Towards a unified framework for studying behavioural tolerance to anthropogenic disturbance

Catherine Čapkun-Huot[1], Daniel T. Blumstein[2], Dany Garant[3], Daniel Sol[4], and Denis Réale[1]

[1] Département des sciences biologiques, Université du Québec à Montréal

[2] Department of Ecology and Evolutionary Biology and Institute of the Environment and Sustainability, University of California, Los Angeles

[3] Département de biologie, Université de Sherbrooke

[4] Centre for Ecological Research and Applied Forestries

Corresponding author: Čapkun-Huot, C. (capkun-huot.catherine@courrier.uqam.ca)

Keywords: Learning, Environment, Between-individual differences, Anthropogenic disturbance, Conservation

Highlights

- Behavioural tolerance is a broadly applicable phenomenon observed when animals have a limited or absent reaction to a risky stimulus.
- Tolerance can emerge from genetic, epigenetic, learning, or other ontogenetic differences between individuals.
- Importantly, different mechanisms may explain much variation in tolerance.
- A mechanistically informed, eco-evolutionary theory of tolerance is essential to understand fitness, population viability, and human-wildlife interactions in the Anthropocene era.

Abstract

Animals vary in how much they respond to risk and the extent to which they can modify their responsiveness over time. How and why animals vary has important consequences for understanding demographic and evolutionary responses to novel or rapidly changing environments. Behavioural tolerance is seen when animals do not have any or have a limited behavioural reaction to a potentially risky situation. Tolerance can emerge from genetic, epigenetic or learning mechanisms, and is mediated by the environment. These mechanisms can influence the speed of acquisition, reversibility, specificity, and duration of the resulting tolerance. Mechanistic clarity is therefore essential to predict the eco-evolutionary consequences of tolerance and to understand and manage human-wildlife interactions in the Anthropocene era.

Main text

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, to become pests, to create conflicts with humans, or to become human commensals. 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). Wildlife managers and conservationists often define tolerant individuals as animals that are not bothered by disturbing stimuli. A high behavioural tolerance is seen when an individual has a limited or no reaction to the stimulus. This excludes cases where animals do not detect the stimulus. In contrast, a low behavioural tolerance towards a stimulus becomes evident when animals show high vigilance, issue alarm calls or promptly flee, for instance. Behavioural tolerance can thus be defined as the degree of reaction to a stimulus signalling a potentially risky situation. Such a definition broadens that of tolerance, which also encompasses physiological tolerance (i.e. low sensitivity to a chemical or physical parameter, such as temperature) 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. From an individual's perspective, too little tolerance to benign stimuli will result in missed opportunity costs [2], because tolerance frees up time and energy for essential activities such as foraging or mating. For instance, 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 novel or changing environment, leading them either to go extinct or to thrive.

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 framework that focusses mainly on anthropogenic contexts. In the Anthropocene, developing a mechanistic understanding of factors that make animals behaviourally tolerant to humans and their activities is essential to understand eco-evolutionary dynamics and manage human-wildlife dynamics.

Causes of behavioural tolerance

A variety of processes can drive an individual's behavioural tolerance (Fig. 1). Studying the cause(s) of variation in tolerance is crucial to improve our predictions on how tolerance may change through time and how it may generalize to other stimuli, which allows for better informed wildlife management and conservation.

Tolerance may depend on genetic differences between individuals, both directly and through their effects on morphology, physiology, and behaviour. Morphological defences like armaments, poisons and venoms, aposematic signalling, or camouflage can increase tolerance. For example, camouflaged bird species tolerate closer human approaches [5]. Behavioural traits expressed in novel or risky situations must also affect tolerance. In fact, exploration, boldness or neophilia are often associated with greater tolerance to disturbance [6]. The measure of tolerance will thus sometimes reflect those traits, but tolerance can also be expressed in other situations (Box 1). A variety of other traits (e.g. metabolism, brain structure, sensory abilities) may also affect tolerance because an individuals' tolerance reflects its history, trade-offs between traits, and constraints on those traits. Tolerance can also be sex specific if, for instance, the sexes differ in their baseline stress hormone levels [7]. Genetic differences, both within and between species, can reflect different evolutionary histories and mechanisms such as genetic drift, bottlenecks, or founder effects. These differences may also represent adaptions to historical conditions in which species have evolved. For instance, insular species (e.g. wandering albatross [*Diomedea exulans*] or penguins) that have evolved in the absence of humans, do not react to their approach by fleeing, but they show some physiological stress responses to it (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 ones.

