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INVITED REVIEW

Behavioral responses of wild animals to anthropogenic change: insights from domestication

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Abstract

With nearly all life on earth experiencing direct or indirect effects of human activity, there is an urgent need to understand how organisms do or do not adapt to human-induced environmental change. Domestication was an early crash into the Anthropocene for some species, and the response of animal populations to domestication selection gives us insights on how plastic responses and evolutionary changes interact to determine the fate of wild vertebrates responding to a human-altered world. We consider intentional breeding, managed hunting, and extermination as part of a continuum of anthropogenic agents of ecological selection and highlight shared targets of selection between domestication and human-induced selection pressures more broadly. Many of the traits that predict successful domestication also predict adaptation of wild animals to human-dominated environments. Domestic animals are also a source for feral lineages and for genetic exchange with wild populations. Shared ecological constraints and gene flow thus contribute to convergent or congruent changes across a spectrum of responses to human influence. Evaluating domestication as another source of anthropogenic selection yields insights for conservation and a promising way to understand mechanisms of behavioral adaptation.

Significance statement

In this review, we draw insights for conservation from domestication—the oldest and most intense evolutionary interaction between animals and humans. Domestication is a special case of organisms successfully responding to an abrupt shift towards human-altered environments, and success in those environments depends on the same factors that make some animals easier to domesticate than others. Domestication has the potential to simultaneously inform us how behavior and genetics contribute to the process of human adaptation in animals and provide a window into the processes required for animals to become human-adjacent. Understanding how animals adapt in our presence yields clues as to how contemporary species react to decreasing habitat and increasing contact with humans.

Keywords Bottleneck · Feralization · Plasticity · Parallel evolution · Anthropocene · Tameness

Introduction

Humans have altered the environment for our own benefit, or detriment, at varying levels for at least 50,000 years (Sullivan et al. 2017), including ancient farming (Diamond 2003) and megafaunal extinctions (Broughton and Weitzel

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2018; Smith et al. 2018). Modern conveniences result in light (Raap et al. 2015; Van Doren et al. 2017; Hussein et al. 2021), noise (Francis et al. 2011; Kight and Swaddle 2011; Di Franco et al. 2020), and chemical pollutants (Zala and Penn 2004; Bernanke and Köhler 2009) that can impact ecosystems far from their source. Understanding behavioral, ecological, and evolutionary responses to human-induced rapid environmental change (HIREC; Box 1) is crucial for management of species and their critical habitats (Sih 2013).

Box 1 HIREC and the Anthropocene

Scholars across subfields use several terms to describe how humans alter the environment. The acronym **HIREC**, for human-induced rapid environmental change (Sih et al. 2010), is convenient to describe anthropogenic impacts or changes that influence environmental stability, usually for the worse. HIREC is often used to describe the entirety of damage caused by anthropogenic impacts. Some of the most devastating effects of HIREC result from climate change which in turn drives environmental degradation and habitat loss (Sih et al. 2010). Similarly, the introduction of novel species and growing human populations have a trickle-down effect which negatively affects not only endemic species in areas of introduction, but can also result in habitat use change and population reorganization (Robertson et al. 2013). HIREC-adjacent activities such as agricultural growth, colonization, urbanization, and commercialization continue to result in damaged and novel niche spaces, which can negatively affect native biodiversity (Boivin et al. 2016)

The pervasiveness of HIREC has led us into a new geological epoch characterized by pollution, climate change, land use change, deforestation, and the burning of fossil fuels (Crutzen 2006): the **Anthropocene**. Human manipulation of animals in the form of domestication is a large contributor to the fundamental reorganization of ecosystems that marks the Anthropocene as a distinct era (Lewis and Maslin 2015)

Domestication constitutes a special and radical form of HIREC from an animal's point of view, with humans imposing dramatic and often intentional selection that results in striking divergence from wild populations. The empirical substrate of Darwin's theory of evolution was founded on heritable variation documented by pigeon (family *Columbidae*) breeders (Darwin 1868). We define domestic animal species as those whose reproduction and food supply are controlled by humans, resulting in distinct phenotypic, genotypic, and behavioral differences (typically traits that are useful to humans) compared to wild ancestors (Zeder 2012). This definition highlights that domestication is an evolutionary process. Approaches from archeology, anthropology, and historiography have long been used to reconstruct histories of population structure and selection pressures of domestic species (Zeder 2018). More recently, understanding the evolution of domestication has been revolutionized by advances in comparative genomics (Barrera-Redondo et al. 2020; Frantz et al. 2020). This interdisciplinary information provides an intriguing opportunity to compare a wide taxonomic breadth of species that have a shared evolutionary history of anthropogenic selection. The behavioral and genetic consequences of domestication selection have received extensive attention. In particular, researchers have suggested that a combination of specific factors are required for species to be domesticable (Diamond 2002; Zeder 2012; Larson and Burger 2013; Larson and Fuller 2014), and that domestication selection results in the evolution of predictable suites of correlated traits and genes (Wilkins et al. 2014; Sánchez-Villagra et al. 2016; Wilkins 2020; Hou et al. 2020). Can these findings shed light on which species are most likely to persist in the face of HIREC, and how we expect these species to evolve? In this review, we focus on how contemporary approaches to understanding domestication could help us predict and manage behavioral responses to anthropogenic change more broadly.

Humans as a source of selection on behavior: domestication as a special case of adaptive evolution in the Anthropocene

From the perspective of animals under domestication, as with animals under HIREC, fitness is maximized by thriving in a human-impacted environment (Fig. 1). Successful adaptation to HIREC requires the ability to live near humans or human-altered environments. Similarly, ancient animals that initiated a commensal path to domestication were adapting to and/or exploiting humans rapidly altering the landscape. The process of domestication can shed light on how animals adapt to life under a human footprint. Zeder (2012) identified three pathways to domestication: (1) commensal relationships, (2) prey for humans, and (3) direct manipulation of breeding.

