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Predator avoidance: Mechanisms

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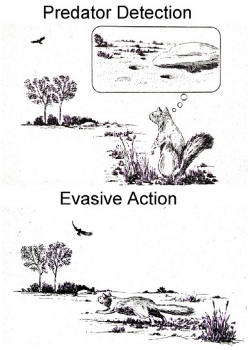
Abstract

Mechanistic research on antipredator behavior focuses on identifying the causes and consequences of how prey cope with predators. The perceptual aspects of predator recognition are emphasized, focusing on the olfactory, auditory, and visual recognition cues used to identify predators. Predator recognition can result from learning to associate a predator with a threatening circumstance, a process that enhances survival and compensates for historical inconsistencies in predator encounters that have not acted as sources of natural selection. If predator configuration and the circumstances of predator encounters have been consistent in the evolutionary time frame, then natural selection can shape the evolution of predator recognition. Relaxed selection from predators has different effects on the persistence of innate predator recognition depending on the complexity of perceptual integration.

Graphical abstract



Keywords

Conditioned inhibition; Habitat affordances; Mechanistic science; Pavlovian conditioning; Predator recognition; Recognition context; Relaxed selection; Selective habituation; Stimulus generalization; Theory of mind

Key points

- Predators can be recognized via innate and learned perceptual processes.
- Olfactory, auditory, and visual systems are reviewed.
- Predator-avoidance involves assessment of microhabitat contexts.
- Antipredator behavior can persist under conditions of relaxed natural selection.

Introduction

This chapter describes how prey species cope with their predators, focusing primarily on behavior at the mechanistic level of organization that includes neurophysiological processes. Emphasis is given to predator-recognition systems involving olfaction, audition, and vision. The complexity of the contextual aspect of how predators are recognized and dealt with in different microhabitats reveals the complex interaction of learned and innate antipredator systems. Examples include descriptions of robust predator-avoidance behavior in which natural selection has been relaxed for extended time periods.

The relationship of mechanistic science and higher-order systems

This discussion focuses on the antecedent causes of antipredator behavior from a mechanistic perspective. The antipredator behavior of different organisms will also be described from the perspective of different levels of organization and time scales of change. As typically used in biology and psychology, the term *mechanism* characterizes a world-view perspective that maintains that reality is best represented as stable and fixed (Overton and Reese, 1981). Any change in this stability results from antecedent causes that are specifiable. This perspective has its origins in the atomist tradition in pre-Socratic Greek philosophy and later refined into the tradition of formal hypothesis testing in the early 17th century by Francis Bacon (Bacon, 1620/1939). During the late 19th century, British and American empiricists, like Thomas Chamberlin, promoted the testing of multiple hypotheses using eliminative induction to identify antecedent causes and consequences of discontinuity (Chamberlin, 1890). In short, the empiricist–positivist–-inductivist perspective of modern analytic philosophers attempts to explain change in the stability and continuity of the object of inquiry by antecedent causal sequences that can be decomposed into simpler elements at lower levels of organization. When trait stability over evolutionary time is considered as primary and change requires explanation, it must be noted that the ubiquitous, mechanistic term "selection pressure" does not characterize the differential filtering process of natural selection that shapes evolutionary change. The less common expression "sources of natural selection" will be used instead to describe the historical circumstances in which prey species failed to detect and recognize predators as threats as well as failed to engage in appropriate antipredator behavior. With the decline or absence of these sources of selection, the ability to recognize predators remains intact in some species for long periods, leading to the inquiry of the mechanisms of trait stability or slow reorganization (Lahti et al., 2009).

As an extension of mechanistic science, control-systems theory incorporates higher levels of organization with multiple goal-directed reference signals and error-correcting feedback loops that regulate behavior over time (Powers, 1973). Nevertheless, while causal relationships are easiest to describe at the lowest level of organization with one-way causation, higher levels of organization involve the complex integration of regulatory elements with two-way causation that are more difficult to describe as having antecedent causes. The highest levels of organization in a system can be difficult or impossible to characterize in this manner, especially if a large number of higher-order relationships exhibit emergent properties that preclude decomposition into simpler elements. As a result, empirical research in antipredator behavior consists typically of assessing causal relationships of perception and action at lower levels of organization.

One interesting facet of control-systems theory relevant to assessing proximate time scales of change in antipredator behavior is that simpler elements at low levels of organization react much more quickly to causal sequences than elements at higher levels of organization that incorporate much more generality in various inputs. As will be discussed, prey can engage in periodic or sustained vigilant behavior while foraging with the goal of evaluating their state of vulnerability based on various microhabitat qualities that include nearness to refuge and the ability to detect predators. Such tonic "nonconsumptive effects" (Preisser et al., 2007), such as prolonged wariness when predators are first detected and then disappear from view, operate at the highest level of the organism–-environment relationship or cognitive level. Although predators are more likely to be detected by prey with tonic states of vigilance, this redirection of attention has energetic costs that impact prey health, growth, and fecundity, especially when vigilance is directed at detecting predators that use sit-and-wait ambush tactics (Caro, 2005; Lima and Dill, 1990). Experimental manipulations of this phenomenon in natural settings typically require the presentation of predator models to engender antipredator behavior.

Affordances

James J. Gibson developed the ecologically relevant perceptual theory positing that perceivers extract information from their environment as fluid "space–time events" that do not require partitioning into a succession of immediate time steps that are reconstructed by the perceiver into a single event (Gibson, 1979). Perception is thus an ongoing activity that involves the detection by the perceiver of the *invariant* features of the environment that can include an invariant pattern over time (Michaels and Carello, 1981). The ecological perception approach asks how an animal knows what to do in complex settings with enormous amounts of information and what information needs to be ignored. This view readily acknowledges that natural selection can shape the active properties and selectivity of information gathering, especially habitat features that are useful (Withagen and Michaels, 2005). Such selectivity permits the recognition of predators, including how they might constitute a particular kind of threat and how the physical properties of the environment might be used differently to evade predation. In some contexts, antipredator behavior includes assessment of the temporal properties of predators and, for knowledge that a predator is nearby but out of view, expectations of the likelihood of it remaining in the area.

