

## Review

## Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence?

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**Intelligence in large-brained vertebrates might have evolved through independent, yet similar processes based on comparable socioecological pressures and slow life histories. This convergent evolutionary route, however, cannot explain why cephalopods developed large brains and flexible behavioural repertoires: cephalopods have fast life histories and live in simple social environments. Here, we suggest that the loss of the external shell in cephalopods (i) caused a dramatic increase in predatory pressure, which in turn prevented the emergence of slow life histories, and (ii) allowed the exploitation of novel challenging niches, thus favouring the emergence of intelligence. By highlighting convergent and divergent aspects between cephalopods and large-brained vertebrates we illustrate how the evolution of intelligence might not be constrained to a single evolutionary route.**

### Cephalopods Intelligence: an Evolutionary Conundrum

Cognitive complexity varies dramatically across species, from simple reflexes to sophisticated **intelligence** (see [Glossary](#)) supporting high **behavioural flexibility**. Traditionally, primates have been considered the pinnacle of cognitive complexity, thus representing the primary target for investigating the evolution of intelligence. Evidence collected in monkeys and apes led to specific hypotheses about the conditions favouring the emergence of intelligence. Firstly, primate intelligence has thought to have evolved as an adaptation to cope with particularly challenging socioecological niches ([Box 1](#)). Two key factors are considered to have driven this adaptation: the need to find and process food (Ecological Intelligence Hypothesis [[1–3](#)]), and the demands of complex social bonds (Social Intelligence Hypothesis [[4–6](#)]). Second, the positive correlation between brain size and the long developmental trajectory reported in primates [[7](#)] suggests a coevolutionary scenario for the evolution of these traits. The slow life history might have been necessary to overcome the costs of a large brain and/or a consequence of the reduced extrinsic mortality resulting from enhanced intelligence [[8,9](#)].

More recently, indicators of complex cognition have been reported in distantly related lineages, most notably cetaceans, elephants, corvids, and parrots [[10–12](#)]. This discovery allows us to investigate the evolution of intelligence beyond primates and thus deepen our understanding of this process. Differences in evolutionary history and brain structure between apes and these taxa suggest that (i) intelligence emerged multiple times independently [[13](#)]; and (ii) distinct neural substrates such as the avian nidopallium and the mammalian cortex, can support equivalent cognitive sophistication [[14](#)]. Despite these differences, the socioecological challenges faced by cetaceans, elephants, corvids, and parrots appear to be comparable to those of apes. Thus, intelligence might have evolved convergently in these groups in response to similar selective pressures [[10–12](#)]. Furthermore, as with primates, a tight link between brain

### Highlights

The most influential views on the evolution of intelligence suggest that intelligence coevolves with slow life history in response to socioecological challenges; however, these conclusions are primarily focused on large-brained vertebrates.

Cephalopod molluscs strongly challenge the most accepted hypotheses on the evolution of intelligence: cephalopods evolved complex brains and high behavioural flexibility together with fast life histories and in simple social environments.

Surprisingly, the evolution of intelligence in cephalopods has been largely overlooked, thus leaving this evolutionary conundrum unsolved.

Discussing differences and similarities between cephalopods and large-brained vertebrates, may shed light on fundamental aspects of the evolution of intelligence.

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**Box 1. Main Hypotheses for the Evolution of Intelligence**

The most accepted hypotheses for the evolution of complex cognition can be divided into two categories. The Ecological Intelligence Hypothesis suggests that complex cognition evolved to meet the challenges associated with finding and processing food [1–3]. Specifically, features such as spatiotemporally dispersed food, generalist diets, and extractive foraging are considered key drivers in this process. Conversely, the Social Intelligence Hypothesis accredits the evolution of intelligence to the demands of group living, such as maintaining complex and enduring social bonds, deception, cooperation, or social learning from conspecifics [4–6]. To date, support for both the Ecological Intelligence Hypothesis [96–99] and the Social Intelligence Hypothesis [100,101] has been demonstrated in different groups, mainly among mammals and birds. It must be noted however that these hypotheses are not mutually exclusive *per se* and that more recent approaches have worked towards frameworks accounting for both ecological and social pressures [68,102].

