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Are we chemically aposematic? Revisiting L. S. B. Leakey's hypothesis on human body odour

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Aposematism entails a mutually beneficial avoidance of signal emitters by heterospecific signal receivers. The celebrated palaeoanthropologist L. S. B. Leakey hypothesized that humans are chemically aposematic, suggesting that our body odour repels large carnivores because they associate our 'bad smell' with what he alleged is our unpalatable flesh. Unpalatability, however, is one of many unprofitable traits potentially denoted by aposematic signals. Moreover, aposematism may arise in interactions with offenders other than predators. Here, I propose that the body odour of humans and, historically, of hominins denotes chemical emitters who exhibit formidable defensive traits, including large body size, agility, vigilance and the capabilities of deploying projectiles and other weapons and/or marshalling group defences. This hypothesis maintains that selection acts against (1) offenders, including carnivores, that fail to avoid chemicals from hominins, and (2) hominins who fail to emit distinguishing chemicals, thereby giving rise to a chemically mediated avoidance that is mutually beneficial, i.e. chemical aposematism. This hypothesis is examined in light of information on free-ranging New and Old World carnivores that avoid humans and on non-domesticated mammals suspected or confirmed to avoid human scent.

ADDITIONAL KEYWORDS: aposematism – body odour – chemical aposematism – human scent – synomone.

'I believe that one of the best ways to protect yourself from bears is to at least smell human.' S. Harkrader, in Porch (1990)

INTRODUCTION

Speculation over the years on the role of human body odour has generated a fund of anecdote and legend (Stoddart, 1990). Recent discussions of human scent focus on evidence attesting to its socio-sexual functions and effects (see de Groot *et al.*, 2017). In a different vein, L. S. B. Leakey (1967), the celebrated palaeoanthropologist, hypothesized that our body odour repels large carnivores because they associate it with what he alleged is our unpalatable flesh. Hence, Leakey's hypothesis purports aposematism, which entails a mutually beneficial avoidance of signal emitters by heterospecific signal receivers. Although traditionally observed in the context of predator–prey interactions, aposematic signals, considered broadly, also avert hazardous encounters between inimical signal receivers and signal emitters in other types of relationships, e.g. between competitors (Jablonski *et al.*, 2013).

Here, I examine the plausibility of Leakey's hypothesis in light of current views on the evolution of aposematism, considered broadly, and of information on free-ranging New and Old World carnivores that avoid humans, and non-domesticated mammals that are suspected or confirmed to avoid human scent. I suggest that the body odour of humans and, historically, of hominins denotes chemical emitters who are capable of mounting formidable (chiefly behavioural) defences, and that hominin chemical emissions evolved as an aposematic signal fostering a mutually beneficial avoidance of hominins and other potentially offending species. [Literature citations originally featured in most of the quoted passages here are omitted; citations that are featured in quoted passages are not included in the References section. Readers should consult the quoted sources for their supporting references.]

LEAKEY'S HYPOTHESIS

A chief inspiration for Leakey's hypothesis came not from his iconic fossil discoveries, but instead from

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camping in the Serengeti (Leakey, 1967). It was there that he or his students, on separate occasions, were approached by up to five African lions (*Panthera leo*), some of which entered their tents. The lions sniffed at their heads and walked away without attacking them. Leakey (1967: 5) recounted these tense encounters and speculated as follows: 'I seriously believe that one of things which protected many early primates, including early man, in the defenseless days before he had weapons or tools, and when he was living on the ground, was that he was unpalatable to the carnivores.… Whether man's natural immunity to large carnivores is smell by itself – they certainly sniff at us – or whether it is a combination of smell plus knowledge of how flesh tastes, I do not know, but I am convinced that a major defense mechanism of the earlier stages of protoman and early man was neither weapons nor canine teeth, nor claws nor physical strength, but his nature-endowed characteristic of being unpalatable, of not being good food for large carnivores.'

CRITICAL RECEPTION

Literature reviews of primate anti-predator defences over the past few decades fail to mention Leakey's hypothesis (Anderson, 1986; Cheney & Wrangham, 1987; Isbell, 1994; Stanford, 2002; Treves & Palmqvist, 2007), and only a few of his contemporaries commented on it. Quigley (1971: 523) did not explicitly cite Leakey for his hypothesis but stated: 'It is generally agreed that human flesh is normally repugnant to felids, although it has also been suggested that they may become addicted to it.' He posited (op. cit.: 524) that 'Man's success in survival over the millions of years during which he was a grassland resident without either fangs or weapons depended, thus, on behavior.… Furthermore, men were rare and widely scattered, and their flesh may have been distasteful to the ordinary predators.'

