New coping styles for a new world

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Abstract

Humans currently occupy all continents and by doing so, modify the environment and create novel threats to many species; a phenomenon known as human-induced rapid environmental changes (HIREC). These growing anthropogenic disturbances represent major and relatively new environmental challenges for many animals, and invariably alter selection on traits adapted to previous environments. Those species that survive often have modified their habitat or their phenotype through plasticity or genetic evolution. Based on the most recent advances in this research area, we predict that individuals with highly plastic capacities, those that are generally shy, with high cognitive abilities and stress responses – in other words, individuals displaying a reactive phenotype – would better perform in human-modified landscapes than their counterparts' proactive phenotypes. Moreover, we hypothesize that when human presence reduces predation, this decouples commonly associated traits resulting in a new range of phenotypes, with individuals characterized by low aggressiveness and physiological stress responses but high boldness, cognitive abilities and plasticity. We coin these individuals as "preactive", being part proactive and part reactive. While supported by some studies, demonstrating the existence of this new coping style will require additional multivariate studies investigating behavioral and physiological responses to multiple challenges in HIREC impacted species.

INTRODUCTION

The ecological importance of phenotypic trait variation within species is gaining increasing attention (Forsman & Wennersten 2016; Roches *et al.* 2018). Recent results demonstrate that intra-specific variation can play a considerable role on the biodiversity of an ecosystem, comparable or even stronger than variation across species (Roches *et al.* 2018). Individuality, which is also referred to as personality, is a statistical phenomenon characterized by individual variation being less than between individual variation and individuals differ along a behavioral dimension (Roche *et al.* 2016). By definition, this implies comparisons with other group members, *i.e.* an individual is bolder than another in multiple contexts and throughout time (Réale *et al.* 2010). Boldness, activity, aggressiveness and sociability/gregariousness are among the most studied personality traits (PTs). Covariation between personality traits defines a behavioral syndrome (Sih *et al.* 2004; Bell 2007). Recent work has integrated molecular and endocrinological mechanisms to further distinguish bold, aggressive and active individuals from their counterparts (Réale *et al.* 2010). The concept of syndromes relates to the older notion of coping styles (Koolhaas *et al.* 1999), which highlights differences between reactive and proactive individuals in their capacities to respond to a challenge. Hence, reactive animals, those that are relatively shy, less aggressive and less active, are also characterized by high hypothalamic-pituitary-interrenal/adrenal (HPI/A) responses and low sympathetic activity compared to proactive ones in response to a stressor (Koolhaas *et al.* 2010). A very large body of literature has also demonstrated that individuals differ in a range of behavioral and physiological traits that are generally associated with being reactive or proactive, and many of these have ultimate consequences on traits associated with fitness in specific environments (see Table 1 for details).

A population is therefore behaviorally and physiologically structured along a continuum of reactive to proactive individuals. From an ecological point of view, this structure has major implications for the ecosystem's dynamics since it drives intra-population competition as well as inter-species interactions (Bolnick *et al.* 2011; Sih*et al.* 2012). From an evolutionary point of view, variability in coping styles is also of primary importance since it determines a population's capacity to adapt to environmental changes and therefore determines the response to natural selection (Dingemanse & Réale 2005). There is therefore an urgent need to acknowledge individual coping style as an important conservation actor in addition to the species diversity that is commonly considered by ecologists and managers (Brodie *et al.* 2018).

Through extensive harvesting, environmental pollution, habitat fragmentation, the introduction of exotic species, tourism, urbanization and climate change, humans modify the strength and direction of natural selection. This has profound consequences on the behavior and physiology of many species. Because of the relative explosion in the rate at which these anthropogenic disturbances have proliferated across the world, they are collectively referred to as human-induced rapid environmental changes or HIREC (Sih *et al.* 2011). Only few areas are still unaffected by HIREC, and therefore physiological responses of species to HIREC are of primary importance for conservation issues. While behavioral responses to HIREC have previously been reviewed (Sih*et al.* 2011; Tuomainen & Candolin 2011; Sih 2013; Wong & Candolin 2015), the associated underlying physiological mechanisms of the differences in coping style have been relatively ignored. Here, we focus on the multiple physiological and behavioral processes by which HIREC modifies the coping style structure of populations. A recent study demonstrates that one of the most important HIREC, climate change, facilitates the dominance of proactive species (i.e., fast-growing and opportunistic), and this has direct consequences on biodiversity (Brustolin *et al.* 2019). Based on recent literature, we propose that evolutionary responses to HIREC at the intraspecific level may generally favor reactive individuals in the wild. This evolutionary response is the consequence of three distinct time-related steps from habitat changes (migration or dispersal), to genetic evolution, detailed below.

