Predator-prey interactions as drivers of cognitive evolution

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Abstract

Despite decades of research, how and why cognition varies between and within species remains hotly debated. Social interactions and environmental variability are the leading hypotheses for cognitive evolution, but these factors fail to account for large amounts of cognitive variation. Evidence is mounting that interactions between predators and prey are a key driver of cognition, but research on the link between predation and cognition has been deemed largely unfeasible until now. Here, we outline how predator-prey interactions may drive cognitive evolution and maintain cognitive variation – we formalise this as the *Predatory Intelligence Hypothesis (PIH)*. The PIH posits the cognitive challenges associated with predator-prey interactions drive a cognitive co-evolutionary arms race between predators and prey promoting bidirectional enhancements in cognition. Our synthesis provides a series of predictions, methodologies and future directions for research that will facilitate uncovering the role of predation in the evolution of intelligence.

Introduction

Why does **cognition**—the processes by which individual animals acquire, process, store, and act on information from the environment [1] —vary so greatly among individuals, populations, and species? The drivers of cognitive variation are amongst the most hotly debated topics in biology. One of the predominant hypotheses for the evolution of cognition, the **Social Intelligence Hypothesis** (SIH), posits that the challenges associated with social life select for greater cognition. The need to maintain and coordinate multiple relationships, monitor conspecific group members and outsiders, identify suitable cooperative partners, and outwit conspecifics in "Machiavellian" interactions [2,3] are a few of a number of challenges presented by the social environment that are argued to favour greater cognition. Although the SIH has empirical and theoretical support, a recent meta-analysis of 103 studies found that >40% of cognitive variation remains unaccounted for [4]. In contrast, the **Ecological Intelligence Hypothesis** (EIH) posits that cognition is shaped by the challenges of food acquisition, environmental variability and heterogeneity, and uncertain climatic conditions, which promotes the ability to recognise and respond to environmental cues [5-10]. Both the SIH and EIH have received significant empirical attention across the last 50 years but continue to return conflicting results across space, time, and taxa [7,11-13].

Another long-posited driver of cognitive variation is the interactions between predators and prey [14-16]. In their seminal paper exploring the evolution of intelligence, Byrne and Bates [14] stated that **predator-prey interactions** are an "ecological theory yet to be fully evaluated", which still largely holds true today. Other authors have considered predation as a confounding factor that limits causal inference when testing how sociality shapes cognition[17]. They argue that predation can drive spurious correlations, making it essential to account for its influence on sociality to fully understand the relationship. Some renditions of the EIH incorporate the interplay between hunting behaviour and cognitive evolution [18,19], suggesting that perhaps the need to acquire resources (prey) drove the emergence of predator cognition. However, predation is largely peripheral to the central predictions of the EIH, which focus on vegetative dietary diversity and environmental variability [13,20] and ignores how predation selects for cognition in prey. In predator-prey interactions, animals must rely not only on direct behavioural cues but also on indirect cues, that are intended to be hidden. This reliance on cryptic and indirect cues, and rapid response to direct cues (e.g., spotting a predator) presents a set of unique and complex cognitive demands that are not adequately captured by the EIH.

Predator-prey interactions are thought to drive cognitive variation via the cognitive challenges that accompany the processes of both hunting and avoiding predation. For example, in obtaining food or avoiding death an animal might rely on cue recognition, spatial and temporal memory of dangerous locations and times, response times and social hunting, and predator avoidance challenges such as group coordination and social learning (Figure 1). In some species, enhanced cognition is a clear driver of prey survival through avoidance of predation [21,22]. Additionally, exposure to high levels of predation drives increases in brain and telencephalon size in guppies (*Poecilia reticulata*) [23,24]. Further, female guppies with larger brains are better able to assess predation risk, reducing their time spent investigating predators prior to responding [25]. At a macroevolutionary scale, prey who have evolved physical antipredator defences (e.g., body armour and spines) show correlated reductions in brain size, suggesting that physical defences reduce the need for the advanced cognitive abilities required for behavioural predator avoidance [26].