Animals with well-developed senses are active perceivers of structural invariants that include environmental features that engender particular kinds of action. Any information perceived, however, must be considered in the context of what it offers or affords the perceiver. From the perspective of perceivers with excellent climbing ability, a large steep boulder and tall tree share the same affordance of an elevated perch for evading terrestrial predators. Looking out is another affordance of a high perch, permitting predator detection and monitoring. Conversely, such predators would likely perceive the same structures as not affording accessibility to prey and indication that the predator was detected if alarm calls were emitted. Trees, however, would afford relative protection from avian predators attacking on the wing as would bushes, shrubs, and thickets that preclude prey seizure; both California ground squirrels and vervet monkeys recognize this affordance and readily dash to nearby bushes after spotting hawks and eagles. Both boulders and trees might afford access to adjacent structures if the predator can climb, and for trees with wide crowns, the low weight-bearing properties of thin branches can afford protection. During daytime attacks, baboons can evade heavier-bodied predators with facile climbing ability, such as leopards and pythons, by seeking refuge on thin branches near the edge of the crown, and macaques and langurs choose the crown edge as primary sleeping sites. In cold habitats, tall conifers are selected by colobine monkeys as sleeping sites to avoid leopards and for thermoregulation.

Escape to burrows affords rodents immediate refuge from nonburrowing predators, but burrows are also places of danger for digging predators and especially venomous snakes that use burrows for thermoregulation and ambushing. Rock squirrels and California ground squirrels recognize this difference in burrow affordance based on predator type, because they become wary of burrow entrances in a sustained or tonic manner after engaging rattlesnakes above ground that are no longer in view.

Other examples include perception of distance to refuge by both diurnal and nocturnal rodents that prefer traveling next to structures that occlude overhead detection. Well-studied laboratory open-field experiments illustrate the aversive arousal of rats and mice exposed in the center of an arena. Their quick scurrying to adjacent walls suggests that they immediately sense their vulnerability to overhead threats. Although not as well documented, animal trails afford guidance, ease of travel to known resources, and the opportunity to detect partially concealed predators along the way. In the latter context, trails afford familiar routes with landmarks, patterns of vegetation, and engender motor learning along the route that facilitates escape. For diurnal mammals with widely spaced eyes, repeated travel without aversive consequences engenders habituation, enabling the rapid detection of partially concealed ambush predators. Trails with a smooth, well-trodden substrate also allow less energy expenditure during transit, and species as diverse as rodents and ungulates move easily and fluidly without appearing disabled to predators. In particular, elephant shrews recognize the affordances of well-maintained trails, spending up to 25% of their time on trail maintenance.

Predator recognition

The recognition of predators by prey is paramount for survival, and, in some species, natural selection has engendered the evolution of well-integrated perceptual capabilities coupled with higher-order inferences of how predators hunt in specific settings. Depending on the prey species, predator recognition involves the use of different sensory modalities, some of which detect gradients in intensity and conspicuousness of predator features that are perceived in both static and dynamic contexts. For example, predator-experienced moose exhibit a heightened wariness to the odors and playback vocalizations of familiar and novel predators in contrast with predator-naïve moose, suggesting that predator exposure engenders a broad "climate of fear" affecting moose readiness to respond appropriately (Berger et al., 2001).

Natural selection can also promote selectivity in how prey learn about predators. In historical situations in which prey encountered predators in highly variable contexts without predictable properties, natural selection operated on prey success in learning to recognize specific morphological characteristics of predators in different settings. In circumstances where stealthy sit-and-wait predators attack quickly during the day or at night, minimizing the ability of prey to assess the predator's physical appearance, prey that escape learn to be wary of specific locations where they were previously attacked. Learning in both contexts can occur rapidly with several aversive experiences. In laboratory studies using contextual fear conditioning, laboratory rats can exhibit one-trial learning by freezing in an experimental apparatus in which they received painful electric shocks the previous day. Such rapid associative learning of a specific spatial location as dangerous is analogous in nature to an animal escaping a painful bite by an unseen predator in a specific setting and later avoiding that area. This evolutionarily "prepared" associative learning of the predictors of dangerous circumstances is contrasted by much slower "unprepared" learning, requiring many more trials to make less urgent or ecologically relevant associations. In low-visibility habitats used by stealthy predators for hunting during the day, or less stealthy predators hunting in dark burrows and at night, some prey have evolved sensory specializations for predator recognition that involve the assessment of the direction and amplitude of specific sounds and detection of predator scent which is diffused and provides much less information on predator location (Kats and Dill, 1998).

Olfactory predator-recognition cues

Marine invertebrates are sensitive to predator odors and evidence of predatory activity, such as the alarm odors of crushed conspecifics that is evident in 25 genera of gastropods. Snails can distinguish the odors of predatory and nonpredatory crustaceans as well as food and refuge. In particular, crabs that eat snails are especially provocative, as characterized by the ability of the gastropod mollusk *Littoraria* to distinguish the odor of their blue crab predator from fiddler crab and grass shrimp odors. Sea urchins respond to large sea stars within 5–10 cm upstream by moving their spines defensively with gaping pedicellariae. Odor discrimination can occur early in development when other sensory modalities are undeveloped. Among aquatic larvae, western toad tadpoles from Oregon can distinguish the odors of predatory garter snakes, backswimmers, and giant waterbugs from those of roughskin newts and rainbow trout that treat these tadpoles as unpalatable.