1. **Commensalism** was the first step in domestication of many widespread species, starting with dogs (*Canis lupus* or *C. l. familiaris*; Vilà et al. 1997). Commensal relationships were established when wild animals fed on human food waste or preyed on other animals attracted to human settlements. Over time, these species became closely tied with humans. Species that were domesticated through this pathway include cats (*Felis catus*) hunting prey near villages in western Asia (Driscoll et al. 2007), and ducks (*Anas platyrhynchos*) foraging in rice paddies in China (Zhang et al. 2018). The commensal pathway illustrates the continuum between domestication and adaptation to HIREC.
2. The **prey** pathway to domestication includes species that were initially hunted for food. Archeological evidence suggests that managed hunting—preferentially targeting males over reproductive females—arose in multiple hunter-gatherer societies (Zeder 2012). At the end of the Pleistocene, the large game species pre-

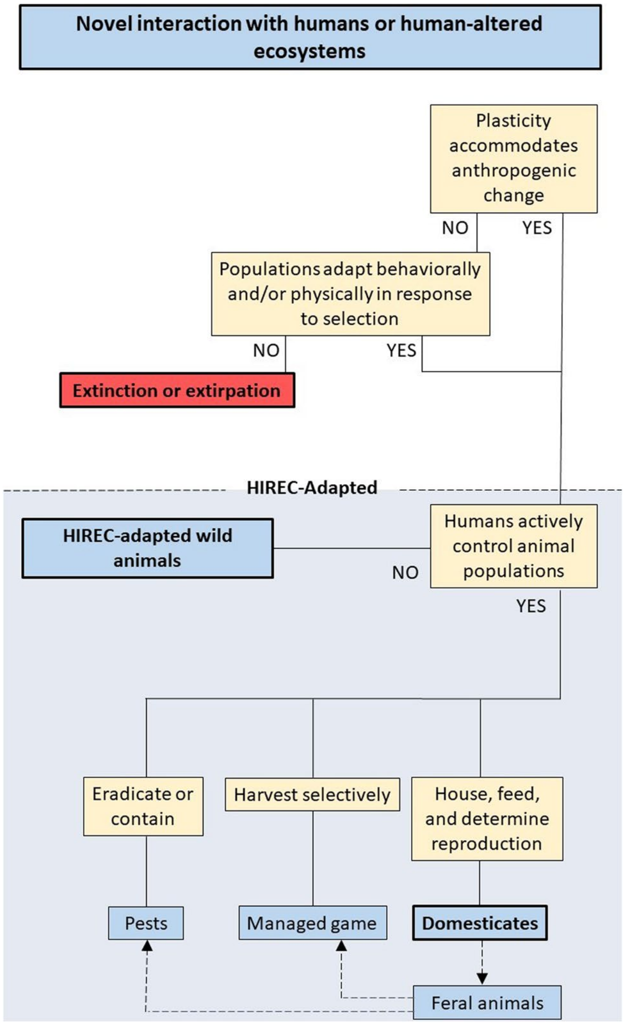

Fig. 1 Evolutionary fate of populations is subject to novel interactions with humans. Each species has a unique history of domestication, feralization, and gene flow. Despite this, broad characterizations can be made of the steps leading to human-adapted animals across a continuum: pests, managed game, domesticates, and HIREC-adapted wild animals. If populations fail both to produce appropriate plastic responses and adapt in response to selection, human-induced changes to the environment may lead to extinction or extirpation. Animals that survive or thrive under HIREC without human control over reproduction and feeding are considered HIREC-adapted wild animals. Despite the dichotomy shown in the figure, there is a continuum of human control over these activities ranging from loosely managed game populations and pests, through free-ranging domestics like backyard turkeys, to tightly controlled domestics like thoroughbred horses. Feral populations routinely arise from domestic ones and may subsequently face the same selection pressures as managed, pest, or wild lineages

ferred by hunters were starting to become scarcer due to a combination of climate change and hunting pressures (Broughton and Weitzel 2018), so humans transitioned to herding animals, notably cattle (wild *Bos primigenius* to domestic *B. taurus*; Helmer et al. 2005) and goats (wild *Capra aegagrus* to domestic *C. hircus*; Daly et al. 2021).

(3) **Directed domestication** typically occurred in regions already experienced with early domestication of other species (Larson and Fuller 2014). It typically involved selection on partially domesticated animals and resulted in traits that would be detrimental to survival in the wild. Direct manipulation of animal breeding goes back at least as far as the purposeful domestication of horses (*Equus caballus*) for hunting their wild relatives, which later evolved into utilizing horses for transport, warfare, and milking (Olsen 2006). Other animals like rabbits (*Oryctolagus cuniculus domesticus*) and carp (*Cyprinus carpio*) were originally brought to Rome to be raised in leporaria and piscinae, or special enclosures used to raise and breed secondary food sources that did not require herding (Balon 1995; Larson and Fuller 2014). Rearing fish for entertainment or pets as a direct form of domestication selection became popular shortly after (Balon 1995). The popularity of this activity is shown by an account involving Lucullus, a politician in the late Roman Republic, who was accused by Cicero of neglecting politics because of his fish (Balon 1995).

Domesticability and adaptation to HIREC

Just as the vast majority of species are negatively impacted by anthropogenic change (Wagner et al. 2021), the vast majority of species fail to adapt to domestication. An influential paper by Diamond (2002) identified six criteria, all of which must be met for a species to be domesticable. Only one of these—social dominance hierarchies, exploitable by humans to control groups of animals—is not clearly pertinent to adaptation to humans more broadly. The rest of the criteria are:

(1) *Adapts to human-provided diet:* Food is frequently a motivator for the ancestors of domestic species to make initial contact with humans (Larson and Fuller 2014). In fact, diet is so important that signatures of selection are found for genes that allowed for dogs to consume starch-rich foods, which helped facilitate the domestication process (Axelsson et al. 2013). Today, domestic and HIREC-adapted wild species both eat from novel food sources and consume novel food items in anthropogenic environments (Fig. 2).

(2) *Fast growth rate and short birth spacing:* species that have long birth intervals prolong the domestication process. Domestic chickens (*Gallus domesticus)* exhibit extreme selection for decreased birth spacing, with some breeds laying 300 eggs a year (Bell 2002; Fig. 2).