Kortlandt's (1980) perspective on the responses of carnivores to the 'strong body odour' of primates contrasts markedly with that of Leakey. Kortlandt (1980: 80) cited a kairomonal effect (*sensu* Blum, 1977) associated with body odours, not an evolved function, positing that 'those carnivores that hunt by scent should always have been able relatively easily to follow primate spoors, and hominid footprints particularly.'

Kortlandt (1980) maintained that early hominins defended themselves against their predators and food competitors with weapons; specifically, thorn branches. He dismissed Leakey's unpalatability hypothesis (op. cit.: 84): 'The idea is ingenious, but from an ecological point of view it is inconceivable that a readily accessible source of meat would remain unexploited for 10 or 20 million years, during which the Carnivora showed a very fast evolution, as well as highly adaptable foraging strategies. The only near-exception that comes to mind are the skunks which are eaten only by raptorial birds. At any rate the apes and man are not skunks. Moreover, Brain (1970, 1978) has proved beyond reasonable doubt that leopards did prey on robust australopithecines at Swartkrans roughly about 1 1/2 million years ago.'

Schaller & Lowther (1969: 330) questioned Leakey's supposition regarding the general unpalatability of primates: 'We find little evidence for such an assumption. Leopards readily eat other primates, such as baboons and even gorillas, and tigers eat rhesus monkeys and langurs. The readiness with which some of the big cats learn to feed on man is well known, and hyenas, too, kill and eat people. The big cats react to man, and presumably did so to the early hominids, as to another predator, not as to a typical primate, judging by their aggressive and flight behavior.'

PREDATION AND UNPALATABILITY

Large carnivores, particularly cats, pose an ancient and recurring threat to hominins. As Loveridge *et al.* (2010: 172) stated, '…human deaths due to large cats are not a thing of the past. Human deaths and injuries caused by lions are relatively common in central and southern Tanzania, with around 563 Tanzanians killed between 1990 and 2004. Similar numbers of people are killed and injured in the Sundarbans of India and Bangladesh, with 294 people killed between 1984 and 2001 in the Indian Sundarbans and 79 people killed between 2002 and 2007 in the Bandgladesh Sundarbans.' Tigers (*Panthera tigris*), which of the large cats are the most prolific killers of humans, killed ~34 075 people in India during the 19th and early 20th centuries (Shepherd *et al.*, 2014). In the 20th century, 12 600 people are estimated to have been killed by tigers, with up to 800 deaths per year from attacks in Asia, chiefly India. In the Americas, jaguars (*Panthera onca*), although rarely reported to attack humans in the wild (Shepherd *et al.*, 2014), occasionally prey on the Aché, a tribe of hunter-gatherers indigenous to Paraguay; jaguar predation accounts for 8% of the mortality of adult Aché tribesmen (Hill & Hurtado, 1996).

As earlier authors had remarked (Schaller & Lowther, 1969; Kortlandt, 1980), documentation of predatory and other attacks on humans by carnivores seems inconsistent with the notion of hominin unpalatability. However, a host of experiential and circumstantial factors are acknowledged to influence the propensity of carnivores to attack humans, making it difficult to relate the literature on this topic to Leakey's hypothesis. Tigers, for example, sometimes attack humans in response to harassment rather than hunger (Gurung *et al.*, 2008). When humans attempt to scavenge from the fresh kills of pantherines, a strategy that may have been adopted by early hominins, they are frequently attacked (Treves & Naughton-Treves, 1999). African lions may commence preying on humans when unintentionally provisioned with human carcasses, or they may learn to prey on humans from pride-mates (Kerbis Peterhans & Gnoske, 2001). Interestingly, some of this literature supports the idea that humans are less preferred as prey. For example, dietary specialization on humans has been observed when natural prey are absent, depleted or removed (Kerbis Peterhans & Gnoske, 2001; Gurung *et al.*, 2008). According to the so-called infirmity hypothesis (Yeakel *et al.*, 2009), pantherines that are sickly, injured, aged or emaciated, and thus unable to secure natural prey, often resort to preying on humans (Kerbis Peterhans & Gnoske, 2001; Gurung *et al.*, 2008). Although intriguing, the relevance of these observations to human defence is unclear.

