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Response

Strategies for red wolf recovery and management: a response to Way (2014)

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Recently, Way (2014) provided a commentary introducing strategies to improve red wolf *Canis rufus* recovery and management. In so doing, Way (2014) critiqued Hinton et al. (2013) because he believed our review neglected management strategies to address three critical issues associated with red wolf recovery efforts. The purpose of Hinton et al. (2013) was to provide a historic context of red wolf recovery, summarise management strategies for the wild population, and suggest areas of ecological research to assist recovery. Our review was specific to identifying areas of research necessary to pursue full recovery of red wolves, rather than identifying flaws within the administrative and legal framework that red wolf recovery was conducted under. As noted in Hinton et al. (2013), a major impediment to implementing appropriate management for red wolf recovery is limited knowledge about red wolf ecology. Site-specific management is fundamental to restoring wild populations of red wolves and channelling limited research efforts into specific areas of concern is crucial to accrue knowledge necessary to develop practical options for improving conservation strategies. Therefore, we disagree with Way (2014) that Hinton et al. (2013) neglected management issues.

We fully embrace the exchange of ideas among researchers, and critiques of scientific articles are fundamental to the advance of science. Indeed, scientific debate is essential and we reviewed Way (2014) in that light. Because of our involvement in red wolf recovery efforts, we empathise with the overall message of Way (2014) to better protect red wolves from human-caused mortality, and to better manage the effects of hybridisation and inbreeding in the wild population. However, we believe Way's (2014) interpretation of these issues in the context of recovery efforts in eastern North Carolina neglected real conditions in the designated recovery area. Although Way (2014) provides eight strategies for achieving red wolf recovery via social and political channels, we only focus on the three primary management needs discussed by Way (2014) because the broad administrative and legal changes suggested in Way's (2014) eight strategies were beyond the scope of Hinton et al. (2013).

The goal of our response to Way (2014) is to advance the discussion of red wolf recovery by clarifying issues related to human-caused mortality, hybridisation, and inbreeding in the wild red wolf population in eastern North Carolina. Anthropogenic factors are broad and affect most aspects of red wolf ecology such as habitat selection (Dellinger et al. 2013), survival (United States Fish and Wildlife Service 2007, Sparkman et al. 2011) and interspecific interactions (Bohling and Waits 2015, Hinton et al., in press). As noted in Hinton et al. (2013), ecological challenges to red wolf recovery such as hybridisation, inbreeding and demographics are difficult to compartmentalise because they are intrinsically intertwined and sensitive to anthropogenic factors, specifically the effects of low survival rates caused by human activities. Below, we discuss inbreeding and hybridisation to provide clarity on what we know about the occurrence of these phenomena in the wild population, and why we disagree with several of Way's (2014) suggestions to overcome these issues. Finally, we discuss how human-caused mortality affects red wolves and suggest management strategies to address these issues that differ from Way (2014).

Inbreeding in wild red wolves

Small, endangered populations are susceptible to the effects of inbreeding because of their isolation and limited choice of unrelated mates (Charlesworth and Charlesworth 1987, Hedrick and Kalinowski 2000, Charlesworth and Willis 2009). The primary concerns associated with inbreeding in red wolves are decreasing reproductive rates and increasing susceptibility to environmental change and disease that are associated with increasing relatedness (Rabon and Waddell 2010, Brzeski et al. 2014). In Hinton et al. (2013), we suggested inbreeding levels of wild red wolves were likely high and that the effects of inbreeding depression on red wolf survival and hybridisation rates remained unknown. Recently, Brzeski et al. (2014) found large inbreeding coefficients (average $f = 0.154$) in wild red wolves when evaluating the extent of inbreeding and inbreeding depression. They concluded that large inbreeding coefficients in the wild population resulted from background relatedness associated with few founders (n = 12), numerous matings with close relatives and no gene flow from other wild red wolf populations. Although Brzeski et al. (2014) found little effect of inbreeding and inbreeding depression on reproductive and survival performance of wild red wolves, they reported that the effects of inbreeding depression were strongest for body size such that more inbred individuals were smaller. Body size was not observed to have a direct effect on red wolf fitness, but was suggested to indirectly influence fitness by influencing the ability of red wolves to acquire territory and secure reproductive opportunities (Brzeski et al. 2014). As noted in Hinton et al. (2013) and Hinton and Chamberlain (2014), examination of morphological characters of red wolves and coyotes *C. latrans* could highlight traits that may have genetic, evolutionary and ecological importance. Inbreeding may have a greater effect on red wolf morphology than previously thought and its influence on hybridisation between

