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Review

The Adaptive Value of Numerical Competence

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Evolution selects for traits that are of adaptive value and increase the fitness of an individual or population. Numerical competence, the ability to estimate and process the number of objects and events, is a cognitive capacity that also influences an individual's survival and reproduction success. Numerical assessments are ubiquitous in a broad range of ecological contexts. Animals benefit from numerical competence during foraging, navigating, hunting, predation avoidance, social interactions, and reproductive activities. The internal number representations determine how animals perceive stimulus magnitude, which, in turn, constrains an animal's spontaneous decisions. These findings are placed in a framework to provide for a more quantitative analysis of the adaptive value and selection pressures of numerical competence.

Highlights

Numerical competence, the ability to estimate and process the number of objects and events, is of adaptive value.

It enhances an animal's ability to survive by exploiting food sources, hunting prey, avoiding predation, navigating, and persisting in social interactions. It also plays a major role in successful reproduction, from monopolizing receptive mates to increasing the chances of fertilizing an egg and promoting the survival chances of offspring.

In these ecologically relevant scenarios, animals exhibit a specific way of internally representing numbers that follows the Weber-Fechner law.

A framework is provided for more dedicated and quantitative analyses of the adaptive value of numerical competence.

Complementing Mechanisms by Evolutionary Function

Numerical competence (see Glossary) is a cognitive ability that is widespread across the animal kingdom [1]. Species from diverse zoological groups, from primates to insects [2–7], can discriminate the number of elements in a set: its **numerosity**. The contemporary study of the mechanisms of numerical competence, both at the behavioral and neural level, is a rich area of investigation in psychology and neuroscience and significant progress has been made over the past decades [1]. However, while we are beginning to understand how numerical competence emerges in the lifetime of an individual, it is largely unknown why numerical abilities exist in evolutionary history. Despite the phylogenetic ubiquity and innate character of a fundamental '**sense of number**' [8–13], the evolutionary basis and ecological pressures that give rise to it are rarely studied. This is surprising, because numerical talent, like any other trait, needs to have a significant advantage for survival and reproduction to emerge and to be maintained over generations. A close look at the literature suggests that numerical competence is indeed of **adaptive value**.

In this review article, I outline the characteristics of numerical representations and how they affect the behaviors of different species in ecologically relevant situations. These findings can provide a framework for more dedicated and quantitative analyses of the adaptive value of numerical competence. Complementing mechanistic insights by evolutionary approaches is needed for an integrative study of the biology of numerical competence.

The Laws of Number Representations

Weber's Law

Animals estimate numerosity not in a precise way, but approximately. Similar numerical values are difficult to discriminate, but discrimination performance is systematically enhanced the more different (or distant) two values are (an effect called 'numerical distance effect'). For example, when frogs (*Bombina orientalis*) chose between two patches of food items, their choice between three and four items is random, but they reliably chose six items over three [14]. Moreover, discrimination becomes systematically less precise in proportion to increasing numbers (termed 'numerical size effect'). For example, even though frogs can discriminate between two and four food items, they fail to discriminate between four and six but yet can discriminate between four and eight [14]. For the sets to be discriminable, the numerical distance between them has to increase

