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Opinion

Toward a unified framework for studying behavioural tolerance

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Behavioural responses are widely held to allow animals to cope with human-induced environmental changes. Less often appreciated is that the absence of behavioural response can also be advantageous. This is particularly true when animals become tolerant to situations that may be perceived as risky, although the actual risk is nonexistent. We provide a framework to understand the causes and consequences of behavioural tolerance. Tolerance can emerge from genetic, epigenetic, or learning mechanisms, each exerting different degrees of influence on its speed of acquisition, reversibility, specificity, and duration. The ultimate impact on fitness hinges on the interplay between these mechanisms and the nature of the stressor. Mechanistic clarity is therefore essential to better understand and manage human–wildlife interactions in the Anthropocene.

Highlights

Animals vary in how they respond to risks, and the extent to which they can modify their responsiveness has important consequences for understanding demographic responses to rapid human-induced environmental changes.

The development of behavioural tolerance toward potentially risky situations may be particularly advantageous in such contexts.

Behavioural tolerance can emerge from a variety of processes, leading to demographic and evolutionary consequences that can widely vary depending on the type of stressor.

We suggest that developing a mechanistic theory of tolerance is essential to understand its consequences for fitness, population viability, and human–wildlife interactions.

What is behavioural tolerance and why does it matter?

Species, populations, and individuals differ in their ability to colonise novel habitats, to deal with anthropogenic changes, and to avoid or get into conflicts with humans. The way organisms cope with human-induced environmental changes has conventionally been ascribed to phenotypic plasticity and evolutionary history [1]. However, an additional factor that demands more thorough consideration is **behavioural tolerance** (see Glossary). Behavioural tolerance can be defined as the degree of reaction to a **stimulus** signalling a potentially risky situation. An individual with high behavioural tolerance has a limited or no reaction to a risky situation. This excludes cases where animals do not detect the stimulus. By contrast, in response to a stimulus signalling a potential risk, an animal with low behavioural tolerance shows, for example, high vigilance, issues alarm calls, or promptly flees. Our definition thus expands the concept of tolerance beyond its conventional use in other disciplines, which also encompasses physiological tolerance (i.e., low sensitivity to a chemical or physical parameter) and ecological tolerance (i.e., the range of environmental conditions in which an organism can live). Most importantly, rather than the processes altering the response to a stimulus signalling a potentially risky situation, behavioural tolerance is the state that emerges from these processes.

Behavioural tolerance can either have positive or negative consequences on fitness. An individual overreacting to benign stimuli, a nonthreatening human approaching, for example, will face missed opportunity costs [2] by using time and energy that it could have devoted to essential activities, such as foraging or mating. On the contrary, a lack of fear to humans can facilitate the acquisition of new resources in human-populated areas by favouring exploration and innovative behaviours (e.g., [3]). This should in turn improve the physiological condition of the individual and hence its survival prospects. However, in other contexts, high tolerance may be fatal and maladaptive [2]. For instance, increased tolerance to human presence can increase vulnerability to poaching (e.g., [4]) or poisoning. These contrasting fitness consequences can affect the demography and evolution of populations exposed to changing environments, leading them either to go extinct or to thrive should tolerance levels be shared by most individuals.

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The term 'behavioural tolerance' is not used consistently in the scientific literature, perhaps because a general framework that defines it and identifies its causes and consequences is still lacking. Although tolerance can be applied to any fear-related behaviours, we develop a mechanistic framework that focuses mainly on anthropogenic contexts. Such a mechanistic perspective on tolerance to humans and their activities is essential to mitigate our impacts on wildlife more effectively.

Causes of behavioural tolerance

A variety of processes can drive differences in behavioural tolerance within (Figure 1) and between species. Studying the cause(s) of variation in tolerance is crucial to understand how tolerance may change through time and how it may generalise to other stimuli.

Tolerance may be under direct genetic control or express heritable variation in morphology, physiology, and behaviour. Morphological defences like armaments, poisons and venoms, aposematic