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red wolves and coyotes remains unknown (Brzeski et al. 2014). Therefore, understanding the effects of inbreeding within the wild red wolf population requires further attention because inbreeding depression could potentially influence the ability of red wolves to competitively exclude coyotes from occupying space on the landscape, or motivate individual red wolves to outbreed with coyotes to avoid incestuous matings (Hinton et al. 2013, Brzeski et al. 2014).

As noted by Brzeski et al. (2014), inbreeding in the wild red wolf population is exacerbated because there are no other wild populations to provide immigrants. Way (2014) suggested reducing the effects of inbreeding depression through genetic rescue. The successful use of Texas cougars *Puma concolor stanleyana* to genetically rescue the Florida panther (*P. c. coryi*) from inbreeding depression is well known (Creel 2006, Pimm et al. 2006, Johnson et al. 2010). Indeed, Way (2014) referenced the genetic rescue of Florida panthers when he suggested performing genetic rescue via carefully controlled augmentation of the captive and wild red wolf population with transplanted eastern wolves *C. lycaon* to outbreed the population. Several studies have suggested that eastern wolves and red wolves are closely-related canids and possibly conspecific (Wilson et al. 2000, Kyle et al. 2008). Therefore, it is possible that Way's (2014) suggestion for genetic rescue is plausible. However, until issues of eastern wolf and red wolf taxonomy are resolved, we believe it is prudent to avoid fostering eastern wolf genetics into the red wolf population because they are not currently recognised as conspecific.

For reasons unrelated to taxonomic issues, we also believe that genetic rescue should currently not be considered to reduce inbreeding depression in the wild red wolf population. Way's (2014) call for genetic rescue is essentially a form of controlled, artificial introgression of eastern wolf genetics to improve red wolf demographics. However, it should be noted that the extant red wolf population has experienced introgression from coyotes, a congeneric species, at least twice during the 20th century. First, red wolves in Texas and Louisiana were suspected to have experienced introgression from the expanding coyote population during the early 20th century (Nowak 1979). Those remnant populations experiencing introgression were described as atypical consisting of sickly individuals occupying marginal habitats and incapable of maintaining self-sustaining populations (Nowak 1979, Phillips and Parker 1988, Carley 2000). As those populations approached extirpation, the United States Fish and Wildlife Service captured individuals to begin the captive-breeding programme. Second, during the early 1990s several hybridisation events occurred in eastern North Carolina, and hybrid canids were able to backcross into the wild red wolf population. As a result, the current wild red wolf population has experienced 3-4% introgression (Gese and Terletzky 2015). Like the Texas and Louisiana populations, without ongoing management, the wild population in eastern North Carolina would likely become extirpated via hybridisation and human-caused mortality.

Hybridisation during the early 20th century and early 1990s are responsible for coyote introgression observed in the extant red wolf genome and, in both situations, provided no positive response in red wolf demographics (i.e. increase in reproductive and survival rates). Any potential for genetic rescue likely did not occur because of the deteriorating environmental conditions experienced by those red wolf populations (Hedrick et al. 2010). These events suggest that eliminating excessive mortality of red wolves on the landscape is likely more important to reducing inbreeding depression than using genetic rescue strategies involving eastern wolves. If environmental conditions are too poor for survival, then benefits of genetic rescue will likely be obscured. However, if red wolf genetics and demographics improve because the quality of the environment improves, then genetic rescue will likely not be needed. Genetic rescue, as suggested by Way (2014) might only be considered if red wolf demographics, like those of the Florida panther, did not respond positively to better environmental conditions. Nevertheless, Brzeski et al. (2014) reported no direct effect of inbreeding depression on reproductive and survival performance of wild red wolves. As a result, genetic rescue is unlikely to solve extrinsic forces (i.e. human-caused mortality) responsible for increased levels of inbreeding in the wild population. Therefore, we believe simply increasing the wild red wolf population and its annual growth rates by reducing human-caused mortalities can reduce inbreeding depression without the potential ramifications of introducing genetic material from another species.