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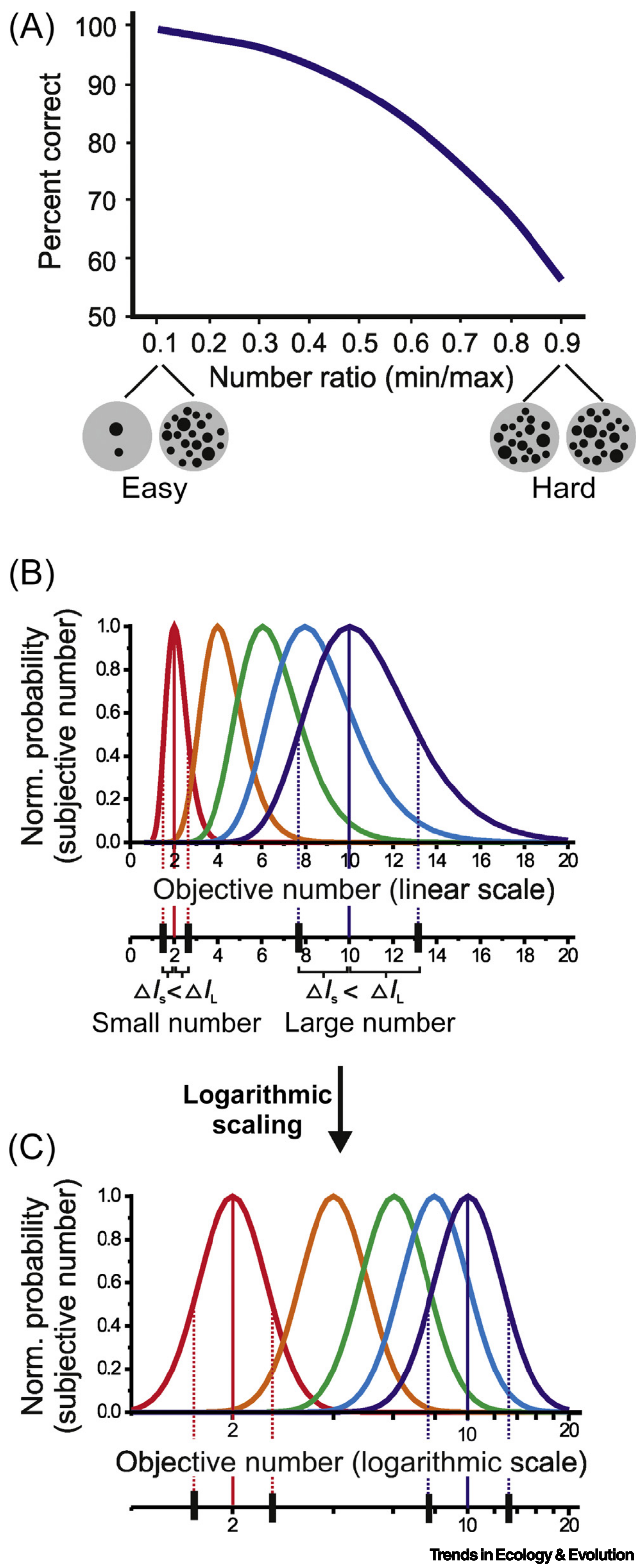

Figure 1. Psychophysical Laws of Animals' Number Discriminations. (A) Ratio-dependency of numerical discriminations. Model performance accuracy of animals in a number discrimination task plotted by the numerical ratio (minimum value/ maximum value) between the stimuli, (after [15,16]). (B) Detailed subjective performance functions for animals' number discriminations. Every colored bell-shaped function (probability density function) indicates an animal's subjective numerical representation of specific objective numbers. In other words, the bell-shaped function shows the likelihood that any number is perceived as being equal to the objective number corresponding to the respective center number of each function. For a given function, the likelihood that a number is judged different than a reference number (center of the functions) increases with numerical distance (numerical distance effect) from the reference number. The just noticeable difference (ΔI) measured at 50% discrimination performance (equivalent to subjective probability 0.5) is denoted both for smaller (ΔI_S) and larger numbers (ΔI_L) relative to the reference number on the number line below. The just noticeable differences are significantly (and in proportion to the numerical values) larger for high numbers (numerical size effect). In addition, the just noticeable differences for a given reference number are always smaller towards smaller numbers and higher towards larger numbers. (C) When the same subjective numerical representations as in (B) are plotted on a logarithmically compressed number scale, the differences become equidistant in perceptual/mental space.

Glossary

Adaptive value: traits that help an organism to survive and reproduce (i.e., that provide greater fitness in its environment).

Approximate number system (ANS): cognitive/mental system that supports the estimation of numerical quantity without relying on language or symbols.

Continuous quantity: continuous and uncountable quantity.

Evolutionarily stable strategy: a strategy (or set of strategies) that, once adopted by a majority of the members of a population, cannot be overturned by any alternative strategy.

Fechner's law: psychophysical law that states that the subjective sensation of magnitudes scales with the logarithm of objective magnitude.

Free-choice experiment: subjects can freely choose between two choices according to preference. A systematic preference of one choice over the other indicates that choice stimuli can be discriminated.

Game theory: the study of mathematical models of strategic interaction among decision-makers. Used to model the biological evolution of successful strategies in groups.

Numerical competence: the ability to represent, discriminate, and process numerical quantity information.

Numerical quantity: see 'numerosity'.

Numerosity: the number of objects/ events; set size; cardinality.