Here, we provide a conceptual synthesis that unites concepts from the study of cognitive evolution and predator-prey ecology to form the *Predatory Intelligence Hypothesis* (PIH), which predicts predation as an important driver of cognitive variation at the individual, developmental, and evolutionary level. The PIH posits that the cognitive challenges associated with interactions with predators and prey create a co-evolutionary arms race that promote bidirectional enhanced cognition. Finally, we present key predictions and ways to test them, that span from individuals to species, from deep time to current day, about predation's role in the evolution of cognition and the maintenance of cognitive variation.

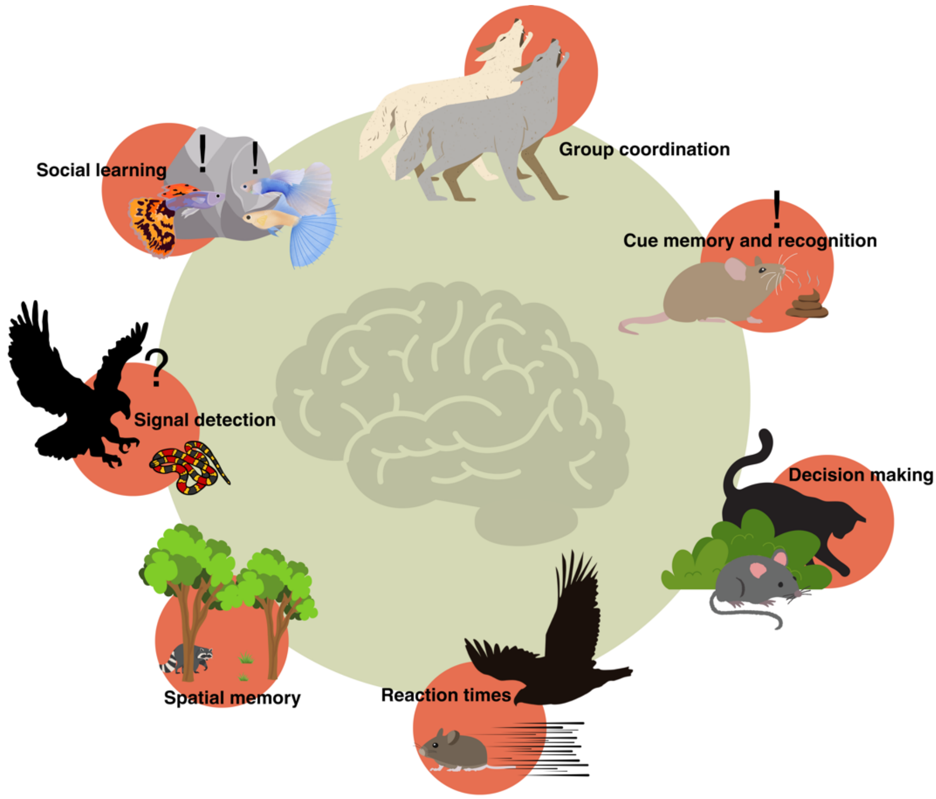

Figure 1. The cognitive challenges of predator-prey interactions. Predator-prey interactions remain largely unexplored as a driver of cognitive variation and evolution despite sharing key mechanisms with other predominant hypotheses of cognitive evolution. Predators and prey must learn to remember and recognise the olfactory, visual and auditory cues of the other member of the interaction [27,28]; prey must make decisions about when to hide, run and forage [29], while predators must make decisions about whether to attack aposematic and dangerous prey [30]. Each member of the dyad must evaluate the cues of the other to make an informed behavioural decision; prey are can be selected for their reaction times [22], the same is likely true for predators; and, predators and prey should remember the locations of the other member of the interaction to either avoid or force an interaction [21]. While only documented in prey [31-33], the ability to socially learn predatory and anti-predator behaviours are central to predator-prey interactions [34]; and, group coordination for hunting prey and avoiding predation presents a key social challenge that is shaped by predation landscapes [35-37].

Box 1. Glossary of key terms and concepts
Antipredator behaviour: any behaviour taken by prey to reduce the likelihood of being killed by a predator. **Bayesian updating:** the process by which individuals integrate new information to update existing knowledge. **Cognition:** the ways in which individual animals acquire, process, store, and act on information from the environment.

Cognitive performance: the success with which an animal solves a problem or learning task, including memory. Measures of cognitive performance may include latency to problem solving or the number of mistakes leading to problem solving.

Inhibitory control: An individual's ability to resist automatic urges.

