



## **BORDERS ON THE RISE: THE UNINTENDED EVOLUTIONARY CONSEQUENCES OF BORDER BARRIERS ON NATURAL POPULATIONS**

**Scott P. Egan, Ph.D.**

**Mattheau Comerford, M.Sc.**

**Glen R. Hood, Ph.D.**

**Linyi Zhang, M.Sc.**

**Kelly L. Weinersmith, Ph.D.**

December 2018

© 2018 by the James A. Baker III Institute for Public Policy of Rice University

This material may be quoted or reproduced without prior permission, provided appropriate credit is given to the author and the James A. Baker III Institute for Public Policy.

Wherever feasible, papers are reviewed by outside experts before they are released. However, the research and views expressed in this paper are those of the individual researcher(s) and do not necessarily represent the views of the James A. Baker III Institute for Public Policy.

Cover image courtesy of Jeffrey Glassberg, Ph.D. (March 28, 2016): View of U.S.-Mexico border barrier in Quitobaquito Springs, Organ Pipe National Monument, Pima County, Arizona

Scott P. Egan, Ph.D.

Mattheau Comerford M.Sc.

Glen R. Hood, Ph.D.

Linyi Zhang, M.Sc.

Kelly L. Weinersmith, Ph.D.

“Borders on the Rise: The Unintended Evolutionary Consequences of Border Barriers on Natural Populations”

## Introduction

Predicting the biological implications of human-made barriers dividing natural populations is a critical and urgent challenge for scientists and policymakers worldwide (Carroll et al. 2014). Inspired by the documented increase of ‘border barriers,’ or anthropogenic barriers along international borders, on a global scale (Figure 1; Vallet 2014; Linnell et al. 2016; Trouwborst et al. 2016), this report addresses the biological impacts of these barriers on natural populations, with a focus on evolutionary changes. While typically built for geopolitical and security reasons, border barriers can also have unintended consequences for biodiversity.

The construction of border barriers is not a new phenomenon (Figure 1; Vallet 2014; Linnell et al. 2016; Trouwborst et al. 2016). From the Great Wall of China, to the Berlin Wall, to the contemporary walls between the U.S. and Mexico, humanity’s history of erecting border barriers spans thousands of years (Linnell et al. 2016; Trouwborst et al. 2016). Current border barriers exist between Israel and the West Bank, Malaysia and Thailand, India and Pakistan, Iran and Iraq, China and Mongolia, and Botswana and Zimbabwe, among others (Linnell et al. 2016; Trouwborst et al. 2016). Given the global scale of border barriers, we know surprisingly little about their impact on ecological and evolutionary outcomes in natural populations (e.g., Lasky et al. 2011). Moreover, there is no clear review directly summarizing the potential evolutionary impacts of border barriers, at a time when biodiversity is rapidly declining on a global scale (Butchart et al. 2010).

There are many reasons for this lack of information, which is partially due to the fundamental characteristics of border barriers. First, border barriers are built between two countries, which have different laws and practices associated with conducting scientific research on the biological impacts of these structures (Trouwborst et al. 2016). Second, border barriers are commonly built for security reasons, and there is often restricted access to these areas on either side as a result. Third, best practices and strategies for mitigating the negative effects of human-made barriers on wildlife could compromise the intended security purposes of border barriers. Fourth, environmental laws intended to protect biodiversity along border areas can be temporarily waived in the interest of national security and safety. Fifth, borders are often created along natural geographic boundaries (Newman and Paasi 1998), therefore border barriers can amplify the historical effects of natural barriers on biodiversity.

This report addresses the evolutionary impacts of border barriers. We summarize data directly from border barriers studies and provide supporting information from studies of other anthropogenic barriers, such as roads, dams, and game fences. To this end, we first provide a brief overview of what can be learned from geographic isolation under natural conditions. Second, we address changes to the movement of individuals and gene flow between populations. Third, we highlight three predicted evolutionary outcomes in response to border walls: (1) divergence due to natural selection and/or genetic drift as gene flow decreases; (2) immediate and long-term changes to effective population size, including population bottlenecks and changes to genetic variation; and (3) inbreeding and

inbreeding depression. For each of these outcomes, we provide evidence from theory and previous studies on the biological consequences of human-made structures to show how local populations can respond to border barriers.

## **Predictions from natural geographic isolation**

Border barriers are a human-made form of geographic isolation, which is defined as population or species that live in areas that are typically near each other but do not overlap in space because of some barrier that keeps them separated. Typically, geographic isolation arises when geographic barriers prevent gene flow between previously interbreeding populations of the same species (Mayr 1963). Geographic isolation has been the subject of extensive research and can therefore provide a framework for what we might observe among populations and species divided by a border barrier (Mayr 1963). Natural geographic barriers can include glaciers, mountain ranges, and continental drift, and physical distance may also be considered a geographic barrier to gene flow (Hutchinson and Templeton 1999).