HUMAN ACTIVITIES MAKE EXPLORATORY INDIVIDUALS CHANGE HABITATS

Proactive individuals are generally more active, explore more and are more likely to disperse (Table 1). Consequently, in situations where HIREC reduces habitat quality, proactive animals can be expected to be the first individuals to leave. This has been previously observed in crabs, where bold individuals were the first to disperse when habitat quality was reduced (Belgrad & Griffen 2018). While studies conducted in the wild are still lacking, some laboratory tests have shown that bold individuals work harder to escape threatening situations. Bolder fish have more attempts to escape laboratory-induced hypoxia (Brelin*et al.* 2005), or tend to avoid the hypoxic environment (Ferrari*et al.* 2016). Bold individuals are also better at avoiding or escaping fishing gear (Diaz Pauli & Sih 2017), which could be related to their higher anaerobic capacities (Table 1) (Killen *et al.*2015).

While leaving a non-suitable habitat might lead to a superior fitness outcome for bold individuals of a given population, this implies that they are subsequently able to successfully find suitable habitat. This is not necessarily an easy task in the context of HIREC, which is often characterized by overall habitat degradation and increases in the presence of ecological traps (Robertson *et al.* 2013).

Previous studies have also found inter-individual differences within a population in the propensity to disperse. Indeed, populations are likely comprised of individuals that differ in consistent ways; dispersers are bold, aggressive and asocial while joiners are rather shy, slow-explorers and social (Cote *et al.* 2010a). Harrison et al. (Harrison *et al.* 2015) also recently differentiated 'resident' from 'mobile' individuals. Mobile individuals tend to explore more, be more active and be less site-specific, and thus, they resemble proactive individuals. In this sense, less socially embedded yearling female marmots (*Marmota flaviventer*) are also more likely to disperse (Blumstein *et al.* 2009), and in the month preceding dispersal these marmots upregulate a suite of specific genes, many of which are associated with migration (Armenta *et al.* 2018). Consequently, in many cases mobile (or proactive) individuals are more prone to change habitats in stressful situations related to HIREC (Fig. 1.1) and this may have evolutionary consequences.

HIRECS FAVOR PLASTIC INDIVIDUALS

HIREC-driven superiority of plastic individuals

Natural selection will favor well-adapted heritable phenotypes in a new environment and lead to genotypic change over time. However, most environmental changes associated with HIRECs seem to occur rapidly and plasticity plays an essential role in determining the phenotype that will survive (Diamond & Martin 2016). Phenotypic changes for individuals exposed to HIREC are largely documented in response to exposition to contaminants, temperature, acidification, environmental noise, etc. Individuals with the best capacities to respond rapidly via changes in behavior (van Baaren & Candolin 2018) or physiology (Taff & Vitousek 2016) are therefore the most likely to survive HIREC, as seen with climate change (Beever *et al.* 2017). In a number of taxa, proactive and reactive phenotypes diverge in their capacities to respond to environmental changes (Table 1). Case studies highlighted the ability of reactive individuals to be more behaviorally plastic in a wide range of circumstances. In rats selected for their aggressive behavior, proactive individuals developed routines, a superior strategy when in predictable environments (or situations) but not when the environment frequently changes (Benus *et al.* 1991).

Plasticity has nevertheless an energetic cost (Moran 1992; Murren*et al.* 2015). Consequently, in a stable environment, proactive individuals, which are less plastic than reactive individuals, are expected to better perform because less energy is invested in coping abilities, memory and learning capacities (Table 1). The costs of plasticity have been demonstrated in great tits (*Parus major*), where fast exploring/proactive individuals performed better in stable environments, while the slow exploring/reactive individuals performed better in a variable and fluctuating environment (Dingemanse & de Goede 2004). And, after transport from UK to Norway, reactive rainbow trout (*Oncorhynchus mykiss*), had greater feeding motivation and started to win dyadic fights against proactive opponents which was not the case prior transportation (Ruiz-Gomez *et al.* 2008). Moreover, reactive rainbow trout are also more efficient at finding food than proactive ones in response to environmental changes (Ruiz-Gomez *et al.*2011). In addition, reactive fish performed better in cognitively complex foraging tasks, even after modifications to their environment (White *et al.* 2017). Similar conclusions were drawn in birds (Verbeek *et al.* 1994) and pigs (Bolhuis *et al.* 2004) where proactive individuals were less successful in reversal learning than reactive pigs, suggesting that proactive individuals display a less plastic behavior. In a monogamous species, the red point cichlid (*Amatitlania siquia*), reactive individuals were better at varying their behavioral profile within pair (Laubu *et al.* 2016) which is important to enhance their reproductive success (Gabriel & Black 2012; Harris & Siefferman 2014). Finally, fish with different coping styles also diverge in their sensitivity to environmental cues. Indeed, reactive individuals have been shown to be more responsive to negative, aversive, stimuli while proactive individuals are more sensitive to positive stimuli (Millot *et al.* 2014).