Innovation: The development of a novel or modified behaviour.

Marginal Value Theorem: A model that describes how individuals make optimal foraging decisions under depleting resources.

Spatial memory: An individual's ability to remember locations and navigation pathways.

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.

Learning: An individual's ability to solve a task that is beyond simple instinctive behaviour (e.g., how to extract a food item).

Behavioural flexibility: The ability of animals to change their behaviour in response to new stimuli or changes in their environment or respond in novel ways to existing stimuli in their environment. A marker for advanced cognition.

Social Intelligence Hypothesis: A hypothesis that predicts that enhanced cognition evolved via the need to keep track of multiple individuals and/or monitor third party relationships and/or maintain complex social relationships.

Ecological Intelligence Hypothesis: A hypothesis that predicts that enhanced cognition evolved to aid animals in foraging and navigating complex and variable environments.

Giving-up density: A foraging experimental procedure that measures foraging decisions in individuals under varying risk conditions.

Predation pressure: A metric that describes the intensity of risk that predators pose to an individual.

The Predatory Intelligence Hypothesis

Predation is an evolutionary force that shapes almost every aspect of the lives of most animals. Animals cannot survive without finding prey or avoiding predation. Hence, predators are under strong selection to be efficient hunters, and prey are under strong selection to avoid predation, although there is substantial asymmetry in this selection [38]. Examples of this evolutionary force are evident when predators and prey are introduced into novel environments [39,40]. For instance, when predatory curly-tailed lizards (*Leiocephalus carinatus*) were introduced to small Caribbean islands, their potential prey, brown anoles (*Anolis sagrei*), became less bold and more arboreal, thereby significantly reducing their risk of predation [41]. For predators, novel prey can drive rapid behavioural [42] and morphological evolution [39], developing traits that promote increased hunting success. Predator-prey theory suggests the outcomes of predator-prey interactions are dependent on the capacity of both predators and prey to appraise each other's physical characteristics and intent, respond during encounters, and alter their behaviour based on previous encounters [27,43]. Perceiving and interpreting information about risk and reward are at the forefront of this coevolutionary arms race. The ability to detect information against background noise, filter information, and overcome stimulus ambiguity to respond appropriately are cognitively demanding [44]. Thus, large components of predatory and **anti-predator behaviours** require skills that are dependent on a significant amount of information processing [44]. Better **cognitive performance** - the ability to rapidly integrate information and respond appropriately – should offer a clear advantage in these life and death encounters [45-47].

Cognition can be an important predictor of prey survival and fitness [4,12,48-50]. African striped mice with enhanced cognition had faster reaction times to a cue of risk, a predator silhouette, and survive longer in the wild [22,50]. Additionally, grey mouse lemurs' (*Microcebus murinus*) combined **cognitive performance** score (calculated from performance in problem-solving, **spatial memory**, **inhibitory control** and causal understanding tasks) positively correlated with survival in the wild, where predators are the primary source of mortality [49]. Pheasants who exhibit enhanced spatial memory skills in the wild are better at avoiding predators [21]. Cognition can also influence anti-predator behaviour. Lab experiments have shown that female guppies with larger brains take less time to recognize and avoid predators [25]. For predators, it is thought that larger brains make predators better hunters due to improved cognitive performance [51]. Increases in the brain size of hominids in Africa corresponds with the decline of predatory megafauna, suggesting that improved cognitive performance may have allowed early humans to eradicate their competitors and predators [51], although this hypothesis is contested [52]. Since cognitive performance is a major predictor of prey survival, predation may have significantly influenced the evolution of cognition. Additionally, predation is likely to actively maintain cognitive variation as no two species, populations or individuals experience identical predatory conditions across their lifecycle. Prey populations living alongside diverse predatory guilds should be under stronger cognitive selection as they must recognise and respond to many different predatory cues predicting predation risk, while populations facing a single predator will have fewer cues to remember. By this logic, the cognitive demand of predator avoidance is substantially higher for prey in ecosystems with diverse predatory pressures. Thus, geographic variation in predatory regimes across a species range should create and maintain cognitive variation (Figure 2).