Geographic isolation decreases gene flow by reducing movement between isolated populations (Wright 1943). Thus, one might predict that as gene flow decreases, populations can diverge and evolve along different paths. Consistent with this prediction, many studies have documented a strong negative association between the amount of gene flow between populations and the degree of divergence in their behavior or morphology (Mayr 1963; Räsänen and Hendry 2008). Moreover, this observation has been supported by verbal and quantitative genetic models demonstrating that as the number of individuals moving between populations decreases, populations can diverge and evolve differently (Räsänen and Hendry 2008).

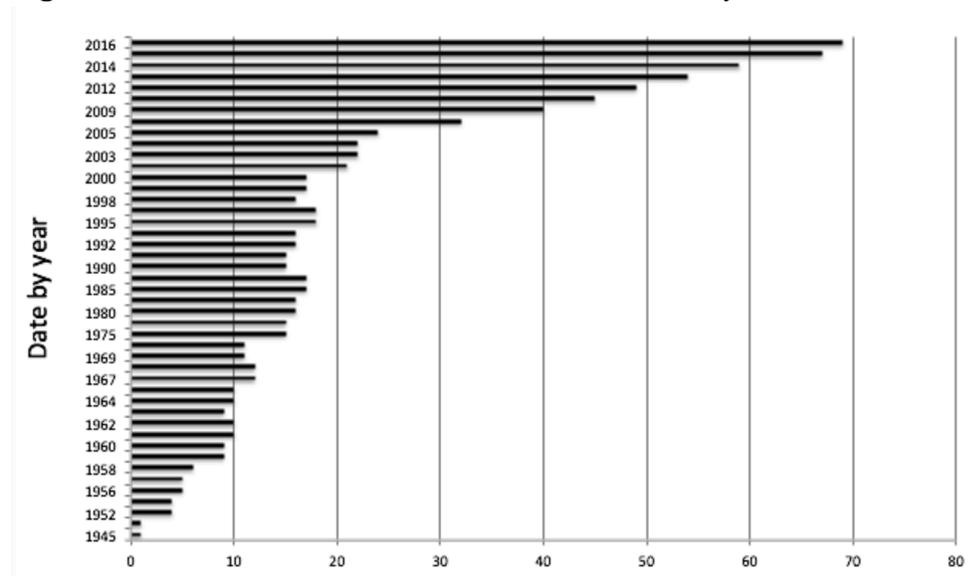
In addition to evolutionary divergence, data on the effects of reduced gene flow between populations suggest a set of correlated or sequential effects that can ultimately lead to decreased fitness and local extinction. First, theory predicts that reductions in gene flow due to changes in geographic barriers are expected to (1) decrease genetic diversity within populations, and (2) increase the effects of genetic drift, which is the influence of random chance on the genetic variation within populations (Nei et al. 1983). These effects should be stronger if the emergence of the geographic barrier also reduces population size (Nei et al. 1975). In certain cases where population sizes decrease dramatically, this can also lead to or increase inbreeding depression, which is the reduced biological fitness of a population as a result of breeding among related individuals that leads to an increase in the expression of deleterious, or harmful, mutations (Nei et al. 1975; Frankham 1995). As population sizes and genetic diversity decrease and inbreeding depression increases, isolated populations may be prone to local extinction due to the lack of genetic variation and inability to respond to future environmental changes (Frankham 1995; Frankham and Ralls 1998), such as the barrier itself and/or sudden shifts in ecological conditions caused by the barrier. Collectively, this work on natural geographic isolation provides a framework for understanding the potential effects of border barriers on natural populations.

## Biological impacts of border walls and other human-made barriers

### *Changes to movement and gene flow*

Human-made barriers reduce animal movement and gene flow through multiple mechanisms, including changing movement directly by physical obstruction and indirectly through behavioral avoidance, or by killing migrants through entanglement (i.e., getting tangled or caught in a barrier) and direct strikes (i.e., hitting a barrier directly, which causes injury and death). These mechanisms can operate independently or in combination to reduce gene flow between populations separated by a barrier.

**Figure 1.** Number of Border Barriers Present Globally



Source: Vallet 2014 and Elisabeth Vallet, University of Quebec at Montreal.

First, border barriers present a physical obstruction to an organism's movement (Aspi et al. 2009; Flesch et al. 2010; Ito et al. 2013). Aspi et al. (2009) found the genetic differentiation between adjacent grey wolf (*Canis lupus lupus*) populations separated by the Finland-Russia border barrier to be similar to the genetic differentiation between more geographically separated wolf populations, suggesting the possible role of the border barrier in reducing genetic exchange between populations. Ito et al. (2013) tracked Mongolian gazelles (*Procapra gutturosa*) and Asiatic wild asses (*Equus hemionus*) across the international border of Mongolia and China. They found that none of the 36 individuals tracked crossed the border during their 2002-2012 study, even though some animals used areas adjacent to the border (Ito et al. 2013). In addition, Flesch et al. (2010) explored the potential impact of border barriers in blocking the migration of a flying species, the ferruginous pygmy owl (*Glaucidium brasilianum*), whose habitat lies along the U.S.-Mexico border area. Flesch et al. (2010) discovered the average flight height is 1.4 meters, well below the height of a 4 meter high border wall, and only 23% of the owls were observed to fly higher than 4 meters. The authors concluded that the construction of a border wall in this region would likely reduce the owls' ability to migrate across the border.

