Potential effects of habitat fragmentation on wild animal welfare

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1. Introduction

The habitats of wild animals change in significant ways, attributable to both anthropogenic and naturogenic causes. Habitat changes affect the welfare of inhabiting populations directly, such as by decreasing the available food, and indirectly, such as by adjusting the evolutionary fitness of behavioral and physical traits that affect the welfare of the animals who express them. While by no means simple, estimating the direct welfare effects of habitat changes, which often occur over a short timescale, seems tractable. The same cannot yet be said for the indirect effects, which are dominated by long-term considerations and can be chaotic due to the immense complexity of natural ecosystems.

In terms of wild animal welfare, it is plausible that the indirect effects of habitat change dominate the direct effects because they occur over many generations, affecting many more individuals. Accounting for such long-term impacts is a crucial objective and challenge for those who advocate for research and stewardship of wild animal welfare (e.g. Ng, 2016; Beausoleil et al. 2018; Waldhorn, 2019; Capozzelli et al. 2020). Despite the seemingly lower tractability of predicting long-term and indirect effects, we must consider all impacts of actions to improve wild animal welfare. Here, we review the welfare effects of one type of habitat change: habitat fragmentation.

Habitat fragmentation refers to the breaking up of a contiguous habitat into smaller, more isolated patches. At least two definitions have been used in previous literature (Fahrig 2003). Most authors have used habitat fragmentation to refer to the combination of habitat break-up and its often associated habitat loss (e.g. Andrén and Andren 1994), while others have used habitat fragmentation to describe only the break-up of a habitat, controlling for the absolute size of the habitat (e.g. Gavish, Ziv, and Rosenzweig 2011). In the remainder of this report, we will use *habitat fragmentation* (or *habitat fragmentation per se* when more clarity is needed) to refer to the breaking up of habitat whilst controlling for habitat loss. This distinction is motivated by the discussion by Fahrig (2003).

1.1. Key takeaways

- It is difficult, but important, to decouple the effects of habitat fragmentation per se from the effects of habitat loss.
- Welfare effects of habitat fragmentation fit into three categories: direct effects (injury, mortality, or protection due to the process of fragmentation), population-level effects (population changes following fragmentation), and evolutionary effects (adaptation of welfare-relevant phenotypic traits and behavioural strategies).
- Habitat fragmentation affects inhabitant populations through the following mechanisms: increased patch number, decreased patch size, increase patch isolation, and increased edge-effects. However, it is rarely possible to isolate the single mechanism responsible for a fragmentation effect.
- Inhabitants are most sensitive to fragmentation with a spatial scale similar to the scale at which they utilise their environment.
- Inhabitants are most sensitive to fragmentation which is novel, unpredictable, and rarely experienced in their evolutionary history.
- Direct welfare effects are short-lived, and can be easily outweighed by population-level and, in particular, evolutionary effects, which occur over a much longer time-frame and therefore affect many more wild animals.
- Population size can increase or decrease following habitat fragmentation depending on a complex combination of fragmentation parameters (such as the patch size and matrix hostility), phenotypic traits (such as resource specialisation), and behavioural strategies (such as dispersal propensity). The welfare consequences of these population-level effects are unclear, being wholly determined by the average welfare of the constituent animals.
- In general, habitat fragmentation can select for increased dispersal ability, decreased parental investment, or phenotypic plasticity in populations affected at the relevant scale. Increased dispersal behavior and decreased parental investment may be associated with lower welfare, in contrast to phenotypic plasticity.
- It is unclear whether more harm results from anthropogenic or naturogenic habitat fragmentation. Naturogenic fragmentation is likely to affect more animals, but they may already be adapted to cope with it.

2. Models of habitat fragmentation

A variety of metapopulation structures that model fragmented habitats of different patch number, size, and isolation, have been studied (e.g. Hanski 1998; Hanski and Ovaskainen 2019). The fragmentation process can be modelled as a transition between metapopulation structures. Commonly used metapopulation structures include (Figure 1):

- Classic Levins metapopulation: small patches with relatively low interaction between patches
- Mainland-island metapopulation: several small "island" patches that are within dispersal distance of a much larger "mainland" patch
- Patchy population: many patches of a variety of sizes with high dispersal between patches
- Non-equilibrium populations: a patchy population where dispersal between patches is very low