When cognition might not improve survival

While enhanced cognitive capacity confers adaptive advantages, maintaining a large brain is metabolically costly [53-55]. Brain size is influenced by life history traits due to energy allocation trade-offs. For example, investment in reproduction in terms of offspring number, offspring size, and frequency of reproduction can limit the energy available to maintain brain tissue, particularly in females [56]. Likewise, the metabolic costs of other life history traits such as longevity, growth rate and age at first reproduction may similarly be traded off against brain size, as part of an overall life-history strategy [57-61]. One explanation is that escape behaviour may be energetically costly and therefore, it pays to allocate energy to muscle tissues directly linked to physiological performance, such as swimming or running ability in circumstances where raw speed is all that is need to escape a predator [62,63]. The development of physical defences also reduces the need for large brains [26]. This may also be the case for species that rely heavily on crypsis to avoid detection by predators, or species that use pursuit deterrent signals which honestly signal either physiological performance or simply that a predator has been seen by potential prey [64]. In some species, anti-predator strategies may not require a high cognitive load (i.e., if fitness is largely independent of cognition). Understanding which species and traits correlate with enhanced cognition is a promising avenue for understanding evolutionary trade-offs driven by predator-prey interactions.

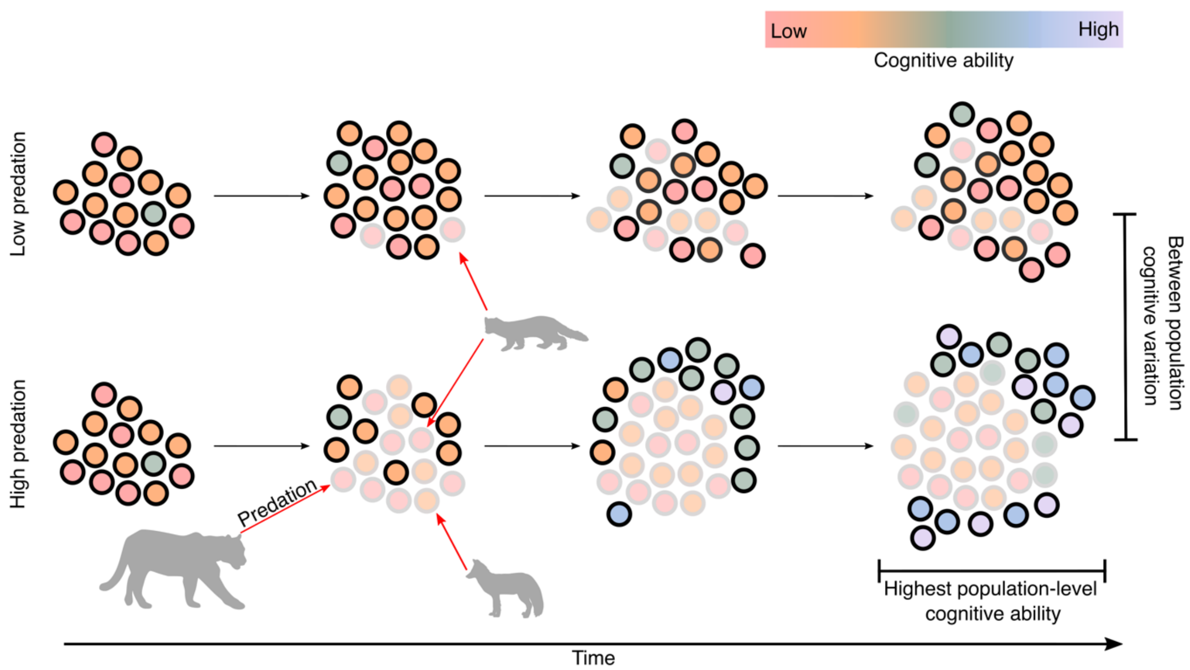

Figure 2. Predation as an evolutionary force shaping cognitive variation. Individuals are represented by the circles in each population, individuals who been predated are greyed out. Enhanced cognition is associated with increased survival and lower predation risk [21,49], suggesting that predation may select for cognitive performance. The two populations pictured above experience low and high predation pressure, selection for cognitive abilities is higher where predation pressure is diverse and amplified, promoting enhanced cognition and driving divergence from the low predation populations. Cognitive variation emerges as predators select for prey cognition differently within and between populations. Predatory functional complexity is therefore expected to generate and maintain cognitive variation among and between prey populations. We predict the same pattern to emerge for predators, but instead of predatory functional complexity, the functional complexity of prey is likely to drive cognitive variation, where hunting many functionally distinct prey species is likely to drive the emergence of enhanced cognition.

