

The ecological causes and consequences of hard and soft selection

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Abstract

Interactions between natural selection and population dynamics are central to both evolutionary-ecology and biological responses to anthropogenic change. Natural selection is often thought to incur a demographic cost that, at least temporarily, reduces population growth. However, hard and soft selection clarify that the influence of natural selection on population dynamics depends on ecological context. Under hard selection, an individual's fitness is independent of the population's phenotypic composition, and substantial population declines can occur when phenotypes are mismatched with the environment. In contrast, under soft selection, an individual's fitness is influenced by its phenotype relative to other interacting conspecifics. Soft selection generally influences which, but not how many, individuals survive and reproduce, resulting in little effect on population growth. Despite these important differences, the distinction between hard and soft selection is rarely considered in ecology. Here, we review and synthesize literature on hard and soft selection, explore their ecological causes and implications and highlight their conservation relevance to climate change, inbreeding depression, outbreeding depression and harvest. Overall, these concepts emphasise that natural selection and evolution may often have negligible or counterintuitive effects on population growth—underappreciated outcomes that have major implications in a rapidly changing world.

KEYWORDS

eco-evolutionary dynamics, evolutionary rescue, global change, hard selection, inbreeding depression, natural selection, outbreeding depression, population dynamics, sexual selection, soft selection

Hard selection is both density- and frequency-independent. For that reason, it is the mathematical geneticist's dream; for the same reason, it is the ecologist's nightmare.

Bruce Wallace, 1975

Don't compare me to the Almighty. Compare me to the alternative.

Political proverb

INTRODUCTION

The realisation that evolution can occur on the same time scale as ecology has fuelled renewed interest in clarifying the links between natural selection and population dynamics (Carroll et al., 2007; Hendry, 2017). This endeavor is especially critical as rapid anthropogenic change threatens populations globally (Kinnison & Hairston, 2007; Stockwell et al., 2003; Trisos et al., 2020). Natural selection is often thought to incur a demographic cost (*sensu* Haldane, 1957) through either increased mortality

or reduced fertility, which places an upper limit on the sustainable rates of adaptive evolution that a population can endure without going extinct (Bürger & Lynch, 1995; Gomulkiewicz & Holt, 1995; Orr & Unckless, 2008). Indeed, this may often be the case for traits undergoing hard selection, where an individual's fitness (here referring to absolute fitness unless otherwise stated; Box 1) is dependent on the match between its *absolute* trait value and the environment and is independent of the phenotypic composition of the population (Wallace, 1975; Box 1). For instance, individuals with lower thermal tolerance limits are more likely to perish as temperatures rise, independent of the thermal tolerances of others in the population. Rising temperatures can cause substantial population declines when many individuals are poorly matched to the thermal environment, and population persistence then depends on whether adaptive evolution can sufficiently reduce thermal mismatch (Killeen et al., 2017). The expectation of population declines and recoveries during adaptation to novel stressors implicitly assumes hard selection (e.g. Bell, 2017; Carlson et al., 2014).

In 1968, several researchers emphasised that natural selection might have little influence on population growth when, in contrast to hard selection, the fitness

of an individual with a given phenotype is *dependent* on the phenotypic composition of the population (Maynard Smith, 1968; Sved, 1968; Wallace, 1968), termed soft selection (Wallace, 1968). To understand soft selection, it is helpful to picture an environment that contains a limited number of ecological 'vacancies' (*sensu* Reznick, 2016) that are critical for survival or reproduction (e.g. territories, mates, survivors of a given predation rate). Relative trait values determine which individuals fill those ecological vacancies. For example, if early arriving migratory birds are more likely to secure an essential breeding territory (i.e. the ecological vacancy), whether an individual's arrival time is sufficiently early to acquire a territory depends on the arrival times of other individuals in the population (Johansson & Jonzén, 2012; Kokko, 1999). In this scenario, the ratio of breeding territories to individuals competing for those territories determines the mean reproductive success of the population, and selection for early arrival time determines which, but not how many, individuals gain a territory (Day & Kokko, 2015). In other words, in the context of soft selection, one individual's loss in failing to acquire an ecological vacancy is often another's gain (i.e. a zero-sum game). The key idea with soft selection is that an individual only needs to be more aggressive, sexier, different, less palatable, faster, etc. than its neighbours to give it an advantage in acquiring food, territories, mates or pollinators, or avoiding harm from herbivores, parasites or predators. Assuming equal selection strength, soft selection should generally have much lower influences on population dynamics than hard selection.

Consideration of hard and soft selection can alter predicted responses to anthropogenic change (e.g. Day & Kokko, 2015). Importantly, these concepts highlight that natural selection and adaptive evolution can proceed with less influence on population growth than may often be expected. However, interactions between hard and soft selection can either increase or decrease extinction risk (Svensson & Connallon, 2019), suggesting that their combined influence on population dynamics can be complex.

Despite significant differences in how hard and soft selection influence, and are influenced by, population dynamics, these concepts have received infrequent attention in the evolutionary and ecological literature. Although many researchers assume selection is hard, soft selection might be the more common form of natural selection (Reznick, 2016; Wallace, 1991). Here, we review the theoretical and empirical literature on hard and soft selection. Although recent work has examined the evolutionary implications of hard and soft selection in meta-populations (e.g. Gallet et al., 2018), we focus on the local population scale and examine how hard and soft selection influence population dynamics. Further, we place these concepts in the broader context of eco-evolutionary dynamics and illustrate their relevance to a range of applied questions involving population responses to anthropogenic stressors.

Box 1 Glossary

Soft selection—A type of natural selection that occurs when the absolute fitness of an individual depends on its trait value relative to that of other conspecifics with which it interacts (i.e. the phenotypic composition of the population).

Hard selection—A type of natural selection that occurs when the absolute fitness of an individual depends on its absolute trait value and is independent of the phenotypic composition of the population.

Population growth—The change in a population's abundance over a given (e.g. annual) time step (N_{t+1}/N_t).

Absolute fitness—An unscaled measure of lifetime individual fitness. Population growth is proportional to the mean absolute fitness of individuals in the population. In this study, fitness refers to absolute fitness unless stated otherwise.

Relative fitness—A scaled measure of individual fitness, where individual fitness is expressed as a proportion of the mean fitness in the population (typical in quantitative genetics) or as a deviation from the maximum fitness (standard in population genetics).

Inbreeding depression—Reduced fitness of offspring with related parents compared to those with unrelated parents.

THE ORIGINS AND DEFINITIONS OF HARD AND SOFT SELECTION

Bruce Wallace introduced the concepts of hard and soft selection to explain why populations can persist despite apparent maladaptation (Wallace, 1968). At that time, population geneticists typically assumed that there was one optimal genotype for a given environment and the presence of any genetic variation should reduce mean fitness (i.e. hard selection). This prediction was at odds with the surprisingly high amounts of genetic variation documented in contemporaneous empirical studies (Harris, 1966; Hubby & Lewontin, 1966). Wallace suggested that soft selection could explain this apparent paradox. If an individual was 'judged' relative to the other conspecifics with which it interacted instead of against a theoretical, ideal organism, high amounts of genetic variation could be withstood with minimal influence on population growth.

To help explain soft selection, Wallace presented a set of equations along with a hypothetical example of N bears competing for K caves in which to hibernate (i.e. ecological vacancies; Wallace, 1991). Individuals must secure a cave to survive. Bears are either aggressive or submissive, and aggressive bears always outcompete submissive bears for caves. A single locus determines the behavioural phenotype, and aggressive behaviour is completely dominant (AA and Aa). The frequencies of submissive and aggressive bears prior to selection are, thus, q^2 and $1 - q^2$ respectively. The strength of selection (s) is one minus the relative fitness of submissive bears. Wallace separated the influence of these competitive interactions on selection into three cases. First, selection does not act when there are fewer bears than caves because every bear can secure a cave independent of its behavioural phenotype (Case 1; Figure 1a,b). Second, all submissive bears will die when there are enough aggressive bears to secure every cave (Case 2). Finally, the strength of selection depends on the proportion of submissive bears that acquire caves when the number of caves is limited but there are too few aggressive bears to fill every cave (Case 3).

Case 1: $s = 0$ for $K \geq N$.

Case 2: $s = 1$ for $K \leq (1 - q^2) N$.

Case 3: $s = 1 - \frac{K - (1 - q^2)N}{q^2 N}$ for $(1 - q^2) N < K < N$.

An outcome of Wallace's soft selection equations is that the strength of selection increases with greater reproductive excess (i.e. $N > K$) and with higher frequency of the advantageous phenotype. As a result, Wallace defined soft selection as being density and frequency dependent (Wallace, 1975). To better understand how this contrasts with hard selection, consider a population of snowshoe hares (*Lepus americanus*) in which predation risk depends on an individual's colour match to the snowless background (e.g. Zimova et al., 2016). Assume

that hares with brown coats are resistant to predation on snowless backgrounds (matched), while hares with white coats have a 50% risk of predation (mismatched). In this example, the relative fitness of the mismatched hares is constant (0.5), and is not influenced by reproductive excess or coat colour frequencies (Figure 1c,d). For this reason, Wallace defined hard selection as being density and frequency independent (Wallace, 1975). Note that these simple depictions of hard and soft selection also highlight differences in their influences on population dynamics (Figure 1).

Importantly, the type of frequency dependence Wallace referred to simply arises from the fact that phenotypes are judged against the phenotypes of others in the population and is more general than negative frequency-dependent selection (e.g. Gigord et al., 2001). The behavioural phenotypes of Wallace's bears are under directional selection because the aggressive bears are always at a competitive advantage, and negative frequency dependence never enters this example. The manner in which Wallace used frequency dependence appears to be a source of confusion surrounding hard and soft selection (Gromko, 1976) and partly responsible for a proliferation of uses of these terms that, although providing critical insights for evolution, deviate from Wallace's initial concept to varying degrees (Box 2). In addition, soft selection is not density dependent *per se*, but is rather dependent on the ratio of density to ecological vacancies.

To further clarify the topic while remaining consistent with Wallace's original concepts, we define soft selection as natural selection that occurs when the absolute fitness of an individual depends on its phenotype relative to that of other conspecifics with which it interacts. In contrast, hard selection is natural selection that occurs when an individual's absolute fitness depends only on its *absolute* trait value and is independent of the population's phenotypic composition. For both hard and soft selection, individual *relative* fitness always depends on the phenotypes of others in a statistical sense because it is a scaled measure (Box 1). The key distinction is that with soft selection there is a causal dependence of individual fitness on the phenotypes of others, whereas with hard selection there is no such causal dependence.