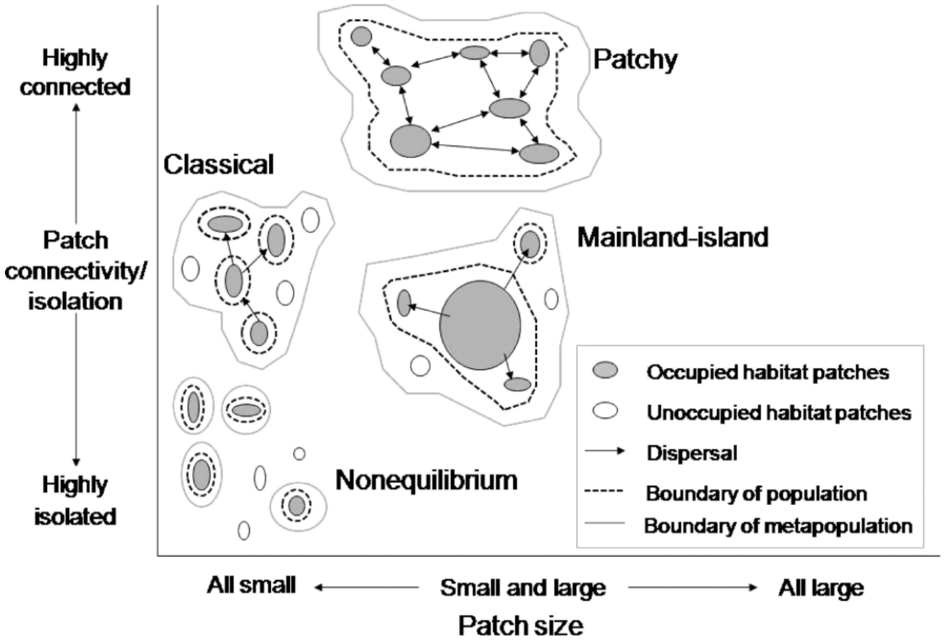

Figure 1: Metapopulation models (Aycrigg and Garton 2014*).*

These metapopulation structures make a binary distinction between habitable patches and the uninhabitable matrix (the region between patches). We can generalise this by including variable matrix habitability, which can take a value between zero (completely uninhabitable) and one (no boundary between patch and matrix). Some types of habitat fragmentation lead to zero matrix habitability, e.g. a road splitting a field into two, while others lead to finite habitability, e.g. a wildfire-managed region of forest which has had flammable undergrowth removed. Matrix habitability is also referred to as matrix permeability, matrix hostility, or matrix quality.

The study of metapopulation structure developed from theories of island biogeography. This field was developed in the 1960s by MacArthur (1969) to study the rich biodiversity of isolated islands, but the theory has since been applied to describe colonisation, survival, and extinction in patches after habitat fragmentation (Harris 2013). This stochastic model allows species occurrence in each patch to vary as a function of patch size and isolation, two key parameters of fragmented habitats. However, these parameters have been shown to be poor predictors of species occupancy in some habitats (Prugh et al. 2008). For example, Schooley and Branch (2009) tested the predictions of this model on the extinction and recolonisation of a population of a rare wetland mammal in a patchy habitat. They showed that patch quality, matrix quality, and spatial connectivity must be included in the model to make accurate predictions in this case.

Even the earliest mathematical models of habitat fragmentation illuminated key parameters that determine the effects on inhabitant populations. For example, using a basic mathematical model of a finite number of habitat patches connected by dispersal whose population undergoes a stochastic exponential growth rate, Roff (1974) demonstrated the importance of high dispersal for the persistence of the metapopulation.

Habitat fragmentation will necessarily lead to increased patch number, decreased patch size, increased patch isolation, and increased edge-length-to-interior-area ratio. One of the aims of habitat fragmentation studies has been to determine which of these mechanisms are responsible for an observed effect on inhabitants. We elaborate on these mechanisms in the following subsections.

3. Parameters of habitat fragmentation

3.1. *Patch number and size*

When a larger habitat patch is broken into two, this doubles the number of habitable patches and halves the area of each patch. That is, there is a reciprocal coupling between these two parameters. For this reason, the effects of patch number and size have traditionally been entangled. Towards the end of the 20th century, there was a debate between biologists that became known as the “SLOSS” - Single Large Or Several Small - debate about whether to conserve large contiguous areas or to separate many small conservation areas.

3.2. Patch isolation and matrix hostility

Patch isolation, and its antonym patch connectivity, is a surprisingly difficult parameter to define. Moilanen and Nieminen 2002 reviewed measures of patch isolation and categorised them into (1) nearest neighbour measures, defined by the distance to the nearest occupied patch and are sometimes weighted by the size of that patch, (2) buffer measures, where occupied patches within a limited neighbourhood of the focal patch are considered equally, and (3) measures that take into account distances to all possible source populations. They noticed that the majority of ecology literature only considers nearest neighbour measures, and showed that studies using such measures are much less likely to find statistically significant effects of patch isolation compared to studies that use more complex measures. For highly fragmented landscapes, they suggest that measures that take into account the distances to all possible source populations will give the best and most consistent performance.

To reduce the dimension of the parameter space, patch isolation and matrix hostility can be combined into one parameter known as the effective patch isolation (Ricketts 2001). This is the distance between each patch weighted by how hostile the matrix between them is. An extremely hostile matrix could force patch inhabitants to have a strong aversion to dispersing to neighbouring patches even if they are relatively close by. The inhabitants could have a similar dispersal aversion when dispersing across a less hostile matrix between well-separated patches. The concept of effective patch isolation allows us to equate these two scenarios. The ease at which inhabitants can disperse between patches is dependant on a combination of patch isolation, matrix habitability, and the dispersal-relevant traits of the inhabitants. The latter is a feature of the species, rather than of the metapopulation structure, leaving the former two to be combined into one parameter.

3.3. Edge length to interior area ratio

As habitat is fragmented, the ratio of the total edge (or ecotone) length to the interior habitat area will increase. This amplifies the effect of edges, which can be either positive or negative to the welfare of the population.

For simplicity, habitat patch edges are often modelled as sharp discontinuities between the habitable interior and the uninhabitable matrix. In reality, patch edges can be smooth gradients between patch and matrix. Even the same edge can be experienced as sharp or smooth depending on the size and dispersal ability of the animal in question. For example, a shear edge between dense forest and open field is a sharp edge for a woodpecker, but a smooth edge for a much smaller and less mobile ant. Further, a habitat edge can be felt by some inhabitants and not others; for example, small aquatic animals will strongly feel an edge between still water and strong currents, which would be hardly noticed directly by a large aquatic animal (Hagen et al. 2012). That being said, if the larger animal depends on the smaller animal for resources, for example through a predator/prey relationship, the habitat edge may still indirectly affect the larger animal.

Albers et al. (2018) used this notion of smooth edges to argue that patch isolation is greater than merely the distance between edges of neighbouring patches. Along the same vein, a parameter known as the depth-of-edge influence was introduced by Saunders et al. (2002) to describe how far into the patch interior an edge affects the inhabitant population.