Fig. 2 Five of Diamond's (2002) six criteria for domesticability (see the Domesticability and adaptation to HIREC section) are also useful for understanding what makes some wild species successful under HIREC. The sixth (not shown) is not relevant to discussion about wild animals and HIREC: social dominance hierarchies used to control groups. 1. *Adapts to human-provided diet* (**a**) Successful domesticates thrive on a wide variety of human-provided food. Cat eating a flour tortilla (photo credit: Amanda Beckman). (**b**) Under HIREC, many wild animals are expanding what is considered their "natural" diet to include resources provided directly or indirectly by humans. *Leptonycteris* spp. feeding at nectar feeder (photo credit: Simon Tye). 2. *Fast growth rate and short birth spacing* (**a**) An extreme of short birth spacing is observed in domestic poultry as evidenced by the high frequency of egg-laying outside the historic breeding season. Five chicks pictured behind metal bars. (**b**) Some non-cavity nesting birds are drawn to nest in human structures. Mourning dove (*Zenaida macroura*) sitting on a nest on top of a green box with a brick wall in the background (photo credit: Chris Jarvis). 3. *Not threatening to humans* (**a**) Secondary rounds of domestication are currently happening for several species to retain juvenile traits and be more suited for indoor life. A small breed of pig (*Sus domesticus*) standing indoors on a rug (photo credit: Vjeran Pavic). (**b**) Animals that humans are willing to feed in public are not considered to be dangerous or aggressive, and typically are not pest species. A grey squirrel (*Sciurus carolinensis*) places its paw in a human's hand that contains food while looking at the person. 4. *Breeds in human-altered environments* (**a**) One extreme of breeding in human environments, dairy calves are quickly separated from their mother after birth in many cases. A black and white photo shows approximately five cattle per small, fenced pen, for dozens of pens. (**b**) While many wild birds will nest on human-created structures, getting wild birds to breed in captivity remains a major obstacle in ornithology research, though some researchers have recently had success. A fledgling dark-eyed junco (*Junco hyemalis*) with an orange band on its leg that was hatched from captive-reared parents in a research population is pictured in an enclosure made of wire mesh with branches, moss, and leaves on the ground (photo credit: Ketterson Lab & Sarah Wanamaker). 5. *Tendency not to panic in enclosures* (**a**) Donkeys (*Equus asinus*) and mules (*Equus asinus* × *Equus caballus*) still perform their duties as pack animals, the reason they were first domesticated, despite the changes to the landscape and infrastructure around them. A mule carrying several sacks on its back and wearing a halter crosses a bridge in front of a stone wall (photo credit: Gil Rosenthal). (**b**) An Italian wall lizard (*Podarcis siculus*), climbs up a brick wall that has crumbled in places to create small crevices. Many animals are drawn to anthropogenic structures because they mimic natural caverns. (photo credit: John Hutchinson)

Similarly, some wild bird species nest in novel human environments and experience higher reproductive success compared to populations in less-disturbed areas (Chace and Walsh 2006; Fig. 2).

(3) *Not threatening to humans:* animals with more amicable and human tolerant dispositions have been historically easier to tame (Belyaev 1979; Diamond 2002). For example, Brubaker and Coss (2015) showed that zebras (*E. quagga*) had longer flight distances than feral horses (*E. c. ferus*) and argued that zebras likely experienced more intense ancient hunting pressure leading to them being more wary and aggressive towards humans, which made the horse more suitable for domestication (Brubaker and Coss 2015). Disposition also influences which domestic animals become indoor pets, and which wild animals humans will approach and feed in public (Fig. 2).

(4) *Breeds in human-altered environments:* species on the edges of the commensal or prey route are especially likely to exhibit reluctance to breed in captivity. However, species can overcome this barrier and breed (naturally or artificially) in social and physical environments drastically different from what was experienced in the wild (Fig. 2). Passerines sing beautifully and are useful for research, and falcons (*Falco* spp.) for catching small prey, but neither have been domesticated due to poor success breeding in captivity (Zeder 2012).

(5) *Tendency not to panic in enclosures:* Last, the well-developed fight-or-flight responses of gazelles (*Gazella* spp.) made them poor candidates for domestication

despite the fact they were a valuable food source (Zeder 2012). Many modern domestic species can tolerate unnatural situations with proper training and reinforcement, but many species moving into human-disturbed habitats do so because they mimic preferred natural areas (Fig. 2).

Some wild species are therefore more likely to adapt successfully to HIREC, including through domestication. Every population encountering a changing environment, however, will experience demographic changes and novel sources of selection that can make them both resilient and more vulnerable to a changing world. Domestication thus represents an extreme test of how species adapt to novel environments caused by humans.

Box 2 Behavioral attributes and outcomes of domestication

Tameness joins "quality" (Rosenthal 2017) and "condition" (Clancey and Byers 2014) as a widely used, sweeping, and vague term in the literature. Domestication always involves selection for "tameness," but the term means different things in different studies. In the classic silver fox domestication study, workers explicitly selected for an attenuated flight response to humans (Belyaev 1979; Trut 1999; Trut et al. 2009), which has been propagated in the literature as "selection for tameness" (Zeder 2012; Sánchez-Villagra et al. 2016; Wilkins 2020). Reduced fear of humans is only part of the dictionary definition of tameness, which also stipulates reduced danger to humans

Animals we consider tame typically go further than not scaring or being scared by humans, exhibiting affiliative behaviors that elicit positive responses from humans. The term **anthropophily** is loosely used in the domestication literature to describe a combination of reduced fear, reduced aggression, and increased socialization with humans. Anthropophily is part of what Diamond (2002) terms **disposition** which also includes behavior towards other domestic animals. Disposition—loosely defined as being prosocial and less aggressive towards humans and other domesticates—is also a key component in tameability, with species with more tolerant dispositions being more tamable

Traits associated with domestic species like tameness and anthropophily can also be rapidly lost. During **feralization**, or when domestic species are released and established in wild conditions, the rapid increase in selection on traits associated with predation, foraging, and mate choice (Johnsson et al. 2016) results in the reduction or elimination of typical prosocial behaviors of domestic species in as little as one generation