Soft selection can be readily generalised from Wallace's heuristic example of bears competing for caves to more complex scenarios. First, Wallace's model assumed truncation selection, but this is not necessary (Charlesworth, 2013). Second, Wallace presented soft selection as directional, but soft selection can involve any mode of selection, including balancing and diversifying (e.g. Svanbäck & Bolnick, 2007). Third, soft selection is equally valid for continuous and discrete traits and applies to quantitative and population genetic frameworks. For example, from a quantitative genetic perspective, soft selection occurs when genes expressed in one individual (e.g. predisposition to be aggressive) alter another conspecific's

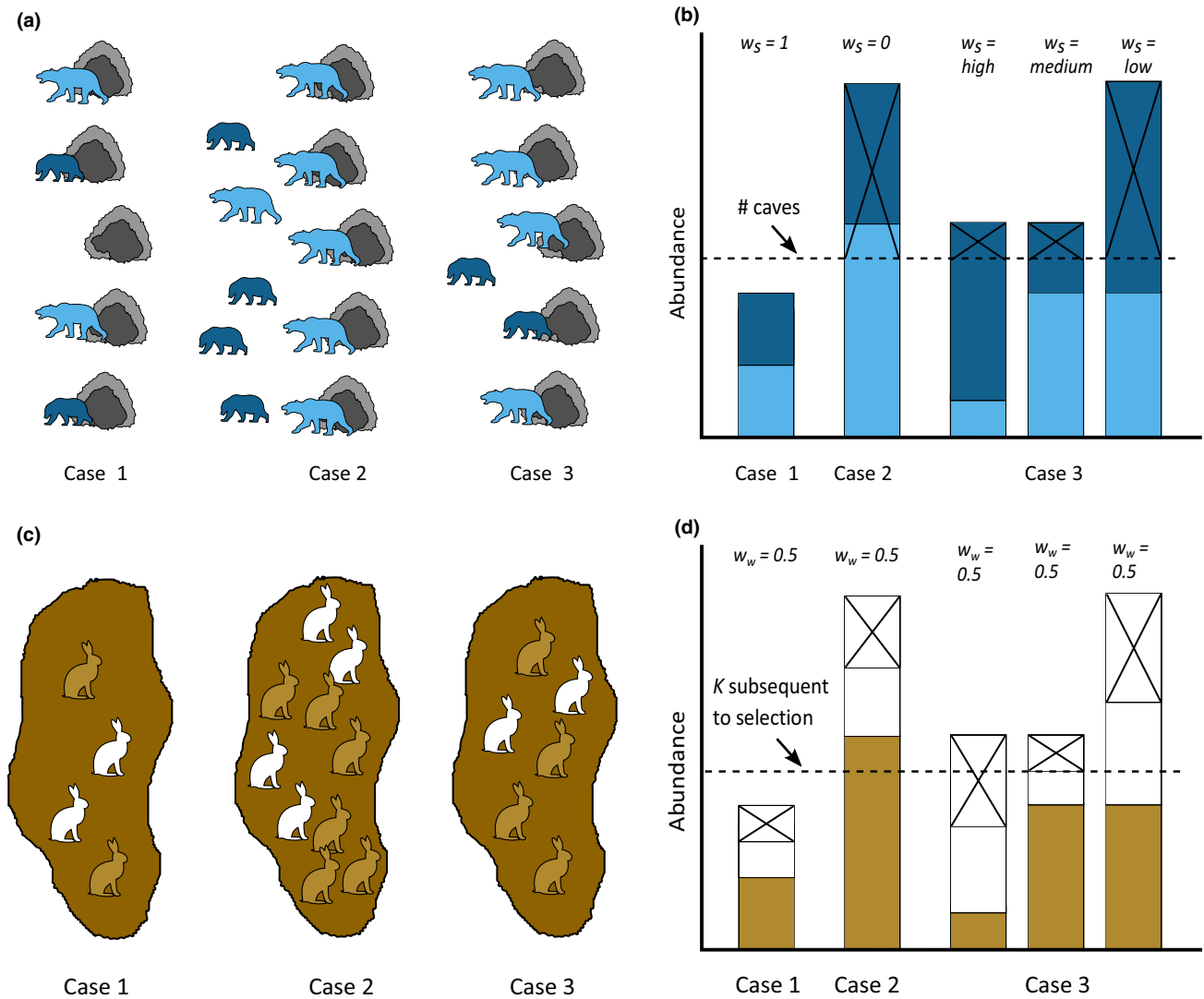


FIGURE 1 Depictions of soft selection occurring in bears competing for caves (a & b) and of hard selection for hares vulnerable to predation (c & d). In the soft selection example (a & b), aggressive bears (light blue) always outcompete submissive bears (dark blue) for a limited number of caves in which to hibernate. In case 1, all bears survive because there are fewer bears than caves and, hence, no selection. In case 2, aggressive bears obtain all caves, and submissive bears are eliminated from the population. In case 3, there are more bears than caves, but not enough aggressive bears to secure every cave, and the strength of selection is dependent on the phenotypic composition and density of the population. In the hard selection example (c & d), white (mismatched) hares have a 50% chance of surviving predation, while brown (matched) hares are resistant to predation. The relative fitness of white hares remains 0.5 irrespective of the phenotypic composition and reproductive excess of the population (d). Selective mortalities are indicated by x's. w_s and w_w are the relative fitness of submissive bears and white hares respectively. The dashed line is the number of caves (b) or the carrying capacity (K) that is due to density regulation that occurs subsequent to selection (d). Cases 1–3 align with the soft selection equations shown in the main text. Note that in the hard selection example, K has no influence on selection, and is included so the ratio of N/K is consistent with the soft selection scenarios. Also note that soft selection does not influence the final population size, while hard selection reduces the final population size when selective mortalities exceed the reproductive excess ($N-K$)

fitness (i.e. indirect genetic effects; Fisher & McAdam, 2019). A range of models touch on the various genetic and evolutionary possibilities outlined above, but often without explicit mention of soft selection (Anderson & Arnold, 1983; Bürger & Gimelfarb, 2004; Clarke, 1973; Engen et al., 2020; Maynard Smith, 1968; Smouse, 1976; Sved, 1968; Svensson & Connallon, 2019). Hard and soft selection can also be generalised to much more diverse ecological scenarios.

THE ECOLOGICAL CAUSES OF HARD AND SOFT SELECTION

Although Wallace focused on intraspecific competition for abiotic resources, soft selection can involve a range of interspecific biotic interactions (Chao et al., 2000; Start, 2020). Returning to the example of coat colouration in snowshoe hares (Figure 1), we previously assumed that predators could not find well-matched hares (e.g. brown

Box 2 Competing definitions of soft selection

Christiansen (1975) applied Wallace's hard and soft selection to two competing models of spatial heterogeneity in selection across discrete habitats (Dempster, 1955; Levene, 1953). Although much of the current use of soft and hard selection is in reference to these models, Levene's model is not soft selection under Wallace's initial intent. In Levene's model, individuals first disperse into two or more habitats, and selection occurs within each habitat. Within-habitat selection depends only on the match between phenotype and the habitat (i.e. hard selection). Next, local density regulation occurs within each habitat type, which results in a consistent contribution of each habitat to the total population size (i.e. hard selection is compensatory). Finally, individuals from all habitats re-pool and mate panmictically. Density and negative frequency-dependent selection emerge in Levene's models at the *global* level, which led to this model being called soft selection. However, relative trait values of individuals never entered this model, which is the critical component of Wallace's soft selection.

A variety of subsequent models (reviewed by Ravigné et al., 2004; also see De Lisle & Svensson, 2017) and some empirical studies (Gallet et al., 2018; Gomulkiewicz & Kirkpatrick, 1992) have invoked soft selection *sensu* Christiansen in the context of evolution in spatially heterogeneous environments or meta-populations (Agrawal, 2010; Ho & Agrawal, 2012; Whitlock, 2002). Their common denominator is the idea that the 'softness' of selection is determined by the extent to which an individual's fitness depends on its phenotype relative to a local average (soft selection) or a global average (hard selection). However, soft selection can also occur globally. For example, global soft selection would occur if individuals from different demes pool in a shared habitat during a certain life stage and phenotype-dependent competition for ecological vacancies occurs among them. Likewise, hard selection does not require a global optimum. For example, habitat heterogeneity can create local optimum trait values against which organisms are judged (i.e. hard selection). The key for Wallace's soft selection is that, at some place and time, selection occurs based on relative trait values among individuals, and frequency and density dependence can emerge at the scale and time that selection occurs.

Research on hard and soft selection *sensu* Christiansen has provided important insights into evolution, including the maintenance of genetic variation (e.g. Gallet et al., 2018; Vale, 2013), and strict adherence to any particular definition is unnecessary. We suggest that authors specify which version of soft selection they are using and acknowledge that the different soft selection models (Wallace vs. Christiansen) are not synonymous.

hares on brown backgrounds), and hence this was an example of hard selection. Another possibility is that predators preferentially target mismatched hares when they are frequent because the search times involved are minimal, but switch to taking better-matched hares when mismatched hares become less frequent because they have no option but to search for longer. This corresponds to soft selection because the fitness of a mismatched hare now depends on how well matched other hares in the population are.

Using a second heuristic example from Chao et al. (2000), if lions prey on the slowest and most peripheral zebras in a herd, the phenotypic composition of the zebra herd determines which, but not necessarily how many, individuals are captured. This example of zebras avoiding predation mirrors bears competing for caves. The initial zebra population size minus the number of predation events determines the number of ecological vacancies (i.e. survivors of a fixed predation rate), and the relative speed and jockeying behaviour of zebras decide which individuals obtain those ecological vacancies. Generally, soft selection arising from interspecific interactions can be broken into two categories: (1) intraspecific competition for a limited biotic

resource and (2) avoidance of negative biotic interactions. For any species that benefits in an interspecific biotic interaction (e.g. predators, herbivores, parasites and mutualists), soft selection can occur due to intra-specific competition for access to, or consumption of, the interacting species (e.g. prey, plants, hosts and the other mutualist respectively). On the other hand, for the species experiencing the negative interaction (e.g. prey, plants and hosts), soft selection is based on the relative ability to avoid harmful interactions.

Interspecific competition adds another layer of complexity to soft selection. When individuals compete for resources with both conspecifics and heterospecifics, an individual's fitness may be determined by their phenotype relative to members of the entire *guild* rather than just their population (a related concept is that guilds and ecosystems involve zero-sum games for energy, see Ernest et al., 2009; Van Valen, 1973). In these cases, the process of phenotypic selection influences not only the evolution of each species (e.g. character displacement; Grant & Grant, 2006) but also their abundances (e.g. competitive exclusion; Violle et al., 2011). To avoid adding more complexity, we do not consider interspecific competition further in this manuscript.