Object tracking system (OTS): visual mechanism that is thought to track up to four objects in a relatively precise but implicit way.

Playback experiment: technique of rebroadcasting natural or synthetic signals to animals and observing their response.

Quorum: the minimum number of individuals supporting a group decision.

Sense of number: intuitive, or instinctive, understanding of numerical quantity (numerosity).

Weber's law: psychophysical law of proportional magnitude discrimination. It states that the just noticeable difference between two magnitudes divided by the reference magnitude is a constant, the Weber fraction.

Box 1. 'Number Neurons' as Proximate Cause of Numerical Competence

The proximate causes of all behaviors are the workings of neurons in the brain. Numerosity-selective neurons, or 'number neurons', that can explain the behavioral approximate number representations [126] have been found in the brains of crows (*Corvus corone*) [127,128], macaque monkeys (*Macaca* spp.) [28,129,130], and humans [131]. As a neuronal reflection of the numerical distance effect, number neurons are tuned to numerosity by exhibiting maximum impulse rates to preferred numerical values with progressively decreasing rates to values more remote from the preferred one. Moreover, as a manifestation of a neuronal numerical size effect, the tuning precision of number neurons deteriorates with an increase in preferred numerical values. In addition to this Weber law signature, the neurons' tuning functions are also best described on a nonlinearly compressed, logarithmic number scale [28,127,128,132] and thus follow the Fechner's law observed in behavior [29,30].

Because such number neurons already exist in naïve animals that have never been trained in the laboratory [12,13], the brain seems to be automatically endowed with an approximate number system (ANS) and its capacity to extract numbers. In support of a putatively innate ANS, artificial number neurons obeying Weber's and Fechner's law spontaneously emerged also in a deep network that was merely trained on visual object recognition, never on numbers [133]. These findings together with the capability of wild animals to spontaneously exploit number suggest that a number sense is based on mechanisms inherent to the brain's sensory systems. Number neurons and numerical competence can emerge as a by-product of exposure to natural visual stimuli, without requiring any explicit training for numerosity estimation. This can explain why animals in the wild and across diverse taxa can readily assess numbers.

in proportion with the absolute magnitudes; the ability to discriminate between quantities is 'ratio-dependent' [15] (Figure 1A). Both distance and size effects are captured by **Weber's law**: the just-noticeable difference, ΔI, divided by the reference value, I, is a constant, c (i.e., $\Delta I/I = c$) [17]. Quantity discriminations that follow Weber's law are a clear signature of the internal **approximate number system (ANS)** that enables representations of all possible estimated numerical values (Figure 1B). The ANS has been found consistently for numerosity judgments in trained animals, from primates [15,18] to bees [7,19], but also for spontaneous numerosity discrimination in a multitude of vertebrate species [20–27].

Ratio-dependency gives rise to two adaptive cognitive capacities: first, the more dissimilar quantities are, the better can they be discriminated. Animals benefit from this phenomenon because dissimilar set sizes are behaviorally more relevant. For instance, while the discrimination of dissimilar numbers of food items promises significant energetic advantage, choosing one of two similar food sets has negligible consequences. Second, animals also benefit from being able to detect absolute numerical differences in small magnitudes compared with large ones. This is because the relative gain of detecting a given absolute numerical difference decreases with increasing magnitudes due to the proportional relationship. For example, it is highly beneficial for an animal to discriminate between one and two food items because the amount doubles, whereas the increase from 10 to 11 items is only by a factor of 1.1. Because judgments are based on perception of stimuli, both relationships are crucial to the understanding of animal decision-making.

Fechner's Law

Studies with trained animals provided a detailed measurement of how animals subjectively represent objective numbers [28–30] (Figure 1B). The resulting bell-shaped performance functions reflect the numerical distance effect. The progressive broadening of the functions, in proportion to increasing magnitude, mirrors the numerical size effect. In addition, a third aspect surfaces on top of Weber's law: relative to a given reference number, animals find it easier to discriminate between smaller numbers and more difficult to discriminate between larger ones. In the example in Figure 1B, an animal could just determine that 8 is a smaller number than 10, but cannot distinguish between 10 and 12, even though the difference is 2 in both cases. For larger numbers, only 13 or above would be discriminable from 10. This effect results in performance functions being mildly asymmetric when plotted on a linear number scale.

