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EFFECTS OF NATURAL AND ARTIFICIAL BARRIERS ON THE GENETIC DIVERSITY OF WILD ANIMAL SPECIES: A REVIEW

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Summary: Barriers are various natural or artificial borders that fragment the landscape. They reduce the habitat, block pathways and separate the populations into smaller segments. A natural barrier may be a sierra, a valley, a river, a sea, the distance between optimal habitats etc. Human-related barriers are the roads, fences and cities.

This article discusses about comparison different barrier types' effects on different species, with the focus on the species size, the barrier type and the effect's strength in the case of multiple species and barriers.

According to the literature the greater barriers mostly have greater effects on species, especially on smaller, non-flying species that are less likely to migrate, but it is revealed that the evaluation is not fully standardized yet. Most of the authors used Wright's F_{st} value, which is an exact number, but researchers have handled it differently. In some cases they were more permissive and ascribed less impact (mostly in the case of low F_{st} values). On the other hand, there are authors who valorized the low F_{st} values because of the possible cascade effect caused by genetic division and changing behaviour.

This review describes the possible effects of barriers, but every species and habitat is unique, therefore the method described should not be regarded as 100% accurate. Comparing by the F_{st} valuesthe effects may be predicted more precisely prior to carrying out the impact studies, thus the additional costs and the impact on the actual species will be easier to estimate.

Keywords: natural barrier, artificial barrier, genetic diversity, review

Introduction

Barriers are various natural or artificial borders that fragment the landscape (Bihari et al., 2011). According to Steeleet et al. (2009), the barrier effect could operate as a permeable filter, hence species with different dispersal potentials, breeding behaviours and/or physiological traits respond differently to topography, and therefore show differences in their patterns of spatial genetic structure across a shared landscape (Sanchez-Montes et al., 2017). A natural barrier may be a sierra, a valley, a river, a sea, the distance between optimal habitats etc. Human-related barriers are the roads, fences and cities that block the passage between territories (McRae et al., 2005). In addition, there are special barrier types. Behavioural barriers act through the phenotype, or the courting behaviour (Garamszegi et al, 2009). Gene-level barriers limit gene transfer by different vectors. This is a real hazard: gene transfer was found to occur between the three domains of life (Archaea, Bacteria, Eucarya) and viruses in all possible ways. To prevent this, organisms "use" degrading enzymes, DNA restriction, recombination and repair, or different codons and receptors (González-Candelas & Francino, 2012).

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Only a few barriers are completely impassable, and the affected species continuously adapt to it. On the other hand, for small species even low-traffic roads act as borders (Andrews, 1990). Fragmented landscapes reduce gene flow, thereby decreasing diversity and the number of individuals, and may finally cause genetic drift and a bottleneck effect. A small population is more vulnerable to environmental changes, so can easily become extinct, and resettlement is also more difficult through the barriers (Andrews, 1990; Cushman et al., 2006; Shirk et al., 2010). When a physical barrier ceases to exist, its impact is drastically reduced within 50–200 generations, but the populations never regain their original status (Irwin, 2002).

Natural barriers

River and lakes

The effectiveness of a river as a functional barrier to gene flow and as an active participant in evolutionary divergence among populations positively relates to the size (width, flow rate and depth) of the river. Hence species differentiation should increase along both sides of the given river from its headwaters all the way to the mouth as the barrier widens and the potential of cross-river gene flow diminishes (Hershkovitz, 1977). However, different results of genetic diversity and differentiation are expected depending upon the species under study, since different species have varied levels of ecological characteristics and potentials of dispersal (Patton et al., 1994). A counting and observation study done on grasshoppers by Willey & Willey (1967) showed that the black canyon of the Gunnison River in Colorado may have had a nearly complete barrier effect on gene flow between populations of the oedipodine grasshopper *(Arphiaconspersa sp.).*Studies conducted on rodents using the mitochondrial cytochrome b gene by Patton et al. (1994) suggested that gene flow rates in *M. hispidus* within the Rio Jurua drainage area (Brazil) were relatively low, and this trend applied equally to gene flow along each bank of the river as well as across it. Similarly, the river Tocantins (Brazil) may have acted as a barrier to gene flow in *Saguinus niger* (small-bodied primates) according to the results of a study based on the D loop of mtDNA conducted by Vallinoto et al. (2006). In this case, the difference between the two populations is larger than between species, thus these populations may also belong to different species. Another small species, the common shrew (*Sorex araneus*) is also exposed to a strong barrier effect. The river Rhone (Switzerland, Italy) and dry slopes hinder its migration, causing 13.9% of the diversity between populations (Lugon-Moulin & Hausser, 2002). Another study on white-tailed deer and the rivers of Michigan (USA) shows a differentiation of r^2=0,396 between populations (Locher et al., 2015). In Portugal the Duoro and Tejo rivers' barrier effect on wild boar populations was studied by Ferreira et al. (2006, 2009). High gene flow rates were observed, which means that the impact of the rivers is not as significant as was thought before. The main factor that formed the genetic structure was more likely a recent bottleneck-effect. In Hungary the effects of Lake Balaton and the river Danube were investigated on wild boars. The results revealed that they had weak effects, in agreement with recent studies (Scandura et al., 2008; Wanjala et al., 2017). In their study using microsatellite loci Cushman et al. (2006) found that the Kootenai River in Americaacted as a barrier to gene flow in bear, however they claimed that the results were poorly supported by evidence.

