Site fidelity as a maladaptive behavior in the Anthropocene

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Site fidelity, or the behavior of returning to previously visited locations, has been observed across taxa and ecosystems. By developing familiarity with a particular location, site fidelity provides a range of benefits and is advantageous in stable or predictable environments. However, the Anthropocene is characterized by rates of environmental change that outpace the evolutionary history of extant taxa, which can result in site fidelity becoming maladaptive. Here we outline the theoretical underpinnings for maladaptive site fidelity and synthesize empirical research supporting its occurrence, and examine it in the context of a related concept, ecological traps, whereby organisms exhibit maladaptive behavior in habitat selection. We then discuss adaptive mechanisms that may enable species with site fidelity to continue to persist in the Anthropocene. With ongoing environmental change, researchers and practitioners should expect fidelity-induced ecological traps to become more common, and initiate projects to identify and understand their origins. Such knowledge will help conserve the widespread and ecologically important behavior of site fidelity.

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Site fidelity is a ubiquitous example of behavioral specialization or rigidity (Berger-Tal and Saltz 2016) in which animals reuse locations that remain fixed in geographic space. Returning to previously visited sites involves spatial memory (Merkle *et al*. 2014), which can be costly to develop and maintain (Dukas 1999) yet provides a rather simple way of choosing where to forage, nest, breed, or migrate. Site fidelity is exhibited at various scales, from daily foraging patches to seasonal migration routes, and has evolved in taxa as diverse as insects (Dyer 1996), birds (Piper 2011), fish (Block *et al*. 2005), reptiles (Broderick *et al*. 2007), amphibians (Bucciarelli *et al*. 2016), and both marine (Horton *et al*. 2017) and terrestrial (Sawyer *et al*. 2019) mammals (Figure 1).

In a nutshell:

- Because Earth's environment has been relatively stable over geologic time, many animals habitually return to places visited in the past to forage, breed, or find shelter, a behavior termed site fidelity
- However, humans are altering habitats much faster than natural change has previously occurred
- Animals that employ site fidelity will have difficulty adjusting to human-induced rapid environmental change because their ability to adjust their behavior in response to habitat alteration is relatively slow
- Researchers and practitioners should expect site fidelity to become more frequently disadvantageous, initiate projects to identify and understand why such changes are occurring, and prioritize conservation of site fidelity behavior

Although site fidelity evolved in predictable environments (Schmidt 2004; Abrahms *et al*. 2018), it can be advantageous in unpredictable environments as well when developing site familiarity is beneficial (Switzer 1993; Piper 2011), or when outcomes are beneficial when integrated over relatively long timescales (Abrahms *et al*. 2018). Site fidelity reduces costs associated with sampling behavior, assessing and choosing habitat, switching locations, and/or natal dispersal. For example, returning to birth sites to breed can be adaptive because an animal survived there, which theoretically provides information about past resource quality (Kokko and Sutherland 2001). Returning to a previously visited location provides information (ie familiarity) that can improve an animal's future dominance interactions, foraging, movement efficiency, predation response, social capital, and local adaptation (Switzer 1993; Piper 2011). Beyond benefits to the individual or population, site fidelity can ultimately play a major role at the ecosystem scale through nutrient and energy transfers (eg subsidizing terrestrial ecosystems with aquatic nutrients) and alteration of trophic interactions (eg population regulation; Bauer and Hoye 2014).

In certain situations, however, site fidelity may be maladaptive, in which the use of a site results in lower fitness than would occur in other available sites. Site fidelity varies among individuals and populations along a continuum, with two of the most common strategies consisting of a "win-stay/