Hybridisation in red wolves

Although hybridisation has been recognised to spur evolutionary change within many taxonomic groups, hybridisation between red wolves and coyotes is caused primarily by anthropogenic factors. Red wolves and coyotes were reproductively isolated prior to European settlement and decades of unrelenting efforts to exterminate red wolves caused remnant, declining red wolf populations to outbreed with expanding coyote populations during the early 20th century (Nowak 1979, 2002). Current populations of red wolves and coyotes in eastern North Carolina exist as two interbreeding species of canids. Hybridisation continues to be a problem for red wolf recovery because it demonstrates that reproductive barriers are currently weak between the two populations. Coyotes are more abundant than red wolves in the Recovery Area and when red wolves cannot locate a red wolf mate, they can consort and breed with coyotes (Bohling and Waits 2015, Hinton et al., in press). Currently, little is known about mechanisms facilitating hybridisation between red wolves and coyotes, but data collected by the U.S. Fish and Wildlife Service and collaborating researchers have provided some insights into red wolf and coyote interactions (Hinton 2014, Bohling and Waits 2015, Hinton et al., in press).

Hybridisation occurs because some red wolves are capable of holding space with smaller-sized coyote mates to form functional breeding pairs capable of defending territories. Red wolves paired with coyotes (hereafter congeneric pairs) are capable of defending territories from other red wolves and coyotes, and breeding pairs are typically disbanded when mates are displaced or die. With few red wolves on the landscape, mating opportunities are likely the primary limiting resource for red wolves. When forming congeneric pairs, red wolves share other limiting resources, such as space and food, with coyote mates. These outcomes demonstrate that consequences of competitive interactions are complicated and may not facilitate reproductive isolation between red wolves and coyotes.

Similar to Rutledge et al.'s (2012) work on historic patterns of eastern wolf and coyote hybridisation, Bohling and Waits (2015) suggested that human-caused disruption (i.e. direct killing) of stable red wolf breeding pairs facilitated hybridisation with coyotes by disrupting patterns of social structure within the red wolf population. Both studies stressed that behaviours associated with maintaining social structure in wolves may be responsible for minimising hybridisation. Hinton et al. (2013) noted that reproductive barriers were likely behavioural, but suggested differences in body size may facilitate differences in spatial and dietary requirements that prevent congeneric pairing between red wolves and coyotes. Indeed, Hinton (2014) observed that red wolves in congeneric pairs were physically smaller and defended smaller-sized territories than red wolves paired with conspecifics. As a result, Hinton (2014) hypothesised that differential use of space and prey between consorting red wolves and coyotes during energetically stressful activities, such as foraging and defending territories, may create incompatibilities between consorting congenerics and prevent successful pair formation. However, as red wolves and coyotes approach each other in body size, similar use of space and prey may reduce incompatibilities between consorting red wolves and coyotes and permit the successful formation of congeneric pairs that create red wolf/coyote hybrids.

Despite recent research indicating intense human-caused mortality facilitates hybridisation between closely-related *Canis* taxa in eastern North America (Benson et al. 2012, Rutledge et al. 2012, Bohling and Waits 2015, Hinton et al., in press), Way (2014) suggested hybridisation is a natural process that may promote preservation of red wolf genes outside the Recovery Area. We recognise that Way (2014) supports ongoing management to minimise hybridisation within the Recovery Area to prevent genetic swamping by coyotes, but we disagree with his suggestion to facilitate hybridisation in areas adjacent to the Recovery Area. Our disagreement hinges on several key points. The concept of hybrids and hybridisation is often misunderstood. As such, the general public almost assuredly would view hybrid canids negatively. There is widespread dislike for coyotes by various special interest groups and rhetoric from these groups has contributed to the generally poor reputation of coyotes with some of the general public. Therefore, promoting hybridisation with a larger wolf species is not a sound way of gaining support for red wolf restoration in local communities weary of large predators, particularly of coyotes. Additionally, Bohling and Waits (2011) found little evidence of hybridisation outside the Red Wolf Recovery Area. This indicates that the Red Wolf Recovery Programme has done an effective job of containing low-levels of hybridisation to areas within the Recovery Area, and that red wolves that have dispersed from the Recovery Area were likely unsuccessful in breeding. Therefore, we see advocating hybridisation as a means of promoting the red wolf genome outside the Recovery Area as counter-productive, because it would create attention over an unwarranted issue, and potentially attract unwanted and negative public perceptions towards red wolf recovery.