4. Causes of habitat fragmentation

Habitat fragmentation can be anthropogenic, naturogenic, or a combination of the two. Anthropogenic causes for habitat fragmentation include the construction of roads, the urbanisation of wild spaces, agricultural expansion, forest management and deforestation, ocean floor dredging, and the variety of fragmentation mechanisms driven by anthropogenic climate change (Scanes 2018).

Naturogenic causes of habitat fragmentation include the creation and diversion of rivers due to changes in weather, volcanic activity, wildfires, floods, and changes in ocean currents, pH, and salinity stratification (Mullu 2016). The habitats of small invertebrates can be fragmented in seemingly innocuous ways, such as previously connected plants becoming isolated due to a strong breeze, isolating the resources on one plant from the inhabitants of another.

In fact, one of the most significant periods of evolutionary change in history was one of large-scale naturogenic habitat fragmentation. The Carboniferous rainforest collapse fragmented a prehistoric mega-forest around 305 million years ago into many smaller “islands”, leading to significant extinction and speciation of many species (Sahney et al. 2010). In particular, the dry weather associated with this fragmentation event severely reduced amphibian populations, who must return to water to lay eggs. Reptiles generally adapted well to the new habitat structure by developing carnivorous traits. This shows how habitat fragmentation can affect populations differently depending on their phenotypic traits and cause adaptation in those traits.

Several mechanisms for habitat fragmentation fall within both the anthropogenic and naturogenic categories. For example, a diverted river could be due to a period of naturally wet weather that is made more extreme due to anthropogenic climate change. That being said, the distinction is instructive because it dictates whether effective ways to improve wild animal welfare involve ecological intervention, societal change, or a combination of the two.

Several authors have assumed that anthropogenic habitat fragmentation is more common and has more significant effects on inhabitant animal populations than naturogenic habitat fragmentation (Mullu 2016). The reasoning behind this claim is that naturogenic habitat fragmentation usually occurs over a longer time frame, giving time for populations to adapt, and that it is usually similar to previous habitat changes that have already been adapted to.

In general, wild animal populations are more sensitive to rapid habitat fragmentation that is unlike that which the populations have adapted to. However, to conclude that anthropogenic habitat fragmentation is more common and more severe than naturogenic habitat fragmentation is largely unjustified. There are two reasons for this. Firstly, whilst habitat fragmentation due to, for example, building new roads and agricultural land occur over short time-scales, this is not true of all anthropogenic habitat fragmentation (Ewers and Didham 2006). For example, anthropogenic climate change, and hence many of its habitat fragmentation effects, occurs over a timescale much longer than the lifespan of all but the most long-lived wild animals. Conversely, some naturogenic drivers, such as wildfires, can rapidly fragment habitats. Given these counterexamples, it is unclear whether the timescale of anthropogenic habitat fragmentation is, as a rule, shorter than that of naturogenic habitat fragmentation.

Secondly, even in the modern era, most animals will experience little to no interaction with humanity. The animal biosphere is dominated numerically by small land invertebrates and small oceanic animals (Tomasik 2009; Bar-On et al. 2018). The majority of the planet's surface is either water, which humans have limited impact on, or land uninhabited by humans, so the vast majority of animals live their lives undisturbed directly by humans, and therefore are unlikely to experience more anthropogenic fragmentation than naturogenic fragmentation. Moreover, the fact that the majority of individual animals are very small suggests that events barely noticeable to humans, like the felling of a branch connecting two trees, are likely to predominate in frequency.

There is also a weaker claim that, to our knowledge, has not been considered. The degree to which animals experience welfare is likely to exist on a spectrum, with some species capable of experiencing a greater degree of welfare than others. If we were to weigh examples of habitat fragmentation according to their effects on welfare, what would emerge as the most impactful causes? Much more research into animal sentience – in particular that of invertebrates – is required to answer this question satisfactorily.

5. Welfare effects of habitat fragmentation

Habitat fragmentation leads to welfare effects that can be categorised into:

- *Direct (or first order) effects:* how animals are injured, killed, or protected by the process of fragmentation.
- *Population-level (or second order) effects:* how population sizes of inhabitants, their predators, or prey, change following fragmentation.
- *Evolutionary effects:* how the traits of affected animals change in adaptation to the fragmentation.

We discuss each category in the following sections. Bear in mind that there is a bias in previous literature towards studying the effects of anthropogenic habitat fragmentation on vertebrates (Tews et al. 2003). We have focused on results that are also applicable to naturogenic habitat fragmentation across a variety of animal species.

Before looking more deeply at each category of welfare effect, it is instructive to observe some general heuristics that broadly hold across each category.

1. **Inhabitants are most sensitive to fragmentation with a spatial scale similar to the scale at which they perceive their environment.** Habitat fragmentation occurs across a range of different scales, from a gentle breeze separating two leaves fragmenting an insect habitat, to large scale forest management affecting large herbivores. Additionally, different species perceive their environments at different scales, from the insect confined

to one plant for the entirety of their short existence, to the deer who can traverse a whole forest section regularly. In general, animals are most sensitive to habitat fragmentation that is on the same spatial scale as the scale at which they perceive their environment (Doak, Marino, and Kareiva 1992). This is closely related to the concept of environmental grain (Hagen et al. 2012).

2. **Inhabitants are most sensitive to rapid or novel fragmentation.** Inhabitants are more able to adapt to slow or common changes in their environment. Rapid or novel fragmentation that has not been adapted to in their evolutionary history will, in general, have more severe welfare effects on inhabitants (Sih, Ferrari, and Harris 2011).
3. **There can be a time-lag between habitat fragmentation and its ecological effects.** Ecological networks respond to changes in the spatial habitat network on different time-scales for different species. Some species react immediately to changes in habitat, whereas others exhibit a time-lagged response (Ewers and Didham 2006). An example of a time-lagged response is *extinction debt*, where future extinction occurs due to past events (Tilman et al. 1994).

