Trends in
Ecology & Evolution

CellPress

Review

Animal cognition and culture mediate predator–prey interactions

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Predator–prey ecology and the study of animal cognition and culture have emerged as independent disciplines. Research combining these disciplines suggests that both animal cognition and culture can shape the outcomes of predator–prey interactions and their influence on ecosystems. We review the growing body of work that weaves animal cognition or culture into predator–prey ecology, and argue that both cognition and culture are significant but poorly understood mechanisms mediating how predators structure ecosystems. We present a framework exploring how previous experiences with the predation process creates feedback loops that alter the predation sequence. Cognitive and cultural predator–prey ecology offers ecologists new lenses through which to understand species interactions, their ecological consequences, and novel methods to conserve wildlife in a changing world.

Highlights

Animal cognition and culture are key components of a species' ecology. Yet, within predator–prey ecology, cognition and culture are rarely considered of importance.

As cognitively complex predators and prey gain experience with predation, individuals learn, gather knowledge, and alter their behaviour to increase their chances of success. Knowledge of the behaviours that promote successful hunting and avoidance may then be culturally transmitted.

Cultural knowledge further governs hunting strategies, prey preferences, spatiotemporal patterns, and predator recognition and avoidance.

Together, animal cognition and culture shape the outcomes of predator–prey interactions.

Incorporating interdisciplinary approaches from animal cognition and culture into predator–prey ecology offers ecologists a chance to enhance their understanding of how predators structure ecosystems in a changing world.

Unresolved complexity in predator–prey interactions

The need to hunt prey, or to avoid being killed by predators, has driven the evolutionary trajectories of organisms across the globe [1]. Predators evolve novel morphologies, behaviours, and life history traits to better hunt prey [2,3], while prey evolve traits to defend themselves, avoid detection, deter predators, and reduce the risk of a predator encounter [4,5]. Predator and prey are entangled in an ecoevolutionary arms race, as improved hunting abilities demand compensatory improvements in prey avoidance and vice versa [6]. These foundational ecological interactions have been understood through the study of **predator–prey interactions** (see Glossary). A range of theoretical, observational, and experimental approaches have highlighted the importance of predator–prey interactions to ecosystem functioning [7]. Predators drive ecosystem processes by directly killing their prey, as reduced prey densities reshape trophic interactions, nutrient cycling, ecosystem engineering, and disease transmission, for example [8,9]. Predators also influence ecosystems nonlethally through the predation risk they pose [8]. The risk of predation influences prey behaviour and physiology, with potential cascading effects [10,11].

The act of predation is the endpoint of a sequence of events [12]. This **predation sequence** first necessitates spatiotemporal overlap between predators and prey, and can advance through the encounter and attack stages, culminating in either prey being killed by a predator, prey escape, or injury for either party [11]. The strong selective pressures exerted across the predation sequence provide predators and prey with opportunities to evolve traits that improve their fitness (i.e., cryptically coloured prey are less likely to be detected) [13]. This classic, ecoevolutionary understanding of predator–prey interactions is being complemented and modulated by a growing understanding that **animal cognition** and culture mediate the outcomes of predator–prey interactions (Figure 1) and concurrently shape the evolutionary trajectories of both predator and prey (Figure 2).

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Figure 1. Animal cognition and culture shape predator–prey interactions. Clockwise from top left: meerkats (*Suricata suricatta*) teach their offspring how to hunt scorpions by removing the stinger prior to consumption [65]. A single individual humpback whale (*Megaptera novaeangliae*) developed a novel hunting strategy of slapping the surface of the water with their tail to increase their hunting success. This strategy spread culturally to more than 600 individuals over 27 years [24]. Burrowing bettongs (*Bettongia lesueur*) learn antipredator behaviour after exposure to predation from cats (*Felis catus*) [89]. The development of tool use culture among long-tailed macaques (*Macaca fascicularis*) enables them to hunt novel mollusc prey, resulting in island-wide decline [57]. Artwork by K. Currier.

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Previous work has suggested that the predation sequence provides opportunities for the use of various cognitive abilities to fine-tune defences and hunting strategies [14]. Cognitive processes involving perception, **learning**, and memory influence an individual's ecology and behaviour and enable the formation of culture [15]. Further, it has been hypothesised that the emergence of complex animal cognition and **animal culture** may be driven by the selective pressures exerted on both predators and prey across the predation sequence [14]. Complex cognition and cultural knowledge transmission can offer individuals and their social groups advantages over other fixed strategies (e.g., **aposematism**), given that learned information and behaviours – such as predator recognition or prey capture strategies – can be developed across an individual's lifespan and transmitted to others within a single generation. Despite acknowledgment that components of animal cognition (e.g., learning [16]) and animal culture (e.g., **ecotypes** [17]) are of importance