The assessment of Leakey's unpalatability hypothesis calls for tests of the consumption or rejection by carnivores of human tissue. Swynnerton (1919: 206–207), who conducted extensive studies on the palatability of insects to vertebrate predators, had early designs on such an experiment: 'I was much disappointed at not securing a lion or a leopard for my trials of the larger mammals, particularly of man, my experiments with the flesh of whom were prompted by Darwin's admitted difficulty in accounting for the smells of the different races and certain other distinctive characteristics in man generally.' A century later, the relative acceptability of humans for consumption by large carnivores remains untested.

CHEMICAL APOSEMATISM

Leakey's (1967; in Quigley, 1971) hypothesis that carnivores avoid the 'bad smell' of humans because they associate it with unpalatable flesh parallels suggestions by other authors that distasteful or toxic organisms emit aposematic chemicals. The feathers and skin of New Guinean birds of the genus *Pitohui*, for example, contain homobatrachotoxin, a structurally complex alkaloid that depolarizes electrogenic membranes and that, owing to this toxicity, presumably thwarts consumers (Dumbacher *et al.*, 1992). Pitohuis also emit a 'strong sour odor' that, like their contrasting orange-brown and black plumage, is believed to be aposematic.

Eisner & Grant (1981), who postulated that 'olfactory aposematism' is widespread in nature, speculated how odours emanating from aposematic organisms may be related to the toxic chemicals they possess: 'Often the organisms involved are identifiable by odors unrelated to the toxins. There is no evidence to indicate that the odors themselves, at their natural concentrations, are intrinsically repellent to predators or play any direct role in chemical defense.… Aposematic odors, one might imagine, could in many instances be no more than odors of incidental origin that have only secondarily, under appropriate predation pressure, and with or without chemical elaboration, taken on a communicative role.' As Diamond (1992: 19) noted for toxin-laden, sour-smelling pitohuis, 'Just as a skunk's striking black-and-white colour constitutes a warning signal distinct from its stink, the pitohuis' stink must be due to a separate chemical; homobatrachotoxin itself is odourless.'

Eisner & Grant (1981) conjectured that chemical aposematism arises by virtue of consumers' learned associations between the 'olfactory concomitants' they posited and the deleterious effects of ingested toxins. Weldon (2013) noted that hazardous or otherwise unprofitable prey also may select for unlearned chemical aversions.

REVISED HYPOTHESIS

The idea that warning signals denote unpalatability was first proposed by Alfred Russel Wallace (1867) for caterpillars whose bright coloration he hypothesized advertises their distastefulness. A panoply of hazardous or otherwise unprofitable traits are also denoted by aposematic signals (see Weldon & Burghardt, 2015). As Eisner & Grant (1981) stated, 'Noxiousness manifests itself in many ways in organisms, as through distastefulness, contact irritancy, pugnaciousness, and possession of defensive glands or mechanical weaponry. Body odors could take on a warning function in all such cases.'

An aposematic function of hominin body odours may be predicated on defences akin to one suggested by Eisner & Grant (1981), pugnaciousness. Humans, other hominins and some non-human primates are formidable adversaries of predators, competitors and other offenders, owing to their large body size, agility, vigilance and abilities to deploy projectiles and other weapons and/or marshall group defences (Anderson, 1986; Cheney & Wrangham, 1987; Isbell, 1994; Stanford, 2002; Treves & Palmqvist, 2007; Willems & van Schaik, 2017). As Hart & Sussman (2009: 162) stated of primate encounters with predators, 'The ultimate act of defense, killing the predator, is atypical but not unknown' (see Cheney & Wrangham, 1987).

I submit that the aforementioned defensive traits plausibly support hominin aposematism. This hypothesis maintains that selection acts against (1) offenders, including carnivores, that fail to avoid chemicals from hominins, and (2) hominins who fail to emit distinguishing chemicals, thereby giving rise to a chemically mediated avoidance that is mutually beneficial, i.e. chemical aposematism. In this hypothetical scenario, the use of weapons, the focus of Kortlandt's (1980) thesis on hominin defences, potentially undergirds rather than competes with a hypothesis on chemical defence.