Mechanisms of selection on prey cognition

Prey are at an almost constant risk of being hunted – consequently, prey have evolved a suite of anti-predator traits and behaviours that increase their survival [64]. Anti-predator behaviours are behavioural adaptations allowing prey to avoid detection, evade attack, fight back, or escape predation [65]. The ability of prey to remember predator cues (olfactory, chemosensory, visual, vibrational, and auditory), identify and recall areas of high predation risk, learn from previous experiences, make decisions, and learn about predation from conspecifics are all cognitively demanding processes, thus cognition is the foundation of many anti-predator behaviours [17,27]. Prey must detect predator cues, integrate this information, and then respond appropriately. This process is constantly repeated through an individual's life, a process known as **Bayesian updating**. Individuals who are more readily able to integrate and react to new signals are likely to have an advantage when it comes to avoiding predation [34,44,66,67]. Further, individuals who can remember and learn when to be vigilant, when and where to flee or hide, and know when to not invest in these costly behaviours are likely to be selected for under predation risk. Cognitive abilities such as pattern recognition, learning ability, causal understanding and spatial memory are all likely to be highly advantageous under these conditions [44]. If cognition significantly reduces predation risk as some have suggested [14,34,49], cognition should provide a clear selective benefit where predation pressure is high.

Mechanisms of selection on predator cognition

Predators have also evolved behavioural strategies to maximise their hunting success and match the diel activity patterns of their prey, recognise prey cues, and use hunting strategies that exploit the morphological vulnerabilities of their prey [68-70]. Predators therefore depend on cognitive abilities such as pattern recognition, learning ability, and spatial memory, among others. The ability to recognise prey search image from the visual environment should allow predators to better detect and hunt prey [71]. Predators who are better able to recognise prey cues (e.g., prey scat) and remember the locations where prey congregate, or areas of previous hunting success are more likely to be successful hunters. Selection for cognitive capabilities may be strongest in predators hunting diverse guilds of different prey types, where predators must remember and integrate a wide variety of cues providing information about prey [28,72]. This may also apply to mimicry complexes, which can be highly diverse with varying levels of protection. For example, one mimicry complex in Australia contained 140 potential mimics from four arthropod orders that included ants, spiders, wasps, bugs and tree hoppers. These ranged from non-defended Batesian mimics to heavily defended Mullerian mimics with protection that included, to a varying degree, spines, cuticle thickness, stinging, mandible size, poison gland size, and aggressive behaviour/communal attack [73]. Mimicry complexes can thus represent polymorphic states, adding to the cognitive load required to navigate a landscape of highly variable prey, although our understanding of these systems is emerging. Nevertheless, in the context of predator cognition, many predators sample potential prey (mimics and models) and need to learn which traits signal distastefulness and at what point a signal may not be accurate or reliable, and whether or not to avoid these potential prey in the future, or, in some cases, how best to get past their defences [74-76]. Other cognitive abilities such as the ability to anticipate and plan for the future (mental time travel[77]) may help predators successfully subdue prey by aiding predators in predicting and responding to anti-predator behaviours. Enhanced cognitive abilities are therefore likely highly beneficial to predators in many contexts [18,78].

Additionally, selection on cognition may be stronger when prey are scarce as each failed hunt has a higher impact on an individual's probability of survival. This is outlined in the **Marginal Value Theorem**. When prey resources dwindle, predators should make optimal decisions around who and where to hunt, maximising their fitness in the process. Inevitably, no foraging is optimal and predators are likely to be selected for their abilities to recognise and respond to prey resource limitation [79]. Then, individuals who best integrate information about food scarcity and adjust their hunting behaviour accordingly are likely to survive.

