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The Effects of Hybridization on Predator-Prey Interactions and its Relation to Climate
Change

by

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Undergraduate honors thesis under the direction of

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Introduction

Hybridization, which is the interbreeding of two closely related species, is not uncommon in nature and can offer insight into evolution. However, it can also give insight into our future. As climate change occurs, species are changing their ranges (Parmesan 2006). This can lead to increased sympatry, thus, potentially increasing hybridization as new hybrid zones are created, as hybrid zones move, and increasing the number and range of existing species with an established hybrid zone. The effects on the parent species are varied; however, wide spread effects are less certain.

Here, I examined literature to study how hybridization affects predator-prey interactions and the implications of climate change (Abrams 2000; Bonsall and Hassell 2007). Four hybrid events will be examined: wolf (*Canis lupus*) × coyote (*Canis latrans*) hybrids, European Wildcat (*Felis silvestris silvestris*) × domestic cat (*Felis catus*) hybrids, mule deer (*Odocoileus hemionus*) × white-tailed deer (*Odocoileus virginianus*) hybrids, and artificially cultured × wild salmonids with focus on two separate species (*Salmo salar* and *Onchorynchus mykiss*).

Wolf - Coyote Hybrids

Hybridization among North American canids is not uncommon, partially due to wide hybridization zones (Roy et al. 1994). The majority of hybridization occurs in the north and northeastern continental United States and southeastern Canada, with no evidence of hybridization between coyotes and grey wolves west of the Rocky Mountains (Pilgrim et al. 1998; Way et al. 2010). The more recent hybridization of coyotes and wolves in the eastern part of the continent is believed to be partially due to anthropogenic facilitation (Leman et al. 1991). Historic deforestation and agricultural land clearing has decreased wolf habitat while at the same time increased suitable coyote habitat bringing the two species closer together and allowing for

more interactions. The eastern wolf (*Canis lupus lycaon*) is believed to be a bridging species, allowing gene flow between coyotes and grey wolves (Rutledge et al. 2010). In the western side of the continent, grey wolves have been recorded attacking coyotes and displaying aggressive behaviors. Coyote-wolf hybrids maybe limited to the eastern half of the continent because of grey wolves' aggression towards coyotes in the west and, consequently, less inclination to breed.

Evidence of introgression is primarily supported by mitochondrial DNA (mtDNA) analyses with coyote mtDNA found in eastern wolf populations (Leman et al. 1991) and by SNP genotyping (vonHoldt et al. 2011). This introgression appears to be unidirectional; coyotes introgressing into eastern and grey wolves. No mtDNA of wolves has been found within sampled coyotes or hybrids, supporting the idea of female coyotes breeding with male eastern wolves (Way et al. 2010). This hypothesis comes from the large size of eastern coyotes compared to western coyotes, suggesting the larger size common in wolves is passed to these coyotes. Whereas diet may play a role (e.g., larger prey items in eastern habitats), it is unlikely as coyotes would first have to be in a size range able to eat larger prey and unhybridized eastern coyotes are of a smaller size (Gittleman 1985; Kay et al. 2009). Unidirectional hybridization is further supported by a lack of wolf Y chromosome DNA found in coyote populations (Rutledge et al. 2010). It is hypothesized that F1 hybrids may backcross into coyote populations, a phenomena that would be undetectable by mtDNA (Leman et al. 2010). Allozyme analysis as a method of detection is also unsuitable due to small amount of differentiation among North American canids (Roy et al. 1994), placing the evidentiary burden principally on mtDNA.

Coyote-wolf hybridization presents far more benefits to coyotes than to wolves. Coyotes in hybrid regions are better predators of deer and able to consume a wider variety of prey due to their larger size, possibly allowing coyote populations to occupy the niche of wolves left open by

their lack of suitable habitat (Kay et al. 2009). Wolves, on the other hand, may become smaller and more coyote-like (Leman et al. 1991; vonHoldt et al. 2011). This would reduce the selection of large prey and possibly more direct competition with coyotes (Gittleman 1985). As this convergence in appearance occurs, it could have negative implications of wolf management. Under the Endangered Species Act (ESA), hybrids of species or subspecies are generally not recognized as protected (Hill 1993). The lack of protection is due to no present policy concerning hybrids, with each species granted protection on a case by case basis (Campton and Kaeding 2005). The recently delisted gray wolf was the only North American canid protected under the ESA, should protection ever be reinstated or given to the eastern wolf the extensive hybrid gene flow could dampen conservation efforts (Way et al. 2010).