If behavioural tolerance results from conflicting physiological, morphological, and behavioural responses, it could also 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 they are less tolerant to risk or disturbance [11]. 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 affects the development of the central nervous system, which, in turn, reduces fear of novelty in adult Norway rats (*Rattus norvegicus*), therefore increasing tolerance towards novel stimuli [12]. Increased paternal care also reduces anxious behaviours in three-spined sticklebacks (*Gasterosteus aculeatus*) by modulating de novo methylation [13]. Parents can also affect their offspring's propensity to take risks through diet. Young blue tits (*Cyanistes caeruleus*) supplemented with taurine have improved cognitive skills and are more risk prone than control individuals [14], 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. [15]).

Throughout its lifetime, an individual can undergo **ontogenetic processes** that can influence its tolerance. For example, ageing, senescence or allostatic load [16] accumulated throughout life can alter tolerance as can experience. Learning, influenced by both genetic and ontogenetic processes, is a major driver of variation in tolerance throughout 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. [17], but sometimes incorrectly, see [18]). Habituation increases tolerance to a stimulus, while sensitisation decreases it. However, and importantly, many other learning processes may lead to changes in tolerance. **Classical or operant conditioning**, amongst 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 (known as food conditioning; e.g. [19]). On the contrary, aversive conditioning methods can be used to reduce tolerance to human proximity (but the effectiveness of the method seems to be mediated by personality; [20]). Other learning mechanisms such as **social learning**, **imprinting**, and **taste aversion** can also result in changes in tolerance.

Considering genetic and non-genetic 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 even sensitisation) to former threats can be much more rapid than the process of habituating to them. Following the cessation of hunting, it took three 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 a few shots (Réale pers. obs.).

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 (see Glossary). For example, tolerating human disturbance may provide abundant and predictable food supplies, improving the condition of individuals [21,22]. In eastern chipmunks (*Tamias striatus*), females inhabiting urban habitats tend to have better body condition compared to females in natural habitats [21]. Human food may also 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 [23]. Tolerance can influence an individual's state through mechanisms other than differential access to food, such as 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 [24]. On the contrary, females can attempt to reduce risk during the reproductive period, as is seen in female Canada geese (*Branta canadensis*) that become less tolerant to human approaches as their eggs' hatching date comes closer [25]. But state can also modify tolerance by modulating learning (see examples in Glossary). Such bidirectional relationships between tolerance and state may result in negative or positive feedback loops. The latter have the potential to cause significant and sudden shifts in tolerance that could worsen human-wildlife conflicts or accelerate extinction, evolution, or the colonisation of new habitats by a population/species.

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 [26]) or spatial personality (i.e. consistent individual differences in spatial behaviours such as habitat use [27]) has been observed in several species. For example, risk-tolerant dunnocks (*Prunella modularis*) select more disturbed habitats than risk-intolerant individuals [28]. In a disturbed environment, an initially tolerant individual can become even more tolerant by regularly encountering disturbing stimuli and becoming habituated to them. Indeed, wildlife is more tolerant to human disturbance in highly disturbed environments compared to low human disturbance environments [29]. Tolerance may evolve if it is heritable (as it appears to be in birds; [30,31]). When individuals in disturbed environments are frequently exposed to stressors, and responding to these stimuli is costly, natural selection can lead to reduced sensitivity to stimuli [32]. Selection for greater tolerance can attenuate some detrimental effects associated with human activities, although at times, 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 [33]. 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 [34]. Since the characteristics of a particular habitat, such as its stability or complexity, can impact learning (e.g. [35]), habitat choice may also influence the plasticity of tolerance. Although studies on the subject are rare, we expect that habitats which are perceived as very risky may impede learning by favouring highly neophobic behaviours (e.g. risk-induced neophobia [36]). Again, we could expect complex feedback loops, either positive or negative, between tolerance, habitat use and other traits, depending on the fitness outcomes of the combination of tolerance and habitat.