Hard selection can also involve both abiotic factors and biotic interactions, and whether a given selective agent (i.e. factor that causes selection) results in hard or soft selection depends on if the absolute or relative trait value in the focal species determines success in the interaction. Using an example involving mutualists, insect pollinators often impose selection on various aspects of flower morphology (Benitez-Vieyra et al., 2006; Galen, 1989), including flower size (Parachnowitsch & Kessler, 2010). If the pollinators only visit a flower that is above a certain size, irrespective of the sizes of the other flowers in the population, they impose hard selection. If, on the other hand, pollinators will still visit flowers regardless of the range of flower sizes in the population but are more likely to visit the relatively larger flowers, they impose soft selection. Generally, hard and soft selection should not be distinguished based on the agent of selection (e.g.

pollinators selecting flowers) but rather on the importance of relative vs. absolute trait values in determining fitness of the focal species (Box 3).

Soft selection is often equated with intraspecific competition (e.g. Charlesworth, 2013), but intraspecific competition can also lead to hard selection. For example, under intraspecific competition for resources due to high density, traits influencing resource use efficiency (e.g. metabolic rates and digestive efficiency) are likely under hard selection because survival is independent of the resource use efficiency of conspecifics (Agrawal, 2010). In contrast, traits influencing resource acquisition ability should be under soft selection because an individual need only be better at acquiring resources than its neighbours to survive under high intraspecific competition (Agrawal, 2010). In other words, both hard and soft selection can involve intraspecific competition and be density dependent.

Box 3 Measuring hard and soft selection

Experiments that manipulate phenotypic composition are required to fully disentangle hard and soft selection and measure their relative strengths. For example, experiments can compare monocultures (uniform social environments) and mixed cultures (heterogeneous social environments) of the phenotype of interest under the same environmental conditions. A relationship between absolute fitness and phenotypes among monocultures provides evidence for hard selection, and a change in that relationship within mixed cultures provides evidence for soft selection (e.g. Weis et al., 2015). For traits that are more continuously distributed, manipulating the mean or variance of the trait, while holding all else constant, should change the absolute fitness of individuals with a given trait value under soft selection (because relative trait values then change), but not under hard selection (Lande, 1976; Svensson & Connallon, 2019). Additional experimental treatments can further disentangle the dynamics of hard and soft selection. For example, when examining soft selection due to intraspecific competition, researchers will typically also want to add density treatments (while resource amounts stay constant), as the strength of soft selection should increase with density in this case. Other treatments of interest include altering the abiotic environmental conditions and the ratio of focal to interactor species for studies examining soft selection due to avoidance of negative interactions.

Deciphering between hard and soft selection in wild populations presents a more significant challenge. Showing that a measure of absolute fitness depends both on an individual's phenotype and the population's phenotypic composition (i.e. mean and variance for continuous traits) provides evidence that soft selection is occurring. This will require measuring a phenotype over multiple selective episodes, either over space, time or both. However, studies must also account for temporal and spatial variation in agents driving selection before inferring to what extent hard and soft selection occurred.

Studies should also aim to examine the demographic costs and evolutionary responses to hard and soft selection. In both observational and experimental studies, the demographic costs of hard and soft selection can be estimated by examining associations between mean absolute fitness (or population growth) and the strength of selection. In addition, evolutionary changes (i.e. temporal trends in breeding values) in the focal trait, and in theory also fitness itself, can be estimated when phenotypic information on traits and fitness are combined with direct or indirect (e.g. pedigree-derived) genetic information (Fisher & McAdam, 2019; Hadfield et al., 2010; Hendry et al., 2018; Kruuk et al., 2008). Modelling approaches that combine selection, inheritance and demography allow for detailed exploration of population responses to environmental change (e.g. Coulson et al., 2017) and will be critical for improving our understanding of the complexities of hard and soft selection.

Further mathematical development is needed to distinguish between hard and soft selection. Models for determining the relative strength of hard and soft selection have been derived for related, but distinctive, versions of the concept (Ho & Agrawal, 2012; Laffafian et al., 2010; Weis et al., 2015). These models can provide results consistent with Wallace's conception of hard and soft selection under some conditions, and might also serve as helpful starting points to derive additional equations.

In addition, soft selection is not density dependent *per se* but instead depends on the ratio of density to ecological vacancies (i.e. reproductive excess). If the number of bears stays the same but a landslide buries half of the caves, the strength of soft selection will increase because the ratio of bears to caves increased (i.e. reproductive excess was greater). Likewise, if the number of zebras remains the same but the number of predation events increases, the strength of soft selection will be greater because the ratio of initial zebras to survivors of predation increased. More generally, the strength of soft selection depends on the per capita amount of resources when intraspecific competition is involved (Agrawal, 2010; Ho & Agrawal, 2012) and the per capita rate of negative interspecific interactions when avoidance of harmful interactions is involved. This suggests that soft selection will be more temporally dynamic than Wallace's example of bears in caves: in addition to variation in density, resource availability can also fluctuate, and when biotic interactions are involved, the density of both species can vary, and both species can evolve (Reznick, 2016; Yoshida et al., 2003).

In addition to being determined by the same ecological factors, hard and soft selection might also operate on the same traits (Weis et al., 2015; Start, 2020; i.e. slushy selection; Clutton-Brock & Pemberton, 2004). In these cases, the hard and soft components of selection might act in opposing or concordant directions. In an experimental test of hard vs. soft selection using *Brassica rapa*, Weis et al. (2015) measured fitness in monocultures and bicultures of early- and late-emerging plants. Comparisons of fitness between monocultures of early and late emergence phenotypes revealed that early-emerging plants had higher fitness (i.e. hard selection), likely due to favourable weather conditions. Likewise, comparisons of fitness between early and late emergence phenotypes within mixed cultures showed that the competitive environment gave early-emerging plants an even greater advantage due to having a head start on growth (i.e. soft selection). Some researchers have suggested that hard and soft selection may often act on the same traits and are better viewed as a continuum rather than discrete categories (Ho & Agrawal, 2012; Start, 2020).

Furthermore, thresholds may be common where selection on a trait transitions from being primarily soft to predominantly hard as the mean phenotype increasingly deviates from an environmental optimum. For example, at warm but not extreme temperatures, individuals that cope better physiologically might be more competitive or better at avoiding negative biotic interactions than individuals with relatively poorer thermal performance (i.e. selection is predominantly soft). However, at extreme temperatures, individuals with lower thermal tolerance limits will be more likely to die for purely physiological reasons (Lutterschmidt & Hutchison, 1997; i.e. selection becomes harder). Similarly, when the mean level of inbreeding in a population is low, individuals that are

relatively more inbred than others might suffer from reduced competitive ability or lower relative ability to escape from predators, for example, but when the mean level of inbreeding is high, survival might plummet regardless of the competitive or predatory environment (Frankham, 1995; e.g. Robinson et al., 2019).

THE DEMOGRAPHIC COSTS OF HARD VS. SOFT SELECTION

Hard and soft selection provide a useful lens to understand how natural selection influences population dynamics. In this section, we discuss the effect of phenotypic selection on vital rates and population growth within the generation that selection occurs. In the next section, we examine the demographic influences of evolutionary responses to selection. It is important to distinguish between *immediate* reductions in mean stage-specific vital rates due to phenotypic selection vs. *net* effects on mean fitness and population growth. Hard selection is always associated with reduced survival or reproductive success during the life stage at which it occurs (compared to a population that is well adapted to those environmental conditions). In contrast, soft selection may have little or no influence on mean vital rates (compared to a population experiencing the same ecological conditions but lacking phenotypic variation). For both types of selection, reductions in stage-specific vital rates may or may not result in a decrease in population growth.

Considering the fitness landscape of a trait undergoing directional selection helps to clarify the immediate influences of hard and soft selection on vital rates. Under hard selection, mean survival (or fecundity) decreases when the mean trait value is further away from an optimum phenotype for the environment (i.e. greater maladaptation; Figure 2a). In contrast, under soft selection, changes in the mean trait value will influence the survival probability of a given trait value but may have little influence on mean survival (Figure 2b; i.e. a zero-sum game).

In an empirical example that mirrors Wallace's illustration of bears competing for caves, Kilgour et al. (2018) compared the survival of aggressive and submissive strains of *Drosophila melanogaster* under different densities and phenotype frequencies. Aggressiveness was under negative frequency-dependent selection, with the strength of selection increasing under high density, competitive conditions (i.e. as the ratio of *Drosophila* to ecological vacancies increased). Survival of aggressive and submissive phenotypes only differed in mixed-phenotype treatments, suggesting selection was soft. Further, mean survival of experimental populations did not differ between uniform and mixed-phenotype treatments or across mixed treatments with different phenotypic frequencies, suggesting that soft selection involved a zero-sum game.

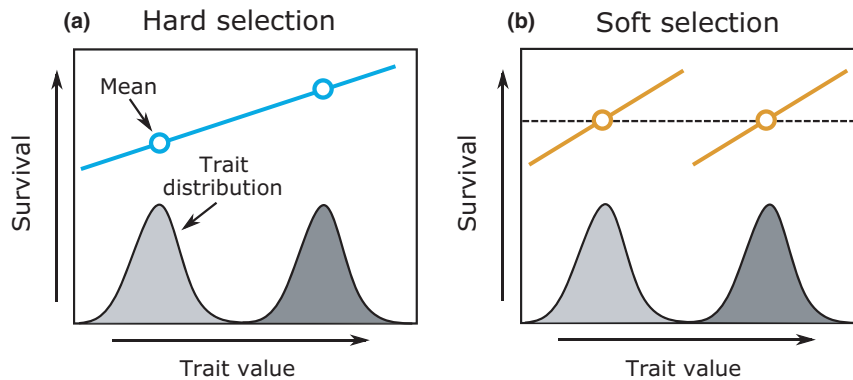


FIGURE 2 The relationship between individual trait values (e.g. thermal tolerance, breeding time, body size, running speed, etc.) and survival probability for hard vs. soft selection assuming positive directional selection. The light and dark trait distributions represent two different populations that are otherwise experiencing the same environmental conditions. Under hard selection (a), the relationship between trait values and survival probability (blue line) does not depend on the phenotypic composition of the population (i.e. trait distribution). The population with the higher mean trait value (dark grey) has higher mean survival (hollow points). Under soft selection (b), an individual's trait value relative to the population mean determines their survival probability (orange lines), and the mean trait value of the population does not influence mean survival (hollow points; dashed line). Note that with compensatory hard selection, a lack of relationship can also result between mean fitness and mean trait value, but in this case, mean fitness is some composite of survival and fertility across multiple life stages

However, soft selection can influence stage-specific vital rates when the phenotypic composition of a population not only influences *which* individuals obtain ecological vacancies but also the *number* of ecological vacancies. For example, territorial defence can influence territory size and, as a result, the number of territories (López-Sepulcre & Kokko, 2005). Further, organisms need to obtain some resources (e.g. food) throughout their lifespan. In these cases, the number of ecological vacancies can be considered the number of individuals the resource-base (e.g. food-base) can support. Strong asymmetries in acquisition ability can create big winners that hoard a disproportionate share of the resources (Weiner, 1985; Weiner & Freckleton, 2010; Yun & Agrawal, 2014), reducing the total number of ecological vacancies. Hence, soft selection will reduce vital rates. However, when resources are extremely limited, such that equal resource distribution among individuals would result in many or theoretically all individuals dying (Miller, 1967; Nicholson, 1957), competitive asymmetries may allow some individuals to hoard enough resources to survive, potentially increasing the mean survival. A similar process could also occur during interspecific avoidance. For example, asymmetries in palatability could create big losers that receive an unequal share of herbivore grazing, potentially increasing or decreasing mean survival. Overall, while hard selection will always reduce stage-specific survival or fecundity, soft selection may increase, decrease or have no effect on stage-specific vital rates. These caveats to zero-sum games under soft selection do not change the general expectation that soft selection is less likely to depress vital rates than hard selection.