Further, some prey species present distinct challenges to their predators. Hunting dangerous prey, for example, may be more cognitively challenging than hunting less risky prey. Dangerous prey can injure predators, potentially reducing their capacity to hunt in the future or even causing death [80]. This added fitness cost likely selects for predators with knowledge of how to hunt dangerous prey, the ability to plan ahead, and the judgement to abort risky hunts. Moreover, generalist predators – which hunt across different functional groups – may face greater cognitive demands than specialist predators [81], as generalists must remember the cues and locations of different prey, store multiple search images, and have memorised distinct hunting strategies – such as solo hunting for small prey and cooperative hunting for large, dangerous prey. Additionally, socio-cognitive traits in group hunting predators that co-operate may also be subject to selection, because individuals that effectively co-operatively hunt prey should derive fitness benefits [82]. Co-operative hunting is at the interface of the PIH and SIH because there should be both selection for the ability to track particular individual conspecifics and their roles in a hunt [83] and the ability to learn from past experience based on how prey behave in particular circumstances and thereafter make adjustments in future hunts. However, to the best of our knowledge, no studies have tested how cognitive abilities shape predator hunting success.

Predators and prey can become engaged in a coevolutionary arms race, where improvements in hunting or predator avoidance require corresponding **innovations** for either member of the pair to restabilise interactions [84]. One exceptional example of this arms race appears between garter snakes (*Thamnophis sirtalis*) and newts (*Taricha granulosa*). Newts have evolved to be highly toxic, deterring predation, in response to this garter snakes evolved a physiological resistance to this toxin, allowing consumption [85,86]. Where physiological and morphological traits may become fixed at adulthood, behavioural plasticity, underpinned by cognition [87], allows individuals to rapidly change their behaviour. The PIH proposes that those with the highest cognitive abilities may be able to engage in quicker and more appropriate behavioural shifts that promote enhanced performance in predator-prey interactions [34,88].

Predicting how predation shapes cognition

Byrne and Bates stated [14] "unfortunately estimating **predation pressure** is generally nigh-on impossible in most environments". While accurate at the time of writing (2007), we have made enormous strides to reduce this constraint. Over the past two decades, advancements in field-based methods - such as camera traps [89], animal-borne cameras, audio recorders, and biologgers [90] – have significantly improved our ability to estimate predation pressure. These methods allow for the tracking and detailed behavioural analysis of individuals during predator-prey interactions which can be correlated with cognitive performance. Recreating deep-time and pre-historic predation pressure has also advanced rapidly with the simulation of ancient predator-prey networks [91-94], allowing the quantification of the number of predators species prey co-existed with. Functional macroecology has also rapidly advanced in the past decade, which has allowed the modelling of historic and current day predation pressure via the traits of predators and prey [95], although these methods provide simple measures of predation (e.g., the number of predators present in a biome), lacking both spatial and temporal nuance of realised interactions. The modelling of ancient predator-prey networks allows the quantification of both the number of predator species a prey species share a coexistence history with and the calculation of the functional complexity of the predator guild (i.e., functional richness and functional uniqueness). Correlating brain size, as a proxy for cognition, with social or environmental variables [4,13,96] has been central to understanding how cognition evolved. With these advances in network and functional ecology, we can now quantify metrics of prehistoric ecological communities (number of predators and functional richness of the predator guild) and correlate these metrics with brain size to ask how predation has driven cognitive evolution through time. In summary, testing how predation shapes cognitive variation is more possible now than ever before. Below, we outline key questions to understand predation's role in the evolution of cognitive variation (Table 1).

Variation in cognition among species

The recreation of now extinct predator-prey interactions [94,97] through network analysis and interaction inference methods can help us understand how interspecific cognitive variation evolved [92]. Ecological networks are further complemented using the traits of these predators to ask whether prey who experienced functionally complex predation (i.e., both pounce-pursuit and ambush predation styles) evolved greater cognition. This can be done at the macroevolutionary scale, using phylogenetic comparative approaches [98,99], which are powerful tools for testing for the correlational evolution of traits. We hypothesise that experiencing predation from multiple predator guilds with distinctive hunting styles presents a greater cognitive burden for remembering and responding to cues and patterns than a single predator, or even multiple predators who are closely functionally related. This prediction is supported by the multi-predator and predator-archetype hypotheses [28,100], which state that individuals who live with multiple functionally similar predators generalise anti-predator responses across their predators. If prey live with a functionally diverse set of predators, anti-predator behaviour generalisation may be more cognitively challenging. Examples of this can be found in prey species that develop unique anti-predator behaviours for functionally diverse predators [101,102]. Developing strategies for the avoidance of multiple predators is likely to be more cognitively taxing than a single predator or predator archetype. This predatory functional diversity should thus select for prey with enhanced cognition as prey may have to craft anti-predator behaviours for each predator species [103,104] (Table 1).