Mule – White-tailed Hybrids

North America is home to two main deer species: the mule deer and the white-tailed deer. Mule deer populate most of the western half of North America whereas white-tailed deer populate a wider range from Canada to northern South America with the possible exception of North American deserts (Innes 2013a,b). The populations of these two overlap extensively and experience hybridization. Hybrids of the two species are rare in the wild and captivity, with the exception of western Texas (Geist 1998). Evidence exists to support the possibility for introgression. The two species also have very different anti-predator behaviors that may be affected by hybridization

Mule deer and white-tailed deer do not exhibit substantial spatial segregation because of shared diets (Anthony and Smith 1977). This keeps them in close proximity when the breeding season arrives, which is roughly the same time period for both species among part of their ranges (Innes 2013a,b). Evidence from mtDNA and serum albumin suggest hybrid individuals exist

throughout the region and backcross into parental species (Hughes and Carr 1993). Hybridization appears to favor introgression from mule deer into white-tailed deer with mule deer does mating with white-tailed bucks, and the F1 does breeding back into the white-tailed population, though opposite parentage is possible (Hughes and Carr 1993; Carr and Hughes 1993). This may partially be due to infertility in male hybrids, preventing F1 males from breeding back into either of the parent population (Hughes and Carr 1993). A notable exception is west Texas, where hybrids are common and F1 males are also fertile and can breed back into populations.

Though hybridization is rare between the two species, at only about two or three percent in some populations (Hughes and Carr 1993), lasting effects can be experienced by the F1 generation and backcrosses. The species differ in escape gait, whether to challenge or flee, and evasion tactics. Both species have distinct escape gaits when fleeing from predators: white-tailed deer gallop while mule deer are more inclined to stot, leaping with an arched back and stiff legs, though will gallop (Lingle 1993; Figure 1). Hybrids between the two have an intermediate escape gait that leans more towards mule deer. A normal stot is four and four, all hooves leaving and contacting the ground simultaneously, conferring increased stability on elevated terrain. A hybrid stot uses the two and two of a gallop. The forelimbs make contact with the ground after the leap before the hindlimbs (Figure 1). Of the three galloping escape gaits, the gallop of white-tailed deer is the fastest. The escape gait appears heavily genetic, and once hybridization occurs the escape gait in subsequent backcrosses does not appear to return to that of a pure member of either species. White-tailed deer and mule deer also differ in their overall predator response. While a white-tailed deer will flee, a mule deer is more likely to stand its ground, group together with its herd, and attack in face of a predator (Lingle 2001). The two species also will take different escape routes when faced with predators, such as coyotes; White-tailed deer prefer

gentle slopes that make quick fleeing downhill easy whereas mule deer prefer rugged slopes that they can ascend and have an advantage while standing their ground (Lingle 2002). When feeding in close proximity, mule deer increase their predation risk by utilizing the same gentle slopes as white-tailed deer.

Domestic cat - Wildcat hybrids

Hybridization in predators does not always affect the capabilities of one to hunt, such as coyotes able to hunt larger prey. In hybrids of domestic cats and wildcats of Europe, the parent species are physically similar which prevents expanded or contracted predation based on size (Krüger et al. 2009). Rather, it is a change in predation based on dietary niche.

European wildcats, an endangered species, hybridize to varying degrees throughout the continent with introgression mainly in the direction of domestic cats to wildcats (Pierpaoli et al. 2003). The most admixed population appears to be in Hungary. Why some regions have more extensive hybridization than others is unknown, though habitat is hypothesized to be a factor (Randi 2008). Wildcats and domestic cats, while having some cross over in diet, have opposite food habits. Wildcats are facultative specialists, feeding on small mammals with a preference for rabbits, whereas domestic cats are generalist and opportunist because, in addition to small mammals, they feed on birds, amphibians, and human food sources (Germain et al. 2009). Hybrids between the two species are in the middle but closer to wildcats; they feed on a wider variety of food sources but, unlike domestic cats, will feed on forest mice. It is here that the hybrids are more likely to encounter their wild parent species and back cross, introgressing domestic genes into the wildcat population.