Age-related changes in antipredator behavior to odor cues are evident in terrestrial vertebrates, notably the broader predatory threat to smaller, more vulnerable juveniles. In a choice test of refuge scented with sympatric and allopatric invertebrate- and snake-predator odors, juvenile Australian scincid lizards avoided refuges scented by predator odors, especially the venomous funnelweb spider, whereas adults failed to distinguish the odors of predators from nonpredators.

Because the chemical attributes of predator recognition can be examined at a low level of organization involving neural pathways, and because prey species can be examined in laboratory settings in either animate or anesthetized states, research on predator-odor recognition has engendered considerable understanding of the integration of olfactory neurophysiology that mediates antipredator behavior. Integrative research has emphasized study of the provocative effects of the predator odor, trimethylthiazoline (TMT) originally isolated from fox feces. Laboratory rats and mice exhibit innate aversion to this odor illustrated by freezing and withdrawing (Kobayakawa et al., 2007). The causal sequences of TMT recognition begin with its activation of odor receptors exclusively in the D-domain glomeruli in the olfactory bulb that transmit information to the olfactory cortex for odor identification. The olfactory cortex projects to many forebrain areas, including the orbital frontal cortex (OFC), which regulates arousal, but the critical circuit for engendering a rapid antipredator response is the olfactory cortex activation of the medial division of the bed nucleus of the stria terminalis (BST). BST activation simultaneously triggers the release of stress hormones via the hypothalamus and pituitary gland and rapid freezing mediated by its direct projection to the midbrain periaqueductal gray (PAG). Although the basolateral complex of the amygdala interacts with the BST, and there is considerable evidence that the amygdala plays an essential role in the production of learned emotional memories, the amygdala plays no substantive role in innate TMT recognition and avoidance behavior. Research using mutant mice has shown that the mouse olfactory bulb has two functional modules, one of which participates in the process of associative learning while the other incorporates specialized neural organization for detecting mammalian predators essential for survival.

Acoustical predator recognition

This facet of antipredator research emphasizes simulations of predator presence to prey using playbacks of predator vocalizations and predator-generated sounds. If the circumstances of acoustic predator recognition enhancing fitness were consistent for a long enough period during evolution, then neural specialization in auditory processing of acoustic structure might be expected to have evolved. If, in the developmental time frame, predator sounds were heard consistently in similar circumstances, but inconsistently in the evolutionary time frame, then learning would be expected to play an important role in acoustical predator recognition. Some facets of sound processes might involve innate perceptual biases that could facilitate learning. For example, captive-born cotton-top tamarins are not responsive to playbacks of predator vocalizations as would be predicted if acoustic predator recognition were innate; nevertheless, these monkeys do respond to low-frequency, noisy sounds that characterize larger body size and potential aggressive threats.

The manner in which bonnet macaques in southern India learn to ignore irrelevant sounds, but react strongly to alarm calls and predator vocalizations, is illustrative of the coupling of two learning processes, conditioned inhibition and Pavlovian conditioning. Conditioned inhibition involves the suppression of attention (i.e., selective habituation) to irrelevant sounds after repeated exposure without emotionally laden consequences, such as fearful running to trees or watching others run to avoid predators. Pavlovian (classical) conditioning results when salient, but initially irrelevant sounds act as predictors of emotionally laden consequences. For example, bonnet macaque infants transported ventrally by their mother on the ground respond to a broad range of loud noises (e.g., conspecific and heterospecific alarm calls) by rapidly clinging harder to their mother to prevent dislodging as she runs to trees and jumps from branch to branch as she climbs. With the exception of alarm calls and predator vocalizations, juveniles begin to ignore ecologically irrelevant sounds by actively observing adult inattention. In particular, watching others run is highly contagious and engenders a fearful emotional state that acts as an unconditioned stimulus maintaining the provocative properties of an ecologically important sound, the conditioned stimulus. In experimental study, playbacks of tiger growls elicited flight in only younger monkeys from Bangalore city where tigers are absent, a property reflecting their sensitivity to loud noises, whereas all monkeys fled in forest troops where tigers are present. Playbacks of eagle calls and leopard growls engender antipredator behavior in Diana monkeys from West Africa (Zuberbühler, 2007). When the leopard-initiated alarm calls of crested guinea fowl are paired with leopard growls in a higher-order Pavlovian conditioning experiment, Diana monkeys treated the guinea-fowl alarm calls as if a leopard were present. This result demonstrates in a natural setting how second-order Pavlovian conditioning of heterospecific alarm calls associated with first-order conditioning of leopard growls would be useful for detecting leopards prior to troop members spotting them.

The ability to selectively winnow out irrelevant sounds while retaining sensitivity to relevant predator sounds via selective habituation is evident in harbor seals in the northwest Pacific (Deecke et al., 2002). Playbacks of the vocalizations of transient mammal-eating killer whales and unfamiliar fish-eating killer whales engendered strong submerging antipredator responses, but there was little submerging to the familiar calls of local fish-eating killer whales that posed no danger.

Novel predator vocalizations that share acoustic properties with sympatric predators can also be evocative due the perceptual process of stimulus generalization. Research on acoustic owl-predator recognition examined the antipredator behavior of migrant and resident tropical birds on the Yucatan Peninsula, Mexico. During playbacks of eastern screech-owl and ferruginous pygmy-owl vocalizations, migratory passerines responded to only familiar screech-owl vocalizations. However, both migrant and resident birds responded to pygmy-owl vocalizations that share acoustical properties with eastern screech-owl vocalizations, allowing migrants to generalize the familiar predator vocalization to the unfamiliar one. Similarly, yellow-bellied marmots in the Rocky Mountains, Colorado, respond to familiar coyote vocalizations and generalize this predator recognition to unfamiliar, but longer duration wolf vocalizations that share similar acoustical properties (Blumstein et al., 2008).