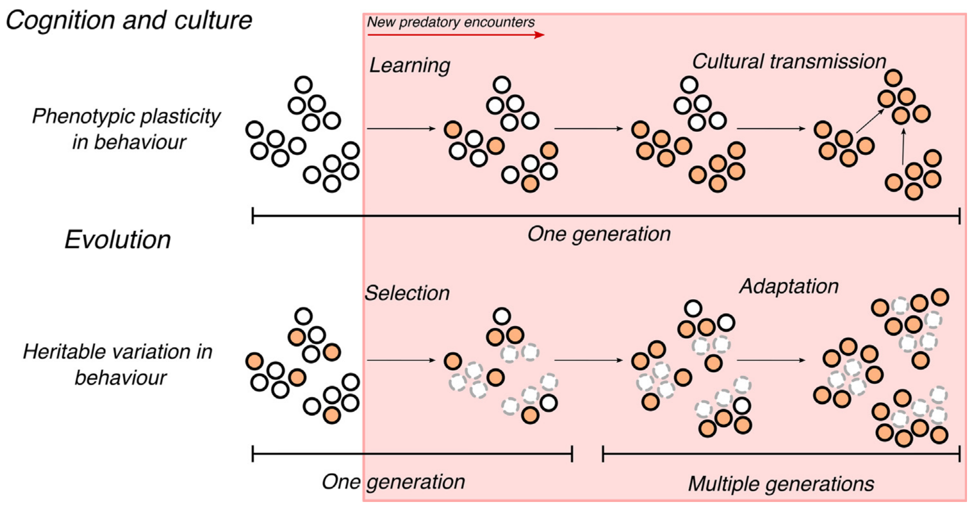

Figure 2. The different mechanisms by which cognition, culture, and evolution spread a novel predatory or antipredator behaviour through a population. Evolution and cognition work through different mechanisms and on different time scales, yet both can lead to changes in a predatory or antipredator behaviour across a population. When a new type of predatory encounter begins to occur in a landscape, individuals of a species with high phenotypic plasticity in behaviour may learn to exhibit a behaviour that improves their performance in the predatory interaction (for prey: improved avoidance of predation, for predators: improved capacity to catch prey). This beneficial behaviour may spread, through cultural transmission, to the rest of the population (top row). Additionally, or alternatively, the new type of predatory encounter may exert selection pressure on a population with heritable variation in the behaviour they exhibit, such that individuals with the genes for a certain type of behaviour are more likely to survive and produce offspring with the genes for that particular behaviour in subsequent generations (bottom row). In this way, the selected behaviour spreads throughout a population through adaptation by natural selection. Importantly, evolution also acts directly on cognition, on the capacity for learning and cultural transmission, and on the degree of phenotypic plasticity displayed in a population. Thus, in some environments (e.g., highly variable ones [90]), having highly complex cognition, the ability to learn accurately and quickly, and high phenotypic plasticity may all be selected for.

to predator–prey interactions, studies have rarely explored how cognition and culture can shape real-world predator–prey interactions.

Here, we review the preliminary work that weaves animal cognition and culture into predator–prey ecology [18] and synthesise the growing evidence that cognition and culture are important forces shaping predator–prey interactions and their influence on ecosystems. We explore how the predation sequence creates opportunities for cognitive development and cultural transmission in both predators and prey. Further incorporation of cognition and culture into predator–prey ecology may unveil novel pathways of evolutionary adaptation across the predation sequence and offer ecologists new ways to understand the causes and consequences of predator–prey interactions.

Cognition as a mediator of predator–prey interactions

Cognition describes the processes by which individual animals acquire, process, store, and act on information from the environment [15]. In essence, cognition serves as the interface between an individual and its environment and is therefore a primary driver of behaviour for animals with complex cognition [19]. Animal cognition research investigates how individuals perceive their environment, learn from previous experiences, make decisions, remember landscapes and landmarks, and solve problems [20].

Predatory and **antipredator behaviours** are dependent upon both innate and learned skills (e.g., cue recognition and search image formation [21]). The capacity to learn and modify attack

Glossary

Animal cognition: the ways in which individual animals acquire, process, store, and act on information from the environment.
Animal culture: behavioural traditions that are socially learned and transmitted within and between generations.
Antipredator behaviour: any behaviour taken by prey to reduce the likelihood of being killed by a predator.
Aposematism: a coloration or set of markings that serves to repel predators by signalling venom, toxins, or unpalatability.
Cognitive test batteries: a sequence of tests that identifies the strengths and weaknesses of an individual within and between cognitive domains.
Ecotype: a distinct phenotype of animal species occupying an ecological niche.
Innovation: the development of a novel or modified behaviour.
Learning: a change in an animal's behaviour that is gained through experience.
Predation sequence: the sequential process through which predation occurs. Comprises of spatiotemporal overlap, encounter, attack, and kill or evade.
Predator–prey interactions: a trophic interaction in which predators hunt prey and prey employ strategies to reduce their likelihood of being killed by a predator.
Vigilance: behaviours that aid surveying the environment to detect prey or potential threats. Commonly utilised by prey to detect predators.

and defence strategies is a crucial tool in the predator–prey arms race, facilitating the development of predatory and antipredator behaviours [21,22]. Further, as both learning and flexibility in behaviour may benefit individuals in multipredator–prey systems, interactions between predators and prey are among the various overlapping hypotheses for the evolution of intelligence [23]. For example, as predators evolve and innovate novel hunting strategies [24], prey may adapt novel counter defences. While prey responses to predator hunting **innovations** have not, to the best of our knowledge, been studied empirically, theoretical modelling suggests that to survive predatory innovations, prey must themselves innovate [25]. Both prey and predator species that exhibit complex cognition may therefore develop increasingly complex cognitive strategies [26]. Thus, predation is thought to be an important evolutionary consideration in the emergence of complex cognition in animals [23,27].