As an endangered species, the risks of hybridization in wildcat populations are much greater than that of many others. This is elevated by their increasingly closer proximity to domestic cats

as humans encroach on and fragment wildcat habitat, running a risk of outbreeding depression (Oliveira et al. 2008).

Hatchery and Wild Salmonid Hybrids

Much like Wildcats, salmonids face a threat from hybridization from a more domesticated relative. Artificially cultured fish from hatcheries undergo artificial selection from humans and vary genetically from wild populations (Cross and King 1983). Escapes from fish culture operations are not uncommon, and the fish can interbreed back into the wild population (Fraser et al. 2010). Whereas artificially selected alleles might offer benefits to wild fish, such as disease resistance, such crosses are not without consequences.

Atlantic salmon (*Salmo salar*), when hybridized with artificially cultured fish, experience several changes, such as morphology and smolt age (Fraser et al. 2010). Among these changes is the anti-predator response. In this case, the anti-predator response is taken as the time for early stages to resume foraging after a predator attack with faster times indicating more willingness to expose oneself to predators still in the area (Houde et al. 2010). Artificially cultured fish have a reduced anti-predator response compared to wild populations with hybrids exhibiting an intermediate behavior. The intermediate anti-predator response, though higher than artificially cultured fish, remains lower than that of the wild parent population (Figure 2). Like the backcrosses of mule deer and white-tailed deer hybrids, the resulting traits of Atlantic salmon hybrids do not fully return to that of wild individuals (Fraser 2010).

Steelhead trout (*Oncorhynchus mykiss*) experiences a similar phenomenon. Fry of artificially cultured fish are more likely to be eaten by predators and in greater numbers than their wild counterparts (Berejikian 1995). Hybrids of the two populations express a greater willingness to risk predator exposure in order to forage (Johnsson and Abrahams 1991). Fry of wild steelheads

must weigh foraging against exposure and make tradeoffs. They may spend more time lower in the water column where they cannot forage as well but are safer from predation. Artificially cultured steelheads, however, are selected for high growth and do not have to make such tradeoffs. Thus, hybridization potentially increases predation and reduces recruitment into adult stocks.

Climate Change and Hybridization

Climate change has affected the range and migrations of species. Expansion and contraction of species ranges and the resulting hybrid zones can be traced throughout the Cenozoic era (Hewitt 2011). Both glacial and interglacial periods served to diverge some species while bring other species into closer proximity. Hybrid zones may have formed repeatedly in some species as climate shifted. Some of these hybrid zones resulted in introgression, as observed at present, while others led to reticulate evolution.

In modern times, species are responding to anthropogenic climate change. In general, species throughout the world are moving closer to the poles of their respective hemispheres (Parmesan 2006). In the Antarctic, species are responding to the loss of sea ice. Species, such as emperor penguins (*Aptenodytes forsteri*), that cannot migrate much further inland, are experiencing population declines while open ocean species are expanding their ranges as the sea ice recedes. Arctic species face a similar plight with more limited migration due to the pole being an ocean rather than a continent. Temperate species are expanding towards the poles as temperate areas change in temperature. Tropical species are invading temperate areas as temperate zones become more suitable habitat.