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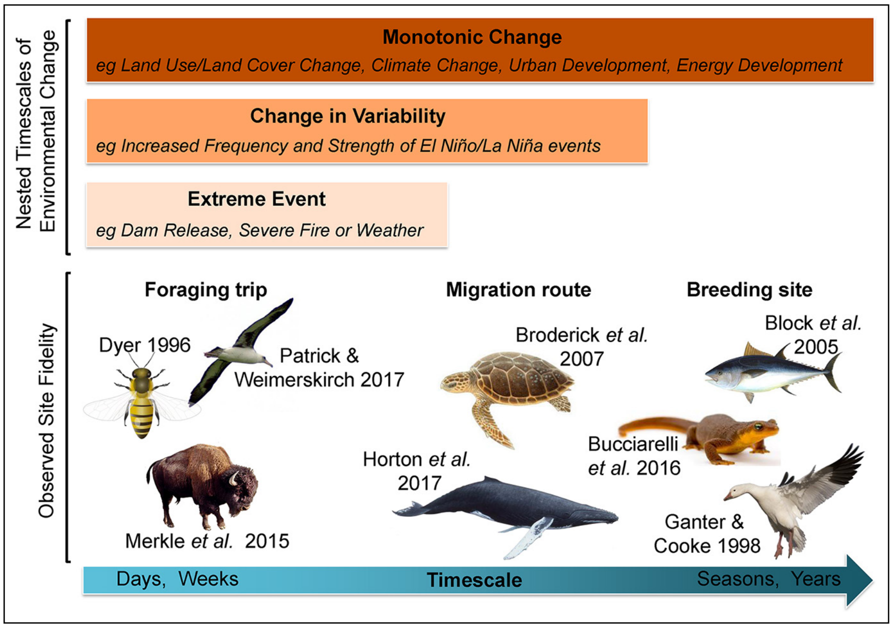

Figure 1. Representation of temporal scales in which site fidelity is observed and at which human-induced environmental change may undermine its adaptive value. Within years, site fidelity can be affected by short-term environmental changes (such as extreme weather events, release of dam water, or severe fires caused by fire suppression regimes). Interannual site fidelity can be affected by increasing environmental variation (for example, more frequent or more intense swings between climatic phases). Perhaps the most detrimental impacts result from long-term, monotonic changes (such as climate warming and land-cover change).

lose-switch" strategy that depends on previous experience, and an "always stay" strategy that is independent of past experience (Switzer 1993). Habitat degradation that shifts spatial patterns in habitat quality could make strong fidelity maladaptive (Kloskowski 2021). Indeed, numerous observational studies have found that individuals with strong fidelity forego the use of higher quality sites in favor of previously visited sites (Williams *et al.* 1993; Merkle *et al.* 2015). For example, experimental manipulation of habitat availability revealed that great tit (*Parus major*) pairs often did not shift from poor-quality habitat to higher quality habitat when vacancies in quality habitat became available. Individuals that did switch tended to be first-year breeders without established territories, suggesting that established individuals were more likely to remain in their occupied site even when high-quality alternatives were present (Krebs 1971).

The effects of maladaptive site fidelity can scale up from individual fitness to population productivity. For instance, food resources on traditional feeding grounds of lesser snow geese (*Anser caerulescens caerulescens*) declined by 50% from 1979 to 1991, and birds that exhibited strong fidelity to these locations had smaller brood sizes (Williams *et al.* 1993). Strong fidelity to breeding sites by Baltic eiders (*Somateria mollissima mollissima*) has also resulted in a drastic decline in their population, as predation on adults at those sites has increased because of population recovery of white-tailed sea eagles (*Haliaeetus albicilla*; Ekroos *et al.* 2012). Similarly, an "always stay" strategy for breeding site selection led to reduced breeding success and a 40% loss in colony size in Cape gannets (*Morus capensis*) following a rapid reduction in prey availability within their foraging range (Pichegru *et al.* 2010). Given the global prevalence of site fidelity and the rapid pace of contemporary environmental change, there is an urgent need to consider how the Anthropocene affects organisms employing this behavior.