A similar approach could be taken with predators who historically hunted many prey species with unique antipredator strategies. It has been hypothesised that animals who forage broadly exhibit enhanced cognition due to the cognitive pressures that come with hunting many functionally diverse prey across large and diverse habitats [7]. Using the network methods detailed above, one could extract the number of prey species a predators species evolved alongside and quantify their functional traits, facilitating the testing of whether functional complexity in historically hunted prey predicts the evolution of enhanced predator cognition. A logical hypothesis follows, that diverse prey guilds promote enhanced predator cognition; however, the presence of one particularly challenging prey species (dangerous, large bodied species) may predominantly drive this pattern given the enhanced selective pressure placed on predators by potentially lethal prey. Evaluating links between prey functional traits and measures of predator cognition are a promising avenue for improving our understanding of how predator-prey interactions shape cognitive variation and drive the evolution of intelligence.

Variation in cognition: from individuals to populations

We also have limited understanding of how predation shapes cognitive development through ontogeny. Similar to how the social environment can shape the cognitive abilities of individuals as they age (individuals living in larger groups exhibit enhanced cognition and improved fitness [12]), predation may have a comparable effect over an individual's lifetime. Juveniles, being the most vulnerable to predation, might be selected for cognitive abilities that promote predator recognition and avoidance. We suggest that developmental predation risk may drive the development of enhanced cognition as a mechanism to improve predator detection and avoidance, similar to how it influences physiological performance required for rapid escape [63]. Longitudinally testing individual cognition from juvenile to adulthood under varying predation regimes will provide insights into which cognitive traits are favoured in differing predation regimes, elucidating the developmental effects of predation on cognition. This approach can be applied to both predators and prey and could be achieve through the cross fostering of eggs in avian or reptilian systems across areas of high and low predation regimes.

Recently, cognitive ecologists have become increasingly interested in individual cognitive variation. By unpacking the drivers of individual variation in cognition, we can address questions that tackle both proximate and ultimate questions surrounding cognitive evolution. This could be done by combining cognitive test batteries with predation risk experiments such as **giving-up density** [105,106] or playback experiments [107]. Combining predation risk experiments and cognitive testing allows for investigation of the mechanisms behind the correlations between enhanced cognition and improved survival in the wild. Both islands and conservation havens are fruitful systems for these questions, where one could ask how predation risk shapes the spectrum of intraspecific diversity in cognitive abilities. As mentioned above, how predator cognitive phenotypes shape hunting performance is an unexplored avenue of research. This means that understanding which cognitive traits enhance hunting success and identifying any mechanisms involved is an important first step. Methods such as GPS tracking and animal-borne video may help identify predation success. Ideal study species should generally be solitary where possible to disentangle individual from group hunting success.

Variation in cognition among prey populations may emerge through context specific predation pressures. Islands are ideal systems for studying how predation influences cognitive evolution because they offer simplified trophic networks, and they can vary naturally in predator and prey species distribution [40-42]. Additionally, there is a growing number of fenced conservation reserves, where prey are either separated from their predators or live under different predator treatments (e.g., native predators only and predator-free) [108,109]. These fenced reserves can function as islands for comparison. Ideally, intraspecific cognitive comparisons should occur across areas of similar environmental complexity as to avoid introducing environmentally driven cognitive selection. It has been hypothesised that lower dietary diversity on smaller islands contributes towards reduced brain size and cognitive performance in predators [110]. Fewer species to hunt may equate to fewer cognitive challenges on islands compared to the mainland, thereby reducing the strength of cognitive selection. This may result in mainland populations exhibiting enhanced cognition compared to those on islands.