5.1. Direct effects

The mechanism of habitat fragmentation can directly affect the wellbeing of its inhabitants. For example, wildfires can cause significant burns to animals who cannot flee or take cover underground, and river diversion can cause flooding of habitats and drowning of inhabitants while opening up new habitat patches in the previous riverbed (Engstrom and Todd Engstrom 2010; Alho and Silva 2012). Burning and drowning being arguably two of the most unpleasant ways to die, direct effects clearly have significant welfare consequences (Tomasik 2016a).

Direct effects tend to be short-lived because they operate on the time-scale of the fragmentation event itself. In general, direct welfare effects of habitat fragmentation are more significant for animals with less dispersal ability because they are less able to evade the fragmentation mechanism (Zielinski and Zachos 2018). In particular, smaller animals such as flightless invertebrates, rodents, and reptiles, who tend to be less capable of moving long distances, tend to be more directly affected than larger animals such as many larger mammalian species.

Smaller patches have less available resources such as food and nesting area. This affects the inhabitants' home range, that is, the area over which they visit regularly, via two competing mechanisms. On one hand, the home range can be reduced because they are confined to a smaller patch, putting up with the reduced resources to avoid the negative consequences of venturing into hostile surroundings. This is likely to be a stronger mechanism for less mobile species and in metapopulations with higher effective patch isolation. This mechanism can lead to starvation and food competition, which will have direct negative consequences on welfare.

On the other hand, the inhabitants' home range can be expanded because the smaller patch size forces the population to disperse outside of its patch to exploit resources in other patches or in the matrix. This is likely to be a stronger mechanism for more mobile species and in metapopulations with lower effective patch isolation. Forcing the inhabitants to employ a strategy of higher dispersal will often lead to lower welfare because individuals who attempt dispersal will encounter hostile environments.

In general, direct effects are more significant the shorter the time-scale of the fragmentation because inhabitants have less time to disperse from the affected regions. In general, direct effects are more significant when the type of fragmentation is rarely experienced by the inhabitants. This is because the inhabitants are less likely to be well-adapted to the disturbance.

5.2. Population-level effects

Mortality and migration caused by direct effects of habitat fragmentation influences population dynamics. Individuals of different populations likely experience different levels of wellbeing average; therefore, effects of habitat fragmentation on population levels are relevant for welfare biology, particularly if one is concerned with total welfare maximisation (Ng 1995).

Fahrig (2003) reviewed 100 studies into the effects of habitat loss and habitat fragmentation and showed that habitat loss generally causes a significant decrease in population size and that habitat fragmentation *per se* has a comparatively smaller effect on population size that is either an increase or a decrease, depending on the specific population traits and nature of the fragmentation. This is an important result which contradicted the previously accepted paradigm that habitat fragmentation leads to a decrease in population size, which, according to Fahrig, is due to not decoupling habitat fragmentation per se from habitat loss. Not controlling for habitat loss has led to confusion as to which mechanism causes the observed effects on population size, biodiversity, and fitness landscape (Didham 2010). In many studies, the significant decrease in population size after habitat fragmentation is due primarily to habitat loss yet is mistakenly afforded to habitat fragmentation per se. In a later review Fahrig reached the stronger conclusion that habitat fragmentation is more likely to increase population size than decrease it. However, a cautious interpretation of this conclusion has been suggested by Fletcher et al. (2018). The conversation is ongoing, with Fahrig et al. recently responding to these criticisms (Fahrig et al. 2019). The effects of habitat fragmentation on population size depend on a complex interaction of multiple interacting variables including population-specific traits, matrix hostility, patch size, patch isolation, and resource distribution, and that general heuristics have limited predictive power (Didham 2010).

Given that habitat fragmentation can be modelled by a change in metapopulation structure, understanding the effects of habitat fragmentation on population size can be achieved by understanding the population size that can be maintained by different metapopulation structures. As discussed above, the SLOSS debate concerns which of two metapopulation extremes - a single large patch or several small patches - support larger populations over time and are most resilient to local and metapopulation extinction (Tjørve 2010; Diamond 1975). This debate boils down to two competing effects:

- Many species, such as many apex predators, require a large patch size to maintain populations. When the patch size gets smaller than a critical size, the population will no longer be able to sustain itself (Fahrig 2003). Therefore, a single large patch can sustain a larger persistent population than several small patches.
- Disturbances such as predation, disease, or habitat change can lead to local patch extinction. Having multiple isolated patches means that local extinctions do not necessarily lead to total metapopulation extinction because individuals dispersing from other patches can recolonise (Schnell et al. 2013). Therefore, several small patches can sustain a larger persistent population than one large patch.

Some species will sustain larger populations in a few larger connected patches while others will sustain larger populations in many smaller disconnected patches. Phenotypic traits, trophic level, and the fragmentation mechanism determine which metapopulation structure would support a larger population of a given species.

In a meta-analysis, Bender et al. (1998) determined that patch size was a strong determinant of population change after habitat fragmentation for edge and interior species, but negligible for generalist species who inhabit both edge and interior. They also made the stronger claim that the changes in population size due to habitat fragmentation *per se* for interior species are, in general, greater than those due to habitat loss. This is a particularly strong claim given the consensus view that habitat loss is the most significant mechanism for population decline (Wilcove et al. 1998). Another meta-analysis concluded that for a large range of species studied (mostly birds), patch size is the most important driver of species persistence (Keinath et al. 2016).