Site fidelity and human-induced rapid environmental change

We are living currently in the Anthropocene, a period signified by human-induced rapid environmental change (HIREC; Sih *et al.* 2011) characterized by swift and widespread land-cover change for such purposes as agriculture and resource extraction (Foley *et al.* 2005). Human-induced climate change has also facilitated global ecosystem alteration (Walther *et al.* 2002), including shifting phenologies and greater environmental variability (Wang *et al.* 2017). Site fidelity did not evolve in such quickly transforming environments. Stated simply, if an animal returns to a given location because of site fidelity, and the relative fitness benefits of that site are reduced because of HIREC, the animal will inherently be more likely to make a maladaptive decision, particularly if other options exist.

An emerging theme that characterizes the Anthropocene is the creation of evolutionary and ecological traps (Robertson *et al.* 2013), which can accelerate population declines (Robertson and Chalfoun 2016; Sigaud *et al.* 2017). Evolutionary traps are situations in which rapidly changing conditions lead to a decoupling of the cue an organism uses to guide its behavior from that cue's fitness outcome. Ecological traps are a subset of evolutionary traps, focused on habitat selection, in which individuals prefer habitats that confer lower fitness over other available options (Robertson and Hutto 2006; Robertson *et al.* 2013; Robertson and Chalfoun 2016). In other words, an ecological trap is characterized by both preference for equal or lower quality sites and a lower fitness outcome derived from the preference (Robertson and Hutto 2006). For example, lizards (*Acanthodactylus beershebensis*) in Israel's Negev desert continued to use areas despite higher rates of predation after the experimental addition of structures that facilitated predator activity (Hawlena *et al.* 2010).

Ecological traps are rooted in habitat selection theory, wherein animals choose between available habitat options given their real or perceived fitness benefit. Whereas site fidelity was originally noted in the scholarly literature on ecological traps as an index of evolved preference of a given site (Robertson and Hutto 2006), the behavior of site fidelity is based on a different decision framework (Merkle *et al.* 2015). With fidelity,