Altogether, reactive individuals have increased behavioral capacities to cope with rapid environmental changes. This is also seen at the physiological level, with reactive individuals showing higher capacities to mount physiological responses required to cope with environmental challenges (Fig. 1.2) due to greater HPI/A axis activation when facing a stress.

Evolutionary shifts observed in response to HIREC

Artificial selection pressures, such as those created by humans, are capable of driving both behavioral and physiological changes in response to selection. For example, fish with bold phenotypes can be preferentially (and unintentionally) harvested, resulting in the selective depletion of bold individuals (Biro & Post 2008). Differences in personality can also result in sampling biases during scientific sampling, with bolder individuals being caught more often (Biro & Dingemanse 2009). Intensive fishing selects on life history traits (growth, maturation, reproduction), but demonstrations of fishing's effects on behavior remained scarce until the last decade (Uusi-Heikkilä*et al.* 2008). Fishing methods are diverse, apparently leading to distinct selection pressures on behavior (Diaz Pauli *et al.* 2015; Arlinghaus *et al.* 2017). Passive fishing (e.g., using long-lining, angling, trapping or gill nets) preferentially catch proactive individuals (Biro & Post 2008; Arlinghaus *et al.*2017), while active gear (e.g., trawls or purse seines) unintentionally targets reactive individuals (Heino

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& Godø 2002; Diaz Pauli *et al.* 2015).

Although hunting has less pressure on wild populations in many places compared to fisheries, it too selects for specific behavioral traits. Madden and Whiteside (Madden & Whiteside 2014) showed for example that shyer pheasant (*Phasianus colchicus)* are more likely to survive to the hunting season than bolder ones. In wild reindeer (*Rangifer tarandus*), a long-term study also showed that hunting pressure is correlated with an increase in flight distance over years, suggesting that populations become shyer because of hunting pressure (Reimers *et al.* 2009). Ciuti et al (Ciuti *et al.* 2012) drew similar conclusions with elk (*Cervus elaphus*), where harvested individuals were bolder. In this context, hunting leads to the same result than passive fishing, selecting for bold individuals and therefore favoring reactive phenotypes. Inversely, the less active animals die from active hunting techniques, such as when dogs are used to chase animals, as seen in bear-hunting (Leclerc *et al.* 2019). As a consequence, the HIRECs linked to fishing and hunting seem to favor one coping style over the other depending on whether the harvesting technique is active or passive.

Rapid environmental changes also may lead to evolutionary changes in the physiology and behavior of wild populations. For instance, climate change has been demonstrated to favor selection for highly plastic individuals over multiple generations (Nussey *et al.* 2005). In addition, multigenerational exposure to high temperatures reduces standard metabolic rate (Pilakouta *et al.* 2019). Global climate change may lead to the reduction of migratory distances in birds (Visser*et al.* 2009), and this phenomenon is an evolutionary response to selection (Pulido & Berthold 2010). High plasticity, reduced metabolic rate, and low standard metabolic rate all favor reactive phenotypes, and we may infer that climate change is driving the evolution of reactive phenotypes (Fig. 1.3.2). It is nevertheless worth noting that tropical cyclones seemingly select for aggressive phenotypes (Little *et al.* 2019), and in this case we would infer that proactive individuals are better adapted to survive.

We have long known that populations evolve in response to exposure to pollutants and with the toxification of Earth; this has become a common driver of HIREC. Empirical studies in the lab monitoring the evolution of behavioral and physiological traits following exposure to pollutants are rare, despite abundant evidence of rapid evolutionary responses (Whitehead *et al.* 2017; Saaristo *et al.* 2018). If the exposure to only one pollutant selected one behavioral response (e.g., boldness or activity), it could be attenuated by a plastic behavioral response (Saaristo *et al.* 2018). However, the large number and diversity of pollutants, each with different properties, and the possible interactions between them (Peterson *et al.* 2017; Saaristo *et al.* 2018), as well as the method of exposure, act as multiple environmental stressors for organisms which have to continuously adapt to new threats and stressors. We suggest that plasticity, a characteristic of reactive phenotypes, will be the key to cope with the diversity of stressors created by pollution.