Waterfalls have also been listed as a potential barrier to gene flow for the aquatic species. Crispo et al. (2006) studied the effects of waterfalls on gene flow in Trinidadian guppies (*Poecilia reticulata*) along the Marianne River using microsatellite loci. Their results suggested that the waterfall along this river had a significant effect on gene flow between populations of *P. reticulata*. However, Shaw et al. (1994) attributed the genetic divergence to stochastic factors. The Strait of Gibraltar is a place where at least 14 km of open sea separates the two shores from each other. Scientists studied 3 groups of common bat (*Myotis myotis*) from each side, with 20 individuals per group. The bat samples were investigated using 6 microsatellite and mtDNA markers. The authors did not find any combination between individuals from different shores, which means that the 14km of open sea completely isolates the groups (Castella et al., 2000).

Mountains and suboptimal areas

Amphibians' dispersal and population connectivity are often affected by slope, elevation and mountain ridges. Several phylogeographic and population genetic studies have suggested that genetic variation among amphibian populations are pronounced for populations separated by these geographical features. For example, landscape genetic analyses based on microsatellite loci in Columbia spotted frogs (*Rana luteiventris*) concluded that landscape features had a profound effect on gene flow between amphibian populations (Funk et al., 2005). However, studies by Zhan et al. (2009) on the population genetic structure of the Chinese wood frog (*Rana chensinensis*) in the Tsinling and Daba Mountain region of Northern China revealed that these mountains had no significant impact on the population genetic structure of *R. chensinensis*. This could be a result of high population connectivity and extensive juvenile dispersal powers. The results of a study on quantifying the differential effect of a major mountain ridge on the genetic structure of four sympatric species with different life history traits revealed that the Sierra de Guadarrama (Guadarrama mountains) act as a strong barrier to gene flow for *P. cultripes* and, to a lesser extent, for *E. calamita, H. molleri and P. perezi* (frog species) and this differential dispersal potential can be traced back to historical genetic variation in amphibian communities (Sánchez-Montes et al, 2017). On the other hand, a small, fast mammal, the common shrew (*Sorex araneus*) can cross passes as high as 500–1000 m, thus the ridges are not considered to act as significant barriers for them (Lugon-Moulin & Hausser, 2002). Studies using both nuclear and mitochondrial DNA markers on Canadian lynx, a North American mammal of the cat family, which is distributed all across North America, indicated that the Rocky Mountains represent a barrier to gene flow in Western Canada (Rueness et al., 2003). Concerns about the vulnerability of mountain lions (*Puma concolor*) to extinction incited the study of the genetic structure of their populations in California by Ernest et al. (2003) using microsatellite loci. The results of the study suggested that there existed a partial barrier of gene flow, indicating that mountainous landscape could affect gene flow in big cats. Markov (1954) studied wild boars (*Sus scrofa*), and suggested that the Rila-Rodopen (Bulgaria) subpopulation differs from the Southern subspecies by morphologicalfeatures. Genov et al. (1991) described two morphological types based on skull size measurements. Both studies conclude that the Balkan Mountains are the barrier between the two ecotypes. This hypothesis was also confirmed by Randi et al. (1992) and Hartl et al. (1993). Between 2000 and 2005 a genetic study was conducted in this area, with 298 samples from Bulgaria and 63 from Germany. According to this study, the Bulgarian population truly separated into 2 genetic groups (Northern-Southern differentiation owing to the Thrakcian valley), but its diversity index numbers are not greater than values in other European populations (Nikolov et al., 2009; Scandura et al., 2008). The results are consistent with the former results, but in their opinion the higher Thracian lowland is the main barrier between the groups, due to the presence of a highway and the lack of big forests (Nikolov et al., 2009). Sprem et al. (2016) investigated the Croatian wild boars. In total 264 blood samples were collected from 10 regions between 2006 and 2009, and three continental, two Mediterranean and one mixed subpopulation was found. The Dinaric Alps showed to be only a weak barrier between subpopulations, whereas distance had a greater effect on gene flow.