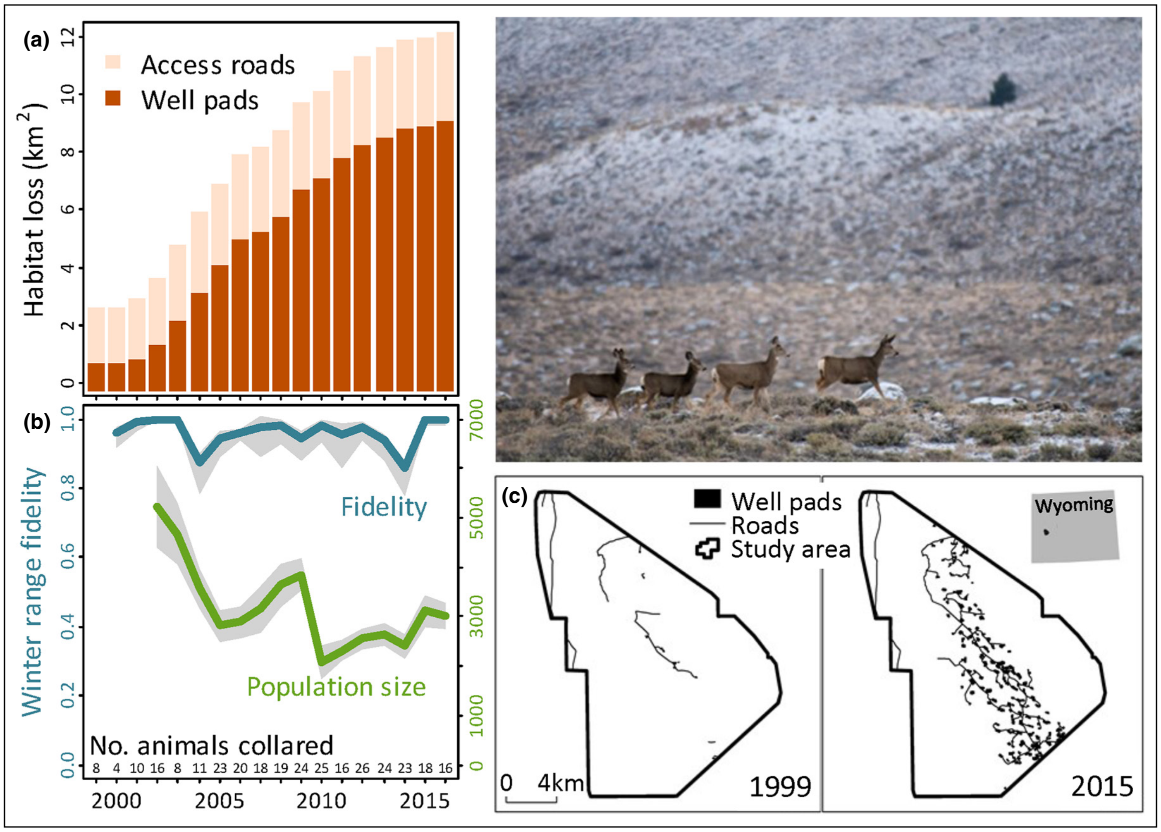

Figure 2. In a natural gas field development in western Wyoming (US), available habitat for overwintering mule deer (*Odocoileus hemionus*) has decreased over the past two decades. (a and c) The cumulative amount of habitat converted to roads and well pads within the gas field has increased. Although this population of mule deer has made fine-scale behavioral changes to avoid habitat close to human infrastructure during winter (Sawyer *et al.* 2017), (b) individuals exhibited strong site fidelity to their winter range prior to development (in 1999); in the subsequent decades, the mule deer population has fallen by 40% (Sawyer *et al.* 2017). See WebPanel 1 for further details. Panel (c) adapted from Sawyer *et al.* (2017). Mule deer image credit: J Riis.

individuals decide whether or not to return to a given site based on previous experience at that geographic location (eg knowledge of the site, reproductive output) and not necessarily because of the habitat conditions at that location (Switzer 1993). To specify site fidelity as a mechanism underlying an ecological trap, we propose the term *fidelity-induced ecological trap* to define situations in which site fidelity, rather than habitat selection, underlies an ecological trap. We envision fidelity-induced ecological traps as scenarios in which individual organisms continue to prefer a site (eg foraging patch, migration route) because of site fidelity, despite the reduced fitness benefits of that site and the availability of other options that may confer higher fitness benefits (sensu Kloskowski 2021).

Whereas previous research has hypothesized that species exhibiting strong site fidelity may be particularly vulnerable to ecological traps (Weldon and Haddad 2005; Hale *et al.* 2015), examples of fidelity-induced ecological traps are increasingly emerging (Ekroos *et al.* 2012; Kloskowski 2021). For example, migratory ungulates often exhibit strong site fidelity (Sawyer *et al.* 2019; Morrison *et al.* 2021); in the western US, populations of mule deer (*Odocoileus hemionus*) continue to return to their traditional winter ranges each year despite human-caused habitat alterations. At the same time, population sizes of mule deer have declined broadly in recent decades (Figure 2; Johnson *et al.* 2017; Sawyer *et al.* 2017). Northern elephant seals (*Mirounga angustirostris*) displaying strong site fidelity in their migrations to the central Pacific Ocean have poorer body condition in anomalous climate settings than their more site-flexible counterparts (Figure 3; Abrahms *et al.* 2018). Likewise, space use patterns of American bison (*Bison bison*) in and around Prince Albert National Park in Saskatchewan, Canada, can be explained by a fidelity-induced ecological trap (Sigaud *et al.* 2017). Although bison mortality risk is higher outside the park from human hunters than inside the park from other causes, bison continue to forage daily on the same farmlands surrounding the park (ie strong site fidelity), thereby contributing to a population decline (Sigaud *et al.* 2017). Similarly, the damming of rivers for hydroelectricity and water resources has caused declines in many fish stocks worldwide, as impassable dams (eg flood control reservoirs) often lead to extirpation of populations of migratory fish with strong site fidelity to natal streams (Liermann *et al.* 2012).

How can site-faithful organisms adapt?