The vernacular perception of "tame" is modulated by affiliative behaviors, morphological traits as interpreted by humans, and other habits like controlled defecation and appropriate interactions with the human-controlled environments. Furthermore, tameness clearly differs between, say, large carnivores and chickens, with the consequences of an aggressive peck far milder for the latter. A brown bear that breaks into vehicles might be defined as "tame" following definitions in the scientific literature on domestication but is clearly not tame in the vernacular sense. Just as with other all-encompassing terms, we are better off unpacking tameness into its constituents, which have distinct neurophysiological and genetic bases

Evolutionary consequences of domestication: insights for adaptation to HIREC

Just as some species respond better to domestication selection than others, domestication selection takes different forms depending on the population being domesticated; consider cattle bred for milk, meat, leather, and fighting (Signer-Hasler et al. 2017). As detailed below, long histories of domestication, feralization, and gene flow with wild neighbors contribute to a unique, often convoluted history for each domesticate. Nevertheless, available evidence suggests core features of the histories of domesticates and many HIREC-adapted lineages: (1) immediate, strong selection from initial interactions with humans, (2) population bottlenecks, and (3) selection for reduced fear and aggression (Box 2).

First, there are immediate phenotypic and fitness consequences of human contact in addition to those imposed by directed selection and breeding. Artificial environments, or human-altered environments, frequently disrupt assortative mating and mate choice (Rosenthal 2017). And initial captivity imposes strong selection on wild animals. A series of studies on hatchery salmonine fishes (family *Salmonidae*) show that captive-reared animals and their descendants often exhibit reduced fecundity compared to their wild counterparts (O'Sullivan et al. 2020). Steelhead trout (*Oncorhynchus mykiss*) lose 40% fecundity per captive generation (Araki et al. 2007) and captive-born Atlantic salmon (*Salmo salar* L.) produce only half (55%) as many offspring as wild populations (Milot et al. 2013). These effects are often transgenerational, with the offspring of captive born individuals also exhibiting lower fecundity (O'Sullivan et al. 2020). Captive offspring survival rates are also lower relative to wild-reared counterparts (Farquharson et al. 2021).

Second, strong domestication selection, along with a small number of founding individuals, invariably results in bottlenecked populations with depleted genetic variations. Reduced effective population size due to bottlenecks from domestication results in the increased probability that mildly deleterious mutations will become fixed (Cruz et al. 2008; Bosse et al. 2019; Fages et al. 2019). In dogs, these mutations can cause complex and physically debilitating genetic diseases like hip dysplasia (Sutter and Ostrander 2004).

Relative to their wild counterparts, domesticated populations thus suffer from increased genetic load—a greater number of deleterious mutations fixing due to drift and hitchhiking with selection targets (Makino et al. 2018; Kim et al. 2021). Strong selection and limited variation, in turn, decrease the efficiency by which these mutations are purged by purifying selection (Cruz et al. 2008; Schubert et al. 2014). Surprisingly, two plant studies suggest that guided selective sweeps can actually purge deleterious variation, resulting in reduced genetic load compared to wild relatives (Kim et al. 2021; Lozano et al. 2021).

Some domestic species—and some animals adapting to HIREC—are more likely to experience histories of population bottlenecks. Larger animals domesticated through the prey pathway are expected to have severe bottlenecks (Larson and Burger 2013). Bollongino et al. (2012) speculated that the severe bottleneck associated with domestication of wild aurochs into cattle was due to the difficulties of managing and distributing a large and aggressive animal.

Animals domesticated on the direct pathway like hamsters (subfamily Cricetinae; Siegel 2012) experienced a much more recent bottleneck associated with heavy selection on breeding over a relatively short time span (Larson and Burger 2013). Genetic bottlenecks are particularly intensified by the fact that small numbers of males have traditionally been bred to multiple females (Warmuth et al. 2012). In the early domestication of large mammals, selective breeding was likely restricted to males, with wild females recurrently introduced to herds (Warmuth et al. 2012; Marshall et al. 2014; Frantz et al. 2020). Archeological evidence suggests that the earliest domestic goat herds were managed differently based on sex; a majority of females were over 2 years old, while the majority of males were harvested before they reached 2 years (Daly et al. 2021). Limiting the number of reproductive males reduces effective population size and, in mammals, the diversity of sex-chromosome haplotypes, specifically on the Y chromosome (Lau et al. 2009).

Selection and drift in domesticated populations are of a piece with adaptation to HIREC more generally. Rare, though highly visible, translocation and captive breeding programs are very similar to directed domestication in that they generate small, often closed populations that experience genetic and cultural bottlenecks (Mock et al. 2004; Snoj et al. 2006; Parker et al. 2012) and strong intentional or unintentional selection (Frankham et al. 1986; Heath et al. 2003; López et al. 2019).

In a broader array of cases, human interaction with wild animals blurs the line with the commensal and prey pathways for domestication, with human-induced selection often yielding harmful changes for populations. Animals of recreational value, like hunting or sport fishing, are often bred and harvested selectively (Fig. 1) due to specific phenotypic characteristics that make them especially desirable to hunters such as large antlers (Double Dime Whitetails 2021) or body size, in addition to preferred behaviors like reduced movement rates (Rivrud et al. 2013; Festa-Bianchet 2017; Leclerc et al. 2019). This "unnatural selection" resulting from HIREC-adjacent living and selection in managed populations has the potential to negatively affect genetic diversity and fitness (Allendorf and Hard 2009).

The third and final thread that most domesticates and HIREC-adapted species share is "tameness," at least in the broader sense of the term (Box 1). Relaxed selection on antipredator responses, selection from human interactions, and learned experience all favor reduced fear of humans (Agnvall et al. 2015, 2018; Sánchez-Villagra et al. 2016). Selection for tameness may typically not involve reduced fear of humans specifically, but an attenuated response to threatening stimuli more broadly in response to release from predation. For example, Providence petrels (*Pterodroma solandri*) on oceanic islands experience a reduced fear of both humans and invasive mammals because of a historic absence of natural terrestrial predators (Bester et al. 2007). Similarly, domesticated Atlantic and Japanese masu (*Oncorhynchus masou*) salmon have an increased risk of predation in the wild because of their maladaptive tendency to stay close to the surface (Reinhardt 2001; Solberg et al. 2020). Increased tameness, loosely defined, is shared across all domestic mammals (Sánchez-Villagra et al. 2016) and may be ubiquitous in animal domestication. Populations under HIREC experience relaxed selection from natural enemies and increased selection on coexistence with humans. This may often favor tameness, except for species that are actively targeted by humans as pests or prey.