AVOIDANCE OF HUMANS AND THEIR SCENT

The approach of humans in the field can be threatening for many non-domesticated mammals. Even large carnivores, including African lions (Valeix *et al.*, 2012), brown bears (*Ursus arctos*) (Moen *et al.*, 2012; Sahlén *et al.*, 2015) and gray wolves (*Canis lupus*) (Karlsson *et al.*, 2007; Wam *et al.*, 2012), adjust their behaviour to avoid encountering humans in a way similar to that of prey evading predators. The risk sensitivity of free-ranging mammals to human approach can be measured as the flight-initiation distance, the distance at which an animal moves away from an approaching threat. Stimulus control studies are needed of the various cues to which large mammals attend in assessing this risk, a daunting logistical challenge, even in tractable field conditions. Nonetheless, field investigators have inferred that some carnivores detect the scent of distant humans and, hence, evade them. Brown bears, for example, are believed to avoid the scent of people as far away as ≥ 0.8 km (Craighead & Craighead, 1971).

In addition to carnivores (Corbett, 1946; Neal, 1977), anecdotal and experimental reports point to other non-domesticated mammals, including ungulates (Murie, 1935; Hubback, 1939; Darling, 1946; Linsdale & Tomich, 1953; Fuller, 1960), rodents (Taylor *et al.*, 1974) and lagomorphs (Norton *et al.*, 1981), that are suspected or confirmed to avoid human scent, whether substrate bound or airborne. Many of these avoidances probably represent kairomonal effects, where would-be prey avoid the scent of human predators; kairomones are semiochemicals that solely benefit chemical receivers, hence the interactions they mediate do not reflect the function(s) of chemicals for signal emitters, namely here, humans (Weldon, 1980). Nonetheless, accounts thus far of the avoidance of human scent indicate the plausibility of hominin chemical aposematism and its independent origins among diverse mammals, including New World taxa whose recent lineages did not interact with ancestral hominins.

These studies also point to the human integument as a source of chemicals eliciting avoidance in numerous mammals (Norton, 1980a, b; Norton & Bryce, 1981; Norton *et al.*, 1981; Conover, 1984; Conover & Kania, 1988; Bates *et al.*, 2007). Human skin has long been known for its unusual surface lipids that feature novel compound classes, carbon-chain lengths, sites of unsaturation and branching patterns (Nicolaides, 1974). As Nicolaides (1974: 25) mused regarding the products of sebaceous glands, a major source of human skin lipids, 'An outstanding property of the unusual lipids of sebum is its extraordinary complexity. Why are so many compounds made? What functional significance could this have? One possible answer is that these substances serve as olfactory messages – a means for chemical communication in the biological world.' Chemicals from various scent sources of humans, including several types of exocrine skin glands, need to be tested systematically for their behavioural effects on heterospecifics.

EXPERIMENTAL STUDIES OF RESPONSES TO HUMAN SCENT

Two species of large mammals in free-ranging populations have been tested in controlled experiments for responses to non-menstrual human odours: the white-tailed deer (*Odocoileus hemionus*; WD), which lives in deciduous forests, grasslands and other habitats in North, Central and South America; and the African bush elephant (*Loxodonta africana*; AE), the largest extant terrestrial animal, which lives in grasslands, plains, dense forests and other habitats in sub-Saharan Africa. Neither species is predaceous, but both are known to attack and kill humans in defence of territories or conspecifics, e.g. offspring; in these contexts, any measure that pre-empts encounters with humans, via semiochemicals or otherwise, may be mutually beneficial. Hence, the avoidance of humans by these mammals may exemplify, and not merely be tangential to, aposematism.

White-tailed deer

Of the non-domesticated mammals studied experimentally for responses to human scent, none has received more attention than WD. White-tailed deer damage more commercially valuable plants in the USA than any other vertebrate; hence, investigations of their responses to the scent of humans (and carnivores) have been undertaken chiefly to identify sources of feeding-deterrent chemicals.