Adaptation to HIREC is markedly slower for organisms with strong site fidelity than taxa with weaker or no site fidelity because adaptation usually occurs over generations rather

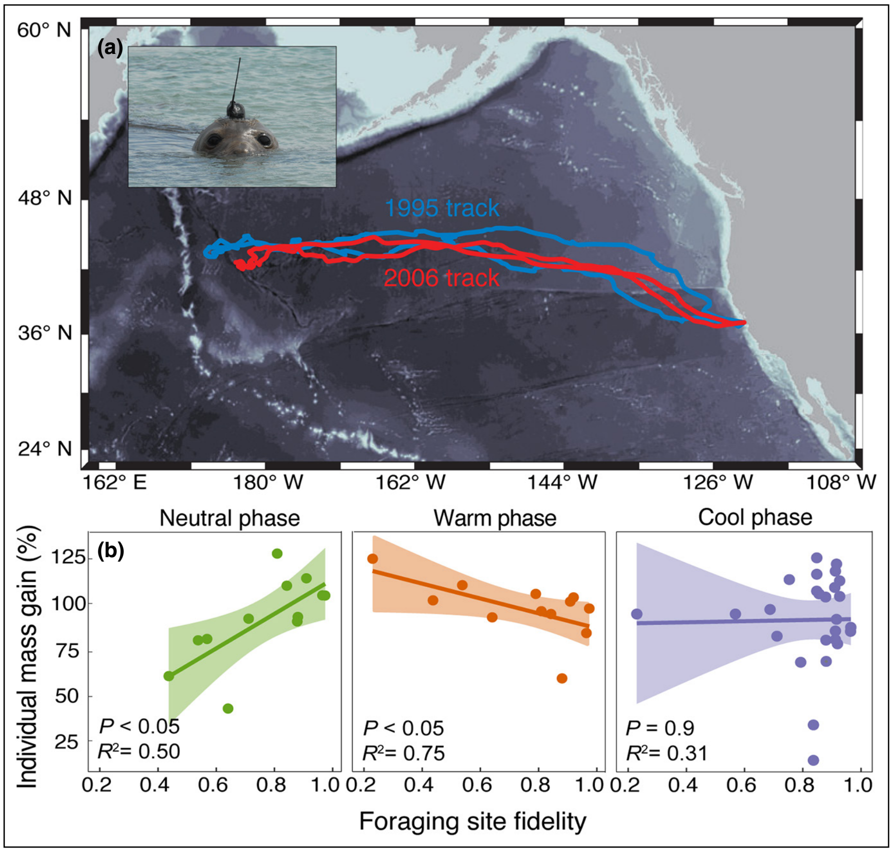

Figure 3. Many female northern elephant seals (*Mirounga angustirostris*) exhibit strong site fidelity to foraging habitats in the North Pacific Ocean during their migrations. (a) Tagging data spanning ~7000 km for the same individual in 1995 and 2006. Quantifying individual-level site fidelity and performance metrics over 10 years revealed that elephant seals with strong site fidelity performed best in average climate conditions, outperforming those that lacked site fidelity (Abrahms *et al.* 2018). (b) However, this pattern was reversed during anomalous climate conditions. Because migration performance is directly linked to reproductive success in northern elephant seals, increasing climate variability projected in the North Pacific may influence the evolutionary benefit of site fidelity to this species. "Neutral", "Warm", and "Cool" phases refer to those of the Pacific Decadal Oscillation. Each colored circle depicts a unique migration from 30 tagged females. Lines and shaded areas represent linear model estimates and 95% confidence intervals, respectively. Figures and data adapted from Costa *et al.* (2012) and Abrahms *et al.* (2018).

than via behavioral plasticity (Berger-Tal and Saltz 2016). Indeed, behavioral plasticity has been linked to the ability of species to adapt to HIREC (Sih *et al.* 2011; Beever *et al.* 2017), and behavioral specialization or rigidity (often characteristic of site fidelity; Abrahms *et al.* 2018) is thought to increase extinction vulnerability (Clavel *et al.* 2011; Berger-Tal and Saltz 2016). We emphasize three ways in which site-faithful species may overcome fidelity-induced ecological traps.