Through expanding ranges, climate change affects hybridization in five major ways: creating hybrid zones, moving hybrid zones, expanding hybrid zones, restricting hybrid zones, and

dissipating hybrid zones. The first, creating hybrid zones, occurs as sympatry increases as ranges shift (Garroway et al. 2010). This can potentially form new hybrid zones such as those between the southern flying squirrel (*Glaucomys volans*) and the northern flying squirrel (*Glaucomys sabrinus*). These two species produce fertile hybrids that backcross into both parental species yet there is no evidence of introgression, indicating a new hybrid zone has formed. The second way climate change affects hybridization, moving hybrid zones, occurs through range shifts of both sympatric species (Buggs 2007). Similar to the previous two, expanding hybrid zones can result from one or both parental species expanding their range into that of the other species. This is a common consequence of invasive hybridization such as what occurs between westslope cutthroat trout (*Oncorhynchus clarki lewisi*) and anthropogenically introduced rainbow trout (*Oncorhynchus mykiss*) (Hitt et al. 2003; Muhfeld 2014). As climate change warms water, the warm temperature inclined rainbow trout has been able to further expand its range into the cold inclined westslope cutthroat trout range (See Figure 3), leading to species becoming genetically extinct through hybrid swarm. The fourth method of change, the restricting of hybrid zones, is a result of the nature of hybrid zones. Similar in method to moving or expanding hybrid zones, populations may move or habitat within the hybrid zone may become unsuitable, discouraging dispersal into the area. Subject to species dispersals, this may lead to a hybrid zone shrinking as less individuals move into the area (Barton and Hewitt 1985). These factors, in more extreme circumstances, may also lead to the fifth outcome for hybrid zones based on climate change: dissipation. Unsuitable habitat may form a reproductive barrier, preventing hybridization between two species. As an example, sea level rise could expand a water body within a hybrid zone, preventing species from coming in contact with one another.

Discussion

As climate changes and more species become sympatric and hybridize, research will need to focus more on how these different hybrid and introgressed species interact. It is my hypothesis that the effects of hybridization are more wide spread. Here, I have used predator-prey interactions to demonstrate this using both predator and prey species.

Wolf-coyote hybrids and wildcat-domestic cat hybrids result from predator hybridization, each parent adapted to a different niche. In both cases, the hybrid individuals can use more food resources than at least one of their parents and introgress this ability back into a parental line through a change in size. In canids, the coyote is an example: normally restricted to medium and small prey, it becomes capable of utilizing large prey and can fill a wolf's niche. However, this comes at a cost at making the wolf a less efficient predator of large prey as introgression leads to a more coyote like appearance and size. In felines, wildcats are an example: wildcats have their diet expanded in the feline hybrid. Usually very selective, wildcat hybrids have their prey items expanded from small mammals to more general small vertebrates as hybridization with domestic cats occurs despite no morphological changes.

Mule deer- white-tailed hybrids and salmonid hybrids are prey species that have their anti-predator responses altered by their hybridization. The deer hybrid exhibits several possible clashes of anti-predator behavior: white-tailed deer will flee using a gallop and prefer gentle slopes to make escape easier whereas mule deer are more likely to stand their ground, utilizing rugged slopes as an advantage, and will stot as a means of escape. Hybrids, however, have an intermediate escape gait. The intermediate escape gait would, hypothetically, reduce fitness of the hybrids. Should they exhibit the white-tailed deer's preference for escape then they would be easier targets for predators depending on the terrain. It would also disadvantageous should the

hybrid have a white-tailed deer's preference for gentle slope but a mule deer's defense of standing its ground in face of predators. Because most hybrids are born to mule does, though, white-tailed behaviors may not be as problematic. However hybrid and backcrossed individuals cannot replicate a pure mule deer's escape gait, leaving them more vulnerable than mule deer when using mule deer anti-predator behaviors. This higher vulnerability to predators is likely a reason hybrid or introgressed individuals are rarely found. Salmonid hybrids between artificially cultured and wild populations also have increased vulnerability due to reduced anti-predator response. Artificial selection favors feeding over caution in artificially cultured salmonids, a trait carried over to their hybrid progeny. Should the hybrid individuals survive to reproduction, backcrosses with wild salmonids may not be able to fully regain a pure wild type anti-predator response.

Within predator-prey interactions, hybridization appears to heavily favor predators. Predators that fill different niches can expand one or both parent species prey selection through behavioral or morphological changes as seen in the feline and canid hybrids, with the exception of wolves, exemplified in this paper. Prey species, however, have evolved different anti-predator responses to predators. When these responses hinder one another or become absent, the hybrid of the two species becomes more vulnerable than its parents to predation losing any benefits from the mixing of genes. It is possible that the opposite holds true for predator and prey: that there are counteracting predatory behaviors and beneficial morphologies for prey. This would be an area of further research.