Reduced movement due to border walls can also occur due to active avoidance of the barrier itself. Unfortunately, very few studies have directly tested the impact of border barriers on animal behavior. However, for other human-made border types like roads or fences, construction is usually accompanied by the removal of vegetation and increased human activities, which change microhabitats and increase human disturbance in the surrounding areas (Mader 1984; Flesch et al. 2010; McCallum et al. 2014). Several studies suggest that animals might develop avoidance behavior in response to these changes. For instance, in the study of the effect of roads on the movement of eight forest-dwelling carabid beetle species (Carabidae; Coleoptera) and two species of mice (*Apodemus flavicollis* and *Celthronomys glareolus*), Mader (1984) found that these organisms rarely crossed roads despite their high mobility. Of the 10,186 individual carabid beetles included in this mark and recapture study, only 11 individuals were captured on the opposite side of the road. Highways also proved to be absolute barriers for both species of mice, as none of the 121 individuals released were found to have crossed these roads. Mader (1984) argued that changes to the microhabitats along the road (e.g., removal of vegetation and microclimate change) and increased human disturbance (e.g., road noise and car headlights) may explain why animals avoid the road barrier. In a more recent example, McCallum et al. (2014) found a decreased appearance of puma (*Puma concolor*) and coati (*Nasua narica*) in areas with barriers (roads, railways, and fences) relative to areas without barriers in four protected areas in Arizona. Similarly, D'Amico et al. (2015) discovered that the presence of a road network decreased the probability of observing red deer (*Cervus elaphus*) by 40% and wild boar (*Sus scrofa*) by 55%. The red deer populations exhibited significant genetic differences consistent with reductions in gene flow associated with roads in this region (D'Amico et al. 2015).

Finally, border barriers can reduce gene flow by killing migrants. Multiple studies have demonstrated the effect of roads on animal mortality, which can impact population persistence, genetic variation, and gene flow (reviewed by Fahrig and Rytwinski 2009; Jackson and Fahrig 2011). In addition, some studies have explored the impact of border barriers on animal mortality specifically (Olson et al. 2009; Pokorny et al. 2017). Pokorny et al. (2017) conducted a ten-month study to estimate the mortality rate of ungulates attempting to cross a razor-wired fence along the 455 km Slovenia-Croatia border. They found 0.12 deaths per kilometer, or over 50 observed deaths in the ten-month period (Pokorny et al. 2017). Olson et al. (2009) described a mass death event due to entanglement of Mongolian gazelles (*Procapra gutturosa*), where hundreds of individuals were found dead after the migration of thousands across the Mongolia-Russia border.

### Three evolutionary outcomes in response to border barriers

#### *Natural selection and genetic drift due to reductions in gene flow*

The changes in migration and gene flow between populations due to border barriers have the potential to induce evolutionary change. In fact, many studies have suggested that border barriers can and do result in evolutionary divergence between populations (Hartl et al. 1991; Aspi et al. 2009; Atwood et al. 2011; Kaczensky et al. 2011). For example, Su et al. (2003) examined populations of six plant species found on either side of the Juyong-guan

section of the Great Wall of China, which was constructed more than 600 years ago. Populations of all six plant species, including wind- and insect-pollinated species, exhibited significant genetic differentiation when separated by the wall compared to populations separated by comparable geographic distances without a wall (Su et al. 2003).

Experiments have also manipulated gene flow between populations and measured evolutionary divergence. In general, experimental evidence shows that gene flow suppresses adaptive evolutionary divergence, such that populations will diverge quickly when barriers are constructed (Reichert 1993; Nosil 2009). Reichert (1993) tested whether gene flow was constraining adaptive divergence in the spider *Agelenopsis aperta*, which exhibited a genetically based difference in antipredator behaviors between environments. In one pair of populations that did not exhibit this difference, Reichert (1993) constructed a barrier to gene flow using fences that reduced dispersal between the environments. After just a single generation, one population evolved the predicted antipredator behavior for that environment, thereby confirming that gene flow was constraining adaptive divergence. In a complementary study, Nosil (2009) reported increased adaptive divergence in genetically based cryptic color patterns between a pair of stick insect (*Timema cristinae*) populations following the construction of a parking lot in the middle of a long-term research site. These two studies provide experimental evidence that human-made structures may reduce gene flow in nature and that these reductions can prompt rapid adaptive divergence in genetically based phenotypes between separated populations.