In contrast with the processes of sound generalization, the distinct sound differences of defensive rattling and hissing by rattlesnakes and gopher snakes are used by California ground squirrels to distinguish these predators when squirrels confront these snakes at close proximity, flagging their tails from side-to-side and throwing loose substrate at these snakes with their forepaws (Owings and Coss, 2008, see Video 1 in the online version at https://doi.org/10.1016/B978-0-443-29068-8.00089-1). The rattling sound also leaks cues to a rattlesnake's body temperature and vulnerability because cooler rattlesnakes strike with lower velocity, reduced accuracy, and more hesitation. Smaller rattlesnakes rattle with lower amplitude and emphasize higher sound frequencies than larger, more dangerous rattlesnakes, and ground squirrels become less cautious when they hear playbacks of the rattling sounds of more vulnerable smaller and cooler rattlesnakes.

Visual predator recognition

The ability of prey to detect and recognize predators visually during the daytime during which the predator's body is immediately distinct from the background as a recognizable Gestalt (unified pattern) can involve the complex perceptual integration of predator features, such as body shape, coloration, texture, and movement. Sit-and-wait ambush predators, such as felids, counter the predator-detection ability of visually adept prey by remaining still, crouching with flattened ears to diminish projecting contours, hiding in vegetation that disrupts body contours, and evolving pattern-blending camouflage. Hunting at night is another way to circumvent visual predator recognition.

Presentations of stationary predator models to active prey have had a long history of revealing the visual cues used for predator precognition. Semi-terrestrial crabs that colonize complex habitats appear to employ binocular vision for navigation and predator recognition. The Kenyan mangrove-climbing crab hesitates when approaching a model of a large crab predator and a simplified rectangular model displaying a horizontal array of large claws (Cannicci et al., 2002). In a much simpler dynamic relationship, experimental study of the semi-terrestrial Neohelice crab has shown that these crabs react quickly to looming predator-like approaches that activate motion-sensitive lobular neurons within the ommatidial columns projecting to the crab's midbrain. The ensuing escape behavior is not a simple reflex because it can be adjusted to reflect direction and speed of the looming object.

Because depth perception is essential for ambushing, predators that rely on vision must face their prey, usually exposing both eyes to prey as a detectable schema. Pike and bass also face their prey using vegetation as cover before striking. Because ambush predators use both eyes to monitor prey, the schema of two facing eyes has been available as a consistent predator-recognition cue during the phylogeny of numerous vertebrate prey species. Research has shown that, during early development, paradise fish larva and jewel fish fry become alarmed by eye-like patterns consisting of two dark spots in the horizontal plane. Two horizontal light-emitting diodes simulating the moonlit eye shine of nocturnal carnivores augment fear in wild house mice associated with foot shock. Similarly, the horizontal arrangement of two concentric circles appears dangerous to a variety of primates, ranging from mouse lemurs to humans.

Social primates in general are excellent detectors of the direction of gaze of nearby conspecifics either as a potential threat or signal of appeasement. Such ability translates well for determining whether predators appear interested. Both common chimpanzees and humans visually fixated the eyes of lions more than they did the eyes of impala presented in computer displays, particularly when the eyes of lions were directed at the viewer rather than averted (Whitham et al., 2024). From a theory of mind framework, this urgent inference that another agent is interested in the perceiver based on its two facing eyes is evidence of a second-order intentional system in which the perceiver has beliefs and desires about the beliefs and desires of others.

As evidence of the speed of assessing predatory interest by bonnet macaques, leopard-experienced forest and leopard-inexperienced urban monkeys start running toward nearby trees with latencies of 200–300 ms after detecting a realistic-looking model leopard with a spotted yellow coat appearing to stare at them in the open (Coss and Ramakrishnan, 2000, see Video 2 in the online version at https://doi.org/10.1016/B978-0-443-29068-8.00089-1). These monkeys react similarly to only a forequarter view of the leopard model, illustrating the threatening appearance of the leopard's facing orientation.

A number of studies of human and non-human primates have documented rapid neural activity during face processing using brain scanning and electrophysiological recordings that provides insight into the rapid assessment of predatory threats. Perception of two facing eyes engenders a cascade of neural activity in the occipitotemporal cortex encompassing pattern recognition that peaks around 170 ms with near simultaneous activation of fearful emotions via interactions of the basolateral amygdala, OFC, and PAG that rapidly initiates flight. Longer cognitive assessment in the 400 ms time frame involves the recruitment of the parietal, medial, and lateral prefrontal cortices that regulate more deliberate action. Wild bonnet macaques respond more slowly to the presentation of a dark leopard morph without the spotted yellow coat that acts as a leopard-recognition cue, and some monkeys continued to monitor the model without fleeing. Presentation of upside-down spotted yellow or dark leopard models also reduces the flight response either by disrupting the leopard's shape or by providing contextual information of a nonhunting cat resting on its back. Despite this postural difference, the spotted yellow coat of an upside-down leopard is still provocative, possibly because spotted patterns activate texture processing via dot-pattern selective neurons in macaque inferotemporal cortex and primates with trichromatic vision are especially sensitive to yellow. The responses of captive-born West Indian green monkeys, sooty mangabeys, pigtailed macaques, and rhesus macaques to leopard models suggest that these primates have also evolved the ability to recognize leopards as predatory threats.