To hunt or avoid being hunted, individual animals rely upon knowledge of each other's spatiotemporal activity patterns [28]. The importance of this knowledge and how it shapes behaviour becomes evident during times of disturbance, such as predator reintroduction. When predators are reintroduced after an extended period of absence, prey must avoid predation without prior lived experience with this particular predator. An example of this behavioural shift comes from the reintroduction of grey wolves (*Canis lupus*) into Yellowstone National Park, USA, in 1995, where elk (*Cervus elaphus*) rapidly began avoiding areas that presented a high risk of encountering a wolf [29]. To reduce the chance of encountering predators, prey learn to recognise their cues (e.g., scat or urine [22]) or may use the corpse of a conspecific to inform avoidance of areas where encountering a predator is likely [10]. Cue association can be learned rapidly and retained for future predatory encounters [30].

For predators, encountering a prey species requires making decisions about who and how to hunt. Predators learn to avoid attacking aposematic prey [31] and make rapid decisions about which species or individuals to prey on based on prey body size and risk [32]. The strategies that predators use to attack prey can be rapidly learned and modified across an individual's lifetime [33]. Similarly, prey can learn strategies that help them reduce the risk of encountering a predator [34]. Best evidence for the ability to rapidly learn and adapt antipredator strategies comes from case studies of prey after the introduction of a predator (Box 1). For example, the introduction of the Tasmanian devil (*Sarcophilus harrisii*) to a devil-free island forced brushtail possums (*Trichosurus vulpecula*) to rapidly learn antipredator behaviours. Possums decreased their foraging activity in devil-dense areas within 3 years of exposure to the predator, reducing their likelihood of encountering a predator [35]. It is also possible that this improved recognition and antipredator behaviour could be driven by an innate recognition mechanism [36]. The conflict between learned and innate responses highlights the need for a more nuanced understanding of when learning-enhanced antipredator behaviours emerge and how (Figure 3 and Box 2). Finally, predator experience shapes whether the predation sequence ends in prey consumption or escape. For example, hyenas (*Crocuta crocuta*) improve their ability to kill prey as they get older. Hyenas commonly hunt in packs, and juveniles join adults on group hunts within 6 months of being born. They learn to hunt prey by observing adults and participating in group kills [37].

Cultural knowledge and predator–prey interactions

Many animals live socially, which may allow them to breed, gather and defend resources, hunt, or protect themselves from predation. A diverse body of literature has emerged documenting that animal social groups possess distinct cultures. Culture generally describes behavioural traditions that are socially learned and transmitted within generations (horizontal transmission) and between generations (vertical transmission) [38,39]. Both vertical and

Box 1. Cognition and culture in novel predator–prey systems

The arrival of new predators, or prey, in ecosystems is a topic of significant research interest and conservation concern [21]. These interactions have typically been studied through an ecoevolutionary lens, exploring the predator–prey arms race that develops during a shared evolutionary history [91]. We explore the role of animal cognition and culture in shaping novel predator–prey interactions [92] across the stages of the introduction process [93], and in doing so provide testable hypotheses for understanding the functioning of novel predator–prey interactions and their effects on ecosystems.

Predator introduction

Upon predator introduction, prey may be subject to heavy cognitive selection pressures, as cognitive ability can predict prey individuals' ability to avoid predation in some species [79,82]. Thus, the introduction of a predator will select for strong learning abilities, shrinking the spectrum of intraspecific variance in learning ability across a population. Additionally, the ability to socially transmit knowledge about how to avoid predation is likely to be selected for [94].

Predator establishment

Prey will improve at recognising and responding to predators with increased experience [16]. Prey will begin to adopt current – or develop new – antipredator behaviours that improve their chances of avoiding predators. Prey continue to be heavily selected for their abilities to learn or socially transmit predator recognition and avoidance behaviours. As predators improve at hunting prey through individual or cultural innovation, prey may be forced to innovate novel strategies themselves to survive [25].

Novel predator range expansion

Prey species on the edge of the introduced predator range expansion may be initially naive, if the predator is novel, but should rapidly learn or adopt antipredator behaviours. If individual home ranges overlap with the home ranges of individuals who are predator-experienced, and the species shows evidence of social learning, prey species may culturally learn about predation risk and cue recognition and thus fare better than other individuals with nonoverlapping ranges when novel predator range expansion occurs. Social learning may function as a mechanism to overcome naivety at the edges of novel predator range expansion (Figure I).