Sea ditches causethe same effects in the open sea as do hollows on land. Three groups of Antarctic octopuses (*Pareledoneturqueti*) were investigated in the Southern Ocean. The results revealed that a distance of 150 km is nothing for the octopuses: there was panmixia between the first two groups (F_{st}=0), but between the second and third groups there was a km-deep ditch, and it almost completely blocked gene flow (F_{st}=0.74) (Allcock et al., 1997). Similar results were obtained with mitochondrial control-region testing on black perch (*Embiotoca jacksoni*) near the California coast (F_{st}=0.59). In this case, the sand spits between atolls were also extremely strong barriers (F_{st}=0.72) (Bernardi, 2000).

Long distances between optimal habitats are difficult to pass for animals. Cougar (*Puma concolor*) tissue samples were collected in 4 states of the USA, and investigated with 16 microsatellite loci. In the area examined 2 populations and 6 subpopulations were found, where the main populations differ extremely significantly with a value of R=0.67, and the subpopulations differ significantly between R=0.14 and R=0.71, depending on the distance (McRae et al., 2005). In a European study, of 3 sparrow species (domestic, Spanish and Italian) were surveyed with 14 microsatellite loci. The researchers found 2 different clusters (Spanish and domestic), and showed that the Italian sparrow is hybridized with the other 2 species. According to their results the former populations lived in small groups in an extensive habitat, therefore hybridization was necessary. Nowadays their populations have increased due to modern agriculture, thus the reproductive barrier is becoming stronger and isolates the species from cross-mating. The Italian sparrows were isolated from the former population by the Alps and the Mediterranean Sea (Hermansen et al., 2011).

Human-associated barriers

Roads, railroads and fences

Almost all countries, both well developed and developing ones have extensive road networks across landscapes. These constitute the primary cause of habitat fragmentation for many animal species, sub-dividing populations with enormous demographic and genetic consequences, therefore affecting effective connectivity between species populations and sub-populations isolated by roads (Corlatti et al., 2009; Forman & Alexander, 1998) and thereby reducing the size of wildlife populations through limiting their ability to move from one area to another (Andrews, 1990).

The road effect depends on the neighbouring species' morphology, physiology and behaviour. It is easier for large mammals to adapt to roads, and they can cross them especially in periods of lower traffic, for example at night (Forman & Deblinger, 1998). Beyond the barrier effect, noise and light also disturb the animals, and collisions decimate the populations (Andrews, 1990). A study of a four-lane highway in Massachusetts reports that the effects of the various factors extend to 100–1000 m from the road itself. The road modifies the landscape, impacts the plant species, the air flow, the microclimate, the water regime etc. (Forman & Deblinger, 2000). The frequency of collisions is increased by the vegetation's proximity to the road and is proportional to the distance from wildlife overpasses (Clevenger et al., 2003). There usually are multiple overpasses/underpasses built on highways, but their efficiency is highly questionable: one study reports an overpass that was only 6% efficient (Ballók, 2011). Caribous (*Rangifer tarandusgranti*) avoid high-traffic roads by 600m and low- or non-traffic roads by 300m (Murphy & Curatolo, 1987). High-traffic roads are usually protected with fences, therefore the two effects mostly occur together. However, in some cases fences are located at political borders, or are erected to protect forests.