It has also been proposed that intelligence might have arisen as a cognitive adaptation to cope with the challenges of predator–prey interactions [86,103–105]. Capturing prey and avoiding predation have dramatic fitness consequences. Thus, it is not hard to imagine how complex cognition allowing flexible behaviours in these domains could be subject to strong positive selection. According to some authors, the cognitive challenges of predator–prey dynamics can be equivalent to those required to compete with group members as in both cases they require interactions with another individual pursuing personal gains [86]. This hypothesis has been discussed for primates [103] and supported from investigations in distinct groups such as fish [106,107], carnivores, and herbivores [108,109].

size and slow life history also exists in birds and other mammals [15,16]. Therefore, similar evolutionary trade-offs might have acted during the evolution of intelligence in distantly related groups of vertebrates.

This convergent evolutionary route, however, cannot explain why intelligence evolved in cephalopods (Figure 1). Coleoid cephalopods (cuttlefish, squid, and octopuses) are shell-less molluscs that are considered among the most cognitively advanced group of invertebrates. They evolved a unique mixture of convergent and divergent features relative to the main groups of intelligent vertebrates (Table 1). On the one hand, cephalopods are endowed with a sophisticated nervous system, which both resembles that of vertebrates in relative size [17] and complexity [18,19] and supports strikingly flexible behavioural repertoires [20–23]. On the other hand, cephalopods do not appear to engage in complex social bonds [24], and have fast life histories with typical lifespans shorter than 2 years, no parental care, and in some cases, terminal reproduction [25].

Here, we present the current reports of behavioural convergence in cephalopods and cognitively advanced vertebrates. We also discuss the factors leading to the emergence of intelligence and fast life histories in cephalopods, highlighting the convergent and divergent aspects between cephalopods and large-brained vertebrates. We contend that vital insights into the evolution of intelligence can be gained by investigating cephalopod cognition.

**Behavioural Convergence**

Intelligence cannot be measured directly, thus, it is typically estimated through morphological and behavioural proxies; namely brain features, and behavioural flexibility. Although different in many aspects, cephalopod brains resemble those of vertebrates in relative size and complexity (Box 2). However, because the cognitive underpinnings of behavioural flexibility have rarely been investigated in this group (although, see [26,27]), current evidence does not allow a fine-grained assessment of intelligence in cephalopods. Flexible behaviours can be supported by simple cognitive mechanisms [28–30], thus, the interpretation of behavioural evidence for intelligence in cephalopods requires caution. Nevertheless, the behavioural convergence between cephalopods and intelligent vertebrates appears remarkable. Below, we highlight the most striking evidence of behavioural flexibility and why these behaviours might require complex cognitive mechanisms.

**Glossary**

**Behavioural flexibility:** the capability to alter a behaviour according to different circumstances, on the basis of previous experience (e.g., learning) or using causal knowledge [124].

**Body pattern:** the combination of chromatic, textural, postural, and locomotor components exhibited by an individual cephalopod at any given moment [23].

**Composite tool:** Two or more tools are manipulated simultaneously to achieve a single outcome [125].

**Flexible tool use:** tool-use behaviours requiring individual and/or social learning to be expressed proficiently, and allowing solving multiple problems through the manipulation of different tools [126].

**Innovation:** ‘the process that generates in an individual a novel learned behaviour that is not simply a consequence of social learning of environmental induction’ [127].

**Intelligence:** the collection of sophisticated cognitive abilities, such as problem solving, complex social cognition, and future planning.

**Semelparity:** reproductive strategy that encompasses a single reproductive cycle before the death. Semelparity differs substantially from iteroparity, whereby individuals undergo multiple reproductive cycles in their life span.



## Trends in Ecology &amp; Evolution

Figure 1. (A) Cuttlefish *Sepia officinalis* (credit egiverga, stock.adobe.com). (B) Caribbean reef squids *Sepio-teuthis sepioidea* (credit kirk, stock.adobe.com). (C) Nautilus *Nautilus pompilius* (credit carljf, stock.adobe.com). (D) Common octopus *Octopus vulgaris* (credit Piero Amodio).

## Box 2. Nervous System of Cephalopods

Cephalopods have a remarkably large nervous system (up to 500 million neuronal cells in the octopus) that comprises a unique mixture of classic molluscan features and more complex vertebrate-like traits [110]. The brain is formed by the aggregation of several ganglia (i.e., lobes) that show the typical neuronal arrangement of invertebrates, with cell bodies surrounding internal layers of synaptic connections [111]. However, the relative size of the cephalopod brain (corrected for body size) [17] and the high density of interneurons resemble that of some vertebrates [19,112,113].