Way (2014) also suggested that continued hybridisation between red wolves and coyotes outside the Recovery Area may enhance the adaptive potential of both species. Hybridisation between red wolves and coyotes does not occur under natural conditions and resulted from human disruption (Nowak 1979, 2002; Bohling and Waits 2015, Hinton et al., in press). Therefore, we do not agree with Way (2014) that ongoing hybridisation on the edges of the core red wolf population provides either parental population with an adaptive advantage or assists red wolf recovery. The numerical discrepancy between coyotes and red wolves is likely to disrupt genetic interactions responsible for the red wolf's unique phenotype and prevent any balance between the gene pools. For example, melanism (black pelage) is absent in western coyote populations but observed in eastern coyote populations (Gipson 1976, Nowak 1979). Because melanism was known to exist in historic wolf populations of eastern North America, past hybridisation may be responsible for melanism in eastern coyote populations (Rutledge et al. 2009). Melanism was observed in the two eastern subspecies of red wolves (*C. rufus floridanis* and *C. r. gregoryi*) during the early 20th century (Nowak 1979). Although melanism was not reported in the western subspecies represented in the reintroduced population, the trait is now considered extinct in extant red wolves. However, melanism is present in coyotes of eastern North Carolina. Of the 264 coyotes evaluated by Hinton and Chamberlain (2014), 15 (5.6 %) were melanistic coyotes with body measurements similar to coyotes with normal-colored pelages. The relatively low occurrence of melanism in coyotes of eastern North Carolina suggests this trait is likely a neutral by-product of past introgression. Also, the absence of melanism in the extant red wolf population suggests introgression can favour the more abundant coyote and purge unique traits from the red wolf. As a result, we believe the suggestions of positive benefits associated with coyote and red wolf hybridisation are currently premature and largely speculative, because no proper assessment has been conducted to detect significant genetic effects upon phenotypic variation and fitness (Hinton et al. 2013).

Way (2014) suggested that hybridisation may enhance the adaptive potential of coyotes. Coyotes colonised most of North Carolina during the late 20th century in the absence of red wolves (DeBow et al. 1998). By the early 2000s, coyotes colonised the Recovery Area in the presence of a red wolf population and ongoing management to prevent hybridisation (United States Fish and Wildlife Service 2007). Coyotes are one of the more adaptable and fecund mammalian species on the North American landscape and their persistence seem to be benefitting from human changes to the landscape. Therefore, we are unsure what benefits an existing coyote population in North Carolina will gain from red wolf introgression that would enhance the adaptive potential of coyotes. More importantly, body sizes of red wolves and coyotes are distinct from one another and hybridisation between red wolves and coyotes guarantees the existence of intermediate-sized canids on the landscape (Hinton and Chamberlain 2014). This is problematic for management strategies to facilitate red wolf recovery in the presence of another canid competitor. Although coyotes greatly outnumber red wolves in eastern North Carolina, red wolves are the larger canid and, on average, adult red wolves weigh approximately 10kg more than adult coyotes (Hinton and Chamberlain 2014). The discrepancy in body mass ensures that red wolves are capable of displacing and killing coyotes. Adult hybrids are statistically larger than coyotes and typically weigh about 6kg less than red wolves (Hinton and Chamberlain 2014). Allowing hybridisation to occur in adjacent areas of the Recovery Area will facilitate increasing the average body mass