However, when plotted on a nonlinearly compressed logarithmic scale, the functions become symmetric and of equal variance (Figure 1C). Thus, as objective numerical values increase, the numerical representations remain equidistant in perceptual (mental) number space. In other words, the subjective sensation of number, S, is proportional to the logarithm of the objective stimulus magnitude, I. This relationship is known as **Fechner's law**: $S = k \cdot \log(I)$ [31]. Because the way in which animals process quantity guides important decisions they make, the behavioral and neural representation of numbers (Box 1) has a strong impact on evolutionary processes [32].

ANS versus 'Object Tracking System'

In addition to the ANS, a second representational system termed **object tracking system (OTS)** is discussed [33]. The OTS is thought to enable storage of one to four visual objects in an unconscious and automatic but relatively precise way [34,35]; larger numbers cannot be tracked, irrespective of the numerical distance. The rare support for the presence of an OTS in animals comes exclusively from spontaneous-choice tasks [36–38], which are suboptimal in deciphering representational systems (Box 2). In addition, reported differences in ratio-dependence for small versus large numbers do not necessary imply the existence of two separate systems [39,40] because only the representation of larger numbers may exhibit sufficient variability that can cause an overlap for adjacent numbers, resulting in a ratio effect [41]. Finally, how implicit object file contents acquired by the OTS are turned into explicit number representations remains elusive. It is therefore unclear whether the OTS really constitutes a separate representational system. The majority of data gathered in spontaneously-behaving animals, and all the behavioral and neuronal results reported in trained animals discriminating controlled stimuli, argue for a single enumeration system, the ANS [15,18,21,28–30].

Box 2. Pros and Cons of Investigating Spontaneous and Trained Behavior

The advantage of field studies and spontaneous choice tests is that they evaluate the ecological validity of numerical competence. However, these approaches also have severe limitations. The most notorious problem is the control for non-numerical quantity factors. Quantity can be continuous and uncountable (e.g., the amount of water) or discrete and countable (e.g., the number of individuals); only the latter type refers to 'numerical quantity' (also termed 'cardinal number', 'set size', or 'numerosity'). While continuous quantity is more concrete and directly related to spatial or temporal dimensions of sensory experience (such as size or duration), numerical quantity is an abstract representation because the sensory appearance of the elements comprising a set is meaningless. For instance, three apples and three alarm calls are both instances of numerical quantity 'three'.

Without specific controls, numerical quantity is usually confounded by continuous quantity. For example, six red apples adopt twice as much red area than three and an animal may simply discriminate the amount of red area rather than the number of apples. A second problem is the unknown motivational status of wild animals, whether they are even willing to choose between quantities. Finally, current approaches are largely confined to test simple abilities, such as relative numerosity judgments that only require 'more than' versus 'less than' decisions. For these reasons, field studies and spontaneous choice tests alone provide only suggestive evidence that animals differentiate numerical quantity.

These problems can be avoided when testing trained animals in a controlled laboratory setting. Using meticulous controls of sensory parameters in computer-controlled stimuli, laboratory studies in conditioned and highly motivated animals unequivocally demonstrate the animals' capability to discriminate and process numerical quantity irrespective of other parameters [2,3,18,128,134,135]. Training studies can also test more advanced numerical capabilities, such as discrimination of various absolute numerosities and switching between numerical rules [136–138].

While field studies with wild animals help us understand which aspects of an animal's environment are crucial drivers of the evolution of numerical abilities, laboratory experiments with trained animals allow for rigorous stimulus control necessary to demonstrate true numerical competence. It is therefore critical to complement results in wild animals with training studies in the laboratory.

Benefits for Survival

To explore how animals spontaneously respond to numerical cues, several approaches are used. First, behavioral observations show if animals use numerical information when interacting with their environment. Second, experimental manipulations, such as presenting conspecific calls during **playback experiments**, allow researchers to test hypotheses about animals' reactions to number information. And finally, **free-choice experiments**, either in the wild or the laboratory, reveal whether animals take numerical cues into account. However, due to methodological constraints, it is not always clear whether animals in the wild discriminate abstract **numerical quantity** or rather concrete **continuous quantity** (Box 2).