According to Forman & Alexander (1998), the term road corridor refers to the road surface including its maintained road sides and any parallel vegetated strips, such as a median strip between lanes in a highway. Roads are highlighted by several theories describing their functional roles in ecosystems such as conduits or filters, habitats, sources and sinks; their effectiveness depends on width, connectivity and usage intensity (Seiler, 2001and Forman & Alexander, 1998). Seiler (2001) describes areas adjacent to road infrastructure as highly disturbed environments, often even hostile for many wildlife species, yet they can still provide attractive resources such as shelter, food or nesting sites, and facilitate the spread of species along with the direction of the road. "Small mammal populations separated by highways may be partially or completely isolated from one another due to low dispersal capabilities, low probability of surviving highway crossing attempts and/or avoidance of the area adjacent to highways" (Reesa & Mill, 2003). Several studies reveal that roads have an impact on seasonal migration, genetic differentiation and diversity and gene flow among populations in many wildlife species. Kociolek and Clevenger examined different fencing techniques and their impact on various groups of animals. According to their results walls higher than 81 cm are strong barriers to small mammals, amphibians and reptiles. When a wall is higher than 150 cm, it also becomes a barrier to medium and large mammals (Kociolek & Clevenger, 2007).

Molecular genetics (microsatellite markers) combined with behavioural and ecological studies was used to understand the impacts of roads on the population structure and connectivity of timber rattlesnakes (*Crotalus horridus*) by Clark et al. (2010). It was revealed that snakes in hibernacula isolated by roads had significantly lower genetic diversity and higher genetic differentiation than snakes in hibernacula in a contiguous habitat. In their population genetic study to compare gene flow adjacent to and across the highway for red-backed vole, deer mice and vagrant shrew, Reesa & Mill (2003) showed a decline in gene flow of 11–37% in all species; capture-recapture methods to compare movement adjacent to and across the highway reported about 2.5 times more movements adjacent to highways than across the highways. Similar results were found by Gerlach & Musolf (2000) in their study on bank vole in Southern Germany and Switzerland.

Roads also increase the mortality rate in some species, and this can in turn influence the sex ratio. For example, in the case of both freshwater turtle species (*Pseudemys floridana, Trachemys scripta, Sternotherus odoratus*) (Aresco, 2005) and barn owls (*Tyto alba*) (Moore & Mangel, 1996) females were shown to be more prone to road kill than males, and hence the decline in population is due to the low number of females. Caswell (2001), Aresco (2005), Rosen & Lowe (1994) and Hels & Buchwald (2001) established that fluctuations in sex ratio affect population growth, especially if the fluctuation leads to a decline in the number of females in the population.

By use of partial Mantel tests, multiple linear regression and coalescent simulations to infer changes in gene flow and diversity of nuclear and mitochondrial DNA markers, Epps et al. (2005) found that highways had a significant effect on gene flow in desert bighorn sheep populations in South-Eastern California. The reduction in genetic diversity of 15% for the past 40 years has been possibly due to habitat fragmentation by human activities, and can subject bighorn sheep to the threat of extinction.

Roads are also often assumed to have insignificant influence on gene flow between populations in large mammals. This could be because it is easy for these animals, especially for fast-moving species, to cross the road/highway. However, high-traffic roads are the major source of mortality for mammals. The Trans-Canada Highway and the effect of crossing on gene flow in grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) was also studied by Sawaya et al. (2014) by comparing genetic data generated from wildlife crossings with data collected from greater bear populations. The results indicated that 47% of black bears and 27% of grizzly bears that used crossings successfully bred, including multiple males and females of both species. However, a genetic discontinuity was detected at the highway in grizzly bears but not in black bears, implying that the highway barred gene flow in grizzly bears.