When human-made structures are created, there is another important effect where the environments are physically changed due to the barrier. This can increase the magnitude of natural selection between environments. For example, Heinen-Kay et al. (2014) sampled three species of *Gambusia* fishes in 43 tidal creeks across six islands in the Bahamas. They found that anthropogenic barriers changed the environmental conditions experienced by populations on one side, including decreased abundance of predators, increased conspecific density (i.e., increased competition), and decreased salinity. This led to consistent evolutionary changes in each of the three species, including changes to male genital shape and allometry (Heinen-Kay et al. 2014). In a separate study of the same three species of *Gambusia* fishes, Giery et al. (2015) found that populations in fragmented habitats had fewer dorsal-fin spots, which is an important trait in mate choice. However, the magnitude and trajectory of divergence differed among species.

Dams and other impoundments along rivers also reduce gene flow and increase the magnitude of natural selection due to changes in environmental conditions. Upstream reservoirs in impounded systems exhibit changes in the resources available to fish, along with abiotic changes to depth and flow rate, which can lead to stronger divergent selection between populations upstream and downstream of the dam. Two conceptually similar studies demonstrate rapid changes in two stream fishes, the bullhead minnow (*Pimephales vigilax*; Haas et al. 2010) and the black-tail shiner (*Cyprinella venusta*; Cureton and Broughton 2014). In each study, comparisons across multiple river systems found changes in morphology between populations, including significant changes to body depth, head shape, and fin placement in the upstream populations in reservoirs relative to the

downstream populations in flowing waters, consistent with the changes to environmental conditions (Haas et al. 2010; Cureton and Broughton 2014).

**Figure 2.** View of a field beyond U.S.-Mexico border barrier in Penitas, Hidalgo County, Texas



Source: Image courtesy of Jeffrey Glassberg, Ph.D. (December 5, 2010)

Random effects causing genetic drift may also play an important role in generating divergence following the construction of a human-made barrier. This may be especially true if the construction of the barrier causes a reduction in population sizes in that area due to phenomena like habitat destruction associated with barrier construction (Nosil 2009) or death due to the barrier itself, such as direct physical strikes, entanglements, or separation of resources (Olson et al. 2009; Pokorny et al. 2017). For example, Nosil (2009) documented a significant decrease in stick insect population associated with a human-made barrier, from over ~140,000 individuals before construction to estimates around 1,200 individuals after the barrier had been built. In addition, Olson et al. (2009) described the death of hundreds of Mongolian gazelles due to entanglement at the Mongolia-China border. Furthermore, genetic drift has greater effects in populations that are already small prior to barrier construction, such as among endangered or threatened species. This is especially critical for the U.S.-Mexico border region, as the ranges of over 100 U.S. endangered species overlap with this area (IPaC 2018).

### *Population bottlenecks and changes in genetic variation*

Population bottlenecks occur when the size of a population is greatly reduced, thereby decreasing the size of the gene pool because much of the genetic variation in the original population has been lost. This may occur in association with border barriers if the creation of a barrier rapidly reduces population size. Severe bottlenecks will reduce genetic diversity (Nei et al. 1975), as will splitting one connected population into multiple smaller populations (i.e., metapopulations) (Gilpin 1991). More genetically diverse individuals and populations often have higher fitness (e.g., Reed and Frankham 2003; Leimu et al. 2006), which allows them to adapt to local environments (e.g., Bridle et al. 2009; Paaby and Rockman 2014; Takahashi et al. 2016). Reductions in genetic diversity and decreased fitness caused by border barriers could thus have important implications for the long-term persistence of populations and species residing along the border.

Studies examining border barriers suggest that these structures influence genetic diversity (Hartl et al. 1991; Aspi et al. 2009; Atwood et al. 2011; Kaczensky et al. 2011), but few studies address this issue explicitly. A study that examined bighorn sheep (*Ovis canadensis nelsoni*) living in the U.S.-Mexico border region found that the sheep do not appear to be negatively impacted by the border, as they exhibit high genetic diversity and show little or no evidence of having gone through a population bottleneck (Buchalski et al. 2015). However, it is difficult to draw broad conclusions about how border barriers impact genetic diversity based on the handful of studies that have directly addressed this issue. Other anthropogenic barriers may provide some insights here as well. For example, roads are also anthropogenic barriers that are frequently associated with a reduction in genetic diversity (Reh and Seitz 1990; Keller and Largiadèr 2003; Epps et al. 2005; reviewed by Holderegger and Di Giulio 2010). For example, a study of the same species of bighorn sheep (*Ovis canadensis nelsoni*) demonstrated that anthropogenic barriers (including roads) that have separated populations for over 40 years are associated with a 15% loss of genetic diversity over this time period (Epps et al. 2005). However, not all studies observe bottlenecks or reductions in genetic diversity associated with roads (Keller et al. 2004; Kuehn et al. 2007; Gauffre et al. 2008). For example, in the flightless ground beetle (*Abax parallelepipedus*), highways result in genetic differentiation but not a loss of genetic diversity or evidence of a bottleneck—likely because of large population sizes (Keller et al. 2004). In general, more work is needed to fully understand the impact of anthropogenic barriers on genetic diversity.