Climate change becomes a greater concern with this in mind for prey species. As hybrid zones change and more species hybridize, more predators may expand their selection of prey and more prey species may become vulnerable. While the increased vulnerability of prey species to

predation would limit backcrossing and introgression, the few hybrid individuals that manage to reproduce will have an impact on their parent species. It is also worth further researching trophic impacts on the expanding niche and generalists behaviors of hybrid and introgressed predators. Effects of climate change on trophic webs and ecosystems have long been a concern but in respect to hybridization it may be an area of neglect, causing more urgency to act than what was previously thought.

Literature Cited

- Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31: 79-105.
- Anthony, R. G., and Smith, N. S. 1977. Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. *Ecological Monographs* 47: 255-277.
- Barton, N. H., and Hewitt, G. M. 1985. Analysis of hybrid zones. *Annual review of Ecology and Systematics* 16: 113-148.
- Berejikian, B. A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2476-2482.
- Bonsall, M. B., and Hassell, M. P. 2007. Predator-prey interactions., 46-61 *in* R.M. May and A. R. McLean, editors. *Theoretical ecology*. Third Edition. Oxford University Press, Oxford, New York.
- Buggs, R. J. A. 2007. Empirical study of hybrid zone movement. *Heredity* 99: 301-312.
- Campton, D. E., And Kaeding, L. R. 2005. Westslope cutthroat trout, hybridization, and the US Endangered Species Act. *Conservation Biology* 19: 1323-1325.
- Carr, S. M., and Hughes, G. A. 1993. Direction of introgressive hybridization between species of North American deer (*Odocoileus*) as inferred from mitochondrial-cytochrome-b sequences. *Journal of Mammalogy* 74: 331-342.
- Cross, T. F., and King, J. 1983. Genetic effects of hatchery rearing in Atlantic salmon. *Aquaculture* 33: 33-40.

- Fraser, D. J., Houde, A. L. S., Debes, P. V., O'Reilly, P., Eddington, J. D., and Hutchings, J. A. 2010. Consequences of farmed-wild hybridization across divergent wild populations and multiple traits in salmon. *Ecological Applications* 20: 935-953.
- Garroway, C. J., Bowman, J., Cascaden, T. J., Holloway, G. L., Mahan, C. G., Malcolm, J. R., Steele M. A., Turner G., and Wilson, P. J. 2010. Climate change induced hybridization in flying squirrels. *Global Change Biology* 16: 113-121.
- Geist, V. 1998. *Deer of the world: their evolution, behaviour, and ecology*. Stackpole Books.
- Germain, E., Ruetten, S., and Poulle, M. L. 2009. Likeness between the food habits of European wildcats, domestic cats and their hybrids in France. *Mammalian Biology-Zeitschrift für Säugetierkunde* 74: 412-417.
- Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia* 67: 540-554.
- Hewitt, G. M. 2011. Quaternary phylogeography: the roots of hybrid zones. *Genetica* 139: 617-638.
- Hill, K. D. 1993. *Endangered Species Act: What Do We Mean by Species*, The. *BC Env'tl. Aff. L. Rev.* 20: 239.
- Hitt, N. P., Frissell, C. A., Muhlfeld, C. C., & Allendorf, F. W. 2003. Spread of hybridization between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1440-1451.
- Houde, A. L. S., Fraser, D. J., and Hutchings, J. A. 2010. Reduced anti-predator responses in multi-generational hybrids of farmed and wild Atlantic salmon (*Salmo salar* L.). *Conservation Genetics* 11: 785-794.