At a Floridian highway a 1.1-m-high concrete wall was erected. Tunnels (2.4*2.4*44 m) were built under the road to facilitate passing. Next year the former number of roadkills (2411) decreased by 93.5% to 158. Only 13 vertebrates were hit, 12 amphibians/reptiles and a coyote. The wall also protected the larger mammals from getting hit, even though only one otter and one lynx were spotted in the culvert (Dodd et al., 2004).For timber rattlesnakes roads with less than 3000 cars/day are weak barriers, and roads with more than 10000 cars/day are strong barriers (Clark et al., 2010). Near the French A11 motorway (4 lines, average traffic 2000 cars/hour, no culverts) agile frog (*Rana dalmatina*) populations were surveyed. 7 populations live far from the highways, and another 4 live close to it. The conditions were similar, except for the distance from the road. Heterozygosity was significantly lower in the fragmented populations (H_{obs}=0.151 vs H_{obs}=0.358), and the fixation indices were greater (F_{st}=0.238 vs F_{st}=0.022). In addition, lower density and increased mortality both endanger the populations living near the highway (Lesbarreres et al., 2006). This effect was also confirmed in another study, where the roads closer than 1.5 km to the lakes had significant impact on frog density ($F_{1,30}$=9.680, p=0.0046) (Carr & Fahrig, 2001). Roads are strong threatening factors to amphibians, especially in the mating season, when the species are migrating. Building culverts is a good method for protecting them, but the tube’s length, temperature, brightness, water level and air flow are all important factors (Forman & Deblinger, 1998; Forman & Deblinger, 2000). In the Doñana Biosphere Reserve a road system's effect was studied by D'Amico et al (2016). The target species were the wild boar (*Sus scrofa*) and the red deer (*Cervus elaphus*). On 40 sampling tracks (200m long, 1m wide) 194 traces and feces were recorded. It was determined that the traffic and the road's surface affect the presence of the species considerably less than the change in vegetation. The road system decreased the potential habitat of the wild boar and the red deer by 55% and 40%, respectively, which could be reduced to 9% by eliminating the unused roads and rehabilitating the landscape.According to Spanish studies, the number of wild boar collisions is strongly correlated with the population density (r=0.86). An average collision costs almost 11000 euros, and happens mostly in areas where the wild boar density is more than 8 individuals/100 ha (Rosell et al., 2008; Rosell et al., 2013).

Kornilev et al. (2006) observed the Eastern boxturtles' (*Terrapene carolina*) behaviour at a railroad. Only 1 of the 12 tracked turtles could crawl over the rails, and another 9 escaped at the railroad crossing. Railroads are also serious threats for larger species. Ito et al. (2008, 2013) investigated Mongolian gazelle (*Procapra gutturosa*) and onager (*Equus hemionus*) populations in the neighbourhood of the Trans-Mongolian railroad line and the Mongolian-Chinese border fences.
In total 33 gazelles and 16 onagers were tracked by radio telemetry. During the monitoring period none of them crossed the railroad, and only one crossed the fences. On the other hand, carcasses were found on the railway, which means that gazelles could pass it. The railroad cuts the gazelles' migration line and decreases their chance to survive in multiple ways. Another group of scientists studied the same railways' Kazakhstanian section and its impact on ungulates (*Saiga tatarica*, *Procapragutturosa*, *Equus hemionus*). According to their study, the vegetation on the Chinese side suits them much better, therefore the species search for a pass to get through (Olson et al., 2013; 2015).

Even flying species are affected by roads and railroads. In Massachusetts, bumblebees were studied in an area cut by a 14-m-wide railroad. The bumblebees trapped were marked and released on either the original or the other side. From the 367 marked bees 31% were observed again on the side where they had been released and only 3 were seen on the other side, and only 11% of the bees crossed the railroad. The conclusion was that even though the road is not a direct barrier, the bumblebees only cross it when this is necessary in order to forage for food (Bhattacharya et al., 2003). Forest birds (owls, hawks, woodpeckers etc.) are the most disturbed by the noise of the roads: they keep away from highways as far as 650 m. Grassland birds are less sensitive to noise pollution, but they are more sensitive to fragmentation (Forman & Deblinger, 1998).

In the case of highly mobile carnivores like bobcats and coyotes, the exceedingly busy Ventura Freeway in the United States affected reproduction of the individuals that crossed to the other side of the road. Combined radio telemetry data and genetically based assignments suggested that 3–32% of the sampled carnivores crossed the freeway over a 7-year period, and the genetic isolation of the population on either side of the freeway showed consistency with a migration fraction of less than 0.5% per generation. The results, therefore, showed that individuals that managed to cross the freeway rarely reproduced (Riley et al., 2006).

In a study the impacts of the Trans-Canadian highway (2 to 4 lines/side, average daily traffic 14000 cars, maximum daily traffic 35000 cars) and Bow Walley road (2 lines, daily traffic 1000–3000 cars) were investigated. In a 3-year period 677 hit animals were found, comprising 47% birds, 46% mammals and 7% amphibians. The result of the analysis was the following: birds and mammals were more likely to be hit on ground level than on raised level (Clevenger et al., 2003).