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 behavioural tolerance is heritable, it can also influence the evolutionary trajectory of the population and its potential for evolutionary rescue. In the presence of genotype-environment correlation (i.e. genetic variance for tolerance is correlated with genetic variance for habitat choice), disentangling the genetic dimension from the plastic (e.g. learned) dimension of tolerance at the phenotypic level is challenging [37]; however, it is essential to predict evolutionary and conservation implications of tolerance.

Environmental effects

Behavioural tolerance is repeatable: individuals show consistent differences in tolerance through time (e.g. [31,38]). It is thus 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 (see Fig. 1 and Box 2). We expect individuals to be less likely to develop or evolve tolerance towards novel, risky, unpredictable and generalised stimuli.

Environmental conditions during exposure to a stimulus can also influence behavioural tolerance (Fig. 1). Abiotic factors, such as habitat structure, influence perceived predation risk [39]. Eastern chipmunks are more vigilant in open habitats compared to forested ones primarily due to their increased vulnerability to predation [40] and under windy conditions as it can be more challenging to detect predators [41]). 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 [42]. 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 [43]. In contrast, vervet monkeys (*Chlorocebus pygerythrus*) are less neophobic in presence of conspecifics [44]. 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 [45]. 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 to them [46].

The environment that individuals have experienced can affect their tolerance. This includes competition and predation, two major forces shaping behaviour. For instance, when there is more competition for food, individuals may become more tolerant of disturbances (as suggested by [47] in the context of depleting resources such as in [48]). 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. [49] found that female *Brachyhraphis episcopi* from areas with high predation had lower stress responses to confinement compared to 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 [50], and older female elk (*Cervus elaphus*) adjust certain behaviours to escape hunters [51,52]. The risk of parasitism may also affect tolerance; animals avoid areas with faeces reflecting high risk of transmission [53,54]. 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 [55]. Pollution may impact tolerance. For instance, antidepressants present in water lower fear responses in fishes [56] and contaminants in urban stormwater wetlands reduce antipredator responses to olfactory cues in tadpoles [57] (see [58] for a review on the effects of contaminants on animal 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 [59]). 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 [60]. Likewise, the size of the home range of terrestrial vertebrates tends to be smaller in urban regions [61]. 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 [61]. 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 is key to clarify the multidimensional impacts of human activities on wildlife (see also [17,62]).

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. in the context of nature-based tourism, see [63]). Fortunately, such transfer seems unlikely (e.g., [64,65]), mainly because tolerance, at least when acquired through habituation, appears to be specific to temporal, spatial and behavioural variables [59]. Yet, studying fear generalisation is an important topic [62] with many applied implications.

Conclusion

We have discussed various causes and consequences of behavioural tolerance to: (1) clarify some misconceptions about tolerance that are widespread in the literature, and (2) propose a unified framework to study the multiple facets of tolerance. Studying the mechanisms and the consequences of tolerance will help better understand and manage human-wildlife coexistence.

Acknowledgements

This work was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC). C.Č.H. work was supported by postgraduate scholarships from the NSERC and the Fonds de recherche du Québec – Nature et Technologies.