Table 1. Key predictions under the Predatory Intelligence Hypothesis. We have opted not to list specific brain regions that could be targets of selection because the Predatory Intelligence Hypothesis can be applied across a broad diversity of taxa with a wide range of brain morphology (e.g., invertebrate vs vertebrate); however, individual studies may wish to make brain

region-specific predictions based on their study species. The same applies to the genes and neurotransmitters that may underlie antipredator behaviour.		
Predictions	Rationale	Systems/methods
Both predators and prey		
Behavioural flexibility, cooperation, spatial memory, and associative learning abilities are positively associated with predatory and anti-predatory success.	Behavioural flexibility allows individuals to rapidly respond to changing circumstance while hunting and avoiding predation. Cooperation facilitates more effective hunting and defence. Spatial memory allows better memory of beneficial locations. Associative learning allows individuals to better gather and incorporate information.	Populations and individuals: Cognitive test protocols paired with biologgers and foraging or avoidance experiments to correlate a cognitive trait with a predatory (number or diversity of prey consumed) or behavioural outcome (reduced foraging in presence of predatory cue). There is also opportunity to test this on captive-raised animals such as guppies (split clutch design) exposed to different levels of simulated predation from different predator types followed by brain imaging and processing.
Prey		
Prey under risk of predation from multiple, functionally distinct predators will exhibit enhanced cognition compared to those experiencing predation risk from few or a single predator.	The challenges associated with increasing predatory functional complexity – e.g. learning and remembering the cues of multiple predators – selects for greater cognition.	Species: Network analysis methods that quantify predation pressure paired with brain size measurements. Populations and individuals: comparisons across islands or conservation havens with different predator numbers.
Associative learning, spatial memory and causal understanding abilities including the neural architecture, neurotransmitters and genes that promote these abilities are positively associated with appropriate anti-predator behaviour.	An improved ability to associate cues with risk, remember locations of previous risk and associate predation with mortality risk offer prey fitness benefits. Enhanced cognition should allow individuals to respond more quickly and appropriately.	Populations and individuals: cognitive testing protocols paired with predation risk experiments such as giving-up densities or playback experiments.
The evolution of cognition is linked to predation risk through time.	Increased functional predator diversity should be associated with enhanced cognitive ability in prey. This creates both intra- and interspecific variation in cognition	Species: Network analysis methods that quantify predation pressure and can map shifts in predation pressure and community assembly. Network

	across space and time. Across time, brain size is one metric of cognitive ability that should change bidirectionally (increase/decrease) in response to higher or lower predator diversity.	metrics can be paired with brain size measurements.
Predators		
Generalist predators who hunt the highest numbers of functionally distinct prey will exhibit enhanced cognition compared to predators more specialised to fewer prey types.	The challenges associated with increasing prey functional complexity – e.g. learning and remembering multiple predator-avoidance strategies – selects for greater cognition.	Species: Network analysis methods that quantify the number of prey predators hunt paired with brain size measurements. Populations and individuals: comparisons between areas where predators hunt prey communities with varying functional complexity
Mesopredators will exhibit enhanced cognition compared to apex predators.	Individuals that both hunt and avoid predators (i.e., mesopredators) should experience stronger selection on cognitive ability and associated traits.	Species: Network analysis methods that quantify the predation risk and prey mesopredators experience and hunt paired with brain size measurements. Populations and individuals: cognitive comparisons between ecologically similar apex and mesopredators (e.g., among the canids).
Predators that hunt co-operatively have greater cognitive ability (behavioural flexibility, inhibitory control, spatial learning, associative learning) than similar sized predators that hunt alone.	Co-operation in a dynamic situation such as a co-operative hunt (e.g., chimps hunting colobus monkeys) likely requires greater cognitive ability than hunts involving a single predator.	Species: cognitive comparisons between closely related species that do and do not cooperatively hunt (e.g., group hunting and solitary hunting felids).

Conclusions

A key issue in psychology, behavioural and evolutionary ecology, and allied disciplines is how we explain the extensive variation evident in cognitive ability and proxies thereof, such as brain size, in a wide range of taxa, including at the population and individual level. Well established hypotheses such as the SIH and EIH provide important explanatory power to account for variation in cognitive ability, but overall, they fall short in many systems. We describe the *Predatory Intelligence Hypothesis* (PIH), formalising the role of predator-prey interactions as a driver of cognitive ability. We have listed a series of testable predictions and discussed how technological advances in monitoring behaviour in the wild may be leveraged to improve our understanding of the factors driving cognitive ability. We hope that by formalising the PIH, we will stimulate new research to address variation in cognitive ability that is currently unaccounted for.

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