Foraging

Finding food is an obvious necessity for heterotrophic organisms to survive. The optimal foraging theory [42] states that animals, when faced with two or more food options, benefit if they can choose the patch that provides the greatest energetic gain. Often, this is the patch with more numerous food items, so the default is that animals 'go for more'. Indeed, animals from different species of vertebrates [4,5,14,36,37,43–50] to arthropods [51] and mollusks [52] show a spontaneous preference for more food items (Figure 2A, Key Figure). Sometimes, when live prey is dangerous, 'going for less' can also be an adaptive strategy [53]. In addition, the satiation state of animals affects the choice of the amount of food-foraging decisions [52].

Food items are particularly difficult to control for non-numerical parameters, such as volume or hedonic value of food patches, and animals may (also) be sensitive to such non-numerical cues when foraging (Box 2). This explains why studies that try to control for such factors sometimes find a preference for larger rather than more numerous food items [50]. Such preferences could also be explained by optimal foraging models in cases where handling difficult prey is relatively costly compared with searching for prey [54].

Navigation

Navigation is of paramount importance for animals that travel great distances. For instance, forager honeybees (*Apis mellifera*) can enumerate landmarks to estimate travelling distance (Figure 2B). About a fifth of the bees trained to collect sugar water at a feeder between the third and fourth tent in a row of four tents used the number of landmarks passed to find their way [55]. More recently, different cohorts of bees were trained in a flying tunnel to find the feeder at one of five yellow stripes distributed on the tunnel wall as landmarks [56]. In transfer trials in new tunnels, these bees searched in the vicinity of the learned landmark number, even when the spatial layout or the type of landmarks was changed. The desert ant *Cataglyphis* uses some sort of 'step counter' mechanism to measure distance to locate its nest after returning from foraging trips [57]; however, whether ants really measure the number of strides or rather integrate the magnitude of leg-position–sensor (proprioceptive) feedback is currently unknown. Finally, rats (*Rattus norvegicus*) trained to enter a specific box defined by ordinal rank (e.g., 'fourth box') among an array of boxes, reliably found the correct box even when sensory cues were tightly controlled, the boxes were switched with each other, or the overall number of boxes changed [58,59]. This indicates that animals not only rely on numerical quantity (cardinal number) but also on numerical rank (ordinal number) when finding their way [60,61].

Quorum Sensing

Sensing a **quorum**, the minimum number of individuals supporting a group decision, is frequent in social insects [62,63]. When an ant colony must relocate, the individual assessments on potential new nest sites is formed into a collective decision by ants using a quorum threshold, namely the number of ants within a new nest site [64]. Similar quorum-based decisions are found in

Key Figure

Animals Exploit Numerical Information in Different Ecological Contexts

(See figure legend at the bottom of the next page.)

other insects [65,66] and sometimes lead to conformist bias (an exaggerated tendency to copy the majority) [67]. In three-spine sticklebacks (*Gasterosteus aculeatus*), the traveling direction of solitary fish is determined by the number of conspecifics going in each direction [68,69] (Figure 2C). Importantly, such quorum responses improve the accuracy and speed of decision-making under predation risk [68]. Similarly, carnivores use a quorum in the context of movement decisions by assessing the number of vocalizing group members [70,71]. Finally, in baboons (*Papio anubis*) the probability of individuals to follow a group depends on the number of initiators; individuals are most likely to follow when there is high agreement among many initiators [72]. Here, Fechner's law has been demonstrated in wild animals: baboons' quantity-based decisions about the direction of troop movements are best captured by models that use approximate-number comparisons with a nonlinearly compressed scale [16]. These decisions made by wild baboons rely on numerical cues and not on non-numerical factors [16] (Box 3).

Avoiding Predation by Hiding

Seeking shelter among large groups of companions is a common passive form of antipredator behavior [73]. For example, individual fish inserted in an unfamiliar environment tend to join the larger of two shoals [74,75] (Figure 2D). The fish can discriminate one versus two, two versus three, and three versus four fish. For larger numbers, mosquitofish (*Gambusia holbrooki*) discriminate four versus eight and four versus ten but not four versus six or four versus seven; discrimination is therefore ratio-dependent [38]. While some authors interpret the discriminability of small numbers (<5) as evidence for an object file mechanism [38], others found that fishes' discrimination obeys Weber's law across both small and large numbers [6,75]. Some prey animals adopt more sophisticated strategies: elks (*Cervus elaphus*) minimize predation risk by wolves (*Canis lupus*) by either living in small herds that are rarely encountered by wolves, or by gathering in large herds that reduces the chance that any particular individual will be the victim [76].