Urbanization, ecotourism and domestication, have all been found to increase boldness of affected populations (Geffroy *et al.* 2015b). Effects of urbanization on bird behavior have been extensively studied and show that living in urban areas leads to reduced flight initiation distance (Samia *et al.* 2015), and higher risk-taking behavior (Miranda *et al.* 2013). However, adaptation to an urbanized environment also requires substantial individual plasticity. For instance, in response to urban noise, great tits increase their pitch during mating calls to increase the likelihood that potential mates receive the signal (Slabbekoorn & Peet 2003). Similar results have been seen in killer whale (*Orcinus orca*) which increased the amplitude of their calls as a function of background noise levels related to ships or tourism boats (Holt *et al.* 2009). In terms of physiology, reduced stress reactivity was also observed for urban individuals (Partecke *et al.* 2006; Atwell *et al.* 2012). Taken together, these studies show that urban areas select for more proactive individuals. In the context of domestication, individuals are often selected for either their docility or their reproductive potential. Both types of selection types lead to bolder individuals in response to both human and potentially other predators (Geffroy *et al.* 2015b), and reduced HPI/A reactivity (Rauw *et al.* 2017), which favors proactive individuals. In the context of both, urbanization and domestication, humans create a "human shield" (Berger 2007), where selection pressure is relaxed and bold individuals are favored. Disappear

RESHUFFLING THE CARDS OF NATURAL SELECTION

Are there ecological consequences of vanishing proactive phenotypes?

Many studies have noted the essential role of keystone species that warrant specific conservation efforts due to their central position for the functioning of a community (Mills *et al.* 1993; Paine 1995; Betts *et al.* 2015), and whose extinction or massive population decline could have massive consequences on community structure (Cortés-Avizanda *et al.* 2015). Recent work has focused on the essential role played by some individuals in a group and coined the term keystone individuals (Modlmeier *et al.* 2014; Pruitt & Keiser 2014). Modelmeier et al. (2014: p55) defined these individuals as having "a disproportionally large, irreplaceable effect on other group members and/or the overall group dynamics relative to its abundance".

The vanishing of proactive phenotypes could first have consequence in terms of group composition and population dynamics as these individuals are likely to be keystone individuals. As noted above, proactive individuals tend to disperse more, while reactive individuals are more likely to join newly colonized areas (Cote *et al.* 2010a). If new populations are composed only from reactive individuals, this may constrain dispersal and space use. For instance, group mean personality scores (boldness, activity, and sociability) of some feral guppy (*Poecilia reticulata*) populations was not associated with exploratory propensity. Rather, group exploratory propensity was driven by the personality of key individuals whereby slow individuals tended to slow down exploration rates of the shoal (Brown & Irving 2014). In mosquitofish (*Gambusia affinis*) mean group personality appeared to also drove group dispersion patterns in the expected pattern (group with many asocial individuals disperse further) although there were no keystone individuals identified (Cote *et al.* 2010b). Because exploration is likely associated with resource harvesting patterns, we can envision that HIREC may modify these patterns and have consequences at other trophic levels. Thus, if a system evolved with a mix of shy and bold individuals, and HIREC systematically eliminated one type, we should expect changes in species composition.

The disappearance of one phenotype could also have substantial consequences on prey-predator relationships. In a recent review, it was considered that a proactive or a reactive response of a prey largely depends on the predictability of an encounter with a predator (Creel 2018). The former response will have an energetic cost (fleeing) while the latter would have stress-mediated cost, by activating the HPI/A axis (Creel 2018). However, this approach largely ignored intrinsic differences in coping abilities between individuals of the same species and rather considered that all individuals are able to mount a similar response according to the situation. Here we suggest that the type of response would also depend on the personality of each individual, although ecological consequences would be the same. If proactive individuals vanish from the population, then responses to a predator consisting of displaying aggressive behavior, modifying activity periods, or engaging in particular patterns of vigilance (Creel 2018) would likely be quite different. Rather, the reactive response will be systematically produced, with all its associated stress-related costs. For instance, in the snowshoe hare-lynx system, predation risk increased glucocorticoid production with direct consequences in the decline of offspring production (Krebs *et al.* 1995). Hence, we can expect that always mounting a reactive response to predatory encounters would lead to chronic stress and its associated consequences in terms of reproductive success.