Swihart *et al.* (1991) demonstrated that WD in Connecticut, USA, are averse to browsing on Japanese yews (*Taxus cuspidata*) and eastern hemlocks (*Tsuga canadensis*) when these plants are treated with the urine of native carnivores, but not when treated with human urine. Swihart *et al.* (1991: 774) speculated that interactions with humans had been relatively brief in evolutionary terms, 'thereby mitigating against the development of innate responses to human odors.' Nunley (1981: 631) argued otherwise:

'The archaeological record shows that deer have been the prey of human predators in North America alone for at least 10 000 years. In just the relatively short period of time since the arrival of Europeans, the feeding patterns of North American white-tailed deer have undergone a shift from a primarily diurnal to crepuscular and, even more frequently, nocturnal schedule. In addition, some experts hold that, as a result of increased pressure by human predators in the same period, the inquisitive-natured white-tailed deer is giving way through natural selection to a wilder-natured deer. These are good examples of the sorts of behavioral microevolution which might have produced an aversion to human or human female odors.'

As in the study by Swihart *et al.* (1991), neither Nunley (1981) nor other investigators (March, 1980; Sullivan *et al.*, 1985; Berger *et al.*, 2001) have consistently elicited avoidance in WD or other cervids with human urine. Instead, agriculturalists discovered that WD are repelled by the scent of human hair. During the 1970s, organic gardeners in the USA used balls of human hair to deter WD and reduce crop damage, thereby avoiding the use of synthetic repellents (Webster, 1978). By the early 1980s, growers of fruit, ornamental trees and nursery crops in Ohio, USA, reported that human hair was their most commonly used WD repellent, rating it a minor to major deterrent of browsing (Scott & Townsend, 1985).

Experimental studies at various field sites confirm that WD are averse to the scent of human hair. In Connecticut, USA, bags of hair suspended on apple (*Malus pumila*) trees significantly reduced browsing damage by WD on buds (Conover & Kania, 1988). In a study with Japanese yews, a preferred winter food of WD, damage to plots treated with human hair averaged 34% lower than in control plots (Conover, 1984). In Alabama, USA, bags filled with hair placed along the perimeters of crop plots partly or completely reduced browsing damage, depending upon the type of crop present and the distances at which the bags were spaced; unprotected plants in control plots were severely damaged (Norton, 1980a, b; Norton & Bryce, 1981). A summary comparison of 12 studies of various commercial and natural repellents, including carnivore urine and faecal scents, rated human hair intermediate in its efficacy as a deterrent of WD and other cervids, with a higher composite score (2.1 on a 0–4 scale) than those of two commercial wildlife repellents (El Hani & Conover, 1998).

Human hair associated with crops has been shown to repel WD at distances of ~3 m (Norton, 1980a, b; Norton & Bryce, 1981). However, the deterrence of WD with hair in feeding bioassays, as with chemical repellents in general, may be influenced by the palatability of the experimental plants (Conover & Kania, 1988; El Hani & Conover, 1998). It is difficult, in any case, to extrapolate from the repellent effects of human hair observed in feeding experiments to interactions with humans in normal field conditions. Free-ranging WD reportedly detect olfactory cues and flee from humans > 0.5 km away (Rue, 1962). Anecdotal observations of another cervid, the red deer (*Cervus elaphus*) in Scotland, suggest that it detects the scent of humans as far away as 0.8 km (Darling, 1946). Field studies are needed to ascertain the ranges at which animals respond to human body odour and to evaluate the influences of wind, thermals, humidity and other environmental parameters on its detection.

African bush elephant

African bush elephants in the Amboseli National Park, Kenya, encounter several ethnic groups, including the Kamba and the Maasai. The Kamba are the most numerous of the agricultural and village-living tribes and currently pose little threat to AE. The Maasai are nomadic, cattle-herding pastoralists whose young men ceremoniously demonstrate their virility by spearing AE. Long-term anecdotal observations suggest that AE are averse to the sight, sound and smell of the Maasai (Kangwana, 2011). Bates *et al.* (2007) demonstrated that AE distinguish between these tribes on the basis of chemical cues, exhibiting heightened aversion to the scent of the Maasai.