An experiment on emergence timing in *Brassica rapa* demonstrated that soft selection can reduce survival (Weis et al., 2015). Mortality was higher in mixed

cultures of early- and late-emerging plants than in monocultures. This is likely because early-emerging plants gained a substantial competitive advantage for access to light, inhibiting late-emerging plants from growing. However, despite differences in early-life survival, the total reproductive output was similar in monocultures and bicultures (Weis et al., 2015). This finding suggests that increased mortality due to soft selection was compensated for by increased reproductive output of the survivors, consistent with the law of constant yield in the plant literature (Weiner & Freckleton, 2010). This experiment highlights that even when selection does reduce a vital rate, population growth can remain unaffected.

A reduction in stage-specific vital rates due to selection may not translate into decreased population growth for several reasons. First, selection may not be strong enough to influence population growth appreciably. Second, the vital rate that selection affects may have a limited influence on population growth (Mills, 2013). For example, inbreeding in bighorn sheep (*Ovis canadensis*) reduced adult female fecundity, but matrix projections suggested that this had little effect on population growth (Johnson et al., 2011). Third, as discussed in the example of *Brassica rapa*, selective mortality or reduced fertility is often partially or entirely compensated for by increased fitness in a later life stage, which we refer to as compensatory selection.

To further explain compensatory selection, assume a simple ceiling model of density dependence where K individuals survive to adulthood due to a fixed number of territories. Reproductive excess occurs because more juveniles are born each year than there are territories ($N_{\text{juveniles}} > K$). Hard selection acting on a juvenile phenotype reduces their numbers to $N_{\text{survivors}}$. If $N_{\text{survivors}} > K$, selection has only eaten into the reproductive excess, and population growth is unaffected. In other words, selection

is fully compensatory. On the other hand, if $N_{\text{survivors}} < K$, selective mortalities are additive, and a population decline will occur (Figure 1d). Selection can also be compensatory under more complex models of density dependence (Ratikainen et al., 2008; Reed et al., 2015), and, in some cases, compensation could even increase population growth (e.g. Abrams, 2009; McIntire & Juliano, 2018).

A study on great tits (*Parus major*) provided empirical evidence for compensatory hard selection. Directional selection for earlier egg-laying in great tits is more intense in warmer springs when phenological mismatch with caterpillar prey is substantial (Husby et al., 2009). This is likely due, in a large part, to hard selection because the fledglings of mothers that miss resource peaks will starve regardless of the hatching timing of other families. Selective mortality of fledglings in mistimed nests reduced local competition and increased post-fledging survival, resulting in no effect on population growth even though the mean number of fledglings was lower (Reed et al., 2013a, 2013b). Compensatory selection also likely occurred in a population of pink salmon (*Oncorhynchus gorbuscha*) that has undergone a rapid evolutionary change in adult migration timing (Kovach et al., 2012, 2013b). The near elimination of late

migratory phenotypes aligned with the second highest stream temperatures on record (Kovach et al., 2012), suggesting hard selection due to thermal mismatch. However, shifts in migration timing did not influence population growth (Kovach et al., 2013a), possibly because density-dependent reproductive success compensated for reduced adult survival (Fukushima et al., 1998).

Hard and soft selection can also interact to influence population growth (Svensson & Connallon, 2019). Soft selection can either increase or decrease the demographic cost of subsequent or concurrent hard selection on the same, or a correlated, trait. Using body size as an example, soft selection can favour larger individuals that have a competitive advantage for resources (e.g. territories; Johnsson et al., 1999), and subsequent hard selection may favour larger body size in colder conditions and smaller body size in warmer conditions for physiological reasons (Gardner et al., 2011; Sheridan & Bickford, 2011; but see Siepielski et al., 2019). If hard and soft selection act on body size in the same direction, soft selection helps to improve the match between the mean body size and the optimal body size, reducing the strength of hard selection and thus its influence on vital rates and population growth (Figure 3a). Instead, soft selection may

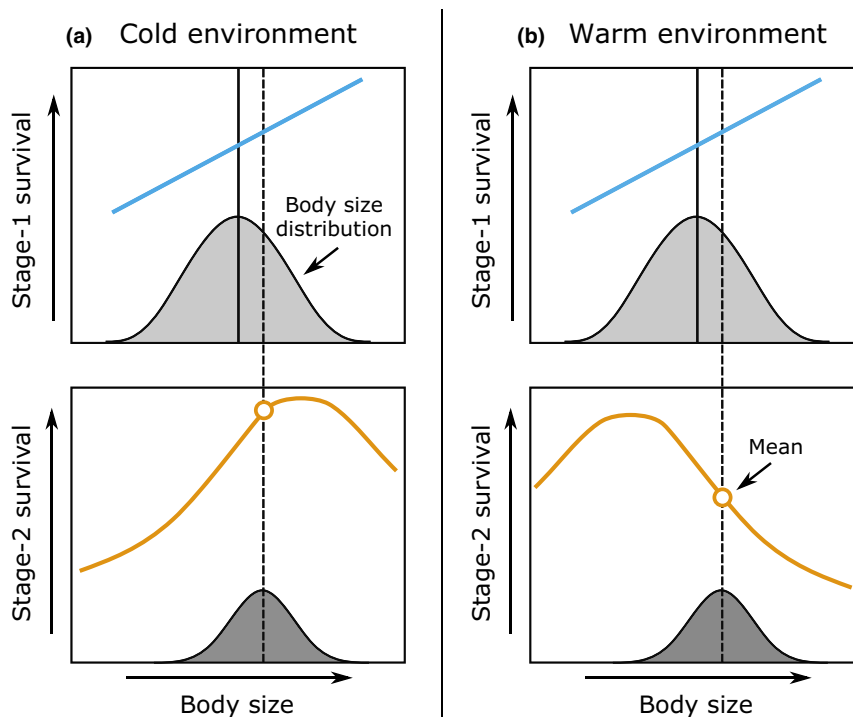


FIGURE 3 A hypothetical example of soft selection followed by hard selection at a later life stage on body size in two populations inhabiting cold (a) vs. warm (b) environments. At life stage 1, larger individuals outcompete smaller individuals for a limiting resource and thus have higher survival (blue lines; upper panels). The solid and dashed vertical lines represent the mean body size before and after soft selection respectively. The survivors of stage 1 are larger on average at the start of stage 2 due to soft selection. The strength of hard selection during life stage 2 depends on how close the mean phenotype (post-soft selection) is to an environmental optimum (orange curves; lower panels). During stage 2, the optimal body size is larger in the colder environment and smaller in the warmer environment for thermoregulatory reasons. In the cold environment (a), soft selection during stage 1 decreases the strength of hard selection on stage 2, and mean stage 2 survival is high (hollow point). In contrast, in the warm environment (b), soft selection increases the strength of subsequent hard selection, and mean stage 2 survival is low (hollow point). The light grey and dark grey distributions represent the trait distributions prior to soft selection and hard selection respectively

oppose subsequent hard selection on body size, which would lead to a greater decline in survival or reproduction (Figure 3b).

THE DEMOGRAPHIC IMPLICATIONS OF EVOLUTION UNDER HARD AND SOFT SELECTION

Although we have thus far examined the effect of phenotypic selection on population growth, hard and soft selection can also have unique influences on how evolutionary responses to selection affect population dynamics. Despite reducing population growth in the generation that selection occurs, hard selection is expected to increase mean fitness in subsequent generations (Fisher, 1930). In cases where the environment changes abruptly or gradually across generations, adaptive evolution via hard selection can sometimes avert extinctions (i.e. evolutionary rescue; Bell, 2017; Hufbauer et al., 2015). For example, yeast (*Saccharomyces cerevisiae*) exposed to mostly lethal salinity initially experienced a rapid decline. However, as salt-tolerant phenotypes increased in frequency, population declines were often reversed within several generations (Bell & Gonzalez, 2009). With continuous environmental change, evolutionary trait shifts may lag behind a moving environmental optimum (Bürger & Lynch, 1995; Lynch & Lande, 1993), leading to sustained hard selection. The inability of adaptive evolution to keep pace with environmental change can threaten long-term population viability (Quintero & Wiens, 2013; Radchuk et al., 2019).

However, adaptive evolution can sometimes have negligible effects on population growth or abundance. Soft selection involving a zero-sum game allows for rapid trait evolution over multiple generations with minimal influence on population dynamics (e.g. Fisher & McAdam, 2019), and thus high rates of sustainable evolution (e.g. Maynard Smith, 1968; Sved, 1968). The population size may also remain stable under evolution via hard selection when selective reductions in vital rates are compensatory. This is a type of cryptic eco-evolutionary dynamic (Kinnison et al., 2015), because evolution in response to hard selection is preventing or limiting maladaptation that might otherwise result in a population decline but there is no apparent change in population growth (e.g. Reed et al., 2013b).