It is important to note further that recognition of a predator includes the context in which it is detected. Evaluation of the background surround in which the predator is detected mediates the choice of evasive action by prey and this context varies in complexity. The fast reaction times of primates fleeing from a rapidly approaching predator involves the simple perception of a looming threat that activates strong emotions in the amygdala and rapid flight activation by the PAG. As the flight sequence unfolds, prey must choose appropriate evasive behavior as a function of predator location, an assessment process similar to that of observing conspecific social interactions. Nonhuman primates share with humans the highly conserved patterns of intercortical connectivity involved in evaluating the contextual properties of social interactions, such as connections between the dorsomedial frontal cortex and precuneus that likely play an important role in organizing the spatial aspects of flight decision making. But further, magnetoencephalography (MEG) used to record rapid brain activity coupled with behavioral tasks have been used to study natural-scene perception in humans (Bar et al., 2006). Such studies are relevant to understanding how the contextual properties of perceiving predators in diverse microhabitats influence flight activity. In nonhuman primates with similar brain organization, the first phase of contextual assessment visually involves predator detection mediated at the subcortical level by the superior colliculus (SC) that can also recognize two facing eyes (Nguyen et al., 2014). As inferred from human studies using MEG, the second phase of flight decision making while perceiving the predator in a complex spatial array of habitat features involves the nearly simultaneous linking of different brain areas by phase locking their neural activity. Once the predator is identified specifically via the inferotemporal cortex, coupled with background scene processing by the adjacent parahippocampal cortex and retrosplenial complex, the prefrontal cortex and OFC can orchestrate the patterning of flight behavior.

Predatory snakes are a threat to variety of rodents with large venomous snakes capable of eating young or small monkeys. Whereas venomous snakes constitute major dangers during unexpected encounters, larger pythons and boa constrictors constitute more systemic predatory threats and can be dealt with effectively if detected early; thus, large snakes are provocative to juvenile and adult monkeys. An experimental study using snake models revealed that the Indian python was the only model snake among a series of smaller model venomous and nonvenomous snakes that engendered alarm calling by wild bonnet macaques (see Video 3 in the online version at https://doi.org/10.1016/B978-0-443-29068-8.00089-1).

One major cue for identifying partially occluded snakes in leaf litter is the crosshatch scale pattern. In experimental presentations, captive-born rhesus macaques are more vigilant toward a snake model with a crosshatch pattern than one without. Large snake-scale patterns, such as repetitive ovals and diamonds, appear to act as predator-recognition cues to white-faced capuchins in Costa Rica that can distinguish models of a boa constrictor and neotropical rattlesnake from a model scorpion eater snake, a noncapuchin predator without large snake-scale patterns (Meno et al., 2013, see Video 4 in the online version at https://doi.org/10.1016/B978-0-443-29068-8.00089-1).

Recognition of a repetitive snake-scale pattern is clearly innate in California ground squirrels as evidenced by their precocious ability to recognize a gopher snake and a textured strip resembling a gopher snake the first day pups use vision to navigate. The innate properties of snake recognition are also evident in the fast reaction times for expressing protective behavior. For example, in humans and wild bonnet macaques, unexpected detection of a nearby snake engenders immediate freezing, startling, or jumping back with latencies as brief as 200 ms. Such a fast reaction precludes higher-order cognition as apparent from interviews of experienced herpetologists surprised by snakes; they mentioned that they became consciously aware of the snakes mostly after the event. The visual processes underlying the innate aspects of snake recognition involve the same brain loci used for face recognition, but with different neural specializations useful for processing highly periodic patterns characterizing crosshatched snake scales, repetitive bands, and blotches (Kawai, 2024). In Japanese macaques, electrophysiological recordings from the pulvinar, a structure receiving direct topographic projections from the SC, suggests that both structures are involved in evaluating snake dangerousness via their striking or relaxed postures (Le et al., 2014).

At the neocortical level of neural organization, research on cats has shown that the first phase of integrating moving gratings resembling snake scales into a global coherent pattern involves higher-order motion analysis by area V1 in the primary visual cortex. In nonhuman primates, top-down neural pathways involving area MT in visual cortex and cortico–thalamo–cortical loops play important roles in the perception of high-resolution images of snakes. Because of the smaller numbers of retinotopic projections to the SC than the visual cortex, low-resolution images of snakes are detected more rapidly via the SC and pulvinar that sends projections to the amygdala. Also, to facilitate rapid responses to snakes to avoid envenomation or being seized by pythons, the OFC inhibiting physiological arousal is less activated during snake perception, allowing concomitant snake recognition by the occipitotemporal cortex and concomitant amygdala activation to drive freezing and jumping responses by the PAG. As evidence for elevated involvement of the amygdala and reduced involvement of the OFC during interactions with snakes, rhesus macaques with bilateral lesions to the OFC showed initial retention of snake fear whereas bilateral lesions of the amygdala eliminated emotional expressions of fearfulness. Similarly, recognition that a rattlesnake is dangerous by snake-naïve rock squirrels during a staged rattlesnake encounter is not disrupted by bilateral OFC lesions, but this removal of OFC inhibition of the amygdala increases sympathetic nervous system arousal substantially.

With evidence of ecologically relevant biases for detecting and recognizing snakes, learning can play an important role in fear augmentation or reduction. Watching an experienced rhesus macaque observing a snake fearfully on video enhances selective learning in captive-born monkeys that a snake is dangerous, while watching a similarly fearful response to flowers on video does not enhance fear of flowers. With this result, it seems reasonable to argue that, with numerous snake encounters in the wild, fear should increase with age. With the exception of pythons, which are provocative to all age classes, and unexpected encounters with snakes, adult bonnet macaques are less excited by snakes than juveniles; adults do remain vigilant when they forage near snakes, a property consistent with processes of selective habituation when snakes do pose a direct threat.

Persistent wariness following predatory attacks

Sustained vigilance (hypervigilance) after prey survive a predatory attack has been equated in humans to combat-related post-traumatic stress disorder (Zanette et al., 2019). For example, zebrafish are an established animal model for inferring the biological properties of other species. These fish typically react strongly to chemical alarm cues that emerged from a predatory attack. When exposed to zebrafish skin odor indicative of a predatory event, zebrafish exhibit anxiety like wariness when placed in an unfamiliar tank compared with controls exposed to the odor of rainbow trout (Thapa et al., 2024). The emotional aspect to this olfactory cued behavior would involve the amygdaloid complex receiving projections from the olfactory bulb known to be involved in fear conditioning. Extended visual wariness of a novel setting would likely include the neurological changes in the optic tectum, the evolutionary homolog of the SC. As an example of enhanced neural-transmission efficacy, African jewel fish chased by a net for 9 min exhibit rapid enlargement of dendritic spines on tectal interneurons that change the efficacy of neural circuits, an effect persisting for 24 h (Burgess and Coss, 1983).