In a 55*40 km area in France, 1148 roe deers (*Capreolus capreolus*) were sampled. This location is bisected bya 4-line highway with 3 wildlife overpasses. The landscape is also fragmented by canals and the Garonne river.One population with 2 subpopulations was shown by the statistical analyses. The resultsreveal that a highway with properly designed overpasses is still a weak barrier and a few weak barriers together can cause differentiation (Coulon et al., 2006). In Michigan the white-tailed deer was studied, and again the barrier with the strongest effect was the highway (Locher et al., 2015). However, large mammals like bears can easily cross the highways. In Canada, a 45-km-long highway section (fenced with 2.4-m-high fence) has 25 overpasses. The bears can easily pass through them, thus the differentiation levels for black (*Ursus americanus)* and grizzly bears (*Ursus arctos*) are only Fst=0.007 and Fst=0.02, respectively (Sawaya et al., 2014).

Some fences are built for reasons other than fencing off roads, for example for protecting forests or defending national borders. In these cases there are no road effects, so these fences simply block passage. Worldwide more than 40 national borders are fenced (Feischmidt & Szerbhorváth, 2017). According to a hypothesis the large herbivore populations that are fenced into areas smaller than 250 km^2 (other references suggest 500 km^2) first increase their densities. When the density reaches a certain limit, the animals overutilize the habitat, which causes a decline in the number of individuals (Macnab, 1983). The abnormal increase in density was verified by Ostfeld (1944), but the habitat degradation wasn't observed in his review, where small mammals were studied. Even so in game preserves the forest is chewn up to the deer's height – evidently larger mammals can make greater impact. In Hungary's southern borders a 175-km-long fence was built in 2015. Its impacts have not been studied, but it cuts through the habitat of the southern mole rat (*Nannospalax montanosyrmiensis*), a highly endangered species represented only by a few hundred individuals (2015:444) (Németh et al., 2015). At the border between the USA and Mexico scientists found that the border decreased the habitats of the species studied by 28% on average, and also more than 50% of the small home-range species were at risk because of the barrier (Lasky et al., 2011).
In Australia fences are built to exclude dingoes, and in those protected territories the density of kangaroos and emus is significantly greater (Caughley et al., 1980). The surroundings of the fences are also avoided by red deers (*Cervus elaphus*) (Ballók, 2011); megaherbivores such as the African elephant (*Loxodonta africana*) also use these territories less intensively, which could affect the entire habitat through a cascade effect (Vanak et al., 2010).

Human disturbance itself can function as a barrier. Urbane populations of the common frog (*Rana temporaria*) have twice greater genetic difference at a distance of 2.3 km (Fst=0.388) than have rural onesat a distance of 41 km (Fst=0.145) (Hitchings & Beebee, 1996). All other human barriers also have a disturbing effect, some of which were mentioned above.

Discussion

It has been determined in recent studies that natural and human-related barriers have a serious impact on the formation of populations and subpopulations, even new species. Natural barriers are usually formed gradually, within a relatively long time, whereas human-related ones can be erected from one day to another and can suddenly cut the former habitat in two and divide the population. The species' body size and ability to migrate greatly influence the barrier's effect. Nevertheless, beyond the physical obstacle there are multipleeffects that make a difference, for example disturbance by light or noise, or a change in the habitat's flora.
As it is evident from the Table 1 below, in the majority of the studies reviewed the barrier's impact fits into the former descriptions, i.e. that motility is the strongest influencing factor. Studies discussing the most barrier types combined with the largest animal body size were compiled into the Table 1. Significant negative effect(s) was/were detected in almost every study. Interestingly, the authors of the articles don't evaluate the same level of impact the same way. Usually Wright's population differentiation index (F_{st}) values were calculated, thus the values between 0.05 and 0.15 are moderate, those between 0.15 and 0.25 are high, and values even higher indicate very high detachment (Wright, 1978). In some cases, however

(for example Epps et al., 2005; Riley et al., 2006), the slightly low F_{st} values were valorised because of the cascade-effect they can cause in the future. Thereforethe impact levels in the Table 1 are different from Wright's level. This strict belief coincides with Irwin's (2002) model study. He calculated that when a barrier ceases to exist, the population's genetic difference plunges suddenly (depending on the motility of the species). However, the differentiation value never reaches 0 again, i.e. the two populations are never reunited. This means that splitting a population into parts leads to permanent changes.