Correlated evolution of traits under domestication

Tameness is only one suite of traits shared across independently domesticated species (Sánchez-Villagra et al. 2016). Across domesticated mammals, domestication results in reduced brain size (Kruska 1996), altered pigmentation (Zhang et al. 2014), and reduced fear of humans (Sato et al. 2020). Captive animals invariably undergo plastic or genetic changes without direct domestication selection, and this effect is also seen with wild animals that are closely associated with humans. For example, white-rumped munias (*Lonchura striata*) kept in captivity, without selective breeding, still developed a loss of pigmentation (Suzuki et al. 2014). Pigmentation loss was also observed in a long-term and free-living study population of house mice experiencing selection for tameness through experimental monitoring and handling (Geiger et al. 2018). Even managed game species meet several common traits of domestication: early age of maturity, group living at a high density, pigment loss, abnormal population age structure, and occasionally increased tameness (Mysterud 2010).

In a celebrated experiment, Belyaev and colleagues (Belyaev 1979; Trut 1999; Trut et al. 2009) selected captive silver foxes (*Vulpes vulpes*) for reduced flight responses to human experimenters ("tameness," Belyaev 1979; Box 2). Direct selection on behavior yielded morphological characteristics found in a range of domestic mammals, notably coat depigmentation and floppy ears. It is worth noting that these experiments built upon an existing selection bias: these foxes were sourced from a Canadian fur farm, where they had been selected for their fur and their ability to breed in captivity (partially through selection for reduced reactivity) for multiple generations (Lord et al. 2020).

Remarkably, when red junglefowl (*Gallus gallus*) were subject to a domestication regime, they converged on traits characteristic of domestic mammals like depigmentation and reduced brain size (Agnvall et al. 2018). Additionally, junglefowl from the reduced fear line exhibited social dominance over junglefowl selected for high fear when presented with feeding, drinking, and dust bathing access in a test arena (Agnvall et al. 2014, 2018), although it was noted this result could also be partially due to reduced neophobia in the low fear lines during testing.

There are three broad ways that this "domestication syndrome" (Hammer 1984) could arise: (1) from independent convergence towards similar suites of traits in response to similar selective pressures, (2) from parallel evolution of a small set of underlying traits, and (3) from systemic effects of genetic load and relaxed selection.

First, natural selection favors those animals best adapted to human environments and human-associated pathogens, while selection is relaxed on evading natural enemies and foraging on natural food sources. Furthermore, humans may be imposing domestication selection on the same core traits, like Diamond's (2002) six criteria for domestication. A generally less fearful animal is likely not only less aggressive but may also be less neophobic with food, spaces, and people. Along with thriving on human-associated food and rapid population growth, each of these traits also helps respond to HIREC (Fig. 2).

Second, different species may undergo parallel genetic changes, such that shared mechanisms produce convergent phenotypes across instances of adaptation to humans (Rosenblum et al. 2014). Hou et al. (2020) identified parallel changes in chickens and six domestic mammals in sets of genes, gene families, and functional pathways associated with exploratory behavior, axon cues, and neurotransmission. Dogs and humans experienced parallel evolution for genes involved in metabolism, digestion, and neural processes while adapting to new similar environments (Wang et al. 2014). As a result, similar diseases are seen in both species due to positive selection in parallel genes. Within species, similar phenotypes across different breeds can also be tested for parallelism to see if independent founding lineages for the same phenotype share similar genetic changes. Morphological changes may also arise from parallel genetic mechanisms, as with dwarfism in three independent breeds of chickens (Wang et al. 2017).

Efforts to identify parallel genetic effects on behavior have been mixed. Wilkins (Wilkins et al. 2014; Wilkins 2017, 2020) suggested parallel selection on genes that underlie the formation and differentiation of the neural crest resulted in phenotypic similarities between divergent taxa. Alternatively, domestication could ubiquitously select for parallel shifts in thyroid hormone metabolism that leads to a prolonged juvenile stage (Crockford 2002). VonHoldt et al. (2010, 2018) found that a gene under strong positive selection in dog domestication was associated with Williams-Beuren syndrome, which can cause some afflicted humans to be overly friendly.

Evidence for and against parallel evolution can be found even within the same taxa, like Old World camels, *Camelus bactrianus*, *C. dromedarius*, and *C. ferus* (Fitak et al. 2020). Additionally, convergence but not parallelism was found between two isolated farm-raised salmon populations (Naval-Sanchez et al. 2020). This indicates that the same early domestication pressures do not always result in the same genetic outcome, even within the same species. Furthermore, there is mixed support that domestication syndrome hypotheses have been rigorously tested enough to support one unifying mechanism ((Lord et al. 2020) but see (Zeder 2020)) or that searching for a universal domestication syndrome is important for researching convergent evolution in domestic species (Johnsson et al. 2021). Despite this, domestication syndrome research continues to yield valuable knowledge about the nature and processes responsible for domestication (Wilkins 2020; Parsons et al. 2020). New research into ancient genomics will continue to update our understanding of this controversial syndrome (Frantz et al. 2020) and undoubtedly shed light on the genetic and behavioral processes resulting in domestication.

Third, general effects of strong domestication selection, both intentional and unintentional, should be expected to both increase genetic load and relax purifying selection on many fitness-related traits. Belyaev's (1979) notion of "destabilizing selection" disrupting developmental pathways is consistent with a contemporary understanding of the phenotypic consequences of reduced heterozygosity and increased fixation of deleterious alleles. Systemic changes in phenotype, from tameness to smaller brain size, may just be manifestations of developmental instability resulting from increased genetic load (Lacy 1997).