The number and function of the lobes differ substantially across cephalopods, depending on species-specific lifestyles [114]. Among the various lobes that constitute the cephalopod brain, the vertical lobe plays a pivotal role in learning and memory in all coleoids [60,115], and has been compared to regions of the mammalian cortex and avian nidopallium [113,116]. In contrast to birds and mammals, the processing of motor and sensory inputs in cephalopods is only partially dependent on the central brain. The optic lobes, a pair of large nervous structures located outside the cartilaginous capsule of the brain and connected to the retinae of the lens eyes, are essential for the computation of visual input [113]. Furthermore, the processing of chemotactile information and of the motor programmes is performed through the concerted action of higher centres (i.e., the inferior frontal lobe system, [19,113]) and the nervous system of the arms. In the octopus, the peripheral neural components encompass up to 60% of the total number of cells and embed the neural information for the execution of basic movements of the arms [117] in a stereotyped autonomous way as in natural motions [118]. Thus, the nervous system of cephalopods represents a striking example of embodied organization, in which the central brain acts as a decision-making unit that integrates multimodal sensory information and coordinates the motor commands executed by the periphery. These idiosyncratic features of the nervous system as well as the suggested lack of somatotopic organisation of the central brain [119] (however, see [22,110]) might have evolved to allow cephalopods to cope with the computational constraints associated with the molluscan body plan and physiology (e.g., coordination of flexible appendages) [110,117].

Table 1. Convergent and Divergent Features between Cephalopods and Large-Brained Vertebrates<sup>a</sup>

	Trait	Cephalopods	Corvids	Cetaceans	Apes
Morphology	Manipulative appendages	Suckered arms and tentacles	Beak and feet	Rostrum	Hands
	Dexterity	High	High	Limited	High
Senses	Vision	High	High	High	High
	Acoustic	Limited	High	High	High
	Smell chemotactic	High	Limited	Limited	Limited
Brain	Brain–body size ratio	High	High	High	High
	Substrate for complex cognition	Vertical lobe	Nidopallium	Cortex	Cortex
Ecology	Lifestyle	Aquatic	Flight	Aquatic	Terrestrial/arboreal
	Diet	Carnivores	Generalistic	Carnivores	Generalistic
	Extractive foraging	Present	Present	Absent	Present
	Predation	High	Limited	Limited	Limited
Social Life	System	Solitary/anonymous schools	Pairs/groups	Family groups	Groups
	Long-term bonds	Absent	With pair mate	With multiple individuals	With multiple individuals
Behavioural flexibility	Find and process food	High	High	High	High
	Social interactions	Limited?	High	High	High
	Predator avoidance	High	?	?	?
Life History	Lifespan	0.5–2 years	>15 years	>40 years	>40 years
	Parental care of offspring	Absent	Present	Present	Present
	Reproduction	Semelparous strategies	Iteroparity	Iteroparity	Iteroparity

<sup>a</sup>The colours of the cells refer to traits that are variable across the groups (blue), or shared (green) or not shared (orange) between the cephalopods and groups of vertebrates.

### Problem Solving and Tool Use

Problem solving and **flexible tool use** are considered hallmarks of physical intelligence [1,31]. Cephalopods, particularly octopuses, show considerable skills in these tasks. In the wild, octopuses express high flexibility in solving demanding problems, such as feeding on bivalves. According to the size and species of the prey, these animals can use their suckered arms to pull open the valves or drill holes through the shell to inject paralyzing toxins into the prey [32]. These extractive foraging techniques are thought to improve with experience (e.g., the number of holes drilled in the shell) [22]. Like tool use in corvids [33], learning can play a key role in octopus problem solving by allowing the fine tuning of innate predispositions. Critically, octopuses exhibit flexibility not only in solving problems in their natural environment, but also when faced with artificial tasks. For instance, octopuses remove lids from jars and open opaque boxes to acquire hidden prey [34,35], as well as retrieve L-shaped food containers from crevices, with or without visual access to the container and regardless of the spatial orientation of the container [36]. Crucially, the performances of the octopuses in these experiments were incompatible with simpler learning mechanisms (e.g., trial and error) [34,36], supporting the idea that problem solving might entail more complex cognitive abilities.