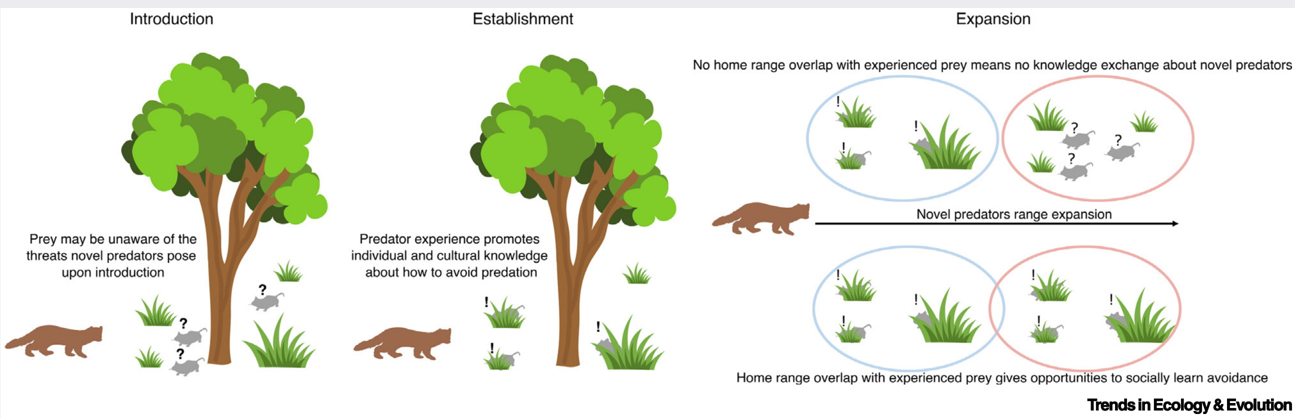

Figure I. Animal cognition and culture drive how prey respond to predator introduction. Prey may be naive to the threat posed by novel predators when predators are introduced. As predators establish and prey become experienced, prey improve their antipredator strategies through individual and social learning. As introduced predators expand their ranges, prey may be naive at the expansion front. However, social learning from spatially overlapping experienced individuals could spread knowledge and buffer naivety.

horizontal cultural transmission of predatory and antipredator behaviours have been documented [24,40,41], demonstrating that innovations, problems solved, and lessons learned from previous experiences are spread to conspecifics, which can then alter the outcomes of predator–prey interactions [42].

Animal culture can mediate the degree of spatiotemporal overlap between predators and prey. For instance, migration appears to be culturally transmitted in many vertebrates [43,44]. Migrating predators may feed on a diverse range of prey species along their route [45,46] and even exploit bountiful stopover sites, as is the case with North American red knots (*Calidris canutus*) that feed on horseshoe crab (*Limulidae* spp.) eggs in Delaware Bay, USA [47]. In addition, predators use knowledge of prey migratory patterns to hunt [46,48]. For example, grey wolf packs travel up