Learning, plasticity, and adaptive responses

The initial response to domestication or other anthropogenic disturbance involves plastic phenotypic changes (Mason et al. 2013). In fact, captivity can induce rapid morphological changes within a few generations (e.g., canids (Siciliano-Martina et al. 2021); Japanese macaques (*Macaca fuscata*) (Kamaluddin et al. 2019); house mice (*Mus musculus*) (O'regan and Kitchener 2005; Courtney Jones et al. 2018)). The associated behavioral evolution depends on genotype-by-environment interactions (Zuk and Spencer 2020), what Marler (1991) termed the "instinct to learn." Due to differences in their natural history and cognitive abilities, some species lend themselves to interact with humans more readily (Zeder 2018). Individual and social learning are key to living with people whether they are out to breed you or not. Reduced fear of humans ("tameness" in the narrow sense) often develops merely as a consequence of learned familiarity with humans, often with unfortunate consequences for humans and animals alike (Herrero et al. 2005). The "dispositional" challenges to domestication involve the instinct to learn; wild horses can be "broken" but zebras cannot (Brubaker and Coss 2015).

Indeed, the tempo and mode of learning are vastly important to domesticability. With the notable exception of pigeons, most domesticated birds are precocial, with extended parental care (Larson and Fuller 2014). Extended parental care is often accompanied by so-called imprinting on caregivers (e.g., Lorenz's (1935) greylag geese (*Anser anser*)). Some species may thus more easily develop "tameness" in the broad sense of reduced fear and increased social affiliation with humans. Many of the characteristics of domestication can thus arise without genic evolution simply through humans "hacking" the ontogeny of social development.

For species under HIREC, behavioral flexibility can be a double-edged sword. On the one hand, learning makes it easier for individuals to survive in a novel environment, and to move across gradients of disturbance. On the other hand, loss of culture may be more difficult to recover from than loss of genetic diversity (Caro and Sherman 2012; Brakes et al. 2019). For example, endangered regent honeyeaters (*Anthochaera phrygia)* kept in captivity have experienced cultural loss of song variants compared to their wild counterparts (Crates et al. 2021). Cultural losses can also result in predator naiveté, with losses to predation cues after a short (50–130 years) period of carnivore (wolf and brown bear (*Ursus arctos horribilis*)) extirpation (Berger et al. 2001). In some cases, cultural losses may also carry negative downstream effects on local ecosystems, as in the case of migratory route loss due to anthropogenic interference (Caro and Sherman 2012). Bison (*Bison bison*), elephants (*Loxodonta africana*), and springbok (*Antidorcas marsupialis*) have all experienced reduced or lost migration routes as a result of agriculture and urbanization (Roche 2008; Caro and Sherman 2012).

Feralization

Domestication is far from irreversible. Many of the most successful domesticates have successfully feralized to the point that they become distinct enough from their domestic ancestors to earn different names: pigs (*Sus scrofa domesticus*) become wild boars (*S. scrofa*), horses become mustangs, and dogs become dingoes (*C. l. dingo*). Even Przewalski's horse (*E. przewalskii*), popularly held as the closest undomesticated lineage to horses, is a feralized domesticate (Gaunitz et al. 2018).

When domestic animals return into wild conditions, selection because of humans is reduced even as animals are again exposed to historic sources of selection like predators and food scarcity. An excellent case study of this is seen in feral chickens in Hawaii; genetic and behavioral analyses indicated that the feral chickens are hybrids originating from an invasion of domestic chickens into wild red junglefowl populations in Kauai (Gering et al. 2015). Additionally, distinct genetic differences are observed in the Kauai feral versus domestic chickens (Johnsson et al. 2016). Furthermore, given enough time, feral animals can be considered truly "wild" again; dingoes were introduced to Australia approximately 5000 years ago, but are designated as native animals and are managed under conservation plans in some areas (Stephens et al 2015). It is not surprising that feral animals thrive in human-disturbed areas. Feral populations constitute a problematic component of HIREC for many natural systems and are often targeted as pests (Hone 1995; Reddiex et al. 2006; Ruscoe et al. 2021). The Providence petrels discussed above, "tame" before ever encountering humans, are easy prey for decidedly untame feral hogs recently descended from domestic pigs.

The apparent ease of feralization stands in contrast with the low success rate of reintroduction of captive-bred wild species (Armstrong and Seddon 2008). In particular, deficiencies in culturally transmitted skills, such as hunting, foraging, and avoiding predators, can be fatal if not taught before reintroduction (Reading et al. 2013). Strategies like supplemental feeding after reintroduction (Ferrer et al. 2017) can also have unintended effects like compromising migratory behavior (Murray et al. 2016). The cultural and genetic profile of successful ferals may lead to useful insights for conservation efforts centered on reestablishing wild populations from captivity. Despite genetic and cultural bottlenecks, and in the face of learned and evolved behaviors and other phenotypes maladaptive for survival in the wild, domestication need not be a dead end for animal lineages (Gering et al. 2019). This observation may be a gem of hope for some wild species pushed to the brink in the Anthropocene.

Gene flow, domestication, and conservation: domestic and human-adapted species

So far, we have discussed domestication and feralization in terms of their utility as models to make predictions and anticipate challenges in conservation. Domesticated animals do mate with their wild relatives, to the evolutionary benefit and detriment of one or both populations (Berthouly et al. 2009; Guarino and Lobell 2011; Frantz et al. 2015; Bolstad et al. 2017). In some cases, humans have actively managed introgression with wild populations to strengthen specific desired traits or to maintain levels of genetic diversity (Murray et al. 2010; Warmuth et al. 2012; Shackelford et al. 2013). Genetic and archeological evidence supports cross-continental gene flow between domestic and wild dromedary populations, a process that contributed to their multiple domestication centers and widespread dispersal (Almathen et al. 2016).

The consequences for wild taxa of mating with domestics are often negative. Domestic escapees, despite having lower fitness in the wild, contribute a migrational load on wild populations and wild-domesticate pairings have the potential to decrease population fitness (Tufto 2017). Domestic escapees have also been shown to alter the age and size at maturation of Atlantic salmon with concerns of introgression contributing to the reduced fitness of wild populations (Skaala et al. 2006; Bolstad et al. 2017). By contrast, gene flow with wild populations has served as an opportunity for genetic rescue in some domestic species (the mouflon (*Ovis orientalis musimon*) and domestic sheep (*O. aries*; Loi et al. 2001); the black-footed ferret (*Mustela nigripes*) and the domestic ferret (*M. putorius furo*; Sandler et al. 2021)). Hybridization with domesticates may sometimes be favored by selection, but the consequences for conservation may be complex (Allendorf and Hard 2009; Todesco et al. 2016).