Just like some species of apes, cetaceans, and corvids, some cephalopod species are tool users. These animals squirt water jets from their funnels (using water as a tool) for a variety of

purposes: to distance scavenger fishes, aid burrowing or remove food remains [37]. These behaviours are unlikely to represent stereotyped actions triggered by undesired stimuli because they are also performed during interactions with floating objects that have been classified as play [38]. In addition to water, octopuses also use solid objects as tools. Several species use stones to block the entrance of their den [39]. Furthermore, veined octopuses assemble pairs of coconut shells into mobile dens and carry them around for future use [40]. This rare example of **composite tool** use in invertebrates might be evidence of complex intelligence for two reasons. First, this tool use might represent a behavioural **innovation** allowing octopuses to protect themselves from predator attacks in habitats where rocky shelters are scarce. Second, because coconut shells are transported to meet apparent future needs and through considerable costs (e.g., conspicuous locomotion), this behaviour might rely on planning capabilities [40]. However, future controlled experiments are required to exclude lower-level explanations (e.g., coconut shells are carried because they became associated with a positive outcome, such as a thwarted attack by a predator).

### Antipredatory Behaviours

The camouflage abilities of cephalopods are perhaps the most iconic evidence of their behavioural flexibility. Through the neuromuscular control of peculiar skin organs (e.g., chromatophores), these animals can alter their **body patterns** almost instantaneously to deceive predators [41,42]. By changing the colour and the texture of their skin, cephalopods can mimic dangerous heterospecifics (e.g., sea snakes [43]) and achieve different kinds of camouflage (e.g., crypsis, countershading, and masquerade) [23]. Cephalopods adjust their antipredatory strategies not only to the features of the substrate [44,45] but also to the type of threat. For instance, young cuttlefish express false eyespots towards visual predators but perform immediate flee responses towards chemosensory predators [46]. Similarly, cuttlefish and squid conceal themselves on the substrate when approached by pelagic fishes but flee away from the bottom when ambush predators are detected [47,48]. The recent discovery that cephalopods change their appearance (e.g., break camouflage) to receive food rewards [49] suggests that these antipredatory responses are not entirely hard-wired but instead entail learning and complex decision-making.

Future research might uncover further antipredatory strategies that are candidates for complex cognition. The BBC Blue Planet II series recently showed a common octopus using its suckered arms to create spherical armour of stones and shells against hunting sharks [50]. This behaviour is functionally similar to the use of coconut shells as a tool by the veined octopuses and might provide further insight into the flexibility of their antipredatory behaviours.

### Social Behaviour

Although cephalopods primarily evolved dynamic skin as an antipredatory weapon [17], their ability to rapidly alter their appearance is also used to communicate visually with conspecifics [23,51]. This sophisticated communication system allows cephalopods to convey honest and deceptive signals simultaneously. By longitudinally splitting the body into two parts, small male cuttlefish can express courtship displays towards a receptive female on one side of their body and deceptive female colourations towards a rival male on the other side of their body [52]. Male mourning cuttlefish have been reported to use this strategy only in front of one female and a single rival male, perhaps because the effectiveness of the female mimicry will be impaired in the presence of multiple males [52]. In a similar vein, male giant cuttlefish adjust their fighting strategy in response to the size and fighting ability of their competitor [53]. Comparable levels of flexibility in a mating context are also observed among octopuses. In algae octopuses, males adjust their mating tactics to their chances of winning agonistic encounters. Specifically, males

avoid mate guarding if larger rivals are around to minimise the risk of fights and of being cannibalised [54].

Behavioural flexibility of cephalopods in social contexts might extend beyond competitive interactions with conspecifics. Preliminary observations indicate that reef octopuses associate with hunting groupers in the Australian Great Barrier Reef [55,56]. In addition, groupers employ the same visual signal to communicate the location of hidden prey to their usual hunting partners, moray eels, and to octopuses [55]. On a superficial level, these interspecific interactions might look like cooperative hunting based on the complementary skills of the two species: speed for chasing prey in open water by the grouper, and capability of reaching prey hidden in narrow crevices by the octopus. Critically, however, no predation by an octopus has been observed in this context, thus, this interpretation remains speculative. Nevertheless, these observations indicate that hunting might provide one useful context within which to investigate the behavioural flexibility of cephalopods in social interaction.