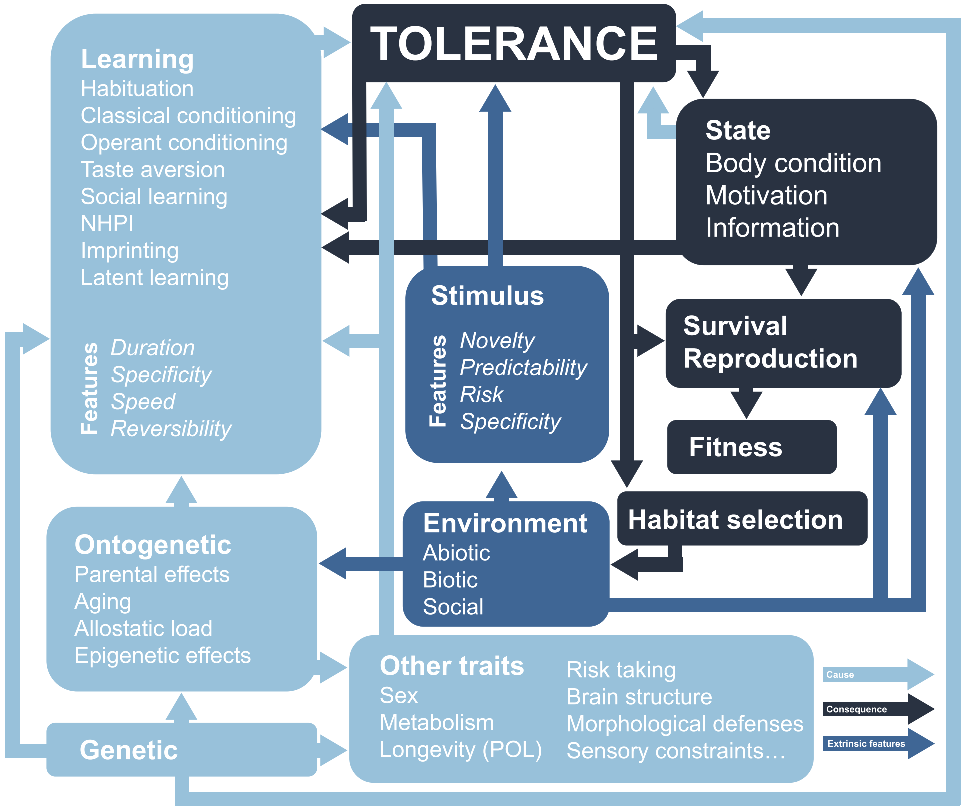

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Figure 1. Causes and consequences of individual behavioural tolerance. Behavioural tolerance is the result of genetic, ontogenetic, and learning processes and can affect an individual's state, its survival, reproduction, habitat selection, and fitness. Causes and consequences of tolerance, and tolerance itself, are modulated by the characteristics of the stimulus and environmental conditions. The consequences of tolerance (e.g., body condition) can cause variation in tolerance, and these feedback loops may cause significant and sudden changes in tolerance. Behavioural tolerance can be measured categorically (an individual does or does not respond to a stimulus) or continuously (individuals differ in the intensity of their response) by means of various metrics. High tolerance to human presence can, for instance, be inferred from short flight initiation distance, low vigilance, low avoidance, low giving-up density, low neophobic responses, short latency to come back to a food patch after a startle test, or extended time spent in areas with potentially threatening sounds, scents, or visual stimuli. Tolerance acquired through learning may differ between mechanisms [e.g., habituation vs. **natal habitat preference induction** (NHPI)] in terms of duration, specificity, speed of change, and reversibility.

Glossary

Behavioural tolerance: degree of reaction toward a potentially risky situation. It can be measured categorically or continuously using a variety of metrics (e.g., flight initiation distance, vigilance, avoidance).

Classical (Pavlovian) conditioning: learning process that leads to a conditioned response by associating a neutral stimulus to an unconditioned stimulus. If classical conditioning explains change in tolerance to the conditioned stimulus, tolerance may decrease without further presentation of the unconditioned stimulus.

Habituation: decline in responsiveness to a stimulus with repeated exposure and that is not explained by motor fatigue, sensory fatigue, or sensory adaptation. Tolerance acquired through habituation may decline without further exposure. Increased responsiveness to a stimulus with repeated exposure is called sensitization.

Imprinting: irreversible learning that occurs during a sensitive period (e.g., learning the identity of parents or habitat early in life). Variation in tolerance explained by imprinting should be stimulus specific.

Latent learning: nonreinforced experience influencing performance later in life. For instance, experience in an environment may improve survival after the introduction of a novel predator. Duration, reversibility, or speed of latent learning are difficult to predict.

Natal habitat preference induction: acquired experience with stimuli in the natal habitat impacting the habitat choice after dispersal. Natal habitat preference induction encompasses habitat imprinting. As with imprinting, variation in tolerance caused by natal habitat preference induction should be stimulus specific and irreversible.

Operant conditioning: type of associative learning that links a behaviour with a particular outcome. If operant conditioning explains variation in tolerance, tolerance should be maintained as long as the reinforcement continues, after which tolerance may change. With sufficiently strong reinforcers, operant conditioning can lead to rapid and reversible changes in tolerance.

Ontogenetic processes: any developmental changes happening over the course of an individual's lifespan.

Parental effects: parental influences on the offspring phenotypes, excluding direct genetic transmission.

signalling, or camouflage can increase tolerance. For example, camouflaged bird species tolerate closer human approaches [5]. Tolerance can also be sex specific if, for instance, the sexes differ in their baseline stress hormone levels [6]. Behavioural traits such as exploration, boldness, or neophilia are often associated with greater tolerance to disturbance [7]. The measure of tolerance will thus sometimes reflect the indirect effect of other traits (Box 1).

Genetic differences in tolerance are not necessarily adaptive but reflect genetic drift, trade-offs, or constraints. However, tolerance may have been shaped by selection to match the conditions in which a species evolved. For instance, insular species that have evolved in the absence of humans show some physiological stress responses yet do not react to an approaching human by fleeing (e.g., [8]). With rapid anthropogenic changes, a species or population's current average level of tolerance may be exapted for these changes or may, inversely, become maladapted. Intolerant species, such as migratory birds that are less innovative and less plastic than resident birds [9,10], may be more vulnerable to anthropogenic disturbance than more tolerant species.

If behavioural tolerance results from conflicting physiological, morphological, and behavioural responses, it is also expected to change with life history (i.e., how an organism allocates its time and resources to produce offspring). For example, slow-lived bird species (i.e., that favour longer lifespan over early reproduction) tend to have longer flight-initiation distances than fast-lived species, which suggests that they are less tolerant to risk or disturbance [11]. Similarly, large-bodied fish are more risk averse and flee earlier than small-bodied fish, probably because larger fish have higher reproductive value [12]. Given that life history has direct effects on the demography and evolution of populations exposed to sudden changes in the environment, identifying the link between behavioural tolerance and life history is crucial to understand how animals cope with human-induced environmental changes.