We know that behavioral variation is an index of genetic variation (Smith & Blumstein 2013). If we selectively reduce phenotypic variation, we are likely reducing genotypic variation. Such a reduction may be ultimately costly if it reduces a population's adaptive potential to what may ultimately be a more variable environment. This loss of behavioral diversity may be particularly acute in conservation management when animals are brought into captivity for breeding with subsequently planned translocations and reintroductions (e.g., Smith & Blumstein 2012; Merrick & Koprowski 2017). We expect captivity to reduce genetic variation and also to eliminate the very variation that may be essential for the wild.

Toward the emergence of a new coping style in predator free-areas

The presence of predators is a key driver that influences the structure of behavioral syndromes (Réale & Festa-Bianchet 2003; Smith & Blumstein 2012). Thus, by extirpating predators, or protecting prey from predation risk, correlations between personality traits may become decoupled (Bell 2005; Bell and Sih, 2007) with a

series of cascading effects on the underlying physiology. The sudden elimination of predators following some HIRECs could render behavioral and physiological traits associated with antipredator responses as "useless". Indeed, natural selection favors antipredator phenotypes that efficiently reduces predation risk. But when the risk is low, these costly phenotypes, including vigilance, high HPI/A activity, or flying capacities, may become counterproductive. Consequently, constraints on these phenotypes are released and the correlation between traits is lost (Fig. 2).

Nevertheless, these effects observed in response to the reduction of predation seem to come with additional constraints related to the presence of human and their associated activities. Indeed, in response to the presence of human, there might be selection for some specific traits leading to new correlation between traits (Fig. 2). However, the direction, intensity and speed of this selection are still unclear, and we therefore face difficulties in predicting animals' responses to human presence.

Response to domestication can be used as a guide to predict the fate of individuals in predator free areas and in interactions with human. Most of our knowledge on the subject comes from foxes (*Vulpes vulpes*) that have been domesticated for now more than 40 generations (Trut 1999), with mixed results. Selection for tameness led to a decrease in fear-related traits (Trut 1999), cortisol production and associated gene pathways (Trut *et al.* 2009) which means that animals are now more bold and proactive (Fig. 1.3.1.3). However, it also decreased aggressiveness (Trut 1999) and increased social cognitive abilities (Hare *et al.* 2005) and neurogenesis (Huang *et al.* 2015), which is consistent with them being more reactive (Rauw *et al.* 2017) (Fig. 1.3.1.3). Notably, however, is that brain size reduction, which often correlates with behavioral flexibility (Sol *et al.* 2005, 2008), characterizes domestication in most species (excluding foxes and mice) (Wilkins *et al.* 2014), and this, associated with the development of routine-like behavior linked to a closed environment (Rauw *et al.* 2017), would suggest that we should expect reduced cognitive skills.

In the case of urbanization (Fig. 1.3.1.2), human contact also leads to increased boldness (Shochat *et al.* 2006; Coleman *et al.* 2008; Møller 2012; Thompson *et al.* 2018), and a reduced HPI/A responses (Atwell *et al.* 2012), which should tend to create more proactive individuals. Nevertheless, urbanization also comes with increased cognitive abilities (Audet *et al.* 2015), and behavioral plasticity (Carrete & Tella 2011; Sol *et al.* 2013; Thompson *et al.* 2018), characteristics of reactive individuals. In the context of urbanization, it is however important to notice the difficulty to determine whether these characteristics emerged from differential colonization according to an individual's traits, or from an evolutionary response that selected for specific traits. In other words, did bold individuals invade towns (Fig. 1.3.1.2, dashed purple arrow), or did shy individuals evolve towards boldness in urbanized areas (Fig. 1.3.1.2, solid grey arrow) (Sol *et al.* 2013)?

In the context of tourism and ecotourism, similar results to those seen with urbanization and domestication have been observed in animals that are in frequent contact with humans. We have seen that boldness has increased (Geffroy *et al.* 2015b; Arroyo *et al.* 2017), as has neurogenesis (Geffroy *et al.* 2018). However, baseline and post stress cortisol responses seem to strongly depend on the intensity with which humans interact with animals, with severe disturbance generally increasing cortisol production (Geffroy *et al.* 2017) (Fig. 1.3.1.1).