In conclusion, the barrier's division effect is unquestionable. Natural barriers have exerted their effects for a long time, therefore intervention in natural processes is only necessary in special cases (for example when species are in danger). On the other hand, human-related impacts appear drastically faster. A river does not "mean" to completely isolate two populations from each other, but we humans build afence for protecting the highway from every animal, therefore it (nearly) completely isolates the two sides.In such cases it is necessary to build wildlife over/underpasses (suitable for every neighbouring species)based on impact studies.Failureto do so has started irreversible processes. Maybe the loss of an allele, a small decline in population density and/or population fragmentation do not appear as a relevant loss at first, but the preservation of biodiversity, and minimizing the possible impacts of future effects are inevitable tasks for conservation.

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Table 1: The effect of various barriers on different types of animals.

Barrier type	Barrier	Species type	Species	Studied species	Effect	Reference
natural	canyon, river	small	oedipodine grasshopper	*Arphiaconspersa*	nearly complete isolation	Willey & Willey, 1967
	drainage	small, swimming	whiskered sole	*Monochirushispidus*	strong (?)	Patton et al, 1994
	river	small	black tamarin	*Saguinusniger*	strong (div=0.086)	Vallinoto et al, 2006
	river	small	shrew	*Sorexaraneus*	strong	Lugon-Moulin & Hausser, 2002
	lake, river	medium	wild boar	*Sus scrofa*	moderate (Fst= 0.066)	Wanjala et al, 2017
	river	big	white-tailed deer	*Odocoileus virginianus*	moderate (Fst= 0.019)	Locher et al, 2015
	river	big	black bear	*Ursusamericanus*	weak (?)	Cushman et al, 2006
	waterfall	small, swimming	Trinidadian guppy	*Poecilia reticulata*	extra strong (Fst=0.302)	Crispo et al, 2006
	sea (14 km)	small, flying	common bat	*Myotis myotis*	complete isolation	Castella et al, 2000
	mountain	small	4 frog species	-	strong	Sánchez-Montes et al, 2017
	mountain	small	chinese wood frog	*Rana chensiensis*	no (Fst=0.0878)	Zhan et al, 2009
	mountain	small	shrew	*Sorexaraneus*	no	Lugon-Moulin & Hausser, 2002
	mountain	medium	Canadian lynx	*Lynx canadensis*	moderate (Fst=0.0422)	Rueness et al, 2003
	mountain	medium	wild boar	*Sus scrofa*	moderate/strong (Fst=0.113-0.206)	Sprem et al, 2016

	mountain, river	big	American puma	*Puma concolor*	weak-moderate	Ernest et al, 2003
	mountain and sea	small, flying	sparrows	-	complete isolation	Hermansen et al, 2011
	trench	small, swimming	black perch	*Embiotocajacksoni*	extra strong (Fst= 0.59)	Bernardi, 2000
	trench	medium, swimming	antarctic octopus	*Pareledoneturqueti*	extra strong (Fst=0.74)	Allcock et al, 1997
	distance	small, swimming	black perch	*Embiotocajacksoni*	extra strong (Fst=0.72)	Bernardi, 2000
	distance	big	American puma	*Puma concolor*	strong (R=0.67)	McRae et al, 2005
	landscape	small	Columbia spotted frog	*Rana luteiventris*	strong, except distance	Funk et al, 2005
	landscape	medium	wild boar	*Sus scrofa*	Nei's distance D=0.002, Wright's Fst=0.05	Randi et al, 1992
	landscape	medium	roe deer	*Capreoluscapreolus*	Nei's distance D=0.0025	Hartl et al, 1993
	landscape	medium	wild boar	*Sus scrofa*	Nei's distance D=0.0032	Hartl et al, 1993
	landscape	medium	wild boar	*Sus scrofa*	moderate (Fst=0.08)	Vernesi et al, 2003
	landscape	medium	wild boar	*Sus scrofa*	strong (Fst=0.172)	Nikolov et al, 2009
	landscape	medium	wild boar	*Sus scrofa*	moderate/strong (Fst=0.138-0.178)	Ferreira et al, 2006, 2009
	landscape	big	red deer	*Cervus elaphus*	Nei's distance D=0.0076	Hartl et al, 1993
human related	road	small	agile frog	*Rana dalmatina*	strong (Fst=0.238)	Lesbarreres et al, 2006
	road, river	small	bank vole	*Clethrionomysglareolus*	moderate (Fst=0.081)	Gerlach & Musolf, 2000
	road	small	small vertebrates	-	increased mortality	Clevenger et al, 2003
	road	small	turtles	-	increased mortality, shifted sex ratio	Aresco, 2005
	road	small	snakes	-	estimated mortality: 22.5/km/year	Rosen & Lowe, 1994