Epigenetic effects in early life can also profoundly shape an individual's tolerance later in life. For instance, maternal behaviours, such as frequent licking and grooming during infancy, affect the

Social learning: variety of processes (e.g., social enhancement, teaching, and copying) whereby individuals come to behave more like others. Social learning can act as an accelerant and rapidly spread a novel behaviour through a population. If social learning explains variation in tolerance, we expect rapid and potentially reversible change.

State: an individual's condition, which includes body and reproductive condition, motivation, and information. State may modulate tolerance directly or through its effects on the propensity to learn.

Stimulus: any external agent or event that calls the attention of the animal.

Taste aversion: avoidance of a food item after experiencing nausea following ingestion. Taste aversion can explain variation in diet and hence differential tolerance to various foods. It is usually irreversible.

Box 1. Disentangling behavioural tolerance from other behaviour traits

The term behavioural tolerance is widely used in the literature on habituation (e.g., [48]). It is also often associated with human-caused disturbances (e.g., [31]), but it can be applied to a much broader range of situations (e.g., predator–prey interactions). However, boldness, exploration, and neophobia are also involved in similar contexts, and the metrics used to quantify them can measure tolerance. For example, flight-initiation distances allow an estimation of an individual's boldness or tolerance, and vigilance toward a novel sound can be a measure of neophobia or tolerance. These traits do intersect with tolerance; while tolerance is the degree of reaction toward a potentially risky situation, boldness is an individual's propensity to take risks, and exploration is an individual's reaction to a new situation involving neophobia, neophilia, and information acquisition mechanisms [68].

Nevertheless, tolerance is not synonymous with boldness, exploration, or neophilia but is an emergent property arising from all these traits. Using the word tolerance does not imply any underlying mechanisms. Tolerance may result from habituation, although it may also be acquired from many other sources (see main text). Unless habituation is properly tested [69], an individual that is not bothered by city sounds is tolerant rather than habituated, and an individual showing low vigilance toward a stimulus could be either bold or neophilic but is, in any case, tolerant toward the stimulus. The use of the term behavioural tolerance thus prevents unjustified inferences about mechanism.

Investigating the causes and consequences of tolerance is critical in the context of human-induced rapid environmental changes. Animals are increasingly confronted with novel human disturbances, but the presence of other stressors in their evolutionary past may affect their current tolerance to anthropogenic stimuli. The concept of behavioural tolerance broadens our perspectives on the causes and consequences of human–wildlife conflicts and on potential mitigation strategies. Many management or conservation scenarios involve attracting or repelling wildlife [70], and analysing the mechanisms of tolerance to human stimuli is essential to improve management. Using the umbrella term 'behavioural tolerance' consolidates different literature on risk perception and fear responses in the context of anthropogenic disturbances and is essential if we aim at reducing the impact of our activities on wildlife.

development of the central nervous system, which, in turn, reduces fear of novelty in adult Norway rats (*Rattus norvegicus*), therefore increasing tolerance toward novel stimuli [13]. Increased paternal care also reduces anxious behaviours in three-spined sticklebacks (*Gasterosteus aculeatus*) by modulating *de novo* methylation [14]. Another way parents can affect their offspring's propensity to take risks is through diet. Young blue tits (*Cyanistes caeruleus*) supplemented with taurine have improved cognitive skills and are more risk prone than control individuals [15], suggesting that parental prey selection may contribute to shaping their offspring's tolerance. The parents' own experience with risk may also influence offspring tolerance through epigenetic mechanisms enhancing risk perception (e.g., [16]).

Throughout its lifetime, an individual undergoes **ontogenetic processes** that can influence its tolerance. For example, ageing, senescence, or allostatic load [17] accumulated through life can alter tolerance as can experience. Learning, influenced by both genetic and ontogenetic processes, is a major driver of variation in tolerance in an individual's lifespan. Changes in a genotype's tolerance can be studied by using the behavioural reaction norm framework (Box 2). **Habituation** is the learning process often inferred from observed changes in tolerance (e.g., [18], but sometimes incorrectly, see [19]). Habituation increases tolerance to a stimulus, while sensitisation decreases it. Many other learning processes may, however, lead to changes in tolerance. **Classical (Pavlovian)** or **operant conditioning**, among others, can also lead to an increase in tolerance like what we observe with habituation. For example, urban environments may promote human proximity tolerance in wild animals through anthropogenic food provisioning, which acts as a reinforcement (food conditioning; e.g., [20]). On the contrary, aversive conditioning methods can be used to reduce tolerance to human proximity (but the effectiveness seems to be mediated by personality [21]). Other learning mechanisms, such as **social learning**, **imprinting**, **latent learning**, and **taste aversion**, can also result in changes in tolerance.

Considering genetic and nongenetic mechanisms is essential to make predictions about the resulting tolerance because each mechanism involved in shaping tolerance may differ in terms of speed of change (i.e., acquisition and loss), reversibility, duration, and specificity of the outcome (Box 3). For example, given the high cost of mortality, dishabituation (or sensitisation) to former threats can be much more rapid than habituating to them. Following the cessation of hunting, it took 3 years for a population of European mouflon (*Ovis aries musimon*) on Kerguelen Island to increase their tolerance to human approach from >80 m to <30 m, whereas they went back to their initial intolerance after hearing a few gunshots (Réale, personal observation).