### *Inbreeding and inbreeding depression*

Inbreeding is the biological phenomenon in which two genetically related individuals mate and produce offspring; it is a symptom of small population size and/or a lack of outbreeding opportunities with genetically dissimilar individuals (Andren 1994). Inbreeding over multiple generations will lead to an increased assembly of recessive deleterious mutations (Charlesworth and Charlesworth 1987). This genetic erosion has negative fitness consequences that are both immediate (e.g., sterility, offspring inviability, and reduced phenotypic plasticity) and latent (e.g., reduced offspring fecundity) (Ralls et al. 1988; Acevedo-Whitehouse et al. 2003). The sum of these resulting fitness costs is referred to as inbreeding depression (Keller and Waller 2002). Populations with inbreeding depression

experience increased risk of extinction (Frankham 1995; Saccheri et al. 1998; Reed et al. 2002). In the special case of border barriers, this extinction risk may be magnified, as inbreeding depression has been shown to reduce a population's ability to overcome environmental change (Lande 1988; Takahashi et al. 2016; Sandner and Matthies 2018).

Theoretical and empirical evidence have also shown that the fragmentation of natural habitats increases inbreeding rates in plant (e.g., Jump and Penuelas 2006) and animal (e.g., Andersen et al. 2004) populations due to isolating effects. Consequently, isolating barriers, such as those constructed along geopolitical borders, have the capacity to dramatically affect inbreeding depression potentials (Reh and Sietz 1990). The small number of studies that have examined the effects of border barriers on inbreeding have found that when such obstacles were coupled with small population size, the probability of inbreeding increased. For example, Aspi et al. (2009) followed grey wolves (*Canis lupus lupus*) that reside along the Russia-Finland border and found strong indicators of inbreeding in the smaller Russian wolf populations. Additionally, inbreeding complicates other challenges brought on by barriers. For example, studies of the ocelot (*Leopardus pardalis*) in the southern U.S. have observed decreased genetic diversity and elevated levels of homozygotes as a consequence of isolation due to anthropogenic habitat fragmentation (Haines et al. 2005). The only viable remedy for mediating the risk of ocelot inbreeding is an effort to reinvigorate gene flow with the larger adjacent Mexican ocelot population (Janecka et al. 2014), and the likelihood of success in reuniting populations on either side of the border would be greatly hindered by the development of a southern border wall dividing the U.S. and Mexico (Lasky et al. 2011). In a related study, Daleszczyk and Bunevich (2009) argue that the removal of a border fence between Belarus and Poland would greatly reduce the probability of inbreeding depression in reintroduced bison populations that were already genetically similar prior to their separation.

The probability of inbreeding can also change when movement corridors in or around border barriers are sealed or altered relative to an organism's natural movement patterns, ranging behavior, and spatial land use. As a result, a herding effect can occur, when large numbers of individuals from the same species are funneled or congregate into an area either adjacent to a barrier or into a smaller core area away from a disturbed barrier habitat (Tracy et al. 2013; Williamson and Williamson 1984). Reh and Seitz (1990) studied the land use effects on the genetic structure of the common frog (*Rana temporaria*) and demonstrated that roads acted as impermeable barriers to frogs, instantaneously reducing local population sizes. They also found that these anthropogenic barriers altered not only the frog's habitat but also its behavior, in that reproduction was favored along roadside ditches rather than in ephemeral ponds. As a result, the roads led to increased adult contact with siblings and therefore more inbreeding. Similarly, fence barriers like those along protected borders have been shown to herd larger herbivores and carnivores. Fence lines have led to the herding of blue wildebeest (*Connochaetes taurinus*) in Kruger National Park in South Africa (Whyte and Joubert 1988), grey wolves (*Canis lupus lupus*) along the Russia-Finland border (Aspi et al. 2009), and African wild dogs (*Lycaon pictus*) in the De Beers Venetia Limpopo Nature Reserve in South Africa (Davies-Mostert, et al. 2013). Consistent with these observations, bobcats

(*Lynx rufus*) and coyotes (*Canis latrans*) spend more time along the sides of major highways than anywhere else in their ranges in California (Riley et al. 2006).

## Conclusions

Border barriers are expanding rapidly on a global scale (Figure 1; Vallet 2014; Linnell et al. 2016; Trouwborst et al. 2016). In this report, we show that border barriers can have unintended but important biological consequences for biodiversity by (1) restricting or altering migration and movement of individuals or populations; (2) inducing changes to the selective environment and increasing the effects of genetic drift; (3) changing effective population sizes and reducing genetic diversity; and (4) increasing inbreeding and inbreeding depression. Despite a dramatic increase in the proliferation of border barriers in recent years and their documented biological impacts on biodiversity, there is much more work to be done. Studies of other anthropogenic barriers can inform predictions on the effect of border barriers and provide a framework for analyzing their impact. As border barriers are being constructed at a near exponential rate, there is a dire need for more research on their evolutionary implications.