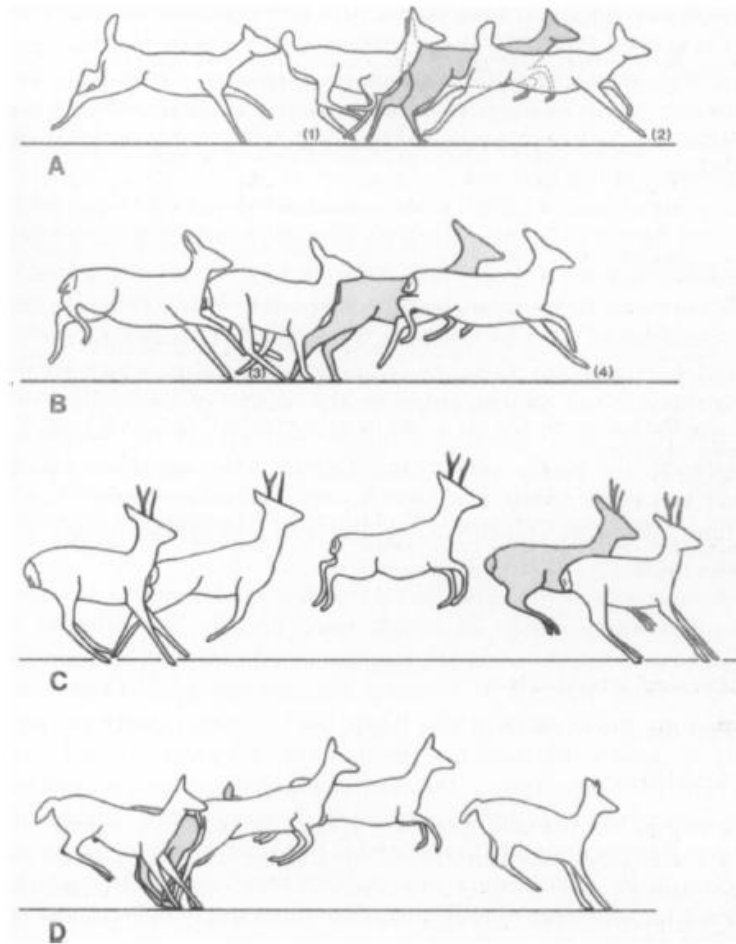
- Hughes, G. A., and Carr, S. M. 1993. Reciprocal hybridization between white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) in western Canada: evidence from serum albumin and mtDNA sequences. *Canadian journal of zoology* 71: 524-530.
- Innes, Robin J. 2013a. *Odocoileus hemionus*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/>
- Innes, Robin J. 2013b. *Odocoileus virginianus*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/>
- Johnsson, J. I., and Abrahams, M. V. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 243-247.
- Kays, R., Curtis, A., and Kirchman, J. J. 2009. Rapid adaptive evolution of northeastern coyotes via hybridization with wolves. *Biology letters*, rsbl20090575.
- Krüger, M., Hertwig, S. T., Jetschke, G., and Fischer, M. S. 2009. Evaluation of anatomical characters and the question of hybridization with domestic cats in the wildcat population of Thuringia, Germany. *Journal of Zoological Systematics and Evolutionary Research* 47: 268-282.
- Lehman, N., Eisenhaver, A., Hansen, K., Mech, L. D., Peterson, R. O., Gogan, P. J., and Wayne, R. K. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution* 45: 104-119.
- Lingle, S. 1992. Escape gaits of white-tailed deer, mule deer and their hybrids: gaits observed and patterns of limb coordination. *Behaviour* 122: 153-181.

- Lingle, S. 2001. Anti-Predator Strategies and Grouping Patterns in White-Tailed Deer and Mule Deer. *Ethology* 107: 295-314.
- Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology* 83: 2037-2048.
- Muhlfeld, C. C., Kovach, R. P., Jones, L. A., Al-Chokhachy, R., Boyer, M. C., Leary, R. F., Lowe, W. H., Luikart, G., and Allendorf, F. W. 2014. Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change* 4: 620-624.
- Oliveira, R., Godinho, R., Randi, E., and Alves, P. C. 2008. Hybridization versus conservation: are domestic cats threatening the genetic integrity of wildcats (*Felis silvestris silvestris*) in Iberian Peninsula?. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 2953-2961.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 45: 637-669.
- Pierpaoli, M., Biro, Z. S., Herrmann, M., Hupe, K., Fernandes, M., Ragni, B., Szemethy, L., and Randi, E. 2003. Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridization with domestic cats in Hungary. *Molecular Ecology* 12: 2585-2598.
- Pilgrim, K. L., Boyd, D. K., and Forbes, S. H. 1998. Testing for wolf-coyote hybridization in the Rocky Mountains using mitochondrial DNA. *The Journal of wildlife management* 62: 683-689.
- Randi, E. 2008. Detecting hybridization between wild species and their domesticated relatives. *Molecular ecology* 17: 285-293.