Based on analogous animal models, sustained combat-like stress enhances glucocorticoids that remodel patterns of interneural connectivity facilitating an increased wariness than would wane slowly. The specific events inducing stress do not have to be contextually associated with the behavioral outcome of elevated wariness. For example, the acute immobilization of laboratory rats increases dendritic arborization in the amygdala that includes the addition of new dendritic spines (Mitra et al., 2005). Such brain remodeling promotes a generalized fearfulness unrelated to the immobilization stressor. That is, the immobilization stressor that increases interneural connectivity in the amygdala generates a noncontextual anxiety that can facilitate a wide range of avoidant behaviors involving other brain structures, such as the OFC that also evaluates levels of reward. The immediate flight of prey in social groups (Fig. 1) would induce stress in fleeing observers that might not have detected the flight-triggering agent. While the process of habituation to nonthreatening predator is transient depending on the predator's visibility to prey, the underlying amydgala-induced anxiety generated from previous flight experiences remains elevated to cope with future threatening contingencies.

Fig. 1 In view of other Cape buffalo, this female flees successfully from an attacking lioness. Photograph by Katherine Murray, Botswana, 2024.

Precocious antipredator behavior

Unlike species with indeterminate growth patterns that exhibit appropriate antipredator behavior at an early age (for fish, see Tulley and Huntingford, 1987), some mammalian young can exhibit inappropriate patterns of antipredator behavior that are clearly endangering. In immature Artiodactyla, such as Thompson's gazelles fawns, the adoption of a prone posture while hiding is a major antipredator defense. However, when disturbed while hiding, these fawns can suddenly expose themselves by stotting (upward jumping) just before taking flight. This adult-like action pattern clearly attracts the attention of nearby mothers as well as predators and can be viewed as a precocious behavior with maladaptive properties. As evidenced by the developmental neurobiology of white-tailed deer, another Artiodactyla, the brain is clearly undeveloped in fawns as emerging patterns of interneural connectivity are in their initial formative stages (Spocter et al., 2018). Similarly in the pups of California ground squirrels, the close investigation of a dangerous gopher snake or rattlesnake shortly after eye opening is clearly maladaptive (Fig. 2).

An explanation for this precocious behavior can be found by examining how neurons grow dendrites within the neuropil. In rat models of neuronal development in neocortex, the formation of primary and secondary dendritic branches are the most consistent aspect of neuronal growth due to the early genetic signaling that guides dendritic growth, spine formation, and axonal proliferation for creating functional neural circuits. Because these proximal dendritic branches are stable developmentally, even under conditions of experiential deprivation (e.g., Volkmar and Greenough, 1972), they provide the primary substrate for the interneural connectivity mediating the expression of innate behavior useful in later stages of development. Despite the increased vulnerability of young individuals to predators, the installation of neural circuits on developmentally stable proximal dendrites rather than more experience-dependent distal ones ensures the reliable expression of predator recognition and avoidance at a latter age when there is an increased likelihood of successful coping with predators.

The effects of relaxed natural selection on antipredator behavior

Unlike the emphasis of evolutionary biologists on explaining how natural selection shapes evolutionary change, studies of relaxed selection examine trait disintegration or trait persistence as relicts when the original sources of selection are diminished or no longer present. The study of antipredator behavior offers unique circumstances for investigating the effects of relaxed selection because the presence or absence of predators and their relative density and prey preferences can be quantified. Moreover, the survival functions of different antipredator behaviors in which failure to respond appropriately immediately impacts fitness are more easily interpreted than many other behavioral traits that affect fitness in a more progressive manner.

An important property of studying the effects of relaxed selection on trait stability is estimating the time scale for changes in the sources of selection from predators. There are several ways to estimate the time frame for the divergence of predator selected- and relax-selected populations. If the predator is exothermic, such as snakes, historical fluctuations in temperature can be estimated from the fossil pollen of temperature-sensitive trees and from sea-surface temperatures derived from temperature-sensitive foraminifera in ocean-core samples. Rising sea-level and the emergence of islands separating prey populations from mainland populations can provide relatively sharp demarcations in gene flow, as can geological events leading to the formation of other barriers to gene flow, such as large rivers. The presence of predators and prey in the same fossil assemblages provides clear evidence

Fig. 2 A 46 day-old California ground squirrel pup, the age of burrow emergence, confronts a devenomated rattlesnake in an artificial burrow.

of historical sympatry, and inferences can be made of possible predator–prey sympatry from fossils appearing in adjacent assemblages of the similar ages. Together, these indices can be linked to genetic distances calibrated to time, showing population divergences in regions with different predator densities. Finally, coarse estimates of time scales of relaxed selection can be made from phylogenetic analyses of species with and without specific patterns of antipredator behavior.

Constraints on trait stability and evolutionary plasticity

There are three constraints at different levels of organization that potentially buffer antipredator behavior from undergoing rapid disintegration under relaxed selection: (1) the shared functionality of coping behaviors to mitigate predation at higher levels of organization, such as elevated vigilance, aggressive mobbing, or flight behavior, (2) neuronal organization at lower levels of organization engaged in the multifunctional processing of perceptual features useful for recognizing different predators, food resources, and variegated habitat features, and (3) the number of predator-recognition cues integrated into a coherent Gestalt.