## References

- Acevedo-Whitehouse, K., F. Gulland, D. Greig, and W. Amos. 2003. "Inbreeding: disease susceptibility in California sea lions." *Nature* 422, no. 6927 (March): 35.
- Andersen, L.W., K. Fog, and C. Damgaard. 2004. "Habitat fragmentation causes bottlenecks and inbreeding in the European tree frog (*Hyla arborea*)." *Proceedings of the Royal Society B: Biological Sciences* 271, no. 1545 (June): 1293-1302.
- Andren, H. 1994. "Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review." *Oikos* 71, no. 3 (December): 355-366.
- Aspi, J., et al. 2009. "Genetic structure of the northwestern Russian wolf populations and gene flow between Russia and Finland." *Conservation Genetics* 10, no. 4 (August): 815-826.
- Atwood, T.C., et al. 2011. "Modeling connectivity of black bears in a desert sky island archipelago." *Biological Conservation* 144, no. 12 (December): 2851-2862.
- Bridle, J.R., S. Gavaz, and W.J. Kennington. 2009. "Testing limits to adaptation along altitudinal gradients in rainforest *Drosophila*." *Proceedings of the Royal Society B: Biological Sciences* 276, no. 1661 (April): 1507-1515.
- Buchalski, M.R., et al. 2015. "Genetic population structure of Peninsular bighorn sheep (*Ovis canadensis nelsoni*) indicates substantial gene flow across US-Mexico border." *Biological Conservation* 184 (April): 218-228.
- Butchart, S.H.M., et al. 2010. "Global biodiversity: Indicators of recent declines." *Science* 328, no. 5982 (May): 1164-1168.
- Carroll, S.P., et al. 2014. "Applying evolutionary biology to address global challenges." *Science* 364, no. 6207: 1245993.
- Charlesworth, D., and B. Charlesworth. 1987. "Inbreeding depression and its evolutionary consequences." *Annual Review of Ecology and Systematics* 18 (November): 237-268.

- Cureton II, J.C., and R.E. Broughton. 2014. "Rapid morphological divergence of a stream fish in response to changes in water flow." *Biology Letters* 10, no. 6 (June): 20140352.
- Daleszczyk, K., and A.N. Bunevich. 2009. "Population viability analysis of European bison populations in Polish and Belarusian parts of Bialowieza Forest with and without gene exchange." *Biological Conservation* 142, no. 12 (December): 3068-3075.
- D'Amico, M., S. Periquet, J. Roman, and E. Revilla. 2015. "Road avoidance responses determine the impact of heterogeneous road networks at a regional scale." *Journal of Applied Ecology* 53, no. 1 (February): 181-190.
- Davies-Mostert, H.T., M.G.L.D. Mills, and W. Macdonald. 2013. "Hard boundaries influence African wild dogs' diet and prey selection." *Journal of Applied Ecology* 50, no. 6 (December): 1358-1366.
- de Paula, A.S., L. Diotaiuti, and C. Galvao. 2007. "Systematics and biogeography of Rhodniini (Heteroptera; Reduviidae: Triatominae) based on 16S mitochondrial rDNA sequences." *Journal of Biogeography* 34, no. 4 (April): 699-712.
- Elias, M., et al. 2009. "Out of the Andes: patterns of diversification in clearwing butterflies." *Molecular Ecology* 18, no. 8 (April): 1716-1729.
- Epps, C.W., et al. 2005. "Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep." *Ecology Letters* 8, no. 10 (October): 1029-1038.
- Fahrig, L., and T. Rytwinski. 2009. "Effects of roads on animal abundance: an empirical review and synthesis." *Ecology and Society* 14, no. 1: 21.
- Flesch, A.D., et al. 2010. "Potential effects of the United States-Mexico border fence on wildlife." *Conservation Biology* 24, no. 1 (February): 171-181.
- Frankham, R. 1995. "Inbreeding and extinction: a threshold effect." *Conservation Biology* 9, no. 4 (August): 792-799.
- Frankham, R., and K. Ralls. 1998. "Conservation biology - Inbreeding leads to extinction." *Nature* 392, no. 6675 (April): 441-442.
- Frantz, A.C., et al. 2012. "Comparative landscape genetic analyses show a Belgian motorway to be a gene flow barrier for red deer (*Cervus elaphus*), but not wild boars (*Sus scrofa*)." *Molecular Ecology* 21, no. 14 (July): 3445-3457.
- Gauffre, B., A. Estoup, V. Bretagnolle, and J.F. Cosson. 2008. "Spatial genetic structure of a small rodent in a heterogeneous landscape." *Molecular Ecology* 17, no. 21 (November): 4619-4629.
- Giery, S.T., C.A. Layman, and R.B. Langerhans. 2015. "Anthropogenic ecosystem fragmentation drives shared and unique patterns of sexual signal divergence among three species of Bahamian mosquitofish." *Evolutionary Applications* 8, no. 7 (August): 679-691.
- Gilpin, M. 1991. "The genetic effective size of a metapopulation." In *Metapopulation Dynamics: Empirical and Theoretical Investigations*, edited by M. Gilpin, 165-175. London: Academic Press.
- Haas, T.C., M.J. Blum, and D.C. Heins. 2010. "Morphological responses of a stream fish to water impoundment." *Biology Letters* 6 (June): 803-806.
- Haines, A.M., et al. 2005. "Evaluating recovery strategies for an ocelot (*Leopardus pardalis*) population in the United States." *Biological Conservation* 126, no. 4 (December): 512-522
- Hartl, G., F. Reimoser, R. Willing, and J. Köller. 1991. "Genetic variability and differentiation in roe deer (*Capreolus capreolus* L) of Central Europe." *Genetics Selection Evolution* 23: 281.