First, adaption may occur through reduction in the intensity of site fidelity. Organisms that employ a "win-stay/lose-switch" site fidelity strategy have greater behavioral flexibility than those employing an "always stay" strategy, and thus are more capable of proximately adjusting their behavior as a result of individual or social information (Doligez *et al.* 2003). For example, whereas bison will continually use and return to the same network of meadows, they can modulate their site fidelity in response to changes in experience (Merkle *et al.* 2014). When a bison recently experiences (ie within days to weeks) poorer quality forage than the current location, the probability of returning to previously visited sites declines. Similarly, male California newts (*Taricha torosa*) can adjust the strength of breeding site fidelity in response to perceived competitive advantage over conspecifics (Bucciarelli *et al.* 2016). Male common loons (*Gavia immer*) likewise increased their breeding success by 41% over 3 years by employing a "win-stay/lose-switch" rule based on the success or failure of the previous breeding attempt (Piper *et al.* 2008). Such behaviors provide a mechanism to try new sites after experiencing a reduction in a site's quality or fitness output, providing a pathway for taxa with site fidelity to cope with HIREC. Nonetheless, the extent to which different organisms can assimilate information about their environment from previous experiences and make informed decisions, such as whether to be site-faithful in different contexts, remains unclear (Chalfoun and Schmidt 2012).

Second, for cases in which there is little to no plasticity in the strength of site fidelity, long-term metapopulation dynamics may facilitate persistence. Whereas site fidelity reduces the probability that a metapopulation might reach carrying capacity over time (Matthiopoulos *et al.* 2005), species that employ strong site fidelity could persist if some individuals in the population occasionally disperse and colonize new areas (Pess *et al.* 2014). Such processes have been observed in salmonids, taxa iconic for site fidelity, in which straying individuals can colonize new habitat (Figure 4; Pess *et al.* 2014). The nature of these straying individuals, however, is poorly understood, and whether the lack of site fidelity is a genetic trait or a product of environmental conditions remains unclear. Adélie penguins (*Pygoscelis adeliae*) also provide a prime example over longer timescales. This species exhibits strong fidelity to breeding sites, and to a lesser extent, foraging sites (Watanuki *et al.* 2003). Climate-driven changes in sea-ice extent are linked to declines over the past several decades across colonies along the Antarctic Peninsula (Ducklow *et al.* 2013). Paleoecological records, however, indicate that dispersal-related fluctuations in the existence and extinction of colonies along a latitudinal gradient in response to climate are "normal" by geological standards

(Emslie *et al.* 2014). Indeed, this process appears to be occurring currently. Although colonies along the Antarctic Peninsula are in decline, those farther south in the Ross Sea have been increasing since the 1950s (Croxall *et al.* 2002). Moreover, the species' dispersal rates increase under stressful environmental conditions (Dugger *et al.* 2010). Thus, intraspecific variation, dispersal, and source–sink dynamics appear to be critical processes for the persistence of species exhibiting strong site fidelity.

Finally, behavioral or physiological compensation may also allow species with strong site fidelity to adapt via natural selection. In such cases, adaptive behaviors or physiologies compensate for maladaptive ones long enough to allow maladaptive behaviors to evolve (Sih *et al.* 2011; Basson and Clusella-Trullas 2015). For instance, prey-switching behavior may allow site-faithful organisms to adjust to changing community and ecosystem dynamics (Baduini *et al.* 2006). Similarly, in some organisms, physiological plasticity in metabolic rates and preferred body temperature can facilitate adaptation to changing environmental conditions (Basson and Clusella-Trullas 2015). Such behavioral or physiological flexibility, if heritable, may then become a target of selection (Sih *et al.* 2011). The challenge with both colonization via metapopulation dynamics and compensation, however, is whether such long-term processes can keep pace with HIREC (Kareiva and Wennergren 1995). Anadromous salmonids provide a glimmer of hope, as they have demonstrated an ability to colonize habitats made available by climate change and restored fish passage (Figure 4; Pess *et al.* 2014).