References (70)

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,

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 Merrick, M.J. and Koprowski, J.L. (2017) Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* 209, 34–44

7 Harding, H.R. *et al.* (2019) Causes and consequences of intraspecific variation in animal responses to anthropogenic noise. *Behav. Ecol.* 30, 1501–1511

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,

9 Sol, D. *et al.* (2010) Evolutionary divergence in brain size between migratory and resident birds. *PLoS One* 5, 1–8

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 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

13 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, 2–7

14 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

15 Donelan, S.C. and Trussell, G.C. (2015) Parental effects enhance risk tolerance and performance in offspring. *Ecology* 96, 2049–2055

16 Guidi, J. *et al.* (2021) Allostatic load and its impact on health: A systematic review. *Psychother. Psychosom.* 90, 11–27

17 Uchida, K. and Blumstein, D.T. (2021) Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. *Behav. Ecol.* DOI: 10.1093/beheco/arab016

18 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

19 Møller, A.P. *et al.* (2015) Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behav. Ecol.* 26, 861–865

20 Found, R. and St. Clair, C.C. (2018) Personality influences wildlife responses to aversive conditioning. *J. Wildl. Manage.* 82, 747–755

21 Lyons, J. *et al.* (2017) Fat and happy in the city: Eastern chipmunks in urban environments. *Behav. Ecol.* 28, 1464–1471

22 Oro, D. *et al.* (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* 16, 1501–1514

23 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,

24 Moran, N.P. *et al.* (2021) Poor nutritional condition promotes high-risk

behaviours: a systematic review and meta-analysis. *Biol. Rev.* 96, 269–288

25 Clermont, J. *et al.* (2019) Plasticity, state-dependency, and individual consistency in Canada goose nest defense behavior. *Behav. Ecol. Sociobiol.* 73,

26 Edelaar, P. *et al.* (2008) Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. *Evolution (N. Y).* 62, 2462–2472

27 Stuber, E.F. *et al.* (2022) Spatial personalities: A meta-analysis of consistent individual differences in spatial behavior. *Behav. Ecol.* 33, 477–486

28 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,

29 Samia, D.S.M. *et al.* (2015) Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* 6,

30 Carrete, M. *et al.* (2016) Heritability of fear of humans in urban and rural populations of a bird species. *Sci. Rep.* 6, 1–6

31 Møller, A.P. (2014) Life history, predation and flight initiation distance in a migratory bird. *J. Evol. Biol.* 27, 1105–1113

32 Møller, A.P. (2008) Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* 63, 63–75

33 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

34 Hill, J.E. *et al.* (2021) A review of ecological factors promoting road use by mammals. *Mamm. Rev.* 51, 214–227

35 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

36 Brown, G.E. *et al.* (2013) Phenotypically plastic neophobia: A response to variable predation risk. *Proc. R. Soc. B Biol. Sci.* 280,

37 Gervais, L. *et al.* (2022) Quantifying heritability and estimating evolutionary potential in the wild when individuals that share genes also share environments. *J. Anim. Ecol.* 91, 1239–1250

38 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

39 Verdolin, J.L. (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav. Ecol. Sociobiol.* 60, 457–464

40 Otter, K. (1994) The impact of potential predation upon the foraging behaviour of eastern chipmunks. *Can. J. Zool.* 72, 1858–1861

41 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

42 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

43 King, A.J. *et al.* (2015) The effects of social conformity on Gouldian finch personality. *Anim. Behav.* 99, 25–31

44 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

45 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

46 Couchoux, C. *et al.* (2018) Signaler and receiver boldness influence response to alarm calls in eastern chipmunks. *Behav. Ecol.* 29, 212–220

47 Blumstein, D.T. (2016) Habituation and sensitization: New thoughts about old ideas. *Anim. Behav.* 120, 255–262

48 Owens, N.W. (1977) Responses of wintering brent geese to human disturbance. *Wildfowl* 28, 5–14

49 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

50 Dieter, C.D. *et al.* (2010) Late summer movements by giant Canada geese in relation to a September hunting season. *Human--Wildlife Interact.* 4, 232–246

51 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, 1–20

52 Ciuti, S. *et al.* (2012) Human selection of elk behavioural traits in a landscape of fear. 279, 4407–4416

53 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,

54 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

55 Demandt, N. *et al.* (2018) Parasite-infected sticklebacks increase the risk-taking behaviour of uninfected group members. *Proc. R. Soc. B Biol. Sci.* 285,