Overall, wild animals exposed to HIREC that relaxes selection on antipredator behavior and increases human contact would likely be bolder but also less aggressive, more plastic in their response, with higher cognitive abilities and lower HPI/A responses. We suggest a new term — "preactive"— in that individuals are part proactive and part reactive. The emergence of this new coping style would be the result of uncoupling initatially associated traits (Fig. 2A), by a first step of relaxed selection due to the creation of a human-shield (Fig. 2B) and a second step where animals associated with humans selectively learn (and/or have evolved) to deal with this new situation by displaying overall decreased aggression, increased boldness and decreased HPI/A reactivity while improving their capacities to be plastic in association with higher neurogenesis (Fig. 2C).

Conclusions

Taken together, HIRECs have profound and potentially cascading effects on wild animals' behavior and physiology that are likely to change the proportion of proactive and reactive individuals in a population, and these changes may lead to changes in species' distribution and abundance. These are the results of three distinct time-related steps: 1) migration of proactive individuals, 2) survival of reactive individuals, and 3) genetic evolution. Based on our current knowledge, we propose that HIRECs which may not systematically relax predation pressure, such as climate change, pollution or harvesting, mostly lead to a genetic evolution towards reactive individuals with reduced boldness and aggressive behavior, and increased plasticity and that these changes are associated with changes in underlying physiology. In parallel, we suggest that other HIRECs which relax predation pressure, such as tourism, urbanization, captivity and domestication, will favor the emergence of a new coping style between reactive and proactive individuals that we refer to as preactive.

While there is now a large literature on individuality and personality traits in nature, we suggest that by systematically investigating the underlying physiological mechanisms, we will be better able to develop predictive models of response to HIREC. Additionally, we emphasize that multigenerational and multivariate studies investigating the effects of HIREC on coping styles are warranted and we hope that future studies will allow us to better understand the conditions and the dynamics of the process that favor the emergence of preactive individuals. Finally, given the vital importance of coping style by environment interactions, we must learn more about the cascading effects of HIREC on ecological systems.

ACKNOLEDGEMENTS

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Table 1. Summary of the observed divergences for traits that are generally associated with the different coping styles: proactive (P) and reactive (R).

Traits	Proactive vs. reactive	References
Behavior		
Boldness	P>R	(Koolhaas *et al.* 1999)
Activity	P>R	(Mas-Muñoz *et al.* 2011; Herrera *et al.* 2014; Geffroy *et al.* 2015a; Wong *et al.* 2019)
Aggressiveness	P>R	(Huntingford 1976; Øverli *et al.* 2004; Castanheira *et al.* 2013)
Exploratory behavior	P>R	(Øverli *et al.* 2006; Millot *et al.* 2009)
Sociality	R>P	(Ferrari 2014; Geffroy *et al.* 2014; Jolles *et al.* 2015)

Traits	Proactive vs. reactive	References
Social dominance	P>R (reversed in a novel environment)	(Øverli *et al.* 2004; Ruiz-Gomez *et al.* 2008; Øverli & Sørensen 2016)
Escape a stressor	P>R	(Brelin *et al.* 2005; Silva *et al.* 2010; Laursen *et al.* 2011; Ferrari *et al.* 2016; Damsgård *et al.* 2019)
Plasticity	R>P	(Benus *et al.* 1991; Bolhuis *et al.* 2004; Ruiz-Gomez *et al.* 2011; Jolles *et al.* 2019), although (Thomson *et al.* 2012) observed the opposite
Dispersal	P>R	(Chapman *et al.* 2011; Myles-Gonzalez *et al.* 2015)
Cognitive abilities		
Behavioral plasticity to solve task	R>P	(Verbeek *et al.* 1994; Bolhuis *et al.* 2004; Ruiz-Gomez *et al.* 2008, 2011)
Sensitivity to positive *stimulus*	P>R	(Millot *et al.* 2014)
Sensitivity to negative *stimulus*	R>P	(Millot *et al.* 2014)
Memory	R longer than P	(Baker & Wong 2019)
Fear learning	R faster than P	(Baker & Wong 2019)
Triggering of self-feeder	R>P	(Ferrari *et al.* 2014; Benhaïm *et al.* 2017)
Neural plasticity	R>P	(Johansen *et al.* 2012; Sørensen *et al.* 2013; Vindas *et al.* 2017a; Sadoul *et al.* 2018; Alfonso *et al.* 2019)
Metabolism		
Glucose	R>P	(Huntingford *et al.* 2010)
Lactate	R>P	(Huntingford *et al.* 2010)
Oxygen consumption	P>R	(Killen *et al.* 2011; Herrera *et al.* 2014)
Metabolic rate (under hypoxia)	P>R	(Killen *et al.* 2012)
Standard metabolic rate	P>R	(Geffroy *et al.* 2016; Yuan *et al.* 2018)
Routine metabolic rate	P>R	(Skov *et al.* 2019)
Resting metabolic rate	P>R	(Huntingford *et al.* 2010)
Anaerobic capacities	P>R	(Killen *et al.* 2015)
HPI/A axis and stress response		
Cortisol level (basal)	R=P	(Tudorache *et al.* 2013; Wong *et al.* 2019)
Cortisol level (post stress)	R>P	(Castanheira *et al.* 2013; Wong *et al.* 2019)
Cortisol basal levels recovery	P faster than R	(Tudorache *et al.* 2013; Wong *et al.* 2019)
Glucocorticoid receptors	P>R (*gr1* in hypothalamus) R>P (*gr2* in whole brain)	(Vindas *et al.* 2017b; Alfonso *et al.* 2019)