Studying and conserving species with site fidelity

Appreciating the role site fidelity plays in causing ecological traps is increasingly important in a rapidly changing world. Ecological traps are a well-documented phenomenon in the Anthropocene (Robertson *et al.* 2013), and evidence for fidelity-induced traps is growing. Both ecological and fidelity-induced traps have clear repercussions for individuals and populations. With ongoing HIREC, research that reveals the costs and benefits of site fidelity strategies will be crucial for anticipating species' responses to future change and identifying effective mitigation measures. Moreover, individual-level behavioral variation within a species can have important consequences for population persistence, and therefore a better understanding of the degree to which site fidelity varies within populations, as well as the causes and consequences of such variation, is critical (Abrahms *et al.* 2018).

Studying site fidelity requires long-term individual-based monitoring, in which habitat choices and resulting space use can be related to past experiences and fitness, along with concomitant datasets of long-term environmental change. In the absence of long-term species monitoring, the inferences made in Figures 2 and 3 would not have been possible. Long-term satellite imagery has facilitated the monitoring of HIREC and its ecological impacts (Foley *et al.* 2005). Furthermore, long-lived species, which are at greater extinction risk than short-lived species (McKinney 1997), often employ site fidelity due to the benefits of site familiarity (Piper 2011) and the increased social cost of relocating sites (Switzer 1993). Because population declines for long-lived species can unfold relatively slowly and include lag effects (Kuussaari *et al.* 2009), long-term monitoring is essential to detect and assess temporal consistency of maladaptive choices.

Knowledge of the role of site fidelity in species persistence provides opportunities for informing conservation efforts. For example, although woodland caribou (*Rangifer tarandus caribou*) display strong fidelity to calving areas, such behavior has not been fully integrated into forest management plans in eastern Canada (Faille *et al.* 2010). Caribou tend to display strong fidelity even in areas that are impacted by human activities (eg logging, road development), which can result in increased predation by wolves (*Canis lupus*)