Consequences of behavioural tolerance for individuals and populations

Tolerance can influence an individual's **state**, like body weight or condition, via differential access to food. For example, tolerating human disturbance may provide abundant and predictable food supplies, improving the condition of individuals [22,23]. In eastern chipmunks (*Tamias striatus*), a species that tolerates the presence of humans well, females inhabiting urban habitats tend to have better body conditions than females in natural habitats [22]. Human food may, however, become an ecological trap for some species. Unhealthy coyotes (*Canis latrans*) show a greater tolerance to human stimuli and rely more on lower-quality food from anthropogenic sources than healthy conspecifics [24]. Tolerance can also indirectly influence an individual's state through enhanced motivation to forage or improved information acquisition to evaluate alternative resources.

Conversely, an individual's state can modify its tolerance. For instance, animals in poor nutritional condition may engage in riskier behaviours around predators or when exposed to novel situations [25]. Instead, females can attempt to reduce risk during the reproductive period, as seen in female Canada geese (*Branta canadensis*) that become less tolerant to human approaches as their

Box 2. Interpreting the dynamics of behavioural tolerance

To study the dynamics of behavioural tolerance, we need to measure the metrics that represent it on different individuals throughout time. We can then use a behavioural reaction norm approach [71]. Figure I shows behavioural reaction norms of three individuals (genotypes a, b, and c) exposed to a stimulus four times in two phases, separated by a phase without the stimulus. T_{ijk} is a behavioural reaction to the stimulus measured on individual *i* during the phase *j* at instance *k*. The dynamics of tolerance (ΔT), resulting from learning processes, for example, are inferred through repeated measures on individuals. As individuals are repeatedly exposed to the stimulus, tolerance decreases (e.g., individual *a* sensitises), increases (e.g., tolerance is reinforced in individuals *b* and *c* through operant conditioning), or stays constant. Assuming a linear response (but nonlinear models could also be used), we can analyse tolerance with the following mixed model:

$$T_{ijk} = \beta_0 + u_{0j} + (\beta_1 + u_{1ijk})x_{ijk} + (\beta_2 + u_{2ik})y_{ik} + (\beta_3 + u_{3ik})x_{ijk}.y_{ik} + e_{ijk}, \qquad \text{[I]}$$

where the intercept of the model (β_0) estimates the initial population tolerance, while u_{0j} is the initial individual tolerance (i.e., the individual deviation from the initial population tolerance). The slope (β_1) of the behavioural reaction with the trial number/time (x_{ij}) represents the population speed of ΔT. Random slopes integrate differences between individuals in speed of ΔT (the individual deviation from the slope, u_{1ij}). Speed can also be estimated independently for phase 0 and 1 by including an interaction between trial number and phase number ($x_{ijk} \times y_{ik}$; β_3 being the population difference in speed between phase 0 and 1 and u_{3ik} being the individual deviation from it). Retention (preserving acquired tolerance through time) is estimated by adding phase number as a fixed effect (β_2; e.g., $T_{1,0}$—$T_{0,0}$; finding the same tolerance at each first trial means no retention). Reversibility is calculated using the difference between tolerance at the last trial of the first phase and the first trial of the third phase (e.g., $T_{1,0}$—$T_{0,3}$; the same tolerance means no reversibility). Experiments could manipulate the time between phases to evaluate its effect on speed and retention. Alternatively, a slightly different stimulus could be presented at phase 1 to test for specificity and compare speed, retention, and reversibility. Residual error is denoted e_{0ij}.

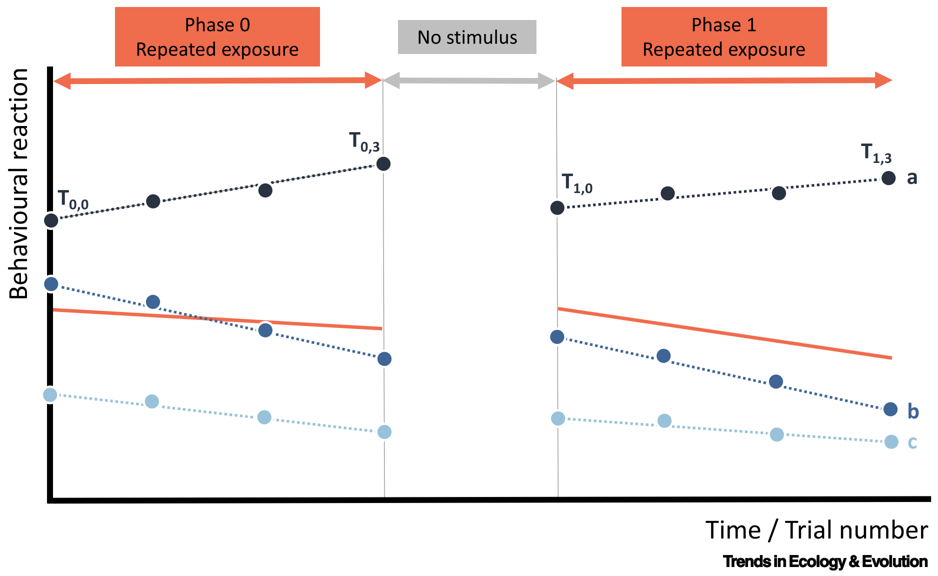

Figure I. The dynamics of tolerance for three individuals (genotypes a, b, and c) displayed using reaction norms. Population ΔT is in orange.

eggs' hatching date comes closer [26]. State can also modify tolerance by modulating learning. Spatial performance is lower in female voles during the breeding period than during the nonbreeding period [27]. Such bidirectional relationships between tolerance and state may result in negative or positive feedback loops. If it occurs in most individuals of a population, the latter have the potential to cause significant and sudden shifts in tolerance that could worsen human–wildlife conflicts and accelerate extinction or facilitate evolution and the colonisation of new habitats.