56 Salahinejad, A. *et al.* (2022) Proximate causes and ultimate effects of common antidepressants, fluoxetine and venlafaxine, on fish behavior. *Sci. Total Environ.* 807, 150846

57 Sievers, M. *et al.* (2018) Stormwater wetlands can function as ecological traps for urban frogs. *Ecol. Appl.* 28, 1106–1115

58 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,

59 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

60 Charuvi, A. *et al.* (2020) A physiological cost to behavioural tolerance. *Behav. Processes* 181, 104250

61 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, 1–8

62 Sih, A. *et al.* (2022) Fear generalization and behavioral responses to multiple dangers. *Trends Ecol. Evol.* DOI: 10.1016/j.tree.2022.11.001

63 Geffroy, B. *et al.* (2015) How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol. Evol.* 30, 755–765

64 Coleman, A. *et al.* (2008) Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*)? *Biol. Lett.* 4, 250–252

65 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

66 Réale, D. *et al.* (2007) Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82, 291–318

67 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

68 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

69 Dingemanse, N.J. *et al.* (2010) Behavioural reaction norms: Animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89

70 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

71 Balkenius, C. (2000) Attention, habituation and conditioning: Toward a computational model. *Cogn. Sci. Q.* 1, 171–214

72 Uribe-Bahamonde, Y.E. *et al.* (2021) The sometimes context-specific habituation: Theoretical challenges to associative accounts. *Animals* 11, 1–17

73 Shettleworth, S.J. (2010) *Cognition, evolution, and behavior (second edition)*, Oxford Uni.

74 Conover, D. 0. and Schultz, E.T. (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends Ecol. Evol.* 10, 248–252

75 Metzgar, L.H. (1967) An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *J. Mammal.* 48, 387–391

76 Davis, J.M. and Stamps, J.A. (2004) The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* 19, 411–416

77 Davis, J.M. (2019) Habitat imprinting and natal habitat preference induction. In *Encyclopedia of Animal Behavior (Second Edition)* (Choe, J. C., ed), pp. 301–305, Academic Press