Eighteen groups of AE, each tested as a family unit, were examined for their responses to the scents of the Kamba and the Maasai by exposing them to cloth garments worn for 5 days by men from these tribes; clean (unworn) cloths served as controls. The family groups ran faster and further and remained tense longer, as evidenced by their erect head posture, sniffing and close proximity to cohorts, in response to Maasai-worn cloths than to cloths worn by Kamba men. The AE fled downwind and away from the human-worn cloths in every trial, never venturing within 10 m of them. They were least averse to unworn cloths and were less likely to move downwind in response to them.

In every trial with human-worn cloths, the family groups fled towards and came to rest in clumps of elephant grass (*Pennisetum purpureum*). Trials with Maasai-worn cloths ended with AE in the tallest grass stands (median height = 1.25 m). In trials with Kamba-worn and the unworn cloths, the AE occupied much shorter stands (0.55 and 0.30 m high, respectively). Given that elephant grass covered only 7% of the study area, it was inferred that AEs sought shelter in grass stands, selecting the tallest stands when confronted with the greatest threat.

Seven of the family groups tested included individuals that had experienced multiple spearings to themselves or members of their family during the previous 30 years; three groups were composed of individuals not known to have experienced the spearing of any individual in their family throughout this period. No familial differences in the strength or types of reactions (speed of travel, distance moved or latency to relax) to the human-worn cloths were observed with respect to spearing history. The strong reactions exhibited even by those groups having had the least experience with spearing suggests that knowledge of the threat posed by the Maasai is transmitted via social learning throughout the local elephant population.

DISCUSSION

Aposematic chemicals belong to a general class of semiochemicals known as synomones, chemicals that mediate interspecific interactions where benefits accrue to both signal emitters and signal receivers (Nordlund & Lewis, 1976). In accordance with the general schemes conjectured for the establishment of synomones (Weldon, 1980), aposematic chemicals arise where (1) a chemically mediated avoidance at one time beneficial for one participant transitions into a mutually beneficial avoidance, (2) an existing, mutually beneficial avoidance comes to be mediated by chemical cues, or (3) a mutually beneficial avoidance comes into being through emitted chemicals. Learned associations between negative encounters with offending heterospecifics and their scent may establish or strengthen avoidances, as possibly reflected by the robust aversions of some animals to the scent of menacing human individuals (Knipe, 1977) or ethnic groups (Bates *et al.*, 2007). Unlearned avoidances probably stem from selection imposed on chemical receivers by dangerous chemical emitters, as Nunley (1981) suggested for the repellence of WD by human scent.

Despite their hypothesized widespread occurrence (Eisner & Grant, 1981; Weldon, 2013), aposematic chemicals have received little experimental attention and, consequently, are seldom mentioned in discussions of chemical defence. In a survey of chemically defended animals, for example, Berenbaum (1995) focused on toxins and other allomones, which are semiochemicals that benefit chemical emitters unilaterally. Of non-human mammals, she cited only the venomous duck-billed platypus (*Ornithorhyncus anatinus*) and the repugnant chemical sprayers, skunks (Mephitidae). Of humans, Berenbaum (1995: 6) wrote: ‘By all rights and purposes, human beings should not utilize chemical defenses; as top carnivores in many food webs, they are rarely if ever consumed by other organisms.’

Berenbaum’s statement regarding humans ignores, among other considerations, chemical deterrents of ectoparasites, notably non-host odours, which repel ectoparasites or inhibit their attraction to hazardous or otherwise unsuitable hosts and, concurrently, forestall injuries to hosts (Weldon, 2010). Tsetse flies (*Glossina* spp.), for example, are large haematophagous Afrotropical flies that transmit trypanosomes, the protozoans that cause trypanosomiasis, to humans and other animals. In the field, tsetse flies avoid human odour because it denotes a host that can catch and crush them during their protracted and painful bouts of biting (Vale, 1969, 1974, 1977, 1979). As Vale (1974: 583) wrote, ‘The intelligence and dexterity of a man make him an extremely hazardous food source and it is not surprising that men are avoided promptly by all food-seeking flies except those which are extremely hungry.’ The odours of nearby men even deter tsetse flies from landing on a preferred host, the ox (*Bos* sp.) (Hargrove, 1976; Vale, 1977). The avoidance by tsetse flies of non-host odours from humans is analogous to the chemical aposematism hypothesized here vis-à-vis predators and other anatagonists, where semiochemicals pre-empt interactions with a harmful species, *Homo sapiens*, and it concurrently becomes less vulnerable to harm.

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