- Heinen-Kayet J.L., H.G. Noel, C.A. Layman, and R.B. Langerhans. 2014. "Human-caused habitat fragmentation can drive rapid divergence of male genitalia." *Evolutionary Applications* 7, no. 10 (December): 1252-1267.
- Hendry, A.P., T. Farrugia, and M.T. Kinnison. 2008. "Human influences on rates of phenotypic change in wild animal populations." *Molecular Ecology* 17, no. 1 (January): 20-29.
- Holderegger, R., and M. Di Giulio. 2010. "The genetic effects of roads: A review of empirical evidence." *Basic and Applied Ecology* 11, no. 6 (September): 522-531.
- Hutchinson, D.W., and A.R. Templeton. 1999. "Correlation of pairwise genetic and geographic distance measures: inferring the relative influences of gene flow and drift on the distribution of genetic variability." *Evolution* 53, no. 6 (December): 1898-1914.
- Information for Planning and Consultation (IPaC). 2018. *Information for Planning and Consultation*. U.S. Fish and Wildlife Service. <https://ecos.fws.gov/ipac/>.
- Ito, T.Y., et al. 2013. "Fragmentation of habitat of wild ungulates by anthropogenic barriers in Mongolia." *PLoS ONE* 8: e56995.
- Jackson, N.D., and L. Fahrig. 2011. "Relative effects of road mortality and decreased connectivity on population genetic diversity." *Biological Conservation* 144, no. 12 (December): 3143-3148.
- Janecka, J.E., et al. 2014. "Loss of genetic diversity among ocelots in the United States during the 20<sup>th</sup> century linked to human induced population reductions." *PLoS ONE* 9: e89384.
- Jump, A.S., and J. Penuelas. 2006. "Genetic effects of chronic habitat fragmentation in a wind-pollinated tree." *Proceedings of the National Academy of Sciences* 103, no. 21 (May): 8096-8100.
- Kaczensky, P., et al. 2011. "Connectivity of the Asiatic wild ass population in the Mongolian Gobi." *Biological Conservation* 144, no. 2 (February): 920-929.
- Keller, I., and C.R. Largiadèr. 2003. "Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles." *Proceedings of the Royal Society B: Biological Sciences* 270, no. 1513 (February): 417-423.
- Keller, I., W. Nentwig, and C.R. Largiadèr. 2004. "Recent habitat fragmentation due to roads can lead to significant genetic differentiation in an abundant flightless ground beetle." *Molecular Ecology* 13, no. 10 (October): 2983-2994.
- Keller, L.F., and D.M. Waller. 2002. "Inbreeding effects in wild populations." *Trends in Ecology & Evolution* 17, no. 5 (May): 230-241.
- Kuehn, R., et al. 2007. "Genetic effect of transportation infrastructure on Roe deer populations (*Capreolus capreolus*)." *Journal of Heredity* 98, no. 1 (January-February): 13-22.
- Lande, R. 1988. "Genetics and demography in biological conservation." *Science* 241, no. 4872 (September): 1455-1460.
- Lasky, J.R., W. Jertz, and T.H. Keitt. 2011. "Conservation biogeography of the US-Mexico border: a transcontinental risk assessment of barriers to animal dispersal." *Diversity and Distribution* 17, no. 4 (July): 673-87.
- Leimu, R., P. Mutikainen, J. Koricheva, and M. Fischer. 2006. "How general are positive relationships between plant population size, fitness and genetic variation?" *Journal of Ecology* 94, no. 5 (September): 942-952.
- Linnell, J.D.C., et al. 2016. "Border security fencing and wildlife: the end of the transboundary paradigm in Eurasia?" *PLOS Biology* 14: e1002483.