It is thought that for all wild animal populations there is a critical patch size, known as the extinction threshold, below which the local population will become extinct (Fahrig 2002). This critical size is dependent on many different factors including their home range, trophic level, niche breadth, and their body size. For example, Slade et al. (2013) found that forest fragments need to be larger than five hectares in order to sustain a population of forest-specialist macro-moth. Fahrig (2002) showed that, in general, habitat fragmentation leads to an increase in the extinction threshold; that is, in more fragmented habitats, larger patches are required to sustain a population.

Pellet et al. (2007) suggested that if the habitability of each patch is not uniform then patch size is only a weak predictor of population size responses to habitat fragmentation. Others have questioned the whole aim of isolating a specific mechanism of how habitat fragmentation affects inhabitants, highlighting that a holistic approach including other parameters such as species traits and matrix hostility must be considered (Prugh et al. 2008).

5.2.1. Patch isolation and matrix hostility

Patch isolation and matrix hostility determine the effective isolation of habitat patches (Ricketts 2001). More isolated patches and more hostile matrix mean dispersal to other patches carries a higher mortality risk. For simplicity, many studies assume that the matrix is uninhabitable or prescribe a “colonisation rate”, which encompasses the effects of patch isolation, matrix hostility, and species traits, such as dispersal ability, that are relevant to movement between patches (Levins 1969). Others have shown that finite matrix hostility is an important factor in population size and evolutionary responses to habitat fragmentation (Vandermeer, Vandermeer, and Carvajal 2001).

Grilli et al. (2015) generalised the classic (Levins 1969) metapopulation model of regularly separated patches, with a uniform colonisation rate between patches, to a model of a randomly fragmented landscape, with a colonisation rate that is related to the relative isolation of each patch. They found that the chance of metapopulation extinction is greater in a regularly fragmented habitat compared to a randomly distributed one. This is likely to be due to the more isolated patches in a randomly fragmented habitat inhibiting metapopulation collapse.

It has been known for some time that increasing the connectedness of fragmented habitat patches can improve metapopulation persistence by making dispersal to and recolonisation of new patches more likely. Habitat corridors (thin habitable regions connecting fragmented patches) and stepping stones (small isolated habitat patch between larger isolated habitat patches) reduce the effective isolation of fragmented habitat patches. The hostility of the matrix surrounding the corridors and stepping stones has a significant part to play in their effect on population persistence (Baum et al. 2004).

By compiling data from 1,015 bird, mammal, reptile, amphibian, and invertebrate population networks on 6 continents, Prugh et al. (2008) determined that patch isolation (as well as patch size) was a poor predictor of population persistence. They assess possible alternate explanations for the low predictive power of patch area and isolation, including (1) patches studied were of an inappropriate scale, (2) particular taxonomic groups or species with certain life-history traits were less sensitive than others, (3) most of the species were “survivors,” able to tolerate disturbance and not threatened with extinction, and (iv) strong effects of the matrix surrounding patches, but show that they are all insufficient to account for the result. This was a surprising result because the paradigm had always been that patch isolation and size were the major determining factors of population size in fragmented landscapes (Levins 1969), but is in agreement with several other analyses, including those by Fleishman et al. (2002) and Pellet et al. (2007).

5.2.2. Edge length to interior ratio

A fragmented landscape will necessarily have an increased ratio of edge length to patch area. This can lead to an increase or decrease in the inhabitants’ population, depending on the complex interconnection of the habitat structure, fragmentation mechanism, and species traits. Habitat fragmentation leads to inhabitants being forced to live closer to a patch edge. Whatever the mechanism that causes hostility of the matrix, whether it be predation, adverse weather, or lack of resources, living closer to the edge could decrease the welfare of inhabitants, particularly interior species.

According to the review by Ries et al. (2004), there are four fundamental mechanisms that cause edge responses: (1) ecological flows, (2) access to spatially separated resources, (3) resource mapping, and (4) species interactions.

(1) Ecological flows involve the movement of organisms, materials, and energy across the habitat edges and are directly related to the resource-specific permeability of the edge. This includes a variety of circumstances including increased sunlight penetrating a forest near its edge, amphibious organisms moving from land into a pond fragment, and debris floating along an ocean current into a coral reef fragment.
(2) Some species require resources that are spatially separated across a habitat boundary, leading to an enhanced density at the edges to maximise access to both resources. For example, a population of dark-eyed junco, a small bird in the American Southwest, demonstrated an edge-exploiting response to habitat fragmentation due to forest wildfire management, reaching their peak abundance at the edge between managed and unmanaged forest patches (Sisk et al. 2003). Being a ground nester and ground forager, the juncos exploited the increased food supply in the managed patches, while exploiting the denser coverage of the unmanaged forest patches for nesting. They populated the edge instead of the interior despite the changes in microclimate across the boundary (in particular, the light intensity, air temperature, and vapour pressure deficit) that deterred the other five bird species in the study from inhabiting the patch edges.
(3) Resource mapping refers to the well-understood fact that the distribution of patch inhabitants will map to the distribution of resources. This is relevant to edge effects because the presence of edges can affect resource distribution. For example, increased sunlight penetrating the edge of a forest patch will lead to a change in the flora at the edge and hence a change in the resource distribution for forest-dwelling herbivores.
(4) Species interactions, such as predator-prey interactions or intraspecific resource competition, involve one population increasing at the expense of another. Avoiding edges to reduce the chance of predation and parasitism is commonplace for mammals, amphibians, and to a lesser extent, birds. Some species, including butterflies (Ries and Fagan 2003), trade less protection from predators for better nesting sites at habitat edges. This is an example of a decision that lowers the welfare of the individual, in this case, due to stress and injury, in order to increase the chance of reproduction. For this population of butterfly, welfare biology concerns are at odds with population-level concerns.