78 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

Figures, tables and boxes

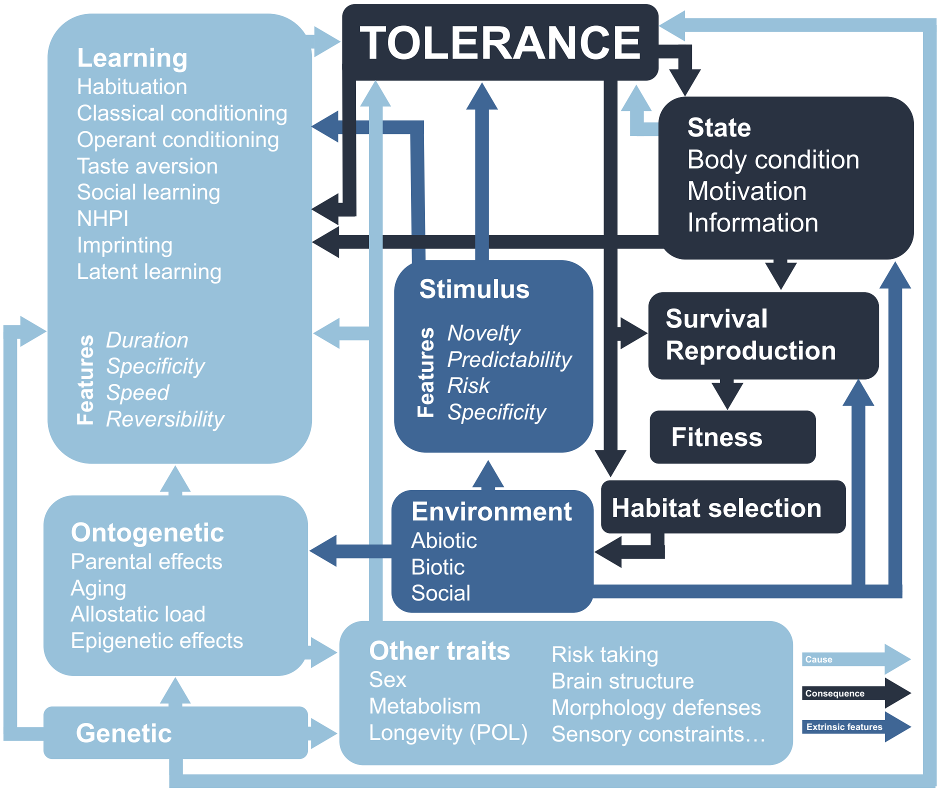

Figure 1. Causes and consequences of individual behavioural tolerance. Behavioural tolerance is the result of genetic, ontogenetic, and learning processes, and can affect an individual's state, its survival, reproduction, habitat selection and fitness. Causes and consequences of tolerance, and tolerance itself, are modulated by the characteristics of the stimulus and environmental conditions. 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.

BOX 1: Disentangling behavioural tolerance from other behaviour traits

The term behavioural tolerance is widely used in the literature on habituation (e.g. [47]). It is also often associated with human-caused disturbances (e.g. [29]), 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 towards a novel sound can be a measure of neophobia or tolerance. These traits do intersect with tolerance: while tolerance is the degree of reaction towards 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 [66].

Nevertheless, tolerance is not synonymous with boldness, exploration or neophilia. Rather, tolerance is constrained by these and other traits and external factors. Tolerance is thus 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 text). Unless habituation is properly tested [67], an individual that is not bothered by city sounds is tolerant rather than habituated. And, an individual showing low vigilance towards a given stimulus could be either bold or neophillic, but is, in any case, tolerant towards the stimulus. The use of the term behavioural tolerance thus prevents unjustified inferences about mechanism.

Most importantly, 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 [68], and understanding what makes an individual tolerant to human stimuli is essential. Using the umbrella term “behavioural tolerance” consolidates different literatures 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.

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** [69]. Figure B2 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 (non-linear models could also be used, see [Čapkun-Huot et al. 2023 in prep]), we can analyse tolerance with the following mixed model:

$$T_{ijk} = \beta_0 + u_{0j} + (\beta_1 + u_{1ijk})x_{ijk} + (\beta_2 + u_{2ik})y_{ik}$$

$$+ (\beta_3 + u_{3ik})x_{ijk}.y_{ik} + e_{ijk}$$

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}.