Box 3. The challenges and promises of mechanistic clarity

Tolerance changes over the course of a lifetime as individuals learn what should or should not be feared. However, the learning mechanisms behind a change in tolerance are difficult to identify. Previous studies (e.g., [72]) have investigated the distinctions between nonassociative types of learning (e.g., habituation) and associative types of learning (e.g., operant conditioning). Some suggested that habituation mechanisms can be associative or nonassociative [73] and that associative and nonassociative influences can happen jointly [74]. Importantly, because learning processes other than habituation can play a part in the dynamics of tolerance, we suggest using the term 'habituation-like processes' rather than habituation to reflect the uncertainty regarding the learning process in nature.

It is essential to distinguish learning mechanisms because they may lead to convergent behavioural tolerances yet with different properties, affecting the costs involved. We lack studies on the features of learning processes (see Features in Figure 1 in main text), although they have important implications for basic and applied ecology. For instance, we expect operant conditioning to change tolerance more rapidly than habituation, provided that strong reinforcers are used. Similarly, tolerance (or intolerance) gained in early life, through imprinting, should be much less reversible than a change in tolerance acquired through social learning later in life. The specificity and duration of tolerance could also be a function of the underlying learning mechanism. Such variation in the features of tolerance could explain variation in the consequences of tolerance. For instance, rapidly acquired tolerance could minimise the costs of missed opportunities (e.g., feeding). Differences in the specificity, duration, and reversibility of tolerance are worth considering when choosing a proper methodology to attract or repel wild animals (see [70]).

The features of acquired tolerance also depend on the features of the stimulus (see Figure 1 in main text). For instance, we expect the predictability and specificity of a stimulus to accelerate the acquisition of tolerance, whereas stimulus novelty should slow tolerance changes. Risk should also be a major modulator of learning because predation is an important selective force. Learned tolerance should also be specific, reversible, and less retained when the risk of predation appears high. Despite the challenges, the study of learning mechanisms is essential for informed application of the proposed behavioural tolerance framework.

Tolerance can also influence habitat choice. Individuals may segregate themselves in a heterogeneous environment according to the level of risk they tolerate. Such matching habitat choice (i.e., phenotype–environment correlation [28]) or spatial personality (i.e., consistent individual differences in spatial behaviours such as habitat use [29]) has been observed in several species. For example, risk-tolerant dunnocks (*Prunella modularis*) select more disturbed habitats than risk-intolerant individuals [30]. In a disturbed environment, an initially tolerant individual can become even more tolerant by regularly encountering disturbing stimuli and becoming habituated to them. Wildlife is more tolerant to human disturbance in high than in low human disturbance environments [31]. Tolerance can sometimes result in the selection of unsuitable habitats, creating ecological traps. This is the case, for example, of mammals that get killed by collisions with cars while moving, foraging, or seeking cover along the roads [32]. Since the characteristics of a particular habitat, such as its stability or complexity, can impact learning (e.g., [33]), habitat choice may also influence the plasticity of tolerance. Although studies on the subject are rare, we expect that habitats that are perceived as very risky may impede learning by favouring highly neophobic behaviours (e.g., risk-induced neophobia [34]).

Because differences in state and habitat choice can influence survival and reproduction, behavioural tolerance has a great potential to affect the absolute fitness of a population. The demographic consequences will depend on whether a substantial portion of the population shares similar levels of tolerance, and this, in turn, depends on how fast animals can adjust their behaviour to the new challenges. When tolerance is heritable (see, e.g., [35,36]), it can also influence the evolutionary trajectory of the population and its potential for evolutionary rescue. When individuals are frequently exposed to stressors, and responding to these stimuli is costly, natural selection can lead to reduced sensitivity to stimuli [37]. Selection for greater tolerance can attenuate some detrimental effects of human activities, although this may prove insufficient. Simulations based on empirical data showed that golden eagles (*Aquila chrysaetos*) exposed to recreational activities suffer detrimental effects despite exhibiting increased tolerance to humans [38].

Environmental effects

Behavioural tolerance is repeatable; individuals show consistent differences in tolerance through time (e.g., [36,39]). It is an intrinsic characteristic of an individual and not merely a product of the current environmental conditions. Nonetheless, behavioural tolerance is highly context dependent. Most notably, tolerance will change with the features of the stimulus (Figure 1 and Box 2). In general, we expect individuals to be less likely to develop tolerance toward novel, risky, unpredictable, and generalised stimuli.