Seeking shelter among social companions has at least three distinct advantages. First, an individual reduces the risk of being predated upon as the number of individuals in the group increases, a phenomenon termed the 'dilution effect', or simply 'safety in numbers' [77,78]. Second, a predator has a harder time singling out an individual that lives in larger groups, the 'confusion effect' [79,80]. And finally, many individuals together have a higher chance of detecting a predator, termed the 'many eyes effect' [81,82].

Avoiding Predation by Mobbing

A more active antipredation strategy is to alarm conspecifics to mob and harass predators. In black-capped chickadees (*Poecile atricapillus*), for instance, the increasing number of (two to five) 'dee'-notes in their 'chick-a-dee' mobbing alarm call conveys information about the progressive dangerousness of a predator [83] (Figure 2E). Two 'dee'-notes suffice for a rather harmless great gray owl, whereas up to five 'dee'-notes are elicited when an agile small pygmy owl has been spotted. Such variations in the number of notes per call in alarm calls have been observed

Figure 2. (A) Corvids of the genus *Corvus* go for more during foraging. (B) Honeybees (*Apis mellifera*) navigate by enumerating landmarks. (C) Three-spine sticklebacks (*Gasterosteus aculeatus*) sense a quorum when deciding on traveling direction. (D) Larger zebrafish (*Danio rerio*) shoals provide better protection against predators. (E) Black-capped chickadees (*Poecile atricapillus*) signal the dangerousness of areal predators via the number of call notes. (F) Wolves (*Canis lupus*) adjust the size of the hunting party according to the prey such as bison (*Bison bison*), the most formidable prey. (G) Lions (*Panthera leo*) assess the number of individuals in their pack before deciding about fight or flight. (H) During courtship, tungara frogs (*Physalaemus pustulosus*) outperform their rivals and increase the complexity of their calls by adding call notes. (I) Beetles (*Tenebrio molitor*) keep track of the number of mating partners a female had. (J) Brood parasites like the brown-headed cowbird (*Molothrus ater*) assess the number of eggs of a host, in this case an eastern phoebe (*Sayornis phoebe*), before depositing their own. All Images shown are from the public domain (Wikimedia Commons).

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Box 3. Number as a Last Resort?

Many animal species seem to represent numerical values. However, as experiments in the wild are usually confounded by continuous quantities, animals may have a preference for non-numerical cues to make adaptive decisions and use number only as a last resort, when no other parameter differentiates stimuli. Indeed, non-numerical cues, such as item size, sometimes play an important role when animals make free choices [50,139–141]. However, this is not to say that numerical information is a last resort. Ample evidence suggests that primates spontaneously and routinely use numerical attributes to arrive at informed decisions. For instance, rhesus macaques (*Macaca mulatta*) that could make matching decisions based on stimulus shape, color, surface area, or number always based their decisions on numerical value when the numerical ratio was favorable [142]. Similarly, movement decisions by wild baboons [72] rely specifically on numerical representations that support approximate number representations [16]. Finally, a study comparing humans' and non-human primates' spontaneous stimulus categorization performances confirmed the numerical bias [143].

Not surprisingly, animals use multiple sources of information, both numerical and non-numerical, to learn about their environment and make decisions [144]. This is to be expected, given that choosing a larger amount sometimes is more beneficial than going for larger numbers. Animals within a population may also vary with respect to their predisposition to use numbers; different strategies coexisting within the same population may be an efficient way to find solutions in a variable environment [55]. Importantly, however, number is not a last resort, but belongs to the set of quantitative parameters that animals can spontaneously exploit.

to denote predator size, type, or distance [84,85]. Some bird species even eavesdrop on heterospecific alarm calls and the contained numerical cues intended for others [86–88]. Moreover, songbirds acoustically recognize the number of individuals initiating mobbing and use this information to decide whether to join in [89]. Thus, numerical assessments are not only used to derive information about the type of predator, but also to decide whether or not to participate in antipredator responses.