In addition to influencing population growth, evolution under hard and soft selection may affect the number of individuals the environment can support. For example, hard selection can increase carrying capacity through the evolution of greater resource use efficiency (Kinnison & Hairston, 2007). Under soft selection, evolution can sometimes alter the number of ecological vacancies, as demonstrated by research on warning colouration evolution (i.e. aposematism). Predators learn

to avoid the most common aposematic warning signals (Chouteau et al., 2016), and the individual fitness of prey depends on how common its warning phenotype is in the population (i.e. positive frequency-dependent selection; for a review of why warning signals may still be polymorphic, see Briolat et al., 2019). Locations with predominantly one warning pattern experience decreased predation rates (Chouteau et al., 2016; Mallet, 1999), suggesting that as a single warning pattern becomes more frequent in a population, the number of ecological vacancies increases. Another, perhaps common, way in which evolution under soft selection can increase the number of ecological vacancies is through diversifying selection to use a greater range of resources in competitive environments (Bolnick, 2004; Svanbäck & Bolnick, 2007).

Much research on how evolution influences demography has focused on life-history traits. Life-history theory predicts trade-offs between faster intrinsic growth rates and better competitive abilities, and the optimal strategy can vary with density (e.g. r-K selection; Reznick et al., 2002). Although hard and soft selection can both occur at any density, the hard-soft continuum may roughly map to the r-K continuum. Using offspring quantity vs. size as an example, at lower densities, the absolute number of offspring matters more for parental fitness (r or hard selection). However, at high densities, the relative offspring size, which determines resource acquisition ability, matters more to parental fitness (Sæther et al., 2016; K or soft selection). Fluctuations in density can cause variation in the optimal number and size of offspring (Sæther et al., 2016), altering patterns of evolution and population dynamics. For example, oscillations in r-K selection promoted stable population cycles in side-blotched lizards (*Uta stansburiana*; Sinervo et al., 2000).

As hard and soft selection may often act on the same traits (Laffafian et al., 2010), considering how their interactions influence evolution and population dynamics is especially critical. Soft selection can either aid or inhibit the scope for evolutionary responses to hard selection to track the optimum phenotype for the environment (Figure 3; Johansson et al., 2015; Svensson & Connallon, 2019), as demonstrated by research on sexual selection (Kokko & Brooks, 2003). Sexual selection may often be soft because the relative phenotype (e.g. display) of individuals of the non-limiting sex influences who secure mates of the limiting sex (the ecological vacancies; but see Zuk et al., 1990). Sexual selection can act in the opposing direction to selection driven by other factors (Andersson, 1994), thus preventing the population's mean phenotype from reaching a fitness optimum for the environment and reducing population growth. For example, male ornaments that attract females, or armaments that deter other males, might also increase vulnerability to predation (Hernandez-Jimenez & Rios-Cardenas, 2012) and parasitism (Moore & Wilson, 2002). In contrast,

both hard and soft selection should often act in the same direction to reduce the frequency of unconditionally deleterious alleles that contribute to inbreeding depression (i.e. purifying selection). Consistent with this prediction, experimental populations of flour beetle (*Tribolium castaneum*) that evolved with high levels of sexual selection subsequently had lower extinction risk under periods of high inbreeding than populations that evolved with minimal sexual selection (Lumley et al., 2015). The extent to which interactions between hard and soft selection influence evolution and population dynamics likely varies considerably across traits and taxa.

HARD AND SOFT SELECTION IN CONSERVATION CONTEXTS

Climate change

Climate change is expected to become a leading driver of extinction in the near future (Trisos et al., 2020; Urban, 2015), and a major concern is that adaptive responses to climate change will be insufficient (Quintero & Wiens, 2013; Radchuk et al., 2019). However, soft selection and compensatory selection might buffer against population declines driven by poor phenotypic matches with changing climatic conditions. For some climate-influenced traits, soft selection may often work in the same direction as, and thus reduce the demographic influences of, hard selection (Figure 3a), which might be the case for thermal adaptation. Sexually selected traits are often condition dependent (Kotiaho et al., 2001), and individuals better matched to the changing thermal environment should have higher conditions and gain reproductive advantages, thereby improving thermal adaptation (García-Roa et al., 2020). Experiments comparing populations that evolved with weak vs. strong sexual selection demonstrate that soft (sexual) selection can increase persistence probability at high temperatures (Parrett & Knell, 2018; Plesnar-Bielak et al., 2012). However, large temperature increases will drive populations towards extinction regardless of buffering from soft selection (e.g. Parrett & Knell, 2018).

Compensatory selection can also buffer against climate-driven extinction, which could partly explain why evidence for population impacts of climate-induced phenological mismatch has remained elusive despite being predicted by the match–mismatch hypothesis (Cushing, 1969; Visser & Gienapp, 2019). For example, cavity-nesting birds are typically regulated by competition for nest sites and food (Newton, 1998), and climate-driven hard selection acting on phenology expressed before density regulation can have a limited impact on population growth, provided that climate change is not too extreme (Reed et al., 2013a, 2013b). These examples have a common theme: soft selection and compensatory selection may buffer against climate-driven population

declines to a point, but significant changes in climate may nevertheless lead to extinction (Trisos et al., 2020).

Soft selection will not always reduce the risk of climate-induced extinction (Figure 3). Research on phenology also demonstrates that hard and soft selection can act in opposing directions and interact in complex ways (Day & Kokko, 2015; Johansson & Jonzén, 2012; Johansson et al., 2014). For example, soft selection may favour early migration to gain territories that counteracts hard selection to match resource peaks (Kokko, 1999; Svensson & Connallon, 2019). This highlights that soft selection might either increase or decrease vulnerability to climate-driven extinction (Svensson & Connallon, 2019), similar to how phenotypic plasticity can either aid or counter adaptation to climate change (Reed et al., 2011). In a counterintuitive example (Day & Kokko, 2015), mismatched migration timing to advancing resource peaks can increase mortality due to hard selection, thus driving population declines. The population declines, in turn, reduce the strength of soft selection for early arrival to secure better territories because competition is weaker. Therefore, although hard and soft selection are now acting in the same direction, increasing mismatch can potentially cause the total strength of selection (the sum of the hard and soft components) to decrease. This can create a feedback loop that increases extinction risk: soft selection due to intraspecific competition weakens as the population becomes smaller, which reduces adaptation and contributes to further population declines via hard selection. Thus, as populations decline due to environmental mismatch, not only will the efficacy of selection decrease due to the increased influence of genetic drift (Lanfear et al., 2014), but the strength of selection may also decrease. In general, understanding hard selection, soft selection and their interactions is important for anticipating likely impacts of climate change on evolutionary adaptation (Aitken et al., 2008), population performance (Beckerman et al., 2003; Benton et al., 2006), range shift dynamics (Best et al., 2007; Cotto et al., 2017) and altered interspecific interactions (Cahill et al., 2013).

Small populations and the extinction vortex

Small, isolated populations face increased extinction risk due to interactions between demographic effects and inbreeding depression (i.e. extinction vortex; Soulé & Mills, 1998). Note that inbreeding depression is the reduction in fitness of inbred *individuals* (Charlesworth & Willis, 2009; Box 1) and does not require that mean fitness decreases. For example, inbreeding depression due to soft selection can involve a zero-sum game (Wallace, 1975). Evolution in response to soft selection can reduce the frequency of deleterious alleles that would otherwise drive population declines through hard selection (e.g. López-Cortegano et al., 2016; Whitlock & Agrawal, 2009), thus weakening the extinction vortex (Lumley et al., 2015).

Soft selection could help explain why some small, inbred populations manage to persist (e.g. Benazzo et al., 2017; Grossen et al., 2020).

Consideration of soft selection could improve the predicted influences of inbreeding depression in population viability analyses (PVAs). The magnitude of inbreeding depression can have strong influences on predicted extinction probability (O'Grady et al., 2006), and common PVAs frameworks implicitly assume that inbreeding depression is due to hard selection against deleterious alleles (e.g. Lacy, 1993). However, if a portion of inbreeding depression is due to soft selection (e.g. Schmitt & Ehrhardt, 1990; or hard selection is compensatory), PVA frameworks will overestimate the effect of inbreeding depression on extinction risk. Accounting for the influences of soft selection and compensatory selection in PVAs would be highly informative but challenging. In any case, soft selection highlights the importance of accounting for multiple estimates of inbreeding depression in population viability analyses.

A promising conservation strategy to alleviate the detrimental effects of inbreeding in small populations is to translocate individuals to assist gene flow, which can increase population growth and, ultimately, persistence probability (i.e. genetic rescue; Bell et al., 2019; Whiteley et al., 2015). Like evolutionary rescue, the expectation of increased population growth with genetic rescue assumes that hard selection had a considerable contribution to inbreeding depression. There is little doubt that inbreeding can cause population declines (Bozzuto et al., 2019) and genetic rescue can reverse these declines (Johnson et al., 2010; Madsen et al., 1999; Robinson et al., 2017). However, measuring increased fitness in intraspecific hybrids compared to non-admixed residents (a common measure of genetic rescue; Robinson et al., 2020) does not guarantee that population growth increased, just as measuring inbreeding depression does not necessarily indicate a population decline. Overall, consideration of soft selection and compensatory selection can influence theoretical and empirical investigation of inbreeding depression and genetic rescue.

Hybridisation, outbreeding depression and captive breeding

Outbreeding depression (i.e. a decrease in individual fitness owing to the genetic admixture of divergent genomes) from human-induced hybridisation, through either release of captive-bred individuals into the wild and introduction of species into their nonnative range, has been of significant concern for decades (e.g. Allendorf et al., 2001; Rhymer & Simberloff, 1996). Consistent with inbreeding depression, outbreeding depression will not lead to decreased population growth if selection against hybrids is soft, and even when hard, ecologically strong but compensatory selection does not necessitate

a population decline when reproductive excess is high. Conversely, a lack of population decline does not suggest that outbreeding depression is negligible. Indeed, soft selection and compensatory selection offer a clear resolution to population persistence and stability despite human-induced outbreeding depression (e.g. Kovach et al., 2015). Few studies have attempted to directly quantify the effects of outbreeding depression on population dynamics (but see Sylvester et al., 2019; Willoughby & Christie, 2019), and we are not aware of any that have considered soft selection.