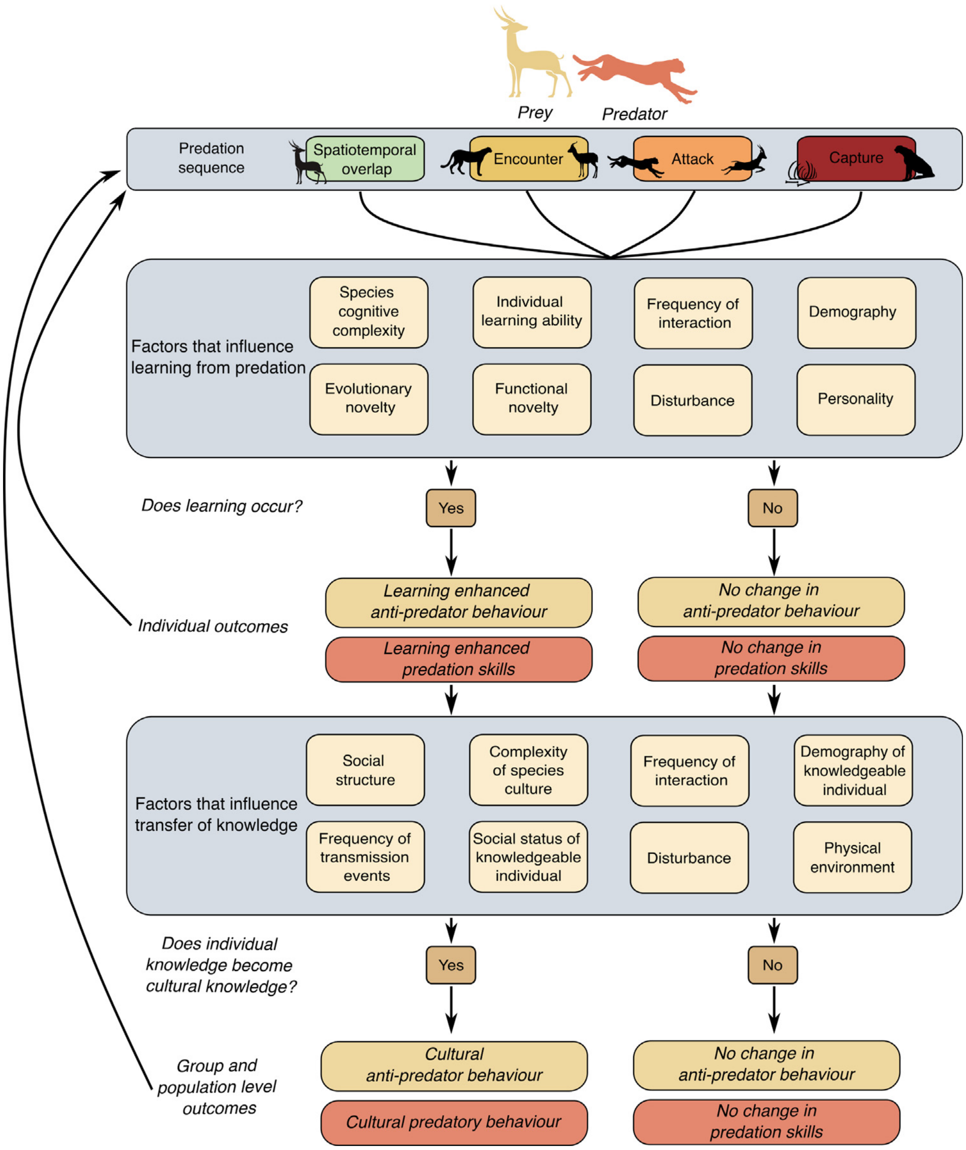

Figure 3. Animal cognition and culture can create feedback mechanisms that alter the predation sequence. This framework considers how one aspect of cognition – learning – shapes predator–prey interactions. Each experience with predation offers learning opportunities to both predator and prey. However, the ability to learn from experiences with predation are driven by individual, ecological, evolutionary, and environmental factors. If both predators and prey are learning from their past experiences with predation, prey should improve at avoiding predators and predators should hunt prey more effectively. In species that learn socially, lessons learned may then be transmitted to other individuals, as mediated by species' social structure, demography, the demography of the knowledgeable individual and the environment. The frequency of the predator–prey interaction may also determine whether individual or social learning occurs. Where cultural transmission occurs, it should be detectable through the spread of novel antipredator and hunting behaviours that improve the chances of individuals, groups, and populations successfully navigating a predator–prey interaction. The factors that shape how animal cognition and culture mediate predator–prey ecology are explored more fully in Box 2 in the main text.

to 500 km to intercept migrant caribou (*Rangifer tarandus*) [49], and North Atlantic right whales (*Eubalaena glacialis*) migrate with their newborn calves hundreds of kilometres to exploit high densities of copepod prey [50,100]. It follows that knowledge of prey movement patterns may therefore be culturally transmitted amongst social predators. Concurrently, migratory and resident prey species experience spatiotemporally variable predation risk across their lives, which can be overcome via social learning about predators [48,51]. Similarly, when prey migrate, they may face both familiar and unfamiliar cues of predation risk, and rely on social information to stay safe at stopover sites [52,53].

The ability to recognise and respond to predators can also be socially learned and culturally retained. Captive-raised predator-naive fathead minnows (*Pimephales promelas*) learned wariness responses to the predatory northern pike (*Esox lucius*) from predator-conditioned conspecifics by observing their responses to predatory chemical stimuli [41]. Predator-naive wood crickets (*Nemobius sylvestris*) socially learn to use complex habitat by watching conspecifics hide from predators and retain this information for future predatory encounters [54]. Further, Cornell *et al.* [55] showed that American crows (*Corvus brachyrhynchos*) learn to recognise the faces of humans who trap them and subsequently avoid these humans or mob them when approached. Naive crows who witness the mobbing responses of crows socially learn the risk these humans pose, creating a culture of mobbing behaviour toward particular individuals. This culture spread, as 5 years later – crows more than 1 km away from the original field site mobbed the humans who trapped their conspecifics.

The development of a hunting culture in predators can determine the attack strategies and hunting success of entire populations of predators. For example, tool use is a behaviour that is commonly socially transmitted in primates and used to hunt cryptic prey [56]. Further, culture can drive the specificity of social group foraging strategies [57,58] and prey preferences [59]. Orca (*Orcinus orca*) form clan-specific ecotypes that are socially learned. Across their global range, orcas adapt their predatory behaviours to prey species availability [17,60,61]. However, clan-specific hunting strategies arise through their ability to learn and remember prey distributions, and by developing and sharing the specialised behaviours needed to hunt each prey species [61,62]. Orca ecotypes drive food web structures in the northern North Pacific Ocean. Whaling at the end of World War II drove a decline in orca prey. This resulted in orcas shifting their prey specialisation to other marine megafauna such as northern fur seals (*Callorhinus ursinus*) and sea otters (*Enhydra lutris*) [63]. Orca predatory specialisation, a function of their culture, is suggested to have driven the sequential megafaunal collapse in the northern North Pacific Ocean [64], demonstrating the power of animal culture to structure ecosystems and alter ecosystem function.

Predictions from a cognitive and cultural predator–prey ecology

Our conceptual synthesis of cognitive and cultural predator–prey ecology provides both insights and predictions to aid in the exploration of how animal cognition and culture are shaping predator–prey interactions. We explore how learned and socially transmitted knowledge can create feedback loops that alter the predation sequence (Figure 3). As knowledge can be gathered from each encounter, learned from, and socially transmitted, animal cognition and culture alter how individual predators and prey engage with each stage of the predation sequence, altering predator–prey interactions. Next, we present a set of predictions exploring which ecological, evolutionary, and behavioural contexts might give rise to learning enhanced and cultural predatory and antipredator behaviours (Box 2).

As predators gain experience hunting prey, we predict that they will improve at tracking the spatiotemporal patterns of their prey and alter their behaviour to improve hunting success with experience. These observable shifts in behaviour are evidence of learning shaping predator–prey interactions. While for prey, experience with predation should lead prey to improve their recognition of predator cues, alter their spatiotemporal activity to be more active at low-risk times and in low-risk areas, and shift their allocation of antipredator behaviours (i.e., **vigilance**) to maximise the likelihood of detecting a predator. If individuals are learning and teaching about predation, there should be detectable shifts in behaviour after the event [65]. When cultural predatory behaviour emerges, predators may be observed altering their hunting behaviour to the socially learned variant and experience increased hunting success after having done so [24]. This increased hunting success is likely to drive ecological change and declines in local prey [57]; however, prey should also increase their investment in avoidance and detection behaviours as threats from predators increase. In prey, when antipredator behaviour is culturally transmitted, prey may

Box 2. What drives the development of cognitive and cultural predator–prey ecology?