Cooperative Hunting

Predatory animals that hunt large and defensive prey often rely on coalition partners to overpower their victims. In wolves, the probability of catching different prey species varies with different optimal intermediate group sizes of a hunting party (Figure 2F) [90]. Because large prey can kick, gore, and stomp wolves to death, large hunting parties encourage individuals to hold back and let others go in for the kill. This can be avoided by optimal group sizes where hunting success depends on each individual's contribution: for elks, capture success levels off at 2 to 6 wolves, while moose (*Alces americanus*) require a mean pack size of 8 [90,91], and for bison (*Bison bison*), the most formidable prey, 9 to 13 wolves are the best guarantor of success [90]. Thus, estimating the optimal number of coalition members is vital, because groups that are too large can have negative effects on cooperation [92].

Numerical cues not only matter to cooperatively hunting mammals, but also to predatory arthropods. *Portia africana,* a communal spider-eating jumping spider, adopts number-informed predatory strategy when preying on tent-building *Oecobius amboseli* spiders [93]. Typically, two *Portia* individuals settle alongside each other at a spider's nest, and when one captures a spider, it is joined by the other to feed alongside it. When deciding whether to settle near a prey spider nest, *Portia* prefer one spider being present over zero, two, or three spiders [93]. Here again, an intermediate group size seems to be optimal for catching prey.

Social Territory Defense

According to **game theory**, animals are expected to assess the strength and relative number of opponents prior to engaging in fights [94,95]. Because larger groups often win such contests [96,97], numerical competence allows for intelligent decisions on whether to attack and risk damaging fights, or retreat and lose territory. In a classic playback study, female lions (*Panthera leo*) were confronted with recordings of either one unknown female intruder roaring or three roaring in an overlapping chorus (Figure 2G) [98]. The lionesses were less likely and less determined to respond aggressively by approaching three simulated intruders than one intruder. In fact, the best predictor of approach probability was the ratio of number of adult defenders to number of intruders [98]. A similar ratio-dependent contest response pattern has been observed in several carnivore species [99–102].

Numerical advantage also affects the outcome of fights in social primates [103,104]. Chimpanzee males defend the group's territories and sometimes kill members of neighboring groups. The number of adult chimpanzee males in a party predicts willingness to respond aggressively [105]. While resources (food, females, and infants) affect the timing of intergroup encounters, the decision to escalate a contest depends primarily on numerical strength [106]. In such intergroup conflicts, the chimpanzees follow predictions made by Lanchester's 'square law' model of combat [107]: individuals in a focal population are willing to enter a contest only if they outnumber the opposing side by a factor of at least 1.5. Numerical advantage determines the outcome of potentially lethal intergroup interactions [108].

Benefits for Reproduction

Courtship

In many species, acoustic communication is important during courtship. Male frogs typically produce 'advertisement' calls to attract females, which choose from many competing males [109]. To surpass rivals, males increase the complexity of their advertisement calls. In male tungara frogs (*Physalaemus pustulosus*), advertisement calls consist of two components, a 'whine' followed by one or more 'chucks' [110]. Competing frogs match or exceed (by one) the number of chucks produced by their rivals and add as many as six chucks (a numerical limit that probably reflects a respiratory constraint [111]) (Figure 2H). This calling behavior of matching or exceeding the number of rival calls has also been observed in other frog species [112–114]. As a sign of adaptive value, females prefer more complex calls (i.e., calls with the greatest number of chucks [115]).

Mating

Estimating quantity improved males' sexual competitiveness. In mealworm beetles (*Tenebrio molitor*), many males mate with many females and competition is intense (Figure 2I). Therefore, male beetles that can discriminate between up to four different female beetles based on odor will always go for more females in order to maximize mating opportunities [116]. After mating, males guard females for some time to prevent further mating acts from other males. The more rivals a male has encountered before mating, the longer he will guard the female after mating [117].

Copulation is a means to an end, namely fertilization. After successful copulation, the sperm continues to compete for the fertilization of the egg. Sperm competition causes a variety of adaptations at the behavioral level. The males' ability to estimate the magnitude of competition determines the size and composition of the ejaculate [118,119]. In the pseudo-scorpion, *Cordylochernes scorpioides*, for example, several males copulate with a single female, with the first male having the best chances of fertilizing the eggs [120]. Because the production of sperm is costly, males assess the number of competitor males that have copulated with a female and adjust by progressively decreasing sperm allocation. These quantity-based behaviors could mark a transition from processing continous to representing discrete quantity.