### Route to Intelligence of Cephalopods

If the above examples of behavioural flexibility in cephalopods can be taken as evidence for a high level of intelligence, then it is necessary to consider why cephalopods, as short-lived invertebrates, should evolve intelligence. The answer to this question is likely to be tightly linked to the dramatic changes in the shells that marked divergence of cephalopods from other molluscs.

Around 530 Mya [57,58] a group of snail-like molluscs experienced a major shift in their morphology and physiology: their protective shell became a buoyancy device. The comparison with nautilus, the only extant cephalopods that retained the external shell, suggests that this key event co-occurred with the emergence of arms, funnel, and crucially, a centralized brain [17,59,60]. The increase in computational power at this stage might have been selected to support arm coordination for locomotion and object manipulation [17,61], as well as navigation in the water column and basic learning processes [62]. Next, around 275 Mya [57,58] the external shell was internalised (in the ancestors of cuttlefish and squid) or lost (in those of octopuses). It has been speculated that competition with marine vertebrates [17] was a driving factor that led to dramatic changes in the lifestyles of these animals (however, see [63]). First, the disappearance of the external shell allowed animals to occupy a wide array of ecological niches. Consequently, modern cephalopods are found in all marine habitats, from tropical to polar waters, and from benthic to pelagic niches [64]. Second, the loss of the protective shell drastically increased predatory pressures and consequently the rates of extrinsic mortality. These novel ecological conditions might not have only played a major role in the emergence of sophisticated biological adaptations (e.g., lens eye, and chromatophores) but also in the coevolution of intelligence and fast life history of cephalopods.

### Which Factors Drove the Evolution of Intelligence in Cephalopods?

The Ecological Intelligence Hypothesis (Box 1) posits that intelligence evolves in response to challenging foraging niches. Cephalopods face ecological problems that are comparable to those of apes and corvids. First, cephalopods exhibit a high level of diet generalism. For instance, South African common octopuses predate on more than 35 species, including crustaceans, gastropods, fishes, other cephalopods, and even conspecifics [65]. Second, cephalopods prey on ephemeral resources that require substantial periods of exploration to be spotted and seized. In the wild, octopuses avoid visiting the same spots that were depleted on previous days [66], suggesting that they need to flexibly update their memory to optimise food-searching activities [24].

Finally, octopuses rely extensively on extractive foraging to feed on bivalves and extract prey from crevices. Extractive foraging is considered a key factor in the evolution of intelligence because these techniques (i) are typically more costly (e.g., due to learning and higher predation risk associated with long-lasting procedures) than alternative foraging strategies; (ii) might require cognitive complexity (e.g., innovativeness) to be developed; and (iii) allow individuals to cover the high energetic demands of large brains [67,68]. Therefore, the ecological challenges faced by cephalopods indicate that the Ecological Intelligence Hypothesis can be an appropriate framework within which to study the evolution of intelligence in this group [61,69].

According to another influential view, intelligence evolves as a cognitive tool to compete with, cooperate with, or learn from conspecifics (Social Intelligence Hypothesis; Box 1). Some cephalopod species live in simple social environments encompassing large but anonymous aggregations (e.g., squid), while others appear to experience only sporadic social interactions (e.g., octopuses) [24]. Thus, they do not engage in complex social bonds like those between mated partners in corvids [70] or group members in apes and cetaceans [71,72]. Building on this, one might conclude that cephalopods have not faced sufficiently challenging social problems to trigger the emergence of intelligence. However, our understanding of the social pressures experienced by different cephalopod species is still very sparse, and therefore a detailed evaluation of the Social Intelligence Hypothesis in this group might be premature.

Although octopuses are typically described as strictly solitary animals [23,24], recent studies have reported long-term occupancy of clumped dens and frequent social interactions in some populations [73–75]. Mated partners have been observed sharing dens and food in the Larger Striped Pacific Octopus [76]. Furthermore, an important consideration here is that different kinds of social challenges might have participated in shaping cephalopod cognition. The mating system of these molluscs is characterised by high promiscuity [77] and short reproductive periods [25,78]. In addition, cannibalism is widespread among cephalopods [79]. These animals have evolved several behavioural and morphological features (e.g., mating tactics [80], mating position [81,82], and secondary sexual traits [83]) to reduce the risk of cannibalism during mating. It is, therefore, possible that large brains supporting fast decision-making and flexible mating strategies [52,54] might have emerged in cephalopods to navigate challenging reproductive environments, in which mating attempts can become fights for life.