Our framework (see Figure 3 in main text) explores how animal learning and culture create feedback loops that alter the predation sequence. We provide a noncomprehensive list of factors that shape how cognition and culture influence the predation sequence, together with predictions for how each factor shapes the role of cognition and culture in predator–prey ecology.

Individual learning

The degree to which individuals learn from predation encounters is likely driven by the complexity of the species' cognition, as species who exhibit more complex cognition are more likely to be capable of detecting and assessing risks, as well as rapid learning and behavioural flexibility (Figure IA) [26,95]. Individual traits are also likely to influence whether individuals learn from previous experiences with predation. For example, individuals who perform better in cognitive tasks are better at avoiding predators (Figure IB) [79,82], juveniles are more likely to rapidly learn and incorporate information (Figure ID) [37,96], and individuals with bold personalities can be worse at learning tasks (Figure IH) [97] and less innovative [98], suggesting they may be worse at avoiding predation. Prey are likely to learn more quickly about evolutionarily and functionally similar predators, as cues, behaviours, and ecologies are similar to their historic predators or prey (Figure IE,F) [33], while learning about novel predators is still likely to occur in the long term [22].

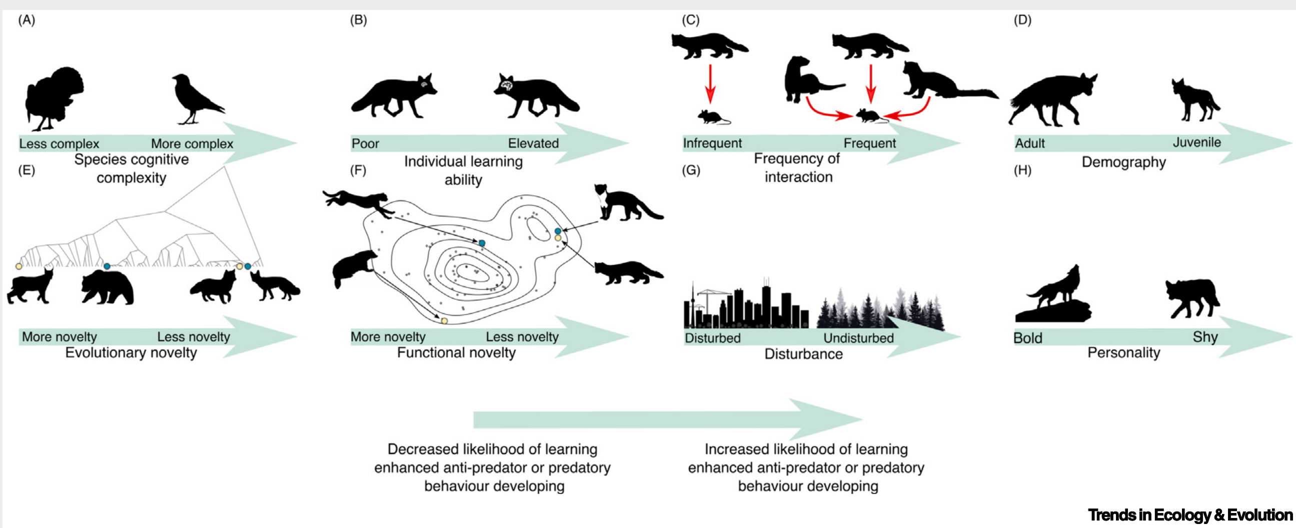

Figure I. Factors that shape how likely a species is to individually develop learned improvements to predatory or anti-predator behaviour.

Cultural transmission

Cultural transmission of improved predatory or antipredator behaviour is more likely in species that live socially and have existing complex cultures that govern other aspects of their ecology [39], as well as in species that have knowledge transmission as a central component of their behaviour and ecology (e.g., meerkats [65]; Figure IIA,B,E). The social status and demography of the individual who possesses the knowledge also determines how likely it is to be culturally transferred. For example, juveniles are more likely to learn from their parents (Figure IID [99]) and social traditions are transferred and maintained by dominant individuals (Figure IIF) [67]. Features of the physical environment can also shape the likelihood of cultural transmission of learning (Figure IIH). A common method for prey to socially learn predator avoidance is through the observation of a conspecific using cover [54], thus a sparsity of cover or the presence of disturbance such as land clearing that reduces cover availability likely limit the emergence of cultural antipredator behaviours.