Brood Parasitism

Brood parasitic birds avoid parental costs by laying their eggs in hosts' nest for incubating eggs and later feeding hatchlings. The host, in turn, develops strategies to avoid being parasitized. In this arms race, both parasite and host rely on numerical information. American coots (*Fulica* *americana*), for example, parasitize their conspecifics. Potential coot hosts seem to enumerate their own eggs, which helps them to reject parasitic eggs [121]. They typically lay an average-sized clutch of their own eggs and later reject any surplus parasitic eggs. Similar behavior is found in wood ducks (*Aix sponsa*), another conspecific brood parasite [122]. Whether brood parasites reject host eggs directly based on numerical discrimination requires more investigation.

Cowbirds (*Molothrus ater*) show an even more sophisticated heterospecific brood parasitism that requires them not only to find a suitable host, but also to precisely time their egg laying (Figure 2J). Cowbird eggs hatch after 12 days of incubation; if the cowbird female lays her egg too late into the host's nest, incubation time will have expired before her chick hatches. However, if she lays her egg too early in the host nest, she risks her egg being discovered and destroyed. Cowbird females therefore closely monitor the host's clutch to synchronize their parasitism with a potential host's incubation [123]. To get timing right, the female cowbird needs to visit a host's nest over multiple days, remember the clutch size from one day to the next, evaluate the change in the number of eggs in the nest from a past visit to the present, assess the number of days that have passed, and then compare these values to decide whether to lay her egg. But irrespective of how careful the cowbird is, the hosts will sometimes detect and destroy the foreign egg. In return, cowbirds show a 'mafia-style' reinforcement strategy [124]: if she finds that her egg has been destroyed, she destroys the host bird's eggs, an additional cost for the host. It is an astounding example of how far evolution has driven some species to exploit numerical cues.

Concluding Remarks and Future Perspectives

The behavioral findings outlined earlier imply that animals in the wild exploit numerical quantity to arrive at fitness-enhancing decisions in various ecological contexts. However, it is necessary to move from primarily suggestive evidence to a deeper understanding of the adaptive value of numerical competence. Later, I identify some of the most pressing questions and offer prospects for the future (see Outstanding Questions).

First, animals' spontaneous sensitivity to number has often been reported as a by-product or accidental finding of studies that had originally been designed to explore other ecological research questions. As a consequence, abstract numerical quantity is almost always confounded by simpler, continuous quantity (Box 1). Thus, field studies specifically geared to numerical competence with tightly controlled stimuli are needed. A future challenge in numerical cognition is to disentangle the relative role and weight of continuous and numerical quantity and how they interact to influence adaptive decisions.

Second, animals that discriminate quantities are constrained by their internal representations that shape how they perceive stimulus magnitude. This, in turn, will influence how animals arrive at ecologically relevant decisions. In models of decision-making, the internal representations of stimuli are usually described by symmetric normal distributions [125]. However, this is a simplification, as numerical quantity representations follow the Weber-Fechner law and show nonlinear compression (Figure 1B,C). To understand fitness-related decisions, the laws of perception and the underlying cognitive and neural machinery must be taken into account.

Third, animals exploit both numerical and non-numerical quantity to make adaptive decisions. Future research needs to show whether different strategies may coexist within the same population. Individuals may flexibly switch between using numerical and non-numerical information as a function of internal and external information [52]. Alternatively, individuals in a population may exhibit heritable differences in their predisposition to use numbers [55], which provides the prospect of opening the study of numerical competence to ecological genetics. In either case, a mixed

Outstanding Questions

Can the relative role and weight of continuous and numerical quantity, and how they interact to influence adaptive decisions, be disentangled?

How do the laws of perception and the underlying cognitive and neural machinery constrain the animals' decision-making in the wild?

Do different strategies to exploit numerical and non-numerical quantity coexist within the same population?

Can the selection pressures and the fitness payoffs of numerical competence be identified in a more detailed and quantitative way?

scheme of quantity sensitivity might turn out to be an **evolutionarily stable strategy** in a variable environment [95].

Fourth, the fitness benefits animals obtain by numerical competence are so far discussed on a rather descriptive and intuitive level. In contrast to other ecological situations, such as forging or mating, quantitative models and theorems are almost entirely missing when studying the constraints of numerical competence. While it is obvious that more food, fewer injuring fights, and more mating opportunities are beneficial for an animal, a scientific understanding requires numbers to be put to these findings. To move the behavioral ecology of numerical competence forward, future research needs to identify both the selection pressures and the fitness payoffs in a more detailed and quantitative way.

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