A third hypothesis suggests that intelligence can emerge in response to the challenges exerted by predators (Box 1). Lacking a protective shell, cephalopods are vulnerable to a wide range of predators (e.g., cetaceans, seabirds, fishes, and other cephalopods) [23,84] that differ substantially in their sensory ecology and hunting strategies (e.g., acoustically, visually, and olfactory-guided). It is accepted that cephalopod evolution has been influenced by high predation pressures exerted by marine vertebrates [17,58]. An iconic example of this is the sophisticated camouflaging behaviour of cephalopods, facilitating rapid and effective concealment from visual predators despite being colour blind [85]. Predator attacks can have dramatic fitness consequences and predator–prey interactions can be as cognitively challenging as intraspecific interactions [86]. Consequently, predation risk might have played a crucial role in the evolution of cephalopod intelligence.

#### Why Cephalopods Did not Evolve Slow Life History?

Traditionally, the evolution of fast life histories in cephalopods has been attributed to physiological constraints (e.g., inefficiency in fat storage metabolism, and high energetic cost of jet swimming) [87]. Focussing on ultimate causes, there might be a complementary interpretation. Fast life histories and **semelparity** are favoured in species with high extrinsic

mortality because high investment in early reproduction is the safer strategy when chances of survival are low in adulthood [88]. By increasing the rates of unavoidable mortality due to predation, the loss of the protective shell might have favoured early senescence, thus preventing slow life history trajectories in cephalopods. The opposite trend might have characterised the evolution of large brained vertebrates (Box 3). A few lines of evidence support this view.

First, cephalopod species experiencing reduced predation have unusually slow life histories. For instance, having retained the protective shell, nautilus live up to 20 years and reproduce several times during their life [89]. Furthermore, as highlighted by Godfrey-Smith [61], the scarcity of predators in abyssal habitats [90] can explain why vampire squids have multiple reproductive cycles [91] and why deep-sea octopuses have the longest egg-brooding period ever reported in the animal kingdom (>50 months, [92]). Second, a negative correlation between longevity and predatory pressure can also be seen in other groups, such as bivalves [93] and social insects [94]. Finally, in opisthobranch molluscs, several groups have lost their protective shell independently from cephalopods. These key events favoured the evolution of sophisticated defence strategies (e.g., crypsis, synthesis of toxic metabolites, and storage of cnidocysts) and crucially, fast life histories in opisthobranchs [95]. Interestingly, opisthobranchs did not evolve large brains and flexible behaviour. This difference between opisthobranchs and cephalopods might, in some cases, be explained by the increase in brain size and complexity that preceded the disappearance of the shell in the latter. Albeit, some groups of opisthobranchs might have lost their shell after the development of alternative defence mechanisms, in other groups, the disappearance of the shell might have pre-dated the emergence of alternative

### Box 3. Predation, Life History and Intelligence in Vertebrates

Predation risk might have played a major role in the coevolution of intelligence and fast life histories in cephalopods. However, it might also have had a significant impact on the evolution of large-brained vertebrates, both directly and indirectly [105].

Dunbar and Schultz [68] have suggested that predation was the main driver for group size in primates. Larger groups then created a demand for enhanced cognitive complexity to cope with the more challenging social environment, thus favouring ecological intelligence to meet the energetic demands of larger brains. If this was the case, then in contrast to cephalopods, predation might have represented an indirect driver for the emergence of intelligence at the initial stage. In addition to group living, other antipredator adaptations such as arboreality, large body size, and flight might have reduced extrinsic mortality in apes, cetaceans, elephants, corvids, and parrots [120], thus favouring the coevolution of slow life histories and intelligence.

Subsequently, key features of slow life histories, such as high investment in a limited number of offspring and long periods of dependency might have resulted in higher demands for cognitively complex antipredator strategies. Since young dependent offspring are subject to higher predation rates [72] (e.g., due to weaker motor coordination, smaller size, and less experience) than adults are, there might be strong selection pressure on the intelligence of the parents to protect offspring from predators. Such selection pressure can explain, for instance, the emergence of complex group coordination in cetaceans to fight against predatory assaults on calves [72]. Thus, at a later stage, predation on offspring might have acted as direct pressure for the evolution of intelligence in large-brained vertebrates. If so, predation might have favoured the evolution of both cognitive (e.g., intelligence) and noncognitive (e.g., life history) adaptations in large-brained vertebrates and in cephalopods – albeit through different evolutionary pathways.