Human-adapted wild populations are more likely to exist near domesticates, and therefore may serve as a conduit for the gene flow of domesticated genes into wild populations. Gene flow has been documented between dingoes and introduced domestic dogs (Stephens et al. 2015), and between European wildcats (*Felis silvestris*) and domestic cats (Oliveira et al. 2008) in urban areas where their ranges overlap. These patterns highlight the need for interdisciplinary approaches to species conservation and documentation in the Anthropocene; if discrete variables describing human-caused environmental alterations, genetic analyses, and ecological knowledge were not all considered, the full scope of these interspecies interactions could not be understood.

Genetic differentiation of domesticates, and human-adapted populations more broadly, operates along the lines we should expect when populations are exposed to ecological divergence. The emergence of new domestic animal species is a special case of ecological speciation (Nosil 2012) which theory and empirical evidence suggest can operate even in the face of extensive gene flow (Heikkinen et al. 2020). Due to strong intentional and unintentional selection in human-controlled environments, domestic species have differentiated even given extensive gene flow with wild relatives (Frantz et al. 2015, 2020; Heikkinen et al. 2020).

Gene flow across human-created ecological gradients

Just as domesticates are under ecological selection and exchanging genes with wild populations, so too are HIREC-adapted wild populations (Berthouly et al. 2009; Mowry et al. 2021). These are animals whose reproduction is not directly controlled by humans, but that have evolved to enhance fitness in a novel ecological niche shaped by humans. Among the best-studied of these are so-called urban exploiters, or species whose population sizes or ranges have drastically grown in human industrial development (Blair 1996). Most of these, like early cats and ducks, are human commensals.

Many studies suggest that animals living in urban environments frequently differ in behavior compared to non-urban conspecifics (Sol et al. 2013). Urban coyotes (*Canis latrans)* display bolder and more exploratory behavior than rural coyotes (Breck et al. 2019), large carnivores decrease daytime activity to reduce time around humans (Ditchkoff et al. 2006), and 21 species of European birds have adjusted their flight initiation distance to match roadway speed limits which can decrease collisions (Legagneux and Ducatez 2013). Recent studies indicate that urban species also exhibit differences in reproductive success (Peach et al. 2008; Bailly et al. 2016) and traits used in mate choice (Candolin and Wong 2019) compared to populations in less-disturbed habitats. It is often unclear whether these traits have evolved due to ecological selection in a novel urban niche, as opposed to drift from genetic and cultural bottlenecks (Johnson and Munshi-South 2017).

Anthropogenic structures, waste, and presence have all demonstrated directional selective effects on the environment (Alberti et al. 2017). In addition to these concerns, urbanization creates chemical (Bai et al. 2017), noise (Kuehne et al. 2013), and light pollution (Cabrera-Cruz et al. 2018), decreases genetic variability (Schmidt et al. 2020), results in habitat loss and fragmentation (Scolozzi and Geneletti 2012), increases the probability of wildlife diseases (Bradley and Altizer 2007), and creates large-scale environmental changes (Zhou et al. 2004; Argüeso et al. 2014).

The presence of anthropogenic structures frequently results in phenotypic adaptation to new opportunities or risks created from their presence. The abundance of bird feeders in the UK has favored longer bills to better exploit these easy meals; great tits (*Parus major*) homozygous for the Col4A5-C collagen gene exhibit increased bill length, and as a result increased reproductive success over heterozygous individuals (Bosse et al. 2017). These longer-billed individuals are more likely to visit bird feeders and spend more time at bird feeders than are heterozygous individuals. Similarly, the human offering of supplemental nectar for hummingbirds (*Calypte ann*a) in urban areas has resulted in a 700-km range expansion over the course of 17 years (Greig et al. 2017). In some cases, the presence of anthropogenic structures can result in phenotypic differentiation, as in *Anolis* lizards adapted to urban heat islands, with higher thermal preferences, longer legs, and a lower humidity tolerance than their arboreal counterparts (Winchell et al. 2018).

Understanding responses to HIREC, including urban adaptations, is an important step in predicting evolutionary responses to climate change and determining how to develop a sustainable and symbiotic relationship between human activities and biodiversity preservation (Johnson and Munshi-South 2017). Similarly, the study of adaptation to human-dominated landscapes provides opportunities to better understand the process of domestication. Indeed, domestic and human-adjacent wild animals display similar features including a loss or decrease of fear of humans and longer breeding seasons (Møller 2010). During the Neolithic period, humans began to sedentarize, rapidly alter the landscape, and domesticate for the first time (Driscoll et al. 2009), indicating domestication has been tied with rapid human development for thousands of years.

Including the commensal domestication pathway, animals have long taken advantage of the opportunities provided by human-altered environments (Driscoll et al. 2009). Habitat generalist, omnivorous, or granivorous birds have greater success in urban areas (Silva et al. 2016). Noise pollution has the ability to filter out species which cannot be heard over the din of the city, resulting in birds that communicate at higher frequencies being better suited for urban life (Francis et al. 2011). But birds can also shift the frequency of their song in response to urban noise (Bermúdez-Cuamatzin et al. 2011). Understanding aspects beneficial to survival in urban ecosystems could serve as an indicator of which species are most likely to be successful in an increasingly anthropogenic world. For example, behavioral plasticity and habitat matching, rather than specific life history traits, have allowed an invasive population of the Barbary ground squirrel (*Atlantoxerus getulus*) to proliferate despite having a founding population of 2–3 individuals (van der Marel et al. 2021).

Synthesis and future directions: what does it take to live in the Anthropocene?

The principles underlying successful domestication and feralization can aid in our comprehension of why some species are thriving while some are imperiled during the Anthropocene. However, an additional and underappreciated aspect that needs to be considered when studying wild species' adaptation to the Anthropocene is the attitudes that humans have towards them.