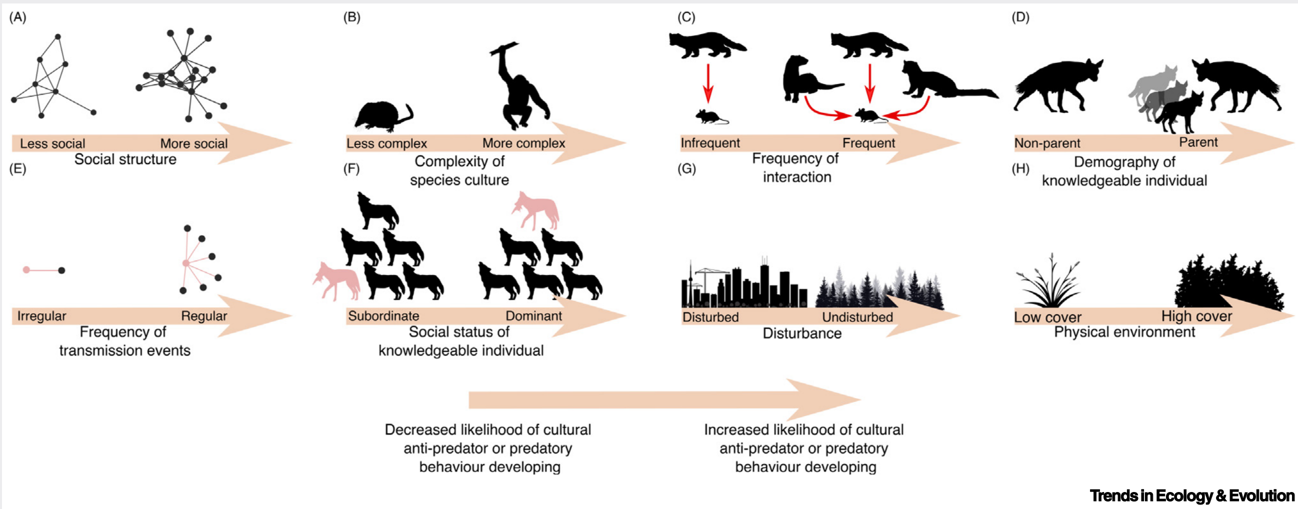

Figure II. Factors that shape how likely a species is to culturally transmit learned improvements to predatory or antipredator behaviour.

learn to hide in cover [54] or increase their allocation in predator detection behaviours [41] after witnessing a conspecific avoid predation. These behavioural changes should be repeated and consistent to be evidence of cultural antipredator behaviour. In the following, we explore the factors that shape the cognition and culture of animals and provide explicit predictions about how and when learning-enhanced and cultural antipredator and predatory behaviour emerge (Box 2).

Frequency of interaction dictates the rate of individual and social learning

The frequency of interactions with the other member of the predator–prey dyad should drive the rate of individual and social learning about predation. More frequent interactions are more likely to drive individual and social learning of predatory and antipredator behaviours, as learning opportunities occur more often and payoff for learning is greater (see Figures IC and IIC in Box 2). Prey populations learn how to avoid predation rapidly when exposed to high densities of predators [16], and predators should be more likely to learn from frequent encounters with the same prey species [33]. Additionally, two key examples of cultural predation stem from predators and common prey; meerkats (*Suricata suricatta*) teaching their young how to remove stingers from their scorpion prey [65], and humpback whales (*Megaptera novaeangliae*) slapping the ocean's surface to kill fish [24] (Figure 1). While little is known about how frequency of interactions shapes how predators hunt prey and prey avoid predation, we predict that the frequency of learning opportunities is a key driver of learning in predators and prey.

Interrogating mismatches between realised and perceived predation risk

Anthropogenic disturbance can result in predator populations at similar densities having distinct relationships with prey and thus effects on ecosystems [66,74,101], while simultaneously influencing the cognition of individuals and the cultural knowledge pathways of social groups (see Figures IG and IIG in Box 2 [20,67]). We suggest that disturbance is an important, largely unconsidered driver of documented mismatches between realised and perceived predation risk [28,68]. We hypothesise that in disturbed areas, predators are less spatiotemporally predictable [69,70]; this makes learning the spatiotemporal patterns of risk more challenging for prey, sometimes resulting in prey not responding appropriately to high-risk scenarios. As disturbance reduces the capacity for social groups to rapidly acquire and transmit information about predation, we predict that prey species that rely on social information to avoid predation will be particularly vulnerable to disturbance. Examples where cognition and culture may aid ecologists include disturbance driving the degree of spatiotemporal avoidance and vigilance in red foxes (*Vulpes vulpes*) towards dingoes (*Canis dingo*) [70,71]; that predation risk exerted by African wild dogs (*Lycaon pictus*) does not always result in prey foraging reductions [72,73]; and that the ability to hunt complex prey appears to be possible from some predators in the absence of disturbance only [10,74] (J.I. Ransom, doctoral dissertation, Colorado State University, 2012)[i]. The exploration of learning, memory, and culture, and how these factors shape predator avoidance, may unveil how knowledge of predators and their patterns influence prey responses to predation risk. Developing a deeper understanding of the cognitive and cultural drivers of predation risk perception and prey avoidance behaviours may uncover whether mismatches between predation risk and prey responses can be explained through the disruption of cultural or cognitive mechanisms that mediate interactions.

Cultural trophic cascades

The cultures of predator populations can determine the densities of their prey [57]. Yet the ecological impact of predator culture goes beyond prey densities, likely shaping prey spatiotemporal patterns and their foraging and vigilance behaviours and thus their effects on vegetation communities. We suggest that explorations of cultural predator–prey ecology may uncover the existence of 'cultural trophic cascades', that is, the multitrophic level ecological effects of cultural development and spread. We predict that the spread of a novel hunting innovation [24] or a cultural prey preference [59] is likely to shape prey species' abundance and behaviour, with flow on effects on community composition and vegetation communities [75–77]. By better understanding the ecological effects of animal culture, we can better predict the effects of disturbance and culture loss on ecosystems and their function.