It must also be noted that adult apes, cetaceans, corvids, and parrots are not exempt from lethal aggression from predators. Thus, it cannot be excluded that predatory pressures in adulthood also participated in shaping their cognition. Supporting this idea, complex communication systems allowing the signalling of distinct kinds of predators have evolved in arboreal primates [121]. Furthermore, it has been recently shown that crows can identify new predators according to their proximity to dead conspecifics [122] and other corvids avoid areas in which a dead conspecific was spotted and actively share this information with other individuals [123]. Hence, it is likely that predation risk on adults might also have participated in selecting intelligence in large-brained vertebrates.



defence strategies (e.g., toxicity) [95]. Thus, lacking a sufficiently complex brain, opisthobranchs might have been constrained to evolve noncognitively, demanding adaptations to cope with novel ecological niches. In contrast, similar conditions might have favoured a further investment in brain growth in cephalopods. Consequently, the camouflage behaviours of cephalopods might require more enhanced cognitive complexity relative to the antipredatory strategies in opisthobranchs.

### Concluding Remarks

The coemergence of flexible behaviour and large brains, together with fast life histories in cephalopods, appears to be, at first, an evolutionary conundrum. In line with Godfrey-Smith [61], we have suggested that this apparent paradox can be explained by analysing the evolutionary history of these animals. The disappearance of the protective shell (i) produced a dramatic increase in unavoidable mortality thus selecting fast life histories, the evolution of alternative protective devices, and, in parallel (ii) facilitated widespread colonization of complex niches, thus driving cephalopods to cope with novel challenging problems. Cephalopod intelligence might have emerged primarily in response to predation and complex feeding contexts. However, social challenges, particularly during mating, might have acted as additional selective pressures in the evolution of their intelligence.

Taken together, cephalopods and large-brained vertebrates might have evolved intelligence through alternative routes in response to partially different pressures and in association with opposite life histories. Thus, the investigation of cephalopods has the potential to unravel new insight into the evolution of intelligence, as well as inspiring new angles in the study of large-brained vertebrates (see Outstanding Questions).

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### Outstanding Questions

#### How Complex Is Cephalopod Cognition?

Behavioural flexibility of cephalopods should be investigated systematically to shed light on its cognitive underpinnings. In turn this will allow us to explore whether behavioural convergence between cephalopods and intelligent vertebrates is indeed supported by comparable cognitive sophistication. For instance, the striking flexibility exhibited by cephalopods during defence, mating competition, and potentially cooperative hunting with fish, raises the possibility that their behavioural interactions with other individuals are not underpinned by simple heuristics, but rather by sophisticated cognitive abilities. Thus, it may be valuable to investigate aspects of cephalopod theory of mind. Namely, whether they can attribute mental states to predators, mating rivals, or cooperative hunting fish. Furthermore, behaviours such as the use of coconut shells as a defensive tool may be the expression of behavioural innovation and planning abilities. As such, it may be worth investigating the extent to which cephalopods can acquire novel tool use behaviours or use these tools to prepare for future scenarios.

#### Which Pressures Led to the Evolution of Intelligence in Cephalopods?

By comparing species that face distinct ecological, predatory, and social challenges, we will better evaluate the relative influence of these factors in the evolution of cephalopods intelligence. For instance, morphological and behavioural proxies for intelligence could be measured in species or populations that are subject to different levels of predation (e.g., density and number of predator species) in order to investigate the influence of predation in the evolution of intelligence.

#### How Relevant Was Predation in the Evolution of Intelligence Across Vertebrates?

Predation has been largely overlooked as driver of intelligence in apes, cetaceans, and corvids. Future research may investigate whether predatory pressure acted only as an indirect

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trigger, for instance, by favouring the arising of novel socio-ecological challenges, or whether it also played a direct role in selecting for enhanced intelligence. Furthermore, it may also be interesting to test the cognitive underpinnings of antipredatory strategies in large-brained vertebrates, particularly those involving the defence of offspring.

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