Environmental conditions can influence behavioural tolerance (Figure 1). Abiotic factors, such as habitat structure, influence perceived predation risk [40]. Eastern chipmunks are more vigilant in open habitats than in forested habitats primarily due to their increased vulnerability to predation [41] and under windy conditions as it can be more challenging to detect predators [42]. The social environment during exposure to a stimulus also affects tolerance. Bold rainbow trout (*Onchorhyncus mykiss*) increase their neophobic response to a novel object after observing shy conspecifics [43]. Bold Gouldian finches (*Erythrura gouldiae*) become less tolerant to a simulated predator when paired with a shy conspecific (and vice versa) through a social conformity process [44]. By contrast, vervet monkeys (*Chlorocebus pygerythrus*) are less neophobic in the presence of conspecifics [45]. Being in a group can also accelerate the acquisition of tolerance according to the risk dilution hypothesis. Zebra finches (*Taeniopygia guttata*) show quicker habituation when they are in social contexts [46]. Signals from conspecifics, such as alarm calls, can also impact tolerance by increasing vigilance or triggering a flight response. A signaller's tolerance influences how other individuals perceive its calls and change their vigilance in response [47].

Competition and predation, two major forces shaping behaviour, can also affect tolerance. For instance, when there is strong competition for food, individuals may become more tolerant of disturbances (suggested by Blumstein [48] in the context of depleting resources, such as in [49]). Intra- and interspecific competition can reduce body condition and increase the cost of missed opportunities, which can, in turn, influence tolerance. Tolerance can also change with historical predation pressures as a mechanism to save energy when faced with threatening stimuli. Brown *et al.* [50] found that female *Brachyhraphis episcopi* from areas with high predation had lower stress responses to confinement than females from streams with low predation. Other animals remain intolerant to high predation risk and avoid high-risk regions instead. Canada geese appear to disperse away from hunting territories before the hunting season begins [51], and older female elk (*Cervus elaphus*) adjust certain behaviours to escape hunters [52,53].

Diseases and contaminants impact tolerance. Animals avoid areas with faeces, reflecting high risk of parasitic transmission [54,55]. Parasite infection can also directly increase risk-taking and tolerance through host manipulation processes in infected individuals and indirectly increase risk-taking in uninfected conspecifics in a group [56]. Pollution can increase tolerance. For instance, antidepressants present in water lower fear responses in fishes [57], and contaminants in urban stormwater wetlands reduce antipredator responses to olfactory cues in tadpoles [58] (see [59] for a review on the effects of contaminants on behaviour).

Beware of apparently benign tolerance

While studying behavioural tolerance to anthropogenic stimuli is crucial to understand how animals cope with human disturbances, this should not be used on its own to infer the impact of humans on wildlife. Tolerance measured on one behavioural trait is not necessarily an accurate indicator of change occurring at the physiological level (see [60]). For example, startled masked lapwings (*Vanellus miles*) that allow closer human approaches incur higher physiological costs through elevated heart rate that lasts longer than individuals who appear less behaviourally tolerant [61]. Likewise, the size of the home range of terrestrial vertebrates tends to be smaller in urban regions [62]. However, this does not imply that tolerant individuals or species found in urban environments are 'adapted' or unaffected by human disturbance. They could be constrained to use urban habitats because of habitat loss [62]. Nevertheless, the absence of correlation between behavioural and physiological measures is not an issue *per se*; it only limits the inferences we can make from a single behavioural measurement. Studying how the plasticity of tolerance in one trait may constrain change in tolerance in other traits, along with changes in survival and reproduction, is key to clarify the multidimensional impacts of human activities on wildlife (see also [18,63]).

Apparently benign tolerance to humans could also be detrimental if it were to transfer to predators. This is especially worrisome since many human–wildlife interactions happen in habitats where humans and predators co-occur (e.g., [64]). Fortunately, such transfer seems unlikely (e.g., [65,66]), mainly because tolerance, at least when acquired through habituation, appears to be specific to temporal, spatial, and behavioural variables [60].

Concluding remarks

Behavioural tolerance can emerge and vary through different pathways and influence an individual's state, survival, and reproduction. It is much more than the simple result of habituation and cannot be equated with other behavioural traits. Tolerant animals are more likely to interact with humans, become considered as commensals or pests, and use anthropic structures designed to manage wildlife [7]. Adjusting attraction or repulsion actions according to individuals', populations', or species' tolerance should improve wildlife management. An interdisciplinary approach to tolerance should not only increase the protection of wildlife but also enhance ecosystem services [67]. Identifying what mechanism(s) underline a change in tolerance and how they affect the properties (e.g., speed of acquisition) of the resulting tolerance will be key to improve management strategies (see Outstanding questions).

Outstanding questions

What factors inhibit or enhance changes in tolerance?

Does the underlying mechanism influence the generalisability of tolerance? For instance, are earlier-life effects, **parental effects**, or genetic drivers more likely to lead to 'general tolerance' compared with more specific tolerances that are acquired through learning?

What are the key differences between learning mechanisms in terms of their speed of generating tolerance and the stability of the tolerance that emerges?

Do learning processes explain differences in tolerance that lead to emergent differences across individuals sharing the same environment? Can this explain variation in niche specialisation?

Are eco-evolutionary dynamics differentially influenced by the mechanisms leading to tolerance?

Do species use different learning processes to adjust their tolerances to new stimuli? If so, why?

Under what conditions is increased tolerance detrimental to an individual?

Does the magnitude of tolerance increase the ability of species to survive in anthropogenically modified environments?

What is the relative role of tolerance compared with other factors (e.g., niche breadth, life history, etc.) in explaining the ability of animals to live in urban environments?

Do cognitive abilities increase the quality of information and the match between shown tolerance and the optimal value of tolerance in a particular situation?

Is habituation possible in the presence of food or does this limit the learning mechanism to conditioning?

Is tolerance strictly context specific or does a tolerance syndrome exist?

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Declaration of interests

No interests are declared.