Traits	Proactive vs. reactive	References
Mineralocorticoid receptors	R>P (whole brain) P>R (hypothalamus)	(Vindas *et al.* 2017b; Alfonso *et al.* 2019)
Corticotropin releasing factor	R>P (whole brain) P>R (hypothalamus)	(Vindas *et al.* 2017b; Alfonso *et al.* 2019)
Cortisol receptor	R>P	(Huntingford *et al.* 2010)
11β-hydroxysteroid dehydrogenase	R>P	(Wong *et al.* 2015)
Neurotransmitters		
Serotonin (Basal)	P=R (brain)	(Øverli *et al.* 2001)
Noradrenaline (Basal)	P=R (brain)	(Øverli *et al.* 2001)
Dopamine (Basal)	P=R (brain)	(Øverli *et al.* 2001)
Serotonin (Post stress)*	R>P (brain stem)	(Øverli *et al.* 2001)
Noradrenaline (Post stress)	R>P (telencephalon and optic tectum) R>P (whole brain)	(Øverli *et al.* 2001) (Alfonso *et al.* 2019)
Dopamine (Post stress)	P=R (brain)	(Øverli *et al.* 2001)
Dopamine D2 receptors	P>R	(Thörnqvist *et al.* 2019)
Serotonin receptor (5-HT1A)	P>R	(Vindas *et al.* 2017a)
Adrenaline and noradrenaline release (Post stress)	P>R (blood)	(Brelin *et al.* 2005; Koolhaas *et al.* 2010)
Immunity		
Immune response	P>R	(MacKenzie *et al.* 2009; Kittilsen *et al.* 2012; Vargas *et al.* 2018a)
Biological clock		
Circadian rhythm	P>R	(Tudorache *et al.* 2018)
Genes involved in biological clock	P [?] R	(Tudorache *et al.* 2018)
Fitness		
Reproductive success	P>R (lab conditions) P>R (lab conditions) P>R (both conditions) R>P (wild conditions) R=P (wild conditions)	(Ibarra-Zatarain *et al.* 2019) (Vargas *et al.* 2018b) (Smith & Blumstein 2008) (Wilson *et al.* 2010) (Smith & Blumstein 2008)
Mating preferences	P>R (lab conditions)	(Godin & Dugatkin 1996)
Mating adjustments	R>P (lab conditions)	(Laubu *et al.* 2016)
Growth	R>P (lab conditions) P>R (lab conditions) P>R (lab conditions) R>P (wild conditions)	(Ferrari *et al.* 2016) (Biro *et al.* 2004) (Damsgård *et al.* 2019) (Adriaenssens & Johnsson 2011)
Survival	R>P (both conditions)	(Smith & Blumstein 2008)