The first constraint of shared functionality in behavioral expression is evident in the antipredator behavior of cat-sized tammar wallabies on Kangaroo island, South Australia, that have been isolated from terrestrial mainland predators, but not large wedge-tailed eagles, for an estimated 9500 years. Presentations of mammalian predator models to inexperienced wallabies engendered heightened vigilance and antipredator behavior typical of mainland wallabies. This finding of visual predator recognition led to the multipredator hypothesis (Blumstein, 2006), positing that antipredator behavior might be buffered from rapid disintegration under relaxed selection from one class of predators if the sources of selection from any extant predators have properties that maintain similar patterns of coping.

With a focus on texture-based predator recognition, the second constraint on evolutionary change at lower levels of organization also involves intertwining multifunctional systems. As discussed earlier, the periodic pattern-processing aspects of rodent, cat, and primate V1 neurons in visual cortex are essential for distinguishing important visual features. Ground squirrels likely employ the same pattern-processing ability to distinguish periodic snake scales and grass seed heads from the complex backdrop of irregular detritus and leaf litter (Coss, 1999). Similarly, dot-pattern selective neurons in the primate inferotemporal cortex that receive input from the visual cortex are attuned to less regularity but have properties theoretically proposed to facilitate pattern segmentation essential for distinguishing spots and rounded patterns. Despite the enormous amount to pleiotropy at the genetic level playing a role in trait stability, any mutations that disrupt the developmental integrity of neural circuitry specialized for these critical visual pattern-processing abilities would thus be scrubbed from the gene pool.

The question remains as to whether under relaxed selection highly conserved neural processes mediating lower levels of visual information processing with broad functionality can protect more specialized neurological processes subserving higher-level pattern recognition from undergoing rapid disintegration. Although such purifying selection accounts for the ancient continuity of visual-texture processing by diverse mammalian species living in different habitats, further specialized neural circuitry clumps visual information, so it pops out to the perceiver as a meaningful Gestalt.

Single-unit recordings of humans engaged in visual-recognition tasks showed that only a fraction of neurons in the medial temporal cortex receiving visual input from the inferotemporal cortex were active out of the hundreds presumably addressed by this memory system and among the millions of neurons activated by a typical stimulus (Quiroga et al., 2008). If applicable to the neural circuitry underlying innate predator recognition, such sparsely distributed coding by only a few million neurons (Lennie, 2003; Reddy and Kanwisher, 2006) could explain how selection is less encumbered in modifying variation in the pattern of interneural connectivity among only a small proportion of units within a bank of many units. Perceptual integration of these neuronal units or patches could thus yield a generalized template for predator recognition (for face-selective patches in macaques, see Moeller et al., 2008). As a result of the much greater historical entrenchment of the neural organization for visual-texture processing than for broader pattern recognition, this latter specialization in information processing is much more plastic in the evolutionary time frame. Although tentative from only a few experimental studies, the robustness of predator recognition under relaxed selection appears to be associated with the number of distinctive predator features integrated perceptually into a meaningful whole. For example, the Spanish subspecies of pied flycatchers relies on two recognition cues for identifying their redback shrike predator: the black band that masked the shrike's eyes and its passerine-like body shape (Curio, 1993). Relaxed selection from shrike predation in the 1000 year time frame is sufficient to induce loss of recognition of a model shrike in nearly all pied flycatchers examined, compared with their ability to recognize more visually complex owl models which is facilitated by the owls' large facing eyes.

West Indian green monkeys imported from West Africa to Barbados Island in the 16th century run up trees like their African counterparts after hearing a playback of a leopard alarm call (Burns-Cusato et al., 2013); these monkeys will also gather and alarm call vigorously at a model leopard and even alarm call at a yellow disk with leopard spots. In the longer time frame of an estimated half million years of relaxed selection from jaguars, black-tailed deer in Northern California appear to have lost their ability to recognize a model jaguar as dangerous because the spotted coat has seemingly regained its original obliterative shading function, disrupting jaguar shape (Stankowich and Coss, 2007). On the other hand, black-tailed deer do recognize a puma model as dangerous and generalize recognition of a large felid shape to a novel tiger model that has less disruptive stripes.

While intuitively simple in their linear configuration, snakes do constitute complex configurations that challenge the recognition process because their appearance can change substantially from coiled to moving in a sinusoidal fashion. Motionless snakes, especially their heads, need to be detected quickly, and coiling disrupts repetitive patterns, leaving the finer-grain snake scales as the only consistent snake-recognition cue. Nevertheless, rattlesnakes and gopher snakes are distinguished in experimental presentations