References

1. Sih, A. *et al.* (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* 4, 367–387
2. Ydenberg, R.C. and Dill, L.M. (1986) The economics of fleeing from predators. *Adv. Study Behav.* 16, 229–249
3. Sol, D. *et al.* (2011) Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS One* 6, e19535
4. Kasereka, B. *et al.* (2006) Vulnerability of habituated Grauer's gorilla to poaching in the Kahuzi-Biega National Park, DRC. *Afr. Study Monogr.* 27, 15–26
5. Møller, A.P. *et al.* (2019) Flight initiation distance, color and camouflage. *Curr. Zool.* 65, 535–540
6. Harding, H.R. *et al.* (2019) Causes and consequences of intra-specific variation in animal responses to anthropogenic noise. *Behav. Ecol.* 30, 1501–1511
7. Merrick, M.J. and Koprowski, J.L. (2017) Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* 209, 34–44
8. Viblanc, V.A. *et al.* (2012) Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC Ecol.* 12, 10
9. Sol, D. *et al.* (2010) Evolutionary divergence in brain size between migratory and resident birds. *PLoS One* 5, e9617
10. Sol, D. *et al.* (2005) Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proc. R. Soc. B Biol. Sci.* 272, 1433–1441
11. Sol, D. *et al.* (2018) Risk-taking behavior, urbanization and the pace of life in birds. *Behav. Ecol. Sociobiol.* 72, 59
12. Gotanda, K.M. *et al.* (2009) Body size and reserve protection affect flight initiation distance in parrotfishes. *Behav. Ecol. Sociobiol.* 63, 1563–1572
13. Caldji, C. *et al.* (1998) Maternal care during infancy regulates the development of neural systems mediating the expression of fearfulness in the rat. *Proc. Natl. Acad. Sci. U. S. A.* 95, 5335–5340