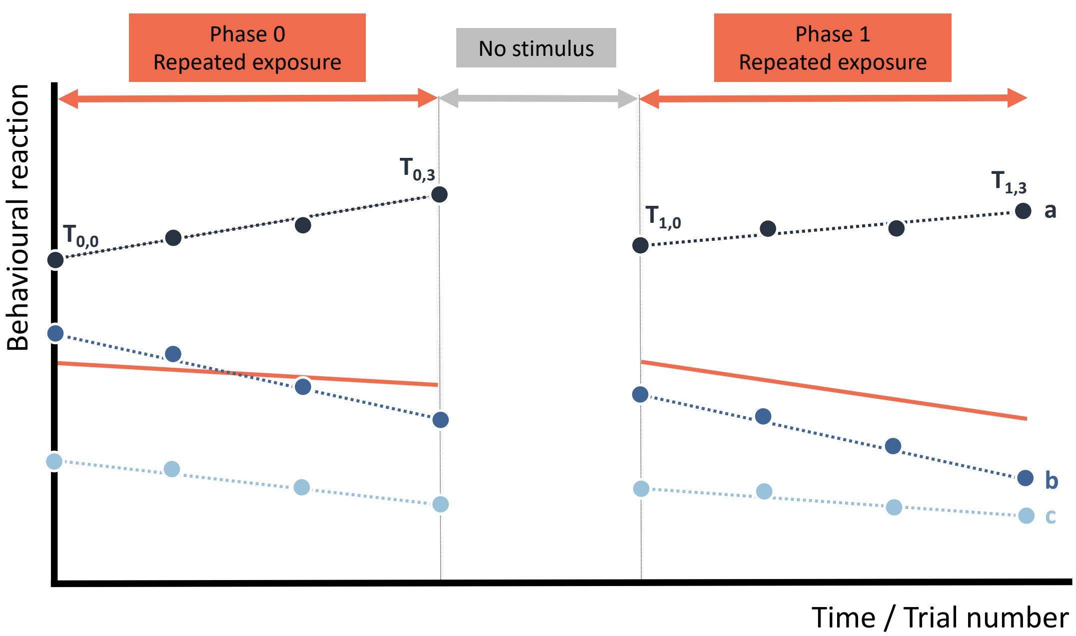

Figure B2. The dynamics of tolerance for three individuals (genotypes a, b, c) displayed using reaction norms. Population ΔT is in orange.

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 [70] have investigated the **distinctions** between non-associative types of learning (e.g. habituation) and associative ones (e.g. operant conditioning). Some suggested that habituation mechanisms can be associative or non-associative [71] and that associative and non-associative influences can happen jointly [72]. 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 Fig. 1), 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 minimize 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 [68]).

The features of acquired tolerance also depend on the features of the stimulus (Fig. 1). 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.

Glossary (501/500)

Classical (Pavlovian) conditioning: learning process that leads to a conditioned response by associating a neutral stimulus to an unconditioned stimulus [73]. If classical conditioning explains change in tolerance to the conditioned stimulus, tolerance may decrease without further presentation of the unconditioned stimulus.

Co- and counter-gradient variation: genetic and environmental determinants combine and increase variation in a trait along a continuum (co-gradient) or oppose and reduce variation in a trait across a gradient (counter-gradient) [74]. Genetically tolerant individuals can learn to become more tolerant (co-gradient) or less tolerant (counter-gradient) to a stimulus.

Habituation: decline in responsiveness to a stimulus with repeated exposure and that is not explained by motor fatigue, sensory fatigue, or sensory adaptation [67]. 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 [73] (e.g. learning the identity of parents, or habitat early in life). Variation in tolerance explained by imprinting should be stimulus-specific.

Latent learning: non-reinforced experience influencing performance later in life. For instance, experience in an environment may lead to higher survival later in life, when a predator is introduced [75]. Duration, reversibility or speed of latent learning are difficult to predict.

Natal habitat preference induction (NHPI): acquired experience with stimuli in the natal habitat impacting the habitat choice post-dispersal [76]. NHPI encompasses habitat imprinting [77]. As with imprinting, variation in tolerance caused by NHPI should be stimulus-specific and irreversible.

Operant conditioning: type of associative learning that links a behaviour with a particular outcome [73]. 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 effects: any developmental changes happening over the course of an individual's lifespan.

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

Social learning: variety of processes (e.g. social enhancement, teaching, 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 (e.g. female geese are less tolerant to human approaching her nest as it happens close to the hatching date [25]) or through its effects on the propensity to learn (e.g. spatial performance is lower in female voles during the breeding period compared to the non-breeding period [78]).

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.

Tolerance: lack of a behavioural reaction to a potentially risky stimulus. It can be measured categorically or continuously using a variety of metrics (e.g. flight initiation distance, vigilance, avoidance).

Outstanding Questions (1780/2000 characters)

What factors inhibit or enhance changes in tolerance?

Does the underlying mechanism influence the generalizability of tolerance? For instance, are earlier-life effects, parental effects, or genetic drivers more likely to lead to "general tolerance" compared to 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 a same environment? Can this explain variation in niche specialization?

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 to 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 this limits the learning mechanism to conditioning?

Generalisability or specificity of tolerance? Tolerance syndrome (response changes with context or not?). Evolutionary response; predictability of individuals in an applied context.