					(observed: 13.5)	
	road	small	amphibians	-	increased mortality (probability of getting hit: 0.34-0.98)	Hels & Buchwald, 2001
	road	small	frog species	-	significant gene flow reduction (p=0.0046)	Carr & Fahrig, 2001
	railroad	small	eastern box turtle	*Terrapene carolina*	1/12 can climb the rails, 9/12 can escape through the crossing	Kornilev et al, 2006
	road	small	timber rattlesnake	*Crotalushorridus*	significant	Clark et al, 2010
	road	medium	coyote	*Canislatrans*	moderate (Fst=0.030-0.037)	Riley et al, 2006
	road	medium	bobcat	*Lynx rufus*	moderate (Fst=0.018-0.064)	Riley et al, 2006
	road	medium	desert bighorn sheep	*Ovis canadensis nelsoni*	strong (Fst=0.012-0.018)	Epps et al, 2005
	road	medium	roe deer	*Capreoluscapreolus*	no (Fst=0.008)	Coulon et al, 2006
	road	medium	wild boar	*Sus scrofa*	no (Fst=0.008)	Frantz et al, 2012
	road	medium	wild boar	*Sus scrofa*	reduce presence probability by 40%	D'Amico et al, 2016
	road	medium	wild boar	*Sus scrofa*	increased mortality	Rosell et al, 2008, 2013
	road	medium/big	ungulates	-	increased mortality	Bruiderink & Hazelbroek, 1996
	road	big	white-tailed deer	*Odocoileus virginianus*	no (Fst=0.019)	Locher et al, 2015
	road	big	grizzly	*Ursusarctos*	no (Fst=0.007)	Sawaya et al, 2014
	road	big	black bear	*Ursusamericanus*	no (Fst=0.02)	Sawaya et al, 2014
	road	big	red deer	*Cervus elaphus*	no (Fst=0.013)	Frantz et al, 2012
	road	big	red deer	*Cervus elaphus*	reduce presence probability by 55%	D'Amico et al, 2016
	road	big	caribou	*Rangifer tarandusgranti*	increased disturbance (mean movement increased to 2-7x)	Murphy & Curatolo, 1987
	railroad	big	mongolian gazelle	*Procapragutturosa*	0 of 16 tracked gazelles cross the	Ito et al, 2008, 2013

					barrier, but its not a complete barrier (carcasses are also found in the fenced area)	
	road, railroad	small,flying	bumblebee species	*Bombus sp.*	most bees remain on their original site (214/217), although relocated bees fly back to their original place (42/45)	Bhattacharya et al, 2003
	road	-	multiple species	-	affects 15-20% of USA land areas	Forman & Alexander, 1998
	road	-	multiple species	-	disturbs animals, increases mortality	Andrews, 1990
	road	-	multiple species	-	*disturbance up to ~1km, increased mortality*	Forman & Deblinger, 2000
	road	-	multiple species	-	low to high risk mostly based on size	Kociolek & Clevenger, 2007
	road	-	multiple species	-	mortality decreased by 65% with wall, strong isolation	Dodd et al, 2004
	fence	small	rodents	-	increased density in fenced area	Ostfeld, 1994
	fence	medium	Mongolian gazelle	*Procapragutturosa*	strong (?)	Olson et al, 2013, 2015
	fence	medium/big	multiple species	-	increased prey density without the predator	Caughley et al, 1980
	fence	big	African elephant	*Loxodonta africana*	increased disturbance (decreased foraging)	Vanak et al, 2010
	fence	-	multiple species	-	decreased habitat use (avg. 28%), main factor of risk (>50%)	Lasky et al, 2011
	fence	-	-	-	habitat degradation when fenced in too	Macnab, 1983

					small area	
	human disturbance	small	common frog	*Rana temporaria*	extra strong (Fst= 0.388)	Hitchings & Beebee, 1996

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