Understanding the genetic changes in dogs, the oldest domestic animal species, is useful for calibrating the maximum end of the scale of human influence. If we understand the genetic changes that humans impose on other species during deliberate domestication, we can gain a better understanding of how wild species might try to shape their own evolutionary trajectory in the Anthropocene. For example, future studies should investigate if pests, which can often be feral or HIREC-adapted wild populations (Gering et al. 2019), that exhibit a reduced fear of humans exhibit signatures of selection in regions functionally similar to those found in hyper-social humans and dogs (vonHoldt et al. 2010, 2018). Further investigations could then tease apart the evolutionary significance of these findings by exploring whether convergence or parallel evolution resulted in observed similarities. Conserved neural systems across vertebrates, notably the social behavior network and the mesolimbic reward system (O'Connell and Hofmann 2011) represent promising candidates for parallel changes resulting from similar social and cognitive pressures arising from domestication and HIREC.

Even as we search for conserved mechanisms underlying the broader challenge of adapting to humans, it is important to recognize that domestication involves unique challenges and opportunities. Commensal species exploit anthropogenic niches, and become domestic once humans begin to encourage this by actively feeding, protecting, and breeding. These differences, particularly regarding prosocial behavior towards humans, are worth remembering as we try to draw insights from domestication selection for the fate of HIREC-adapted species. The broader point is that human attitudes towards a species have important effects on the spectrum of selective forces it has to contend with (Table 1). All domestic species are around today because the human-attributed value of the relationship outweighed the realized costs. Similarly, the evolutionary trajectory for wild animals in the Anthropocene depends on their subjective value to humans (Table 1). Rats (*Rattus* spp.), cockroaches (order Blattodea), and squirrels (*Sciurus* spp.) all share a preference for human-dominated landscapes and the waste produced by humans. Yet squirrels are the only one that people purposely feed in public (Fig. 2). The value that people assign to a given species can determine the selective pressures that species experiences, and therefore its likelihood of survival in the Anthropocene (Table 1). In particular, it can be difficult to rally enough public support to effectively conserve and manage imperiled species unless they are charismatic (Jacobs 2009; Small 2012). For example, surveys sent to Floridian boaters showed that many individuals were aware of and supported Florida manatee (*Trichechus manatus latirostris*; graceful, reminiscent of mermaids) conservation efforts, including actions they could personally take to aid in manatee conservation (Aipanjiguly et al. 2003). However, those same individuals are likely not aware of the threatened Black Creek crayfish (*Procambarus pictus*; small, many legs, lives in mud), which shares a very limited range with the manatee, even exists let alone what can be done to conserve it.

Human interest in particular wild animal species can also lead to outcomes that favor a target species at the expense of an entire ecosystem: rabbits in Australia, starlings (*Sturnus vulgaris*) in North America, and Mozambique tilapia (*Oreochromis mossambicus*) worldwide. Public interest in non-native animals and a lack of ecological knowledge without effective community engagement can lead to cascading consequences (Deak et al. 2019). This is particularly true when considering the presence of invasive species, many of which have an advantage over native species because they are transported (and often subsequently released) in order to serve some function, whether esthetic or practical, for humans. The relationship between domestication and invasion runs deep, with the process of domestication often resulting in movement of animals into new ranges where escaped and released animals have the potential to damage local ecosystems (Lewis and Maslin, 2015). Humans are both the problem with most invasive species, as well as the potential solution. Understanding which phenotypes and behaviors humans prefer in wild or domestic animals could help provide insight into which axes of HIREC and/or early stages of domestication species are experiencing in the Anthropocene.

Summary and conclusion

Animals evolve to exploit humans as a resource and vice versa. The dynamics of conflict and cooperation between humans and animals share many basic properties with coevolving systems more broadly, whether with domestication or adaptation to HIREC (Table 1). Human activities have the ability to influence behavior and genetic makeup of individuals in novel ways through the process of domestication. While there has been significant research on specific aspects of these changes, there are still many questions remaining about how domestication influences global biodiversity and speciation processes. Anthropogenic disturbance, specifically domestication, has been of tremendous use to science, which has surely helped science ring the alarm bells that many wild species are not keeping up with our rapidly changing world. Can science return the favor beyond ringing the alarm bells? Our modern understanding of genomics, combined with early warnings of physiological stress from environmental change (Gabor et al. 2018), can aid our conservation and biodiversity preservation goals through admixture, genetic rescue, and selective breeding programs like those used in zoos to help recover endangered populations.

The study of domestication has the potential to illuminate potential problems in conservation as these domestic and threatened species are often subject to similar limiting factors such as genetic bottlenecking (Moyers et al. 2018), introgression (Chen et al. 2018), human-mediated selection (Frantz et al. 2020). Does the fact that so few species successfully domesticate bode similarly ill for adaptation to

Table 1 Human perception of animals during the Anthropocene can result in divergent selection pressures affecting the way that animals adapt and respond to HIREC conditions. How humans view and respond to specific species and groups affect the way that these animals respond to anthropogenic pressures

If humans…	…selection in the Anthropocene favors individuals that can…	…in HIREC-adapted…
ignore my existence	adapt to novel niches	wild populations (songbirds, wall lizards)
eat me	be tasty and grow fast	domesticated and managed populations (chickens, seabass, white-tailed deer)
hate me	avoid humans; reproduce quickly and abundantly	pests (urban rats and mice)
find me beautiful or sacred	be more beautiful	domesticated and managed populations (koi, swans)
think I could be useful	be useful	domesticated and managed populations (llamas, gambusia)
enjoy my company	be cute and prosocial	domesticated populations (bichons frises, cockatiels)
fear me	avoid humans – or be beautiful, tasty, or useful	wild and managed populations (tigers, German shepherds)

Anthropocene? Compared to the number of domesticated animals, the number of wild HIREC-adapted species is much larger; future studies using genomic tools for comparisons within HIREC-adapted species, and between HIREC-adapted and domestic species, provide an excellent opportunity to study behavioral, convergent, and parallel evolution.

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Declarations

Conflict of interest The authors declare no competing interests.

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