Oftentimes, outbreeding depression may be due to both hard and soft selection. This is likely the case for Pacific salmon, where captive-bred (i.e. hatchery-produced) individuals and their hybrids tend to have markedly reduced fitness in the wild due to rapid adaptation to the captive-rearing environment (Araki et al., 2008; Christie et al., 2014). Reduction in fitness is likely cumulative over many traits, but it generally appears to result from reduced marine survival (Jonsson et al., 2003) and reproductive success during spawning (Thériault et al., 2011). The latter is due, at least in part, to soft selection. Experimental studies have demonstrated that, compared to wild-born fish, hatchery-born females are competitively inferior at acquiring and defending breeding sites, and males have a substantially lower ability to obtain mates (Fleming & Gross, 1993; Neff et al., 2015). However, competitive disadvantages of hatchery-born fish were generally weaker at low densities (Fleming & Gross, 1993), and hatchery-born fish readily breed in the absence of wild fish (Fleming & Gross, 1992). Thus, low abundance of wild-born fish can increase the reproductive success of hatchery-born fish, thereby producing offspring with reduced marine survival. Even if reduced mean fitness is only partially due to hard selection (e.g. O'Sullivan et al., 2020), increased production of hybrids could exacerbate population declines, the exact opposite of the desired outcome of captive breeding programs.

Harvest

Strategic harvest of reproductive excess is at the core of sustainable fisheries and wildlife management (e.g. Boyce et al., 1999). While theoretically and empirically justified when viewed solely in the light of population abundance, the harvest of population excesses can decrease the efficacy of soft selection on traits mediating success in intraspecific competition and reduce the buffering capacity afforded by compensatory selection (Young, 2003). Furthermore, harvest often acts as a selective force (Allendorf & Hard, 2009), especially on traits that are subject to strong sexual selection (e.g. body size, horn size). In a population harvested exactly at maximum sustainable yield, and hence kept at population sizes below which there is strong intraspecific competition for a limiting resource

(e.g. breeding territories), the strength of soft selection will likely be reduced and hence these traits might be more vulnerable to the effects of genetic drift. At best, this might create situations where natural selection cannot act to shift populations towards fitness peaks that are desired by humans (e.g. larger body sizes). At worst, harvest could act to increase the phenotypic maladaptation that many populations of conservation concern already face (Waples et al., 2008), which might prove increasingly worrisome as populations are subject to novel or more acute selective pressures under global change. In either scenario, it is clear that consideration of soft selection is fundamental in predicting the ecological and evolutionary implications of harvest.

CONCLUSION

Hard and soft selection are neglected topics of broad relevance for uniting ecology and evolution (Lowe et al., 2017). Hard and soft selection are connected to demography in fundamentally different ways (Reznick, 2016; Wallace, 1975), and their interactions can have a variety of influences on population dynamics (Svensson & Connallon, 2019). Research that has considered hard and soft selection has revealed unexpected influences of natural selection on population growth (e.g. Day & Kokko, 2015; Sinervo et al., 2000). Interactions between hard and soft selection may also be a common contributor to feedbacks between ecology and evolution (Ferriere & Legendre, 2013; Kokko & López-Sepulcre, 2007). For example, hard selection is more likely to influence density, density can alter the strength of soft selection, and soft selection then affects the strength and demographic impact of subsequent hard selection (e.g. Day & Kokko, 2015). As the links between natural selection and population dynamics are central to evolutionary-ecology (Hendry, 2017), consideration of hard and soft selection may also influence theoretical and empirical evaluation of eco-evolutionary dynamics in communities and ecosystems. However, many aspects of hard and soft selection remain poorly understood, and further research on these topics is needed.

As more studies on hard and soft selection accumulate, we can better address a range of questions, such as: Is soft selection generally stronger or weaker than hard selection? How do the influences of hard and soft selection vary across traits, taxa and types of interspecific interactions? How often and under what conditions does soft selection work in the same vs. opposing direction as hard selection? Do hard and soft selection have differing or cascading influences on meta-populations, communities and ecosystems? How often and to what extent does selection influence population growth and extinction risk? How common are thresholds where selection changes from primarily soft to predominantly hard? Is anthropogenic change 'hardening' selection as populations become increasingly maladapted and reach

critical thresholds? Theoretical work has provided critical insight into some of these topics. Empirical research on hard and soft selection presents a more substantial challenge, particularly in wild populations, but empirical studies will be valuable for testing theory and aiding conservation efforts.

Consideration of these topics can alter predicted extinction risks, a core issue in conservation biology. Encouragingly, population viability assessments that ignore soft selection and compensatory processes may be overly dire because natural selection and adaptive evolution can proceed with little influence on population growth. However, soft selection can sometimes increase extinction risk (Svensson & Connallon, 2019), further emphasising the need to incorporate these concepts into population viability analyses. In addition, similar to adaptive phenotypic plasticity (Simmonds et al., 2020), soft selection and compensatory selection may buffer against population declines (Parrett & Knell, 2018; Reed et al., 2013a), but only up to a point in which mismatch to the environment becomes too severe for persistence (Frankham, 1995; Trisos et al., 2020). Unfortunately, humans are reducing the density of many populations, sometimes intentionally (e.g. harvest), which will often decrease buffering from soft selection and compensatory processes and, in turn, increase extinction risk. Overall, hard and soft selection highlight the need to explicitly consider how the ecological context in which natural selection occurs influences contemporary evolution and its demographic consequences in a changing world.

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AUTHORSHIP

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REFERENCES

- Abrams, P.A. (2009) When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. *Ecology Letters*, 12, 462–474.
- Agrawal, A.F. (2010) Ecological determinants of mutation Load and inbreeding depression in subdivided populations. *The American Naturalist*, 176, 111–122.
- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.
- Allendorf, F.W. & Hard, J.J. (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 9987–9994.
- Allendorf, F.W., Leary, R.F., Spruell, P. & Wenburg, J.K. (2001) The problems with hybrids: Setting conservation guidelines. *Trends in Ecology & Evolution*, 16, 613–622.
- Anderson, W.W. & Arnold, J. (1983) Density-regulated selection with genotypic interactions. *The American Naturalist*, 121, 649–655.
- Andersson, M. (1994) *Sexual selection*. Princeton, NJ: Princeton University Press.
- Araki, H., Berejikian, B.A., Ford, M.J. & Blouin, M.S. (2008) Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, 1, 342–355.
- Beckerman, A.P., Benton, T.G., Lapsley, C.T. & Koesters, N. (2003) Talkin' 'bout my generation: Environmental variability and cohort effects. *The American Naturalist*, 162, 754–767.
- Bell, D.A., Robinson, Z.L., Funk, W.C., Fitzpatrick, S.W., Allendorf, F.W., Tallmon, D.A. et al. (2019) The exciting potential and remaining uncertainties of genetic rescue. *Trends in Ecology & Evolution*, 34, 1070–1079.
- Bell, G. (2017) Evolutionary rescue. *Annual Review of Ecology Evolution and Systematics*, 48, 605–627.
- Bell, G. & Gonzalez, A. (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters*, 12, 942–948.
- Benazzo, A., Trucchi, E., Cahill, J.A., Maisano Delser, P., Mona, S., Fumagalli, M. et al. (2017) Survival and divergence in a small group: The extraordinary genomic history of the endangered Apennine brown bear stragglers. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E9589–E9597.
- Benitez-Vieyra, S., Medina, A.M., Glinos, E. & Cocucci, A.A. (2006) Pollinator-mediated selection on floral traits and size of floral display in *Cyclopogon elatus*, a sweat bee-pollinated orchid. *Functional Ecology*, 20, 948–957.
- Benton, T.G., Plaistow, S.J. & Coulson, T.N. (2006) Complex population dynamics and complex causation: Devils, details and demography. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1173–1181.
- Best, A.S., Johst, K., Münkemüller, T. & Travis, J.M.J. (2007) Which species will successfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. *Oikos*, 116, 1531–1539.
- Bolnick, D.I. (2004) Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, 58, 608–618.
- Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999) Seasonal compensation of predation and harvesting. *Oikos*, 87, 419–426.
- Bozzuto, C., Biebach, I., Muff, S., Ives, A.R. & Keller, L.F. (2019) Inbreeding reduces long-term growth of Alpine ibex populations. *Nature Ecology & Evolution*, 3, 1359–1364.
- Briolat, E.S., Burdfield-Steel, E.R., Paul, S.C., Rönkä, K.H., Seymoure, B.M., Stankowich, T. et al. (2019) Diversity in warning coloration: selective paradox or the norm? *Biological Reviews*, 94, 388–414.
- Bürger, R. & Gimelfarb, A. (2004) The effects of intraspecific competition and stabilizing selection on a polygenic trait. *Genetics*, 167, 1425–1443.
- Bürger, R. & Lynch, M. (1995) Evolution and extinction in a changing environment: A quantitative-genetic analysis. *Evolution*, 49, 151–163.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H. et al. (2013) How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280, 20121890.
- Carlson, S.M., Cunningham, C.J. & Westley, P.A.H. (2014) Evolutionary rescue in a changing world. *Trends in Ecology & Evolution*, 29, 521–530.
- Carroll, S.P., Hendry, A.P., Reznick, D.N. & Fox, C.W. (2007) Evolution on ecological time-scales. *Functional Ecology*, 21, 387–393.
- Chao, L., Hanley, K.A., Burch, C.L., Dahlberg, C. & Turner, P.E. (2000) Kin selection and parasite evolution: Higher and lower virulence with hard and soft selection. *The Quarterly Review of Biology*, 75, 261–275.
- Charlesworth, B. (2013) Why we are not dead one hundred times over. *Evolution*, 67, 3354–3361.
- Charlesworth, D. & Willis, J.H. (2009) The genetics of inbreeding populations. *Nature Reviews Genetics*, 10, 783–796.
- Chouteau, M., Arias, M. & Joron, M. (2016) Warning signals are under positive frequency-dependent selection in nature. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 2164–2169.
- Christiansen, F. (1975) Hard and soft selection in a subdivided population. *The American Naturalist*, 109, 11–16.
- Christie, M.R., Ford, M.J. & Blouin, M.S. (2014) On the reproductive success of early-generation hatchery fish in the wild. *Evolutionary Applications*, 7, 883–896.
- Clarke, B. (1973) Mutation and population size. *Heredity*, 31, 367–379.
- Clutton-Brock, T.H. & Pemberton, J.M. (2004) *Soay sheep: Dynamics and selection in an island population*. Cambridge: Cambridge University Press.
- Cotto, O., Wessely, J., Georges, D., Klonner, G., Schmid, M., Dullinger, S. et al. (2017) A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nature Communications*, 8, 15399.
- Coulson, T., Kendall, B.E., Barthold, J., Plard, F., Schindler, S., Ozgul, A. et al. (2017) Modeling adaptive and nonadaptive responses of populations to environmental change. *The American Naturalist*, 190, 313–336.
- Cushing, D.H. (1969) The regularity of the spawning season of some fishes. *ICES Journal of Marine Science*, 33, 81–92.
- Day, E. & Kokko, H. (2015) Relaxed selection when you least expect it: why declining bird populations might fail to respond to phenological mismatches. *Oikos*, 124, 62–68.
- De Lisle, S.P. & Svensson, E.I. (2017) On the standardization of fitness and traits in comparative studies of phenotypic selection. *Evolution*, 71, 2313–2326.
- Dempster, E.R. (1955) Maintenance of genetic heterogeneity. In: *Cold Spring Harbor Symposia on Quantitative Biology*. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, pp. 25–32.
- Engen, S., Wright, J., Araya-Ajoy, Y.G. & Sæther, B.E. (2020) Phenotypic evolution in stochastic environments: The contribution of frequency- and density-dependent selection. *Evolution*, 74, 1923–1941.
- Ernest, S.K.M., White, E.P. & Brown, J.H. (2009) Changes in a tropical forest support metabolic zero-sum dynamics. *Ecology Letters*, 12, 507–515.
- Ferriere, R. & Legendre, S. (2013) Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. *Philosophical*