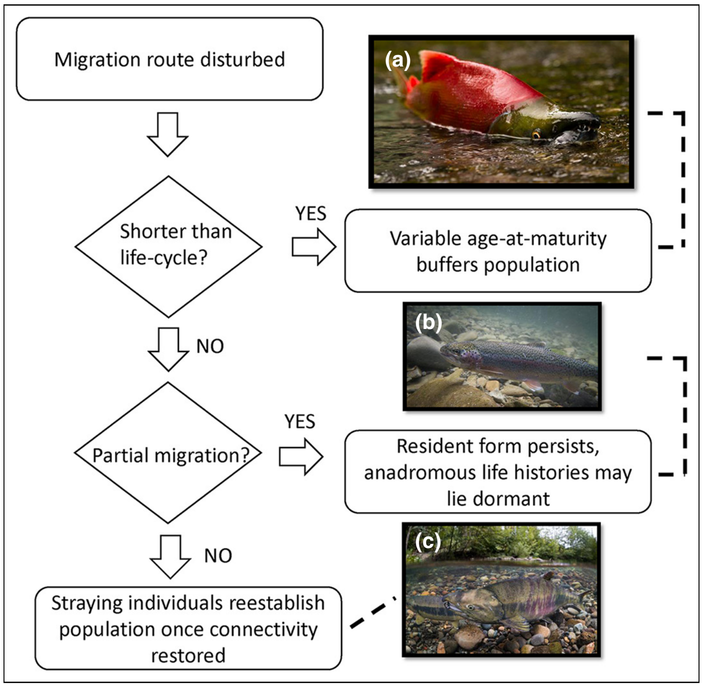

Figure 4. Pathways in which anadromous salmonids with strong fidelity (often migrating >1000 km from marine habitats to breed in their natal streams) can persist if natal streams are disturbed or fragmented. (a) Variation in age-at-maturity creates overlapping generations in species such as sockeye salmon (*Oncorhynchus nerka*), preventing ephemeral disturbances from extirpating populations. (b) In species that exhibit partial migration, such as rainbow trout (*Oncorhynchus mykiss*), resident (ie non-anadromous) life-history forms protect populations from fragmentation lasting longer than a life cycle by allowing individuals to persist upstream of disturbance (Quinn *et al.* 2017). Finally, although most individuals return to their natal stream to spawn, some stray, allowing the species to reclaim lost habitat. (c) Species that lack variation in age-at-maturity or a freshwater resident form, such as chum salmon (*Oncorhynchus keta*), are more prone to extirpation. Chum salmon image credit: J Ching.

through apparent competition with moose (*Alces alces*; Losier *et al*. 2015). Management plans that identify and conserve consistently preferred areas will therefore minimize negative outcomes for site-faithful species. Indeed, where conservation of preferred areas is possible, site fidelity can simplify conservation decisions. In such cases, the clearly defined areas to which animals consistently return provide blueprints for prioritizing sites for protection, habitat restoration, and reintroduction.

Conservation decisions often reflect an implicit assumption that animals choose the best habitat possible and are capable of a high degree of behavioral flexibility (Berger-Tal and Saltz 2016). For instance, off-site mitigation, wherein one site is conserved as mitigation for another site being developed, is increasingly being used in numerous countries to offset the ecological consequences of human development or even achieve net environmental benefits (McKenney and Kiesecker 2010). Yet off-site mitigation may be a futile conservation approach for organisms with strong site fidelity because they lack the short-term behavioral plasticity to "discover" the off-site mitigation areas; for instance, the endangered Gunnison sage-grouse (*Centrocercus minimus*) displays strong site fidelity to lekking grounds, and colonization of unoccupied habitat is rare (Gerber *et al*. 2019). Animals with strong site fidelity may therefore lack the behavioral mechanisms to escape from ecological traps even after experiencing poor outcomes. In such cases, management strategies that promote behavioral flexibility and learning at the individual or population level could be essential (Schlaepfer *et al*. 2005; Greggor *et al*. 2014). For example, translocation of individuals from populations known to be more behaviorally flexible could diversify populations with predominately fixed behaviors (Schlaepfer *et al*. 2005; Sih *et al*. 2011). In addition, where possible, habitat restoration may be a promising investment for conserving taxa with strong site fidelity.

Finally, when very few populations of a given species remain, the potential for metapopulation dynamics to "rescue" or recolonize populations with strong site fidelity may be needed, such as the case for the Adélie penguin colonies outlined above. Notably, when conserving based on a metapopulation dynamics strategy, the conservation of suitable habitat is necessary even if currently unoccupied (Matthiopoulos *et al*. 2005). Such areas can serve as habitat for dispersal of existing populations and for initiation of new populations. For many species, however, HIREC may have already reduced the availability of unoccupied habitat to such an extent that the rate of random subpopulation extinction may exceed the rate of colonization of new places (Kareiva and Wennergren 1995).

Conclusions

Many species rely on the behavioral strategy of returning to previously visited sites to persist. From salmonids traveling hundreds of kilometers to spawn in natal waters to ungulates and marine megafauna tracking their same migration routes hundreds or thousands of kilometers year after year, site fidelity has played a critical role in the evolution and maintenance of global biodiversity (Bauer and Hoye 2014). Site-faithful organisms, however, are having difficulty adapting to HIREC, and are experiencing fidelity-induced ecological traps. Moreover, off-site mitigation efforts (eg habitat banking, conservation easements) to minimize impacts to species that overlap with HIREC-related development (eg residential, agricultural, or energy-related development) are largely ineffective for organisms with strong site fidelity. We urge researchers and conservation practitioners to initiate comprehensive programs to identify and understand fidelity-induced ecological traps, and prioritize the conservation of areas and habitats to which individual organisms tend to return to throughout their lives.

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