Of course, these four mechanisms are interlinked. For example, ecological flows affect resource mapping within a patch and species interaction at the edge, and species interaction overlaps with resource mapping for carnivorous species. Ries et al. (2004) implemented these mechanisms in combination to achieve a conceptual model with high predictive value. However, they also note that new edges formed by habitat fragmentation can open a habitat patch up to novel inputs which can lead to ecological cascades, where several species or populations are affected through several mechanisms. The effects of such a destabilisation of a population can be both significant and unpredictable, especially if the cascade is made up of several levels.

If the matrix is sufficiently hostile, habitat edges can act as impermeable boundaries, which can lead to an accumulation of population at the edge. Desrochers and Fortin (2000) showed that even in the absence of a edge-attraction, a population of chickadees, a forest-dwelling bird, were more densely populated close to edges. They explained that this was due to the boundary acting as a conduit for the movement of the birds. This mechanism has also been observed in voles (Andreassen et al. 1996).

Some researchers have categorised species into either *edge specialists*, who are primarily associated with the perimeter of a habitat, *interior specialists*, who are primarily associated with the core, and *generalists*, who utilise both edge and interior (*e.g.* Brand et al. 2001). Others suggest a categorisation based on edge sensitivity, where some species are significantly affected by a change in the edge-interior ratio while others are not, is more appropriate because it is incorrect to assume that a given species will react to different habitat edges the same way (Ries et al. 2004; Ries and Sisk 2010). That being said, the over-reliance of ecology research on these categorisations has been criticised (Villard 1998).

Increased edge length relative to interior area can affect predator-prey relationships (Fagan et al. 1999). For example, a population of butterflies in a forest fragment may prefer to occupy the patch interior due to increased predation from birds at the open edges. Habitat fragmentation forces the butterflies to live closer to the edge, increasing the chance of predation and the stress and mortality that comes with it. This affects the populations of, and hence has welfare implications for, both predator and prey.

5.3. Evolutionary effects

When a habitat fragments, the change in the environmental pressures may alter the fitness landscape, favoring different phenotypic traits and behavioural strategies than before. The resulting adaptation to this new environment can be either positive or negative for the welfare of the individual animals affected by it because different phenotypic traits and behavioural strategies predispose individuals to different welfare levels.

The ecology literature is weighted towards using life-history traits as predictors of habitat fragmentation sensitivity, rather than the inverse problem of understanding the effect that habitat fragmentation has on the evolution of life-history traits. From a welfare biology perspective, the latter might be at least as important as the former because life history evolution could have welfare repercussions for many generations after habitat fragmentation has abated. That being said, understanding the traits that predispose a population to habitat fragmentation sensitivity is still important for welfare biology because traits which confer resilience to habitat fragmentation are likely to be selected for after fragmentation, and may mitigate direct effects of habitat fragmentation events on individual wild animals.

5.3.1. Life history traits as welfare predictors

The pressures of natural selection determine how members of a population invest in alternative phenotypic traits and behavioural strategies to meet the unique demands of their habitat. Life-history theory describes the variety of such strategies that are related to age- and stage-specific resource investment. When a habitat is changing in an unpredictable way, inhabitants suffer a higher mortality rate and a lower life expectancy, which selects for life-history strategies that involve higher offspring numbers, lower parental investment, and faster development (Stearns 1992).

Life-history theory is crucially relevant to welfare biology because some life-history traits predispose individuals to lower levels of welfare than others. For example, populations of individuals who put more resources into producing a large number of low-fitness offspring at the expense of investing in the successful development of each offspring will have lower life expectancy and reduced ability of individuals to deal with adversity, ultimately leading to lower welfare (Smith and Fretwell 1974). This heuristic can be understood in terms of pace of life theory (Healy et al. 2019), which models syndromes of life-history traits as a spectrum between two extremes: ”fast-living” species, where more energy is invested in reproductive rate, and “slow-living” species, where more energy is invested in mitigating mortality risks. Traits associated with a fast pace of life include high numbers of offspring, low parental investment, fast development rates, and short life expectancy. Traits associated with a slow pace of life include low numbers of offspring, high parental investment, slow development towards high fitness, and long life expectancy. This can be simplified even further to a spectrum between investment in quantity of offspring (fast) versus quality of offspring (slow). Finite resources necessitate a trade-off between these two extremes. The comparatively shorter life expectancies associated with a fast pace of life implies that these individuals have less opportunity to accrue positive welfare before a potentially painful death; thus, animals adapted to a fast pace of life might be expected to have lower net welfare than members of closely related species adapted to a slower pace of life, all else being equal.

Populations adapted to a “slow” life history are generally less able to persist in a fragmented habitat than populations adapted to a faster pace of life. This is a case of the more general heuristic that slow growth and iterative reproduction is a more effective strategy in stable and predictable habitats, whereas traits associated with a fast pace of life, such as earlier maturation, are favored in the presence of changing and unpredictable habitats. The predictive power of this heuristic is particularly strong in mammals, where a meta-analysis of 68 studies across 232 mammalian species found that mammals with lower growth rates, paternal care of offspring, greater mass, larger home ranges, and increased niche specialization had significantly lower abundances in fragmented habitats (Kosydar 2014). Further, a meta-analysis of butterflies and moth populations showed that low reproductive rates are associated with population sensitivity to habitat fragmentation (Ockinger et al. 2010).