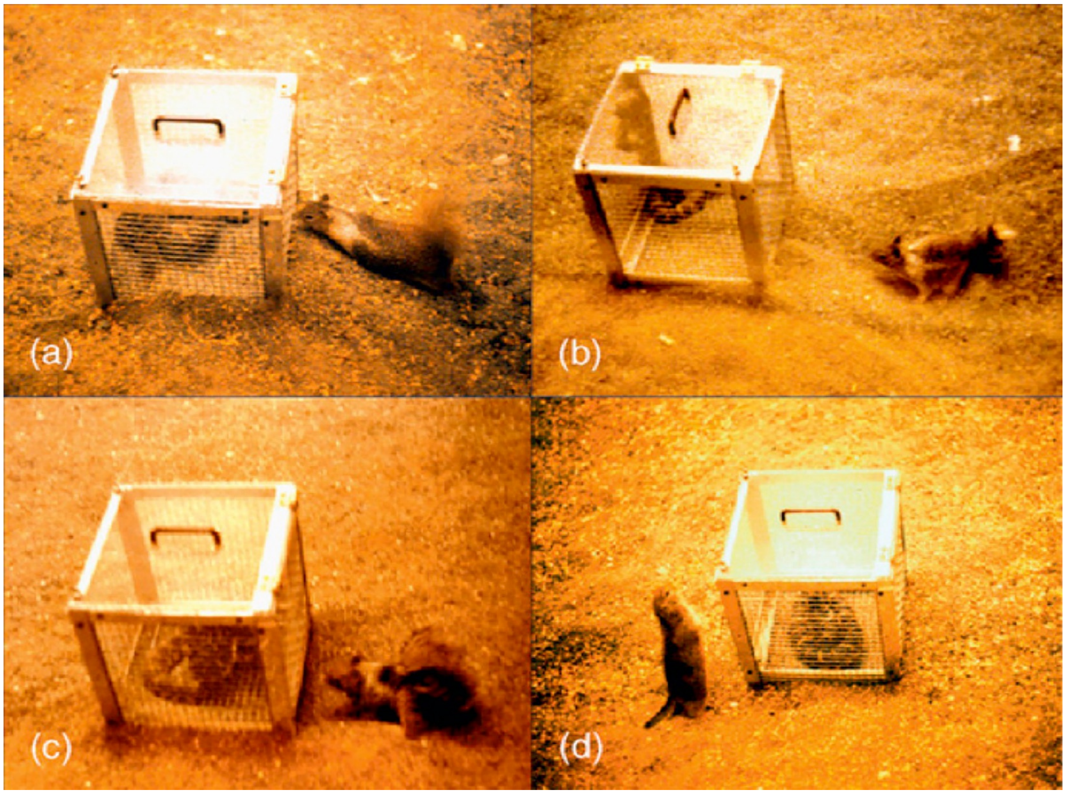


Fig. 3 Evolutionary persistence and loss of snake recognition by ground squirrels. Photographs are taken through a one-way mirrored window during experimental study revealing behavioral differences among California ground squirrels (*Otospermophilus beecheyi*) that currently or historically encountered rattlesnake and gopher snake predators and Arctic ground squirrels (*Spermophilus parryii*) whose ancestors evolved for the past 3 My in snake-free central Alaska. (a) California ground squirrel from the snake-abundant Folsom Lake area harassing a caged rattlesnake by tail flagging vigorously. (b, c) California ground squirrels from the Lake Tahoe basin and Mt. Shasta are shown preparing to harass the rattlesnake by throwing substrate. Tahoe basin and Mt. Shasta squirrels have experienced relaxed selection from snakes for estimated times of 70,000 and 300,000 years, respectively. (d) Arctic ground squirrel exhibiting a vulnerable standing posture indicative of loss of snake recognition. Folsom Lake squirrels exhibit the highest serum-based resistance to rattlesnake venom recorded in this species. Lake Tahoe squirrels show an intermediate loss of venom resistance and squirrels from Mt. Shasta show the same lack of venom resistance as Arctic ground squirrels.

by wild California ground squirrels experiencing relaxed selection for an estimated 300,000 years (Coss, 1999), a time frame in which their serum-based resistance to rattlesnake venom has dissipated completely (Fig. 3).

While the snake-recognition system persists under prolonged relaxed selection, changes in the cohesiveness of antisnake behaviors are evident, and all populations studied show an elevation in sympathetic nervous system arousal. Based on human studies, high states of arousal can compromise behavioral expression, leading to recklessness. As discussed previously with rock squirrels engaging a rattlesnake in staged encounters, lesions of the OFC disinhibit amygdala activity that elevates arousal markedly. In a similar manner, elevated arousal while dealing with snakes in relax-selected California ground squirrel populations might reflect neural reorganization of the OFC due to genetic drift in combination with unrelated sources of selection. From this insight, natural selection from snakes for thousands of years has apparently dampened physiological arousal during snake encounters, which might explain the calmer, more coordinated pattern of antisnake behavior by these squirrels. Although biophysical evidence from rats indicates that the expense of generating neuronal action potentials is high, the persistence of antisnake behavior under relaxed selection argues for sparse coding for the underlying neural circuitry that engenders a low metabolic burden.

A final point should be made about higher-order predator-recognition processes under relaxed selection that include how prey anticipate the motivational states of predators, what actions they might take, and the kinds of habitat features and circumstances useful for evading predation. In experimental presentations, a predator can be recognized visually outside its natural surroundings by inexperienced prey. Nevertheless as mentioned above, it is reasonable to argue that predator recognition evolved to operate most effectively when the predator is embedded in the appropriate context of its typical surroundings. Prolonged relaxed selection is likely to compromise the habitat-related contextual aspects before predator-recognition fails completely, in part, because the integration of predator appearance and background habitat has been historically much more variable than the continuity of predator-recognition cues of shape, texture, sounds, and odor. Future study of relaxed selection should address whether species that continue to recognize predators robustly in appropriate habitats maintain this ability in experimental contexts altered to reflect historical circumstances no longer present.

Conclusion

The examples of predator-avoidance behavior discussed in this chapter provide a backdrop for understanding the interaction of different levels of behavioral organization, with the lowest level involving the mechanistic properties of neural circuitry. At this level of organization, only a few studies provided sufficient information about how the perceptual aspects of predator features are recognized and initiate the appropriate expression of defensive behavior. Mammalian antipredator behaviors, notably those of nonhuman primates, were emphasized because some attributes of neural functions could be interpreted from studies of the specific brain areas of nonhuman primates and humans that are presumably homologous. Such interpretations were directed at explaining their adaptive properties in fostering survival and fecundity.

There are essential aspects of predator avoidance that need to be explored by further study. Natural selection operating on successful predator evasion involves the composite of predator features and the typical microhabitat for these encounters. Predator detection is only the first phase in the process of predator identification. The perceptual saliencies of olfactory, auditory, and visual cues are embedded contextually within varying microhabitat features that typically exhibit much greater complexity. Prey thus need to extract this information from complex arrays of microhabitat features by recognition systems that are reliably invariant either due to historically consistent sources of natural selection or by recognition systems that emerge from neural-circuit plasticity that affords contextual learning. Future field and laboratory studies of antipredator behavior need to consider these contextual relationships in planning experiment protocols.

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