14. McGhee, K.E. and Bell, A.M. (2014) Paternal care in a fish: epigenetics and fitness enhancing effects on offspring anxiety. *Proc. R. Soc. B Biol. Sci.* 281, 20141146
15. Arnold, K.E. *et al.* (2007) Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. *Proc. R. Soc. B Biol. Sci.* 274, 2563–2569
16. Donelan, S.C. and Trussell, G.C. (2015) Parental effects enhance risk tolerance and performance in offspring. *Ecology* 96, 2049–2055
17. Guidi, J. *et al.* (2021) Allostatic load and its impact on health: a systematic review. *Psychother. Psychosom.* 90, 11–27
18. Uchida, K. and Blumstein, D.T. (2021) Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. *Behav. Ecol.* 32, 668–678
19. Bejder, L. *et al.* (2009) Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* 395, 177–185
20. Møller, A.P. *et al.* (2015) Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behav. Ecol.* 26, 861–865
21. Found, R. and St. Clair, C.C. (2018) Personality influences wildlife responses to aversive conditioning. *J. Wildl. Manag.* 82, 747–755
22. Lyons, J. *et al.* (2017) Fat and happy in the city: Eastern chipmunks in urban environments. *Behav. Ecol.* 28, 1464–1471
23. Oro, D. *et al.* (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* 16, 1501–1514
24. Murray, M. *et al.* (2015) Poor health is associated with use of anthropogenic resources in an urban carnivore. *Proc. R. Soc. B Biol. Sci.* 282, 20150009
25. Moran, N.P. *et al.* (2021) Poor nutritional condition promotes high-risk behaviours: a systematic review and meta-analysis. *Biol. Rev.* 96, 269–288
26. Clermont, J. *et al.* (2019) Plasticity, state-dependency, and individual consistency in Canada goose nest defense behavior. *Behav. Ecol. Sociobiol.* 73, 66
27. Galea, L.A.M. *et al.* (1996) Sexually dimorphic spatial learning in meadow voles *Microtus pennsylvanicus* and deer mice *Peromyscus maniculatus*. *J. Exp. Biol.* 199, 195–200
28. Edelaar, P. *et al.* (2008) Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* 62, 2462–2472
29. Stuber, E.F. *et al.* (2022) Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. *Behav. Ecol.* 33, 477–486
30. Holtmann, B. *et al.* (2017) Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. *Proc. R. Soc. B Biol. Sci.* 284, 20170943
31. Samia, D.S.M. *et al.* (2015) Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* 6, 8877
32. Hill, J.E. *et al.* (2021) A review of ecological factors promoting road use by mammals. *Mammal Rev.* 51, 214–227
33. Brydges, N.M. *et al.* (2008) Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks. *Anim. Behav.* 75, 935–942
34. Brown, G.E. *et al.* (2013) Phenotypically plastic neophobia: a response to variable predation risk. *Proc. R. Soc. B Biol. Sci.* 280, 20122712
35. Carrete, M. *et al.* (2016) Heritability of fear of humans in urban and rural populations of a bird species. *Sci. Rep.* 6, 31060
36. Møller, A.P. (2014) Life history, predation and flight initiation distance in a migratory bird. *J. Evol. Biol.* 27, 1105–1113
37. Møller, A.P. (2008) Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* 63, 63–75
38. Pauli, B.P. *et al.* (2016) Forecasting disturbance effects on wildlife: tolerance does not mitigate effects of increased recreation on wildlands. *Anim. Conserv.* 20, 251–260
39. Carrete, M. and Tella, J.L. (2010) Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* 6, 167–170
40. Verdolin, J.L. (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav. Ecol. Sociobiol.* 60, 457–464
41. Otter, K. (1994) The impact of potential predation upon the foraging behaviour of eastern chipmunks. *Can. J. Zool.* 72, 1858–1861
42. Clermont, J. *et al.* (2017) Assessing anti-predator decisions of foraging eastern chipmunks under varying perceived risks: the effects of physical and social environments on vigilance. *Behaviour* 154, 131–148
43. Frost, A.J. *et al.* (2007) Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proc. R. Soc. B Biol. Sci.* 274, 333–339
44. King, A.J. *et al.* (2015) The effects of social conformity on Gouldian finch personality. *Anim. Behav.* 99, 25–31
45. Nord, C. *et al.* (2022) Fear of missing out? Personality and plasticity in food neophilia by wild vervet monkeys, *Chlorocebus pygerythrus*. *Anim. Behav.* 191, 179–190
46. St. Lawrence, S. *et al.* (2021) Does the presence of a conspecific increase or decrease fear? Neophobia and habituation in zebra finches. *Ethology* 127, 1033–1041
47. Couchoux, C. *et al.* (2018) Signaler and receiver boldness influence response to alarm calls in eastern chipmunks. *Behav. Ecol.* 29, 212–220
48. Blumstein, D.T. (2016) Habituation and sensitization: new thoughts about old ideas. *Anim. Behav.* 120, 255–262
49. Owens, N.W. (1977) Responses of wintering brent geese to human disturbance. *Wildfowl* 28, 5–14
50. Brown, C. *et al.* (2005) Differential stress responses in fish from areas of high- and low-predation pressure. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 175, 305–312
51. Dieter, C.D. *et al.* (2010) Late summer movements by giant Canada geese in relation to a September hunting season. *Hum. Wildl. Interact* 4, 232–246
52. Thurfjell, H. *et al.* (2017) Learning from the mistakes of others: how female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. *PLoS One* 12, e0178082
53. Ciuti, S. *et al.* (2012) Human selection of elk behavioural traits in a landscape of fear. 279, 4407–4416
54. Poirotte, C. and Kappeler, P.M. (2019) Hygienic personalities in wild grey mouse lemurs vary adaptively with sex. *Proc. R. Soc. B Biol. Sci.* 286, 20190863
55. Brambilla, A. *et al.* (2013) Don't spit in the soup: faecal avoidance in foraging wild Alpine ibex, *Capra ibex*. *Anim. Behav.* 86, 153–158
56. Demandt, N. *et al.* (2018) Parasite-infected sticklebacks increase the risk-taking behaviour of uninfected group members. *Proc. R. Soc. B Biol. Sci.* 285, 20180956
57. Salahinejad, A. *et al.* (2022) Proximate causes and ultimate effects of common antidepressants, fluoxetine and venlafaxine, on fish behavior. *Sci. Total Environ.* 807, 150846
58. Sievers, M. *et al.* (2018) Stormwater wetlands can function as ecological traps for urban frogs. *Ecol. Appl.* 28, 1106–1115
59. Saaristo, M. *et al.* (2018) Direct and indirect effects of chemical contaminants on the behaviour, ecology and evolution of wildlife. *Proc. R. Soc. B Biol. Sci.* 285, 20181297
60. Higham, J.E.S. and Shelton, E.J. (2011) Tourism and wildlife habituation: reduced population fitness or cessation of impact? *Tour. Manag.* 32, 1290–1298
61. Charuvi, A. *et al.* (2020) A physiological cost to behavioural tolerance. *Behav. Process.* 181, 104250
62. O'Donnell, K. and Delbarco-Trillo, J. (2020) Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: a meta-analysis. *J. Urban Ecol.* 6, juaa014
63. Sih, A. *et al.* (2022) Fear generalization and behavioral responses to multiple dangers. *Trends Ecol. Evol.* 38, 369–380
64. Geffroy, B. *et al.* (2015) How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol. Evol.* 30, 755–765
65. Coleman, A. *et al.* (2008) Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*)? *Biol. Lett.* 4, 250–252
66. Allan, A.T.L. *et al.* (2021) Consistency in the flight and visual orientation distances of habituated chacma baboons after an observed leopard predation. Do flight initiation distance methods always measure perceived predation risk? *Ecol. Evol.* 11, 15404–15416

67. Uchida, K. *et al.* (2023) Managing wildlife tolerance to humans for ecosystem goods and services. *Trends Ecol. Evol.*, Published online November 8, 2023. https://doi.org/10.1016/j.tree.2023.10.008
68. Réale, D. *et al.* (2007) Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82, 291–318
69. Rankin, C.H. *et al.* (2009) Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiol. Learn. Mem.* 92, 135–138
70. Greggor, A.L. *et al.* (2020) The rules of attraction: the necessary role of animal cognition in explaining conservation failures and successes. *Annu. Rev. Ecol. Evol. Syst.* 51, 483–503
71. Dingemanse, N.J. *et al.* (2010) Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89
72. Petrinovich, L. and Patterson, T.L. (1979) Field studies of habituation: I. Effect of reproductive condition, number of trials, and different delay intervals on responses of the white-crowned sparrow. *J. Comp. Physiol. Psychol.* 93, 337–350
73. Balkenius, C. (2000) Attention, habituation and conditioning: toward a computational model. *Cogn. Sci. Q.* 1, 171–214
74. Uribe-Bahamonde, Y.E. *et al.* (2021) The sometimes context-specific habituation: theoretical challenges to associative accounts. *Animals* 11, 3365