Methods for cognitive and cultural predator–prey ecology

The many examples explored in this review demonstrate the potential for cognition and culture to mediate predator–prey interactions, highlighting the need to continue to develop our understanding of how animal cognition and culture shape ecosystems. The melding of ideas and methods from animal cognition research into predator–prey ecology can unveil novel and important links between individual cognition and the ability to avoid predation. Methods such as puzzle boxes (used to quantify problem-solving abilities) and learning tests (used to quantify spatial, associative, and reversal learning [78]) can be correlated with predator mortality data to provide novel insights into the role of cognition in avoiding predation or successfully killing prey [79]. Prey cognitive metrics could additionally be correlated with predation cue recognition and avoidance behaviours [21]. Similar integration could be achieved in predator-focused work, by pairing individual cognitive metrics with data from global positioning system (GPS) collars [80], accelerometers, and/or animal-borne audio recorders [81] that accurately identify predation events.

Explorations of cognitive predator–prey ecology have put forward cognition as a strong determinant of an individual's ability to avoid predation. For example, **cognitive test batteries** of individually identified animals and measures of their antipredator behaviour and mortality in the wild have been combined to reveal links between cognition and predation risk avoidance. This was achieved by Heathcote *et al.* [79] who, prior to releasing juvenile pheasants (*Phasianus colchicus*) into the wild, quantified the individual associative learning scores via a colour discrimination task, reference memory ability with a complex maze task, and working memory with a radial-arm maze test. Pheasant performances in these tasks were then linked to predation risk experienced through the quantification of home ranges and mortality rates. Additionally, Fichtel *et al.* [82] quantified problem-solving abilities with a puzzle box, spatial memory with a maze task, inhibitory control with a cylinder task, and causal understanding using a string-pulling task to demonstrate that individual cognitive performance in grey mouse lemurs (*Microcebus murinus*) positively correlates with survival in the wild, where mortality is primarily driven by predators. These novel and innovative approaches to understanding predation risk pave the way forward for ecologists looking to further integrate these areas of research. Expanding this work to understand how other cognitive attributes – such as problem solving and innovation shape predator avoidance, recognition and habitat selection – are important future avenues of research.

Reintroduction programmes are a prime context for exploring how animal cognition and culture shape predator–prey ecology. Given that animals are in short- or long-term captivity prior to introduction, the quantification of cognitive abilities is more achievable than in wild animals. As many reintroduced prey species are killed by predators [83], individual and aggregated cognitive traits could be combined with post-release tracking to document the role of cognition in navigating novel predation pressures. A similar level of insight into the cognitive traits that influence the ability for predators to rapidly learn to hunt novel prey after reintroduction could be achieved with the same methods. Beyond cognition, the reintroduction of social hunting predators known to develop socially learned hunting traditions that improve their hunting success (i.e., wolves) theoretically allows researchers to accurately document the spread of predatory culture and study the ecological and behavioural responses of prey species to the spread of culture. Methods such as giving-up densities [84] and playback experiments [85] could be deployed across a spatial gradient where the predatory culture occurs and where it does not, or before and after the cultural spread, to assess whether prey shift their antipredatory responses to predators after the development of cultural predatory behaviour. By documenting how these cultures spread throughout populations, we not only deepen our understanding of animal culture, but also how it can shape ecosystems and their function.

Outstanding questions

How does behavioural flexibility, including problem solving and inhibitory control, shape the ability of prey to avoid predation and predators to hunt prey?

How does human disturbance (i.e., human persecution or urbanisation) shape the cognition and culture of wild animals, and what are the consequences for predator–prey interactions?

Can we predict the ecological circumstances and consequences of the change (gain or loss) of animal culture, as mediated by changes in predator–prey interactions?

Does animal culture drive cascading ecological effects, mediated by predator–prey interactions?

Does intraspecific variation in the cognitive capacities of individuals alter predator–prey interactions?

Concluding remarks

There is growing evidence that animal cognition and culture have the capacity to mediate interactions between predators and prey. While the ecological sciences have readily acknowledged the cognitive abilities and cultures of non-human animals, the incorporation of these concepts into ecological research has been relatively slow [86]. We believe that further integration and exploration of cognition and culture in the ecological sciences offers exciting new perspectives for understanding how predators and prey coexist and shape their environments.

There remains a plethora of questions (see Outstanding questions) regarding how cognition and culture can shift predator–prey interactions. Understanding the reach of animal cognition and culture in shaping species interactions is an important endeavour in a changing world, as species and their cultures are rapidly gained and lost, yet the implications of these shifts for ecosystem function are unknown. By quantifying the extent of animal cognition and culture in shaping predator–prey dynamics and their effects on ecosystems, we broaden our understanding of the importance of these mechanisms in shaping the ecology and evolution of predator–prey dynamics. Given the recent uptake in the number of study systems dedicated to understanding the fundamental questions of animal cognition and culture [87] and constantly evolving technologies to do so [88], unpacking the relationship between animal cognition, culture, and predator–prey ecology has never been more feasible.

Acknowledgments

We thank A. O'Neill for inspirational fireside conversations. We appreciate feedback and helpful discussion with K. Zawada, D. Nimmo, and E. Rogers. We thank the editor and two anonymous reviewers for their insightful comments. All illustrations were provided by Keegan Currier Illustration and silhouettes are from PhyloPic.org. E.I.F.W. was supported by a Gulbali Institute DECRA Track Postdoctoral Fellowship while leading this paper.

Declaration of interests

No interests are declared.

Resources

[i]www.proquest.com/openview/a8f90e0d9ad9b35e5b9e8b4afe43f8a5/1?pq-origsite=gscholar&cbl=18750

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