Compared with habitat specialisation and habitat type, the effects of life-history traits on population persistence through habitat fragmentation are generally small (Hagen et al. 2012). However, we are interested in traits that predict population persistence only insofar as it suggests which traits have the potential to be changed after habitat fragmentation, which can have consequences on the welfare of inhabitants. Therefore, life-history traits are of particular interest because they are predictors of population persistence and plastic to evolutionary adaptation. For example, Soga and Koike (2012) showed that voltinism was associated with population persistence in butterfly populations whose forest habitat is fragmented by urbanisation. Univoltine and bivoltine (1-2 broods per year) populations were more susceptible than multivoltine (>2 broods per year) to extinction due to forest fragmentation. This study was an inter-species comparison, but if there is a mechanism by which adaptation can operate on this trait, then we can conclude that habitat fragmentation could cause a change in voltinism towards multiple broods per year. While the mechanism through which multi-voltinism leads to population persistence is unclear, it is plausible that smaller patch size leads to a higher incidence of aversive interactions with the matrix (i.e. hostile environment surrounding the habitat patch), and that the greater number of offspring that is associated with the multivoltine strategy offsets lower survival and welfare among individual offspring.

5.3.2. Phenotypes that predict fragmentation sensitivity

In addition to metapopulation structure, physical traits and behavioural strategies can be predictive of sensitivity to habitat fragmentation (Keinath et al. 2016). Habitat fragmentation also changes the selective pressures imposed on inhabitants by their environment, so to the extent that these traits affect the survival and ultimate reproductive success of an individual’s offspring in a fragmented landscape, they may also be subject to natural selection (Hagen et al. 2012). Given relevant genetic variation in traits such as dispersal ability, phenotypic plasticity, and life history parameters, this leads to changes which could significantly affect the welfare of future individuals in a population.

5.3.2.1. Dispersal ability

The trait most predictive of fragmentation sensitivity is dispersal ability. Dispersal is any movement that has the potential to lead to gene flow, or, equivalently, any undirected movement away from the origin habitat patch (Ronce 2007). This distinguishes dispersal from migration, which describes an obligatory movement to a different habitat due to the uninhabitability of the previous habitat.

It is worth noting that several different methods are used to determine dispersal ability, including direct observation of movement between patches, inference from patch population dynamics, and measurements of anatomical features that are associated with dispersal ability, such as wingspan. Comparisons between studies that use different observational parameters to determine dispersal ability can be prone to error.

In theory, dispersal between habitat patches will occur when the fitness benefits of moving (e.g. the possibility of finding a habitat patch with more resources and evade less favourable conditions) outweigh the costs (e.g. energy expenditure associated with locomotion and the risk of not finding a new patch). Dispersal ability is a combination of a wild animal's dispersal range and their propensity to seek out new habitat.

Dispersal between habitat patches in a fragmented habitat serves two purposes: to avoid adverse conditions, including competition for resources, and to find a more patch with more resources, such as food or mates (Bonte et al. 2012). Inhabitants of a fragmented landscape are presented with a trade-off:

1. On one hand, habitat fragmentation leads to greater competition within each patch due to the reduction of available resources associated with the decrease in patch size. Greater dispersal ability allows inhabitants to explore neighbouring patches, leading to greater resource availability. Additionally, greater patch isolation, which generally follows habitat fragmentation, can be overcome by a greater dispersal ability. Habitat fragmentation presents inhabitants with dispersal barriers and the higher their dispersal ability, the more likely they are to overcome these barriers.
2. On the other hand, if the fragmented landscape has a hostile matrix and highly isolated patches, dispersal is extremely costly due to high dispersal mortality, so having a lower dispersal ability could be a strategy of greater fitness. Habitat fragmentation presents inhabitants with more costly dispersal and the lower their dispersal ability, the more likely they are to avoid these high fitness costs.

In general, the first mechanism dominates, leading to the general principle that higher dispersal ability predicts lower sensitivity to habitat fragmentation (Hagen et al. 2012; Henle et al. 2004; Ockinger et al. 2010). In fact, increased dispersal ability may increase the persistence time of a population by several orders of magnitude (Roff 1974).

That being said, there have been cases where increased dispersal ability is associated with greater population-level sensitivity to habitat fragmentation. For example, Slade et al. (2013) observed that species of macro-moth with higher levels of traits related to high dispersal ability, such as wingspan, were less able to sustain their population in a fragmented forest habitat.

Furthermore, for some species of butterfly, an intermediate dispersal ability is worse for population persistence after habitat fragmentation compared to both a low and high dispersal ability. Thomas (2000) understood this to be due to intermediate dispersal ability allowing individuals to attempt dispersal but they often have insufficient ability to succeed, so miss out on the population benefits of dispersing, yet still pay the large costs associated with attempted dispersal.

There are at least two mechanisms by which increased dispersal ability could have welfare consequences. First, increasing individuals' propensity to explore hostile regions leads directly to individuals finding themselves in unpleasant situations. Second, other welfare-relevant life history traits may be coupled to dispersal ability.

Early models of habitat fragmentation through a change in metapopulation structure with a trade-off between investment in different trait profiles demonstrate that habitat fragmentation causes inhabitants to develop increased dispersal ability (Hanski 1994). The classic trade-off is between investment into survival versus reproduction (Burton et al. 2010). In a fragmented landscape, increased dispersal ability corresponds to increased probability of reproduction at the cost of an increase in mortality rate due to movement through the matrix to a different habitat patch.

Life-history trait models have demonstrated that, at a habitat edge, dispersal ability is selected for at the cost of per-offspring parental investment. Burton, Phillips and Travis (2010) demonstrated, in a model of a habitat that is range-expanding into the previously uninhabited matrix, that populations located near the range edge experience selection for dispersal ability, but also accelerated pace of life in terms of higher reproductive rate paired with higher mortality. Given that habitat fragmentation necessarily involves an increase in edge length per interior area, it is to be expected that higher dispersal ability and faster pace of life would follow.

There are some species for whom an increase in dispersal capability is instead associated with lower levels of reproduction. For example, in a meta-analysis by Guerra (2011) showed that for wing-dimorphic insects, those with higher dispersal ability have fewer offspring. However, they also showed that these offspring are of lower fitness (hypothesized to be due to less parental investment in each offspring) compared to the offspring of parents with lower dispersal ability. The lower parental investment per offspring from highly dispersive parents might plausibly be associated with lower offspring welfare.

While considering the metapopulation as a whole gives us the general result that habitat fragmentation leads to increased dispersal ability, it is possible that subpopulations inhabiting small isolated habitat patches could evolve traits associated with lower dispersal ability. This is possible if the emigrants, who by definition have higher dispersal ability, are not replaced by immigrants, leaving a subpopulation of individuals with low dispersal ability to pass on these traits (den Boer 1990; Cody and Overton 1996). This is most likely to happen in fragmented landscapes that have significant and even directional patch isolation, so that even highly dispersive immigrants are rare.

As an example of an exception to the general rule that fragmentation increases dispersal ability, Baguette et al. (2003) showed that dispersal ability decreased after butterfly habitat was fragmented over a 30-year time-frame. It was concluded that patches became so isolated that the risk of mortality from dispersing between them outweighed the benefits of finding habitable patches. This observed result is in agreement with theoretical metapopulation modelling

(Weigang and Kisdi 2015). This evolutionary response to habitat fragmentation is a mechanism of so-called evolutionary suicide (Sih, Jonsson, and Luikart 2000; Gyllenberg, Parvinen, and Dieckmann 2002).

5.3.2.2. Phenotypic plasticity

Inhabitants of highly variable environments tend to develop more phenotypic plasticity; that is, the ability to change one's phenotypic traits in response to environmental change (Chevin and Hoffmann 2017). Habitat fragmentation can be a stressful change to inhabitants which can lead to increased phenotypic plasticity, allowing increased fitness across a larger range of environments (Hendry, Farrugia, and Kinnison 2008). As discussed above, stresses from habitat fragmentation can come from a variety of mechanisms including increased edge effects, though increase predation from matrix predators, and smaller patch size, leading to increased resource competition.

Under which conditions a population will develop phenotypic plasticity to adapt to a changing habitat rather than increased dispersal ability to evade stressors altogether is unclear, but is thought to be related to the physical scale of the variable habitat in relation to the organisms' dispersal capability, and the dimensionality and timescale of environmental variation within the habitat (Hollander et al. 2014). Similarly, whether a population will evolve traits associated with a faster pace of life or increased phenotypic plasticity depends on how predictable the stressor is and what life stages it affects (Reznick et al. 2002; Hollander et al. 2014). Accelerated pace of life (or higher dispersal) is likely to be a more successful strategy in terms of reproductive fitness when the stressor is unpredictable, because these traits counter the decreased chance of any individual reproducing regardless of what stressor is responsible. On the other hand, increasing phenotypic plasticity is likely to be a more successful strategy when the stressor is predictable, because phenotypic plasticity is typically initiated by a change in specific parameters, such as the temperature of the environment, and so is a trait change directed at increasing fitness over a particular type of environmental change.

5.3.2.3. Body size

Body size is a weak predictor of sensitivity to habitat fragmentation. The predictive power of body size exists by virtue of the relationship between body size and other directly predictive traits (Keinath et al. 2016).

Large body size correlates with a large home range (Jetz 2004). Animals with larger home range size require larger habitat patches to sustain their population, therefore, larger animals are less able to persist when their habitat is fragmented (Hagen et al. 2012). Large body size is also correlated with low reproductive rates and other life-history traits associated with a slower pace of life (Cardillo et al. 2005).

Attempts have been made to relate habitat edge sensitivity (and hence fragmentation sensitivity, since fragmentation always leads to more edge per interior area) to body size and other species traits. However, the relationship between these parameters seems complex. For example, Pfeifer et al. (2017) found that edge sensitivity decreased with body size for forest-core amphibians, but increased with body size for forest-core reptilian species.

5.3.2.4. Resource specialisation

In general, populations that have a narrow feeding or nesting niche are more susceptible to population decline due to habitat fragmentation than populations with a broad resource niche.

A meta-analysis of butterflies and moth populations showed that those with a narrow feeding niche are associated with population sensitivity to habitat fragmentation (Ockinger et al. 2010). The same (but less significant) effect was observed across several studies in bee populations in fragmented habitats (Bommarco et al. 2010). In a meta-analysis of mammalian species, (Kosydar 2014) similarly found that populations with increased niche specialisation had and significantly lower abundances in fragmented habitats.

6. Conclusions

It is clear that habitat fragmentation can affect wild animal welfare. The direction of the welfare effects is less clear and is dependent on the specific nature of the habitat fragmentation and the traits of the inhabitant population. The direct welfare effects follow directly from the fragmentation mechanism and are likely to be negative in the majority of cases. Populations can either increase or decrease in response to habitat fragmentation. Whether this is corresponds to an increase or decrease in welfare depends on whether the welfare of individuals in the population is net-positive or net-negative and on the choice of welfare aggregation method (*e.g.* total or average welfare). Evolutionary effects can correspond to an increase or decrease in welfare, although the mechanisms for decreased welfare seem more likely. The fact that population-level and evolutionary effects can impact welfare for many generations after the fragmentation occurs is reason to believe that they can dominate direct effects.

In summary, the welfare effects of habitat fragmentation depend on:

1. The direct welfare effects of the fragmentation mechanism,
2. The associated population changes,
3. The welfare-relevant traits that are evolved as a consequence,
4. Whether the inhabitants of affected populations have net-positive or net-negative welfare and the method of welfare aggregation,
5. The relationship between life-history traits and individual welfare.

This framework is not unique to habitat fragmentation and could be used to analyse the welfare effects of other environmental changes.

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