic adjustments in interaction rules enabling animals to maintain group cohesion across different ecological contexts [64]. Moreover, whereas models and lab studies have tended to treat individual group members as identical and interchangeable, individuals in natural groups vary and may benefit from responding differentially to different group members. Jackdaws, for example, discriminate
and adjust their responses to different flock members while flying at high speed, keeping track of their mating partner [65] and responding differentially to conspecífics versus heterospecifics [66].

There has long been a tension between the simple interaction rules typically thought to explain collective behaviour and the sophisticated cognitive processes often invoked to explain social interactions in animal cognition research. Studies grounded in the problems animals face in their natural environments, incorporating ecologically relevant heterogeneity, are beginning to bridge this gap. This work is inspiring the development of more realistic mechanistic models of interaction rules that take into account relevant ecological characteristics [67], and is increasingly revealing that taking part in collective behaviour can entail substantial cognitive challenges. Indeed, the information-processing demands that individuals face when acting together as part of a group, including during interactions between groups [68], may represent an important and overlooked selection pressure driving cognitive evolution.

Conclusions
Through this brief review, we have tried to highlight how explicit consideration of natural history can contribute to every stage of cognitive research, from developing research questions to designing experimental protocols and interpreting results. Formal models can also play a key role by making our assumptions explicit, incorporating ecologically relevant costs and benefits and generating a priori predictions. Indeed, there is now a growing body of theoretical research on the ecological and evolutionary role of information processing and the cognitive mechanisms underlying it [69,70]. A greater interplay between theoretical, field and lab approaches has strong potential to deepen our mechanistic understanding of cognitive processes and the developmental and selective forces that shape them.

Conflict of interest statement
None.

Acknowledgements
A.T. was supported by a Leverhulme grant (Grant no. RGP-2020-170) and N.T. by a Swiss National Science Foundation Postdoctoral Mobility Grant (Grant no. P400PB_194397/1).

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