- Mader, M.J. 1984. "Animal habitat isolation by roads and agricultural fields." *Biological Conservation* 29, no. 1:81-96.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge: Belknap Press.
- McCallum, J.W., J.M. Rowcliffe, and I.C. Cuthill. 2014. "Conservation on international boundaries: the impact of security barriers on selected terrestrial mammals in four protected areas in Arizona, USA." *PLoS ONE* 9: 1-11.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. "The bottleneck effect and genetic variability in populations." *Evolution* 29, no. 1 (March): 1-10.
- Nei, M., T. Maruyama, and C. Wu. 1983. "Models of evolution of reproductive isolation." *Genetics* 103, no. 3 (March): 557-559.
- Newman, D., and A. Paasi. 1998. "Fences and neighbors in the postmodern world: boundary narratives in political geography." *Progress in Human Geography* 22, no. 2 (April): 186-207.
- Nosil, P. 2009. "Adaptive population divergence in cryptic color pattern following a reduction in gene flow." *Evolution* 63, no. 7 (July): 1902-1912.
- Olson, K.A., et al. 2009. "Fences impede long-distance Mongolian gazelle movements (*Procapra gutturosa*) in drought-stricken landscapes." *Mongolian Journal of Biological Sciences* 7: 45-50.
- Paaby, A.B., and M.V. Rockman. 2014. "Cryptic genetic variation: evolution's hidden substrate." *Nature Reviews Genetics* 15: 247-258.
- Pokorny, B., et al. 2017. "Border fence: a new ecological obstacle for wildlife in Southeast Europe." *European Journal of Wildlife Research* 63: 1.
- Ralls, K., J.D. Ballou, and A. Templeton. 1988. "Estimates of lethal equivalents and the cost of inbreeding in mammals." *Conservation Biology* 2, no. 2 (June): 185-193.
- Räsänen, K., and A.P. Hendry. 2008. "Disentangling interactions between adaptive divergence and gene flow when ecology drives diversification." *Ecology Letters* 11, no. 6 (June): 624-636.
- Reed, D.H., D.A. Briscoe, and R. Frankham. 2002. "Inbreeding and extinction: the effect of environmental stress and lineage." *Conservation Genetics* 3, no. 3 (September): 301-307.
- Reed, D.H., and R. Frankham. 2003. "Correlation between fitness and genetic diversity." *Conservation Biology* 17, no. 1 (February): 203-237.
- Reh, W., and A. Seitz. 1990. "The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*." *Biological Conservation* 54, no. 3:239-249.
- Reichert, S.E. 1993. "Investigation of potential gene flow limitation of behavioral adaptation in an aridlands spider." *Behavioral Ecology and Sociobiology* 32, no. 5 (May): 355-363.
- Riley, S.P.D., et al. 2006. "Fast-track: a southern California freeway is a physical and social barrier to gene flow in carnivores." *Molecular Ecology* 15, no. 7 (June): 1733-1741.
- Roe, R.H., J. Gibson, and B.A. Kingbury. 2006. "Beyond the wetland border: estimating the impact of roads for two species of water snakes." *Biological Conservation* 130, no. 2 (June): 161-168.
- Saccheri, L., et al. 1998. "Inbreeding and extinction in a butterfly metapopulation." *Nature* 392: 491-494.

- Sandner, T.M., and D. Matthies. 2018. "Inbreeding limits responses to environmental stress in *Silene vulgaris*." *Environmental and Experimental Botany* 147: 86-94.
- Su, H., et al. 2003. "The Great Wall of China: a physical barrier to gene flow?" *Heredity* 90: 212-219.
- Takahashi, Y., et al. 2016. "Lack of genetic variation prevents adaptation at the geographic range margin in a damselfly." *Molecular Ecology* 25, no. 18 (September): 4450-4460.
- Tracy J.A., et al. 2013. "Mapping behavioral landscapes for animal movement: a finite mixture modeling approach." *Ecological Applications* 23, no. 3 (April): 654-669.
- Trouwborst, A., F. Fleurke, and J. Dubrulle. 2016. "Border fences and their impacts on large carnivores, large herbivores and biodiversity: an international wildlife law perspective." *Review of European, Comparative and International Environmental Law* 25, no. 3 (November): 291-306.
- Vallet, E. 2014. *Borders, Fences and Walls: State of Insecurity?* New York: Routledge Publishing.
- Whyte, I.J., and S.C.J. Joubert. 1988. "Blue wildebeest population trends in the Kruger National Park and the effects of fencing." *South African Journal of Wildlife Research* 18, no. 3 (January): 78-87.
- Williamson, D., and J. Williamson. 1984. "Botswana fences and the depletion of Kalahari wildlife." *Onyx* 18, no. 4 (October): 218-222.
- Wright, S. 1943. "Isolation by distance." *Genetics* 28, no. 2 (March): 114-138.