- Transactions of the Royal Society of London. Series B*, 368, 20120081.
- Fisher, D.N. & McAdam, A.G. (2019) Indirect genetic effects clarify how traits can evolve even when fitness does not. *Evolution Letters*, 3, 4–14.
- Fisher, R. (1930) *The genetical theory of natural selection*. Oxford: Oxford University Press.
- Fleming, I.A. & Gross, M.R. (1992) Reproductive behavior of hatchery and wild coho salmon (*Oncorhynchus kisutch*): Does it differ? *Aquaculture*, 103, 101–121.
- Fleming, I.A. & Gross, M.R. (1993) Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecological Applications*, 3, 230–245.
- Frankham, R. (1995) Inbreeding and extinction: A threshold effect. *Conservation Biology*, 9, 792–799.
- Fukushima, M., Quinn, T.J. & Smoker, W.W. (1998) Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Canadian Journal of Fisheries and Aquatic Science*, 55, 618–625.
- Galen, C. (1989) Measuring pollinator-mediated selection on morphometric floral traits: Bumblebees and the alpine sky pilot, *Polemonium viscosum*. *Evolution*, 43, 882–890.
- Gallet, R., Froissart, R. & Ravigné, V. (2018) Experimental demonstration of the impact of hard and soft selection regimes on polymorphism maintenance in spatially heterogeneous environments. *Evolution*, 72, 1677–1688.
- García-Roa, R., García-González, F., Noble, D.W.A. & Carazo, P. (2020) Temperature as a modulator of sexual selection. *Biological Reviews*, 95, 1607–1629.
- Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011) Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26, 285–291.
- Gigord, L.D.B., Macnair, M.R. & Smithson, A. (2001) Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soo. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 6253–6255.
- Gomulkiewicz, R. & Holt, R.D. (1995) When does evolution by natural selection prevent extinction? *Evolution*, 49, 201–207.
- Gomulkiewicz, R. & Kirkpatrick, M. (1992) Quantitative genetics and the evolution of reaction norms. *Evolution*, 46, 390–411.
- Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in Darwin's finches. *Science*, 313, 224–226.
- Gromko, M.H. (1976) What is frequency-dependent selection? *Evolution*, 31, 438–442.
- Grossen, C., Guillaume, F., Keller, L.F. & Croll, D. (2020) Purging of highly deleterious mutations through severe bottlenecks in Alpine ibex. *Nature Communications*, 11, 1001.
- Hadfield, J.D., Wilson, A.J., Garant, D., Sheldon, B.C. & Kruuk, L.E.B. (2010) The misuse of BLUP in ecology and evolution. *The American Naturalist*, 175, 116–125.
- Haldane, J.B.S. (1957) The cost of natural selection. *Journal of Genetics*, 55, 511–524.
- Harris, H. (1966) C. Genetics of man enzyme polymorphisms in man. *Proceedings of the Royal Society B: Biological Sciences*, 164, 298–310.
- Hendry, A.P. (2017) *Eco-evolutionary dynamics*. Nottingham, UK: Princeton University Press.
- Hendry, A.P., Schoen, D.J., Wolak, M.E. & Reid, J.M. (2018) The contemporary evolution of fitness. *Annual Review of Ecology Evolution and Systematics*, 49, 457–476.
- Hernandez-Jimenez, A. & Rios-Cardenas, O. (2012) Natural versus sexual selection: Predation risk in relation to body size and sexual ornaments in the green swordtail. *Animal Behavior*, 84, 1051–1059.
- Ho, E.K.H. & Agrawal, A.F. (2012) The effects of competition on the strength and softness of selection. *Journal of Evolutionary Biology*, 25, 2537–2546.
- Hubby, J.L. & Lewontin, R.C. (1966) A molecular approach to the study of genetic heterozygosity in natural populations. I. The number of alleles at different loci in *Drosophila pseudoobscura*. *Genetics*, 54, 577–594.
- Hufbauer, R.A., Szűcs, M., Kasyon, E., Youngberg, C., Koontz, M.J., Richards, C. et al. (2015) Three types of rescue can avert extinction in a changing environment. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 10557–10562.
- Husby, A., Kruuk, L.E.B. & Visser, M.E. (2009) Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1845–1854.
- Johansson, J. & Jonzén, N. (2012) Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched. *Ecology Letters*, 15, 881–888.
- Johansson, J., Kristensen, N.P., Nilsson, J.-Å. & Jonzén, N. (2015) The eco-evolutionary consequences of interspecific phenological asynchrony – A theoretical perspective. *Oikos*, 124, 102–112.
- Johansson, J., Smith, H.G. & Jonzén, N. (2014) Adaptation of reproductive phenology to climate change with ecological feedback via dominance hierarchies. *Journal of Animal Ecology*, 83, 440–449.
- Johnson, H.E., Mills, L.S., Wehausen, J.D., Stephenson, T.R. & Luikart, G. (2011) Translating effects of inbreeding depression on component vital rates to overall population growth in endangered bighorn sheep. *Conservation Biology*, 25, 1240–1249.
- Johnson, W.E., Onorato, D.P., Roelke, M.E., Land, E.D., Cunningham, M., Belden, R.C. et al. (2010) Genetic restoration of the Florida panther. *Science*, 329, 1641–1645.
- Johnsson, J.I., Nöbbelin, F. & Bohlin, T. (1999) Territorial competition among wild brown trout fry: Effects of ownership and body size. *Journal of Fish Biology*, 54, 469–472.
- Jonsson, N., Jonsson, B. & Hansen, L.P. (2003) The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology*, 40, 900–911.
- Kilgour, R.J., McAdam, A.G., Betini, G.S. & Norris, D.R. (2018) Experimental evidence that density mediates negative frequency-dependent selection on aggression. *Journal of Animal Ecology*, 87, 1091–1101.
- Killeen, J., Gougat-Barbera, C., Krenek, S. & Kaltz, O. (2017) Evolutionary rescue and local adaptation under different rates of temperature increase: A combined analysis of changes in phenotype expression and genotype frequency in *Paramecium* microcosms. *Molecular Ecology*, 26, 1734–1746.
- Kinnison, M.T. & Hairston, N.G. (2007) Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. *Functional Ecology*, 21, 444–454.
- Kinnison, M.T., Hairston, N.G. & Hendry, A.P. (2015) Cryptic eco-evolutionary dynamics. *Annals of the New York Academy of Sciences*, 1360, 120–144.
- Kokko, H. (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68, 940–950.
- Kokko, H. & Brooks, R. (2003) Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici Fennici*, 40, 207–219.
- Kokko, H. & López-Sepulcre, A. (2007) The ecogenetic link between demography and evolution: Can we bridge the gap between theory and data? *Ecology Letters*, 10, 773–782.
- Kotiaho, J.S., Simmons, L.W. & Tomkins, J.L. (2001) Towards a resolution of the lek paradox. *Nature*, 410, 684–686.
- Kovach, R.P., Gharrett, A.J. & Tallmon, D.A. (2012) Genetic change for earlier migration timing in a pink salmon population. *Proceedings of the Royal Society B: Biological Sciences*, 279, 3870–3878.
- Kovach, R.P., Gharrett, A.J. & Tallmon, D.A. (2013a) Temporal patterns of genetic variation in a salmon population undergoing rapid change in migration timing. *Evolutionary Applications*, 6, 795–807.
- Kovach, R.P., Joyce, J.E., Echave, J.D., Lindberg, M.S. & Tallmon, D.A. (2013b) Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PLoS ONE*, 8, e53807.