*Serotonin (5-HT) levels were higher for reactive than proactive ones after stress in the brain stem of rainbow trout (Øverli *et al.* 2001). However, it is important to note that the serotonergic activity (measured as the ratio between 5-HT and its metabolite; (Shannon *et al.* 1986)) was found lower for reactive than for proactive in the whole brain of sea bass (Alfonso *et al.* 2019) and higher in the amygdala homologue of Atlantic salmon (Vindas *et al.* 2017a).
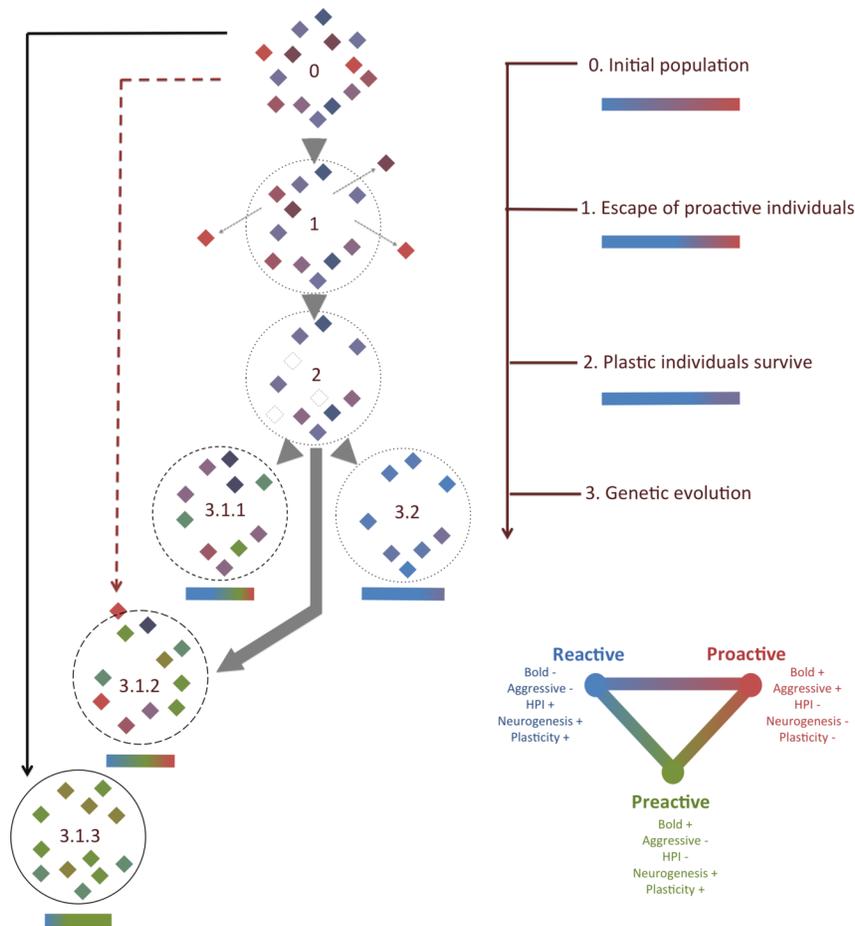
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Figure 1. Temporal consequences of Human Induced Rapid Environmental Changes (HIREC) on the reactive-proactive continuum. Animals are from 0. an initial pristine population exposed to HIRECs with effects on 1. dispersal, 2. phenotypic plasticity, 3. genetic evolution related to HIRECs that produce 3.1. a human predator shield such as 3.1.1. Tourism, 3.1.2. Urbanization and 3.1.3. Domestication or 3.2. that do not produce a human shield (e.g., Climate Change, Pollution or Harvesting). The black arrow represents animals from the initial population directly caught to be domesticated and the dashed purple arrow highlights the fact that some proactive individuals could invade urban areas. The shape of the border of each circle directly correlates to the intensity of human-shield, from no contact (light dashed circle), to high contact (full circle).
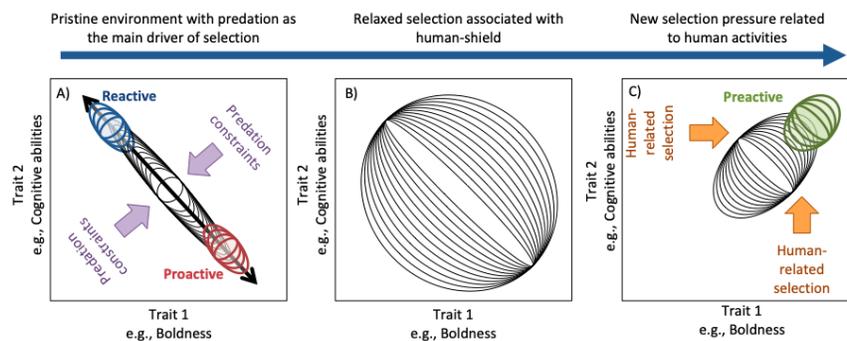
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Figure 2. The decoupling of personality traits leading to the emergence of a preactive coping style. See the section "**Toward the emergence of a new coping style in predator free-areas** " for a full description of the process.