- Roy, M. S., Geffen, E., Smith, D., Ostrander, E. A., and Wayne, R. K. 1994. Patterns of differentiation and hybridization in North American wolflike canids, revealed by analysis of microsatellite loci. *Molecular Biology and Evolution* 11: 553-570.
- Rutledge, L. Y., Garroway, C. J., Loveless, K. M., and Patterson, B. R. 2010. Genetic differentiation of eastern wolves in Algonquin Park despite bridging gene flow between coyotes and grey wolves. *Heredity* 105: 520-531.
- vonHoldt, B.M., Pollinger, J.P., Earl, D.A., Knowles, J.C., Boyko, A.R., Parker, H., Geffen, ., Pilot, M., Jedrzejewski, W., Jedrzejewski, B., Sidorovich, V., Greco, C., Randi, E., Musiana, M., Kays, R., Bustamante, C.D., Ostrander, E.A., Novembre, J., and Wayne, R.K. 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. *Genome Research* 21: 1294-1305.
- Way, J. G., Rutledge, L., Wheeldon, T., and White, B. N. 2010. Genetic characterization of eastern “coyotes” in eastern Massachusetts. *Northeastern Naturalist* 17: 189-204.

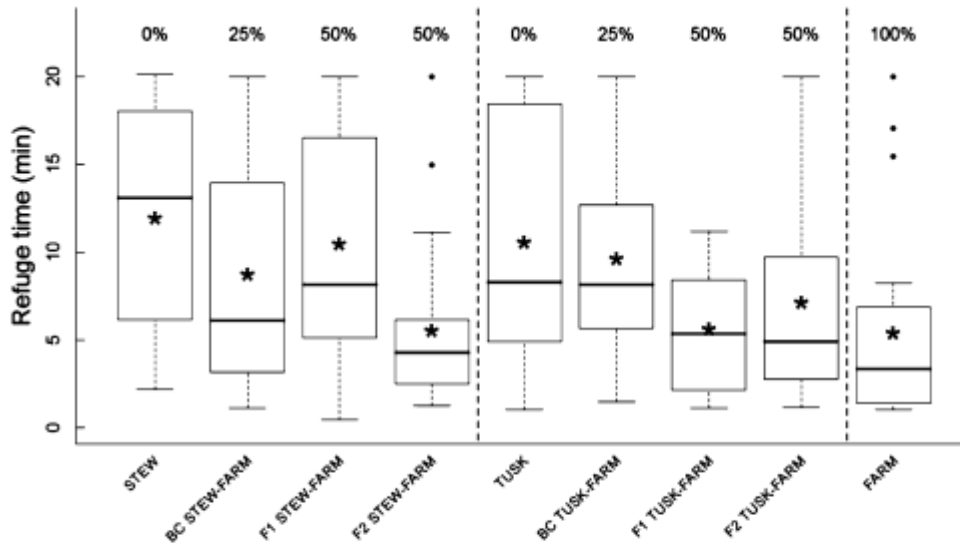
Appendix

Figure 1



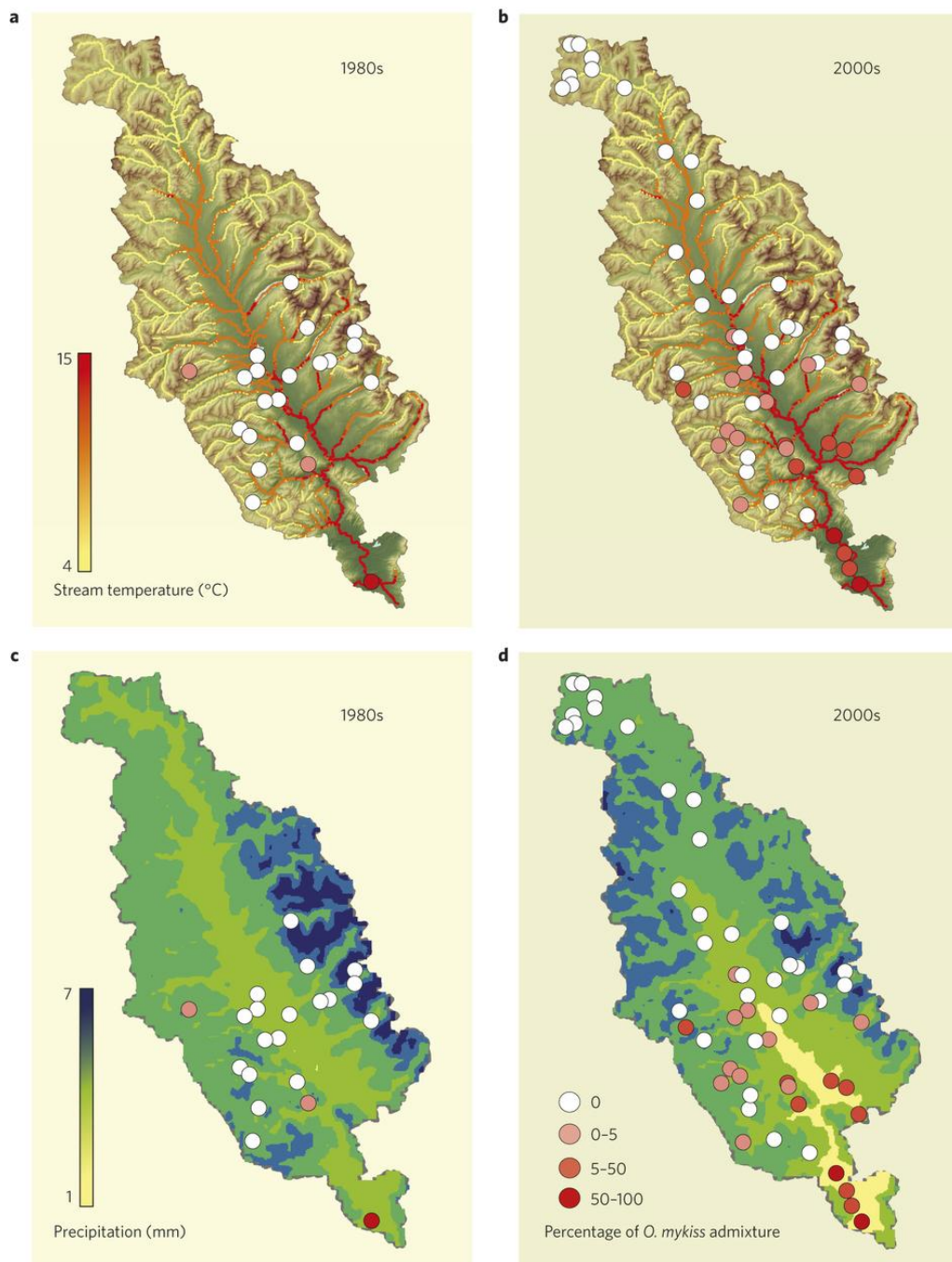
Selected gates of White-tailed deer, mule deer, and their hybrid. A: White-tailed gallop. B: Mule Deer Gallop. C: Mule deer stot. D: Hybrid Stot (Lingle 1992).

Figure 2



Boxplots of refuge time for Atlantic Salmon crosses. STEW and TUSK represent two wild North American populations and BC represents backcrosses. The bold line in the box represents the median and the star represents the mean. Dots represent outliers. The upper and lower horizontal line represent the largest and smallest observation that was not an outlier. Percentages represent the amount of farmed genes in the crosses. Houden et al. (2010)

Figure 3.



Maps showing the spread of rainbow trout hybridization in relation to average decadal summer stream temperature (a,b) and May precipitation (c,d); 1980s (a,c) and 2000s (b,d) (Muhlfeld et al. 2014)