- Kovach, R.P., Muhlfeld, C.C., Boyer, M.C., Lowe, W.H., Allendorf, F.W. & Luikart, G. (2015) Dispersal and selection mediate hybridization between a native and invasive species. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142454.
- Kruuk, L.E.B., Slate, J. & Wilson, A.J. (2008) New answers for old questions: The evolutionary quantitative genetics of wild animal populations. *Annual Review of Ecology and Systematics*, 39, 525–548.
- Lacy, R.C. (1993) Vortex: A computer simulation model for population viability analysis. *Wildlife Research*, 20, 45–65.
- Laffafian, A., King, J.D. & Agrawal, A.F. (2010) Variation in the strength and softness of selection on deleterious mutations. *Evolution*, 64, 3232–3241.
- Lande, R. (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 30, 314–334.
- Lanfeer, R., Kokko, H. & Eyre-Walker, A. (2014) Population size and the rate of evolution. *Trends in Ecology & Evolution*, 29, 33–41.
- Levene, H. (1953) Genetic equilibrium when more than one ecological niche is available. *The American Naturalist*, 87, 331–333.
- López-Cortegano, E., Vilas, A., Caballero, A. & García-Dorado, A. (2016) Estimation of genetic purging under competitive conditions. *Evolution*, 70, 1856–1870.
- López-Sepulcre, A. & Kokko, H. (2005) Territorial defense, territory size, and population regulation. *The American Naturalist*, 166, 317–329.
- Lowe, W.H., Kovach, R.P. & Allendorf, F.W. (2017) Population genetics and demography unite ecology and evolution. *Trends in Ecology & Evolution*, 32, 141–152.
- Lumley, A.J., Michalczyk, L., Kitson, J.J.N., Spurgin, L.G., Morrison, C.A., Godwin, J.L. et al. (2015) Sexual selection protects against extinction. *Nature*, 522, 470–473.
- Lutterschmidt, W.I. & Hutchison, V.H. (1997) The critical thermal maximum: History and critique. *Canadian Journal of Zoology*, 75, 1561–1574.
- Lynch, M. & Lande, R. (1993) Evolution and extinction in response to environmental change. In: *Biotic interactions and global change* (eds Kareiva, P.M., Kingsolver, J.G. & Huey, R.B.). Sunderland, MA: Sinauer Associates Inc, pp. 234–250.
- Madsen, T., Shine, R., Olsson, M. & Wittzell, H. (1999) Restoration of an inbred adder population. *Nature*, 402, 34–35.
- Mallet, J. (1999) Causes and consequences of a lack of coevolution in Müllerian mimicry. *Evolutionary Ecology*, 13, 777–806.
- Maynard Smith, J. (1968) “Haldane's dilemma” and the rate of evolution. *Nature*, 219, 1114–1116.
- McIntire, K.M. & Juliano, S.A. (2018) How can mortality increase population size? A test of two mechanistic hypotheses. *Ecology*, 99, 1660–1670.
- Miller, R. (1967) Patterns and process in competition. *Advances in Ecological Research*, 4, 1–74.
- Mills, L.S. (2013) *Conservation of wildlife populations: demography, genetics, and management*. West Sussex, UK: Wiley-Blackwell.
- Moore, S.L. & Wilson, K. (2002) Parasites as a viability cost of sexual selection in natural populations of mammals. *Science*, 297, 2015–2018.
- Neff, B.D., Garner, S.R., Fleming, I.A. & Gross, M.R. (2015) Reproductive success in wild and hatchery male coho salmon. *Royal Society Open Science*, 2, 1–9.
- Newton, I. (1998) *Population Limitation in Birds*. San Diego: Academic Press.
- Nicholson, A.J. (1957) The self-adjustment of populations to change. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 153–173.
- O'Grady, J.J., Brook, B.W., Reed, D.H., Ballou, J.D., Tonkyn, D.W. & Frankham, R. (2006) Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation*, 133, 42–51.
- O'Sullivan, R.J., Aykanat, T., Johnston, S.E., Rogan, G., Poole, R., Prodöhl, P.A. et al. (2020) Captive-bred Atlantic salmon released into the wild have fewer offspring than wild-bred fish and decrease population productivity. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20201671.
- Orr, H.A. & Unckless, R.L. (2008) Population extinction and the genetics of adaptation. *The American Naturalist*, 172, 160–169.
- Parachnowitsch, A.L. & Kessler, A. (2010) Pollinators exert natural selection on flower size and floral display in *Penstemon digitalis*. *New Phytologist*, 188, 393–402.
- Parrett, J.M. & Knell, R.J. (2018) The effect of sexual selection on adaptation and extinction under increasing temperatures. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20180303.
- Plesnar-Bielak, A., Skrzynicka, A.M., Prokop, Z.M. & Radwan, J. (2012) Mating system affects population performance and extinction risk under environmental challenge. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4661–4667.
- Quintero, I. & Wiens, J.J. (2013) Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecology Letters*, 16, 1095–1103.
- Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C. et al. (2019) Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, 10, 3109.
- Ratikainen, I.I., Gill, J.A., Gunnarsson, T.G., Sutherland, W.J. & Kokko, H. (2008) When density dependence is not instantaneous: theoretical developments and management implications. *Ecology Letters*, 11, 184–198.
- Ravigné, V., Olivieri, I. & Dieckmann, U. (2004) Implications of habitat choice for protected polymorphisms. *Evolutionary Ecology Research*, 6, 125–145.
- Reed, T.E., Gienapp, P. & Visser, M.E. (2015) Density dependence and microevolution interactively determine effects of phenology mismatch on population dynamics. *Oikos*, 124, 81–91.
- Reed, T.E., Grotan, V., Jenouvrier, S., Saether, B.-E. & Visser, M.E. (2013a) Population growth in a wild bird is buffered against phenological mismatch. *Science*, 340, 488–491.
- Reed, T.E., Jenouvrier, S. & Visser, M.E. (2013b) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, 82, 131–144.
- Reed, T.E., Schindler, D.E. & Waples, R.S. (2011) Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology*, 25, 56–63.
- Reznick, D. (2016) Hard and soft selection revisited: how evolution by natural selection works in the real world. *Journal of Heredity*, 107, 3–14.
- Reznick, D., Bryant, M.J. & Bashey, F. (2002) r- and K-selection revisited: The role of population regulation in life-history evolution. *Ecology*, 83, 1509–1520.
- Rhymer, J.M. & Simberloff, D. (1996) Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, 27, 83–109.
- Robinson, J.A., Räikkönen, J., Vucetich, L.M., Vucetich, J.A., Peterson, R.O., Lohmueller, K.E. et al. (2019) Genomic signatures of extensive inbreeding in Isle Royale wolves, a population on the threshold of extinction. *Science Advances*, 5, eaau0757.
- Robinson, Z.L., Bell, D.A., Dhendup, T., Luikart, G., Whiteley, A.R. & Kardos, M. (2020) Evaluating the outcomes of genetic rescue attempts. *Conservation Biology*, 35, 666–677.
- Robinson, Z.L., Coombs, J.A., Hudy, M., Nislow, K.H., Letcher, B.H. & Whiteley, A.R. (2017) Experimental test of genetic rescue in isolated populations of brook trout. *Molecular Ecology*, 26, 4418–4433.
- Sæther, B., Visser, M.E., Grotan, V. & Engen, S. (2016) Evidence for r- and K-selection in a wild bird population: A reciprocal link between ecology and evolution. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152411.

- Schmitt, J. & Ehrhardt, D.W. (1990) Enhancement of inbreeding depression by dominance and suppression in *Impatiens capensis*. *Evolution*, 44, 269–278.
- Sheridan, J.A. & Bickford, D. (2011) Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1, 401–406.
- Siepielski, A.M., Morrissey, M.B., Carlson, S.M., Francis, C.D., Kingsolver, J.G., Whitney, K.D. et al. (2019) No evidence that warmer temperatures are associated with selection for smaller body sizes. *Proceedings of the Royal Society B: Biological Sciences*, 286(1907), 20191332.
- Simmonds, E.G., Cole, E.F., Sheldon, B.C. & Coulson, T. (2020) Phenological asynchrony: A ticking time-bomb for seemingly stable populations? *Ecology Letters*, 23, 1766–1775.
- Sinervo, B., Svensson, E. & Comendant, T. (2000) Density cycles and an offspring quantity and quality game driven by natural selection. *Nature*, 406, 6–9.
- Smouse, P.E. (1976) The implications of density-dependent population growth for frequency- and density-dependent selection. *The American Naturalist*, 110, 849–860.
- Soulé, M.E. & Mills, L.S. (1998) No need to isolate genetics. *Science*, 282, 1658–1659.
- Start, D. (2020) Ecological rigidity and the hardness of selection in the wild. *Evolution*, 74, 859–870.
- Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003) Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, 18, 94–101.
- Svanbäck, R. & Bolnick, D.I. (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, 274, 839–844.
- Sved, J.A. (1968) Possible rates of gene substitution in evolution. *The American Naturalist*, 102, 283–293.
- Svensson, E.I. & Connallon, T. (2019) How frequency-dependent selection affects population fitness, maladaptation and evolutionary rescue. *Evolutionary Applications*, 12, 1243–1258.
- Sylvester, E.V.A., Wringe, B.F., Duffy, S.J., Hamilton, L.C., Fleming, I.A., Castellani, M. et al. (2019) Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. *Evolutionary Applications*, 12, 705–717.
- Thériault, V., Moyer, G.R., Jackson, L.S., Blouin, M.S. & Banks, M.A. (2011) Reduced reproductive success of hatchery coho salmon in the wild: insights into most likely mechanisms. *Molecular Ecology*, 20, 1860–1869.
- Trisos, C.H., Merow, C. & Pigot, A.L. (2020) The projected timing of abrupt ecological disruption from climate change. *Nature*, 580, 496–501.
- Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science*, 348, 571–573.
- Vale, P.F. (2013) Killing them softly: Managing pathogen polymorphism and virulence in spatially variable environments. *Trends in Parasitology*, 29, 417–422.
- Van Valen, L. (1973) A new evolutionary law. *Evolutionary Theory*, 1, 1–30.
- Violle, C., Nemergut, D.R., Pu, Z. & Jiang, L. (2011) Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, 14, 782–787.
- Visser, M.E. & Gienapp, P. (2019) Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3, 879–885.
- Wallace, B. (1968) Polymorphism, population size, and genetic load. In: Lewontin, R.C. (Ed.) *Population biology and evolution*. Syracuse, NY: Syracuse University Press, pp. 87–108.
- Wallace, B. (1975) Hard and soft selection revisited. *Evolution*, 29, 465–473.
- Wallace, B. (1991) *Fifty years of genetic load: An odyssey*. Ithaca, NY: Cornell University Press.
- Waples, R.S., Zabel, R.W., Scheuerell, M.D. & Sanderson, B.L. (2008) Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. *Molecular Ecology*, 17, 84–96.
- Weiner, J. (1985) Size hierarchies in experimental populations of annual plants. *Ecology*, 66, 743–752.
- Weiner, J. & Freckleton, R.P. (2010) Constant final yield. *Annual Review of Ecology Evolution and Systematics*, 41, 173–192.
- Weis, A.E., Turner, K.M., Petro, B., Austen, E.J. & Wadgymar, S.M. (2015) Hard and soft selection on phenology through seasonal shifts in the general and social environments: A study on plant emergence time. *Evolution*, 69, 1361–1374.
- Whiteley, A.R., Fitzpatrick, S.W., Funk, W.C. & Tallmon, D.A. (2015) Genetic rescue to the rescue. *Trends in Ecology & Evolution*, 30, 42–49.
- Whitlock, M.C. (2002) Selection, load and inbreeding depression in a large metapopulation. *Genetics*, 160, 1191–1202.
- Whitlock, M.C. & Agrawal, A.F. (2009) Purging the genome with sexual selection: Reducing mutation load through selection on males. *Evolution*, 63, 569–582.
- Willoughby, J.R. & Christie, M.R. (2019) Long-term demographic and genetic effects of releasing captive-born individuals into the wild. *Conservation Biology*, 33, 377–388.
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G.J. (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, 424, 303–306.
- Young, K.A. (2003) Toward evolutionary management lessons from salmonids. In: Hendry, A.P. & Stearns, S.C. (Eds.). *Evolution illuminated. Salmon and their relatives*. New York: Oxford University Press, pp. 358–376.
- Yun, L. & Agrawal, A.F. (2014) Variation in the strength of inbreeding depression across environments: Effects of stress and density dependence. *Evolution*, 68, 3599–3606.
- Zimova, M., Mills, L.S. & Nowak, J.J. (2016) High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters*, 19, 299–307.
- Zuk, M., Johnson, K., Thornhill, R. & Ligon, J.D. (1990) Mechanisms of female choice in red jungle fowl. *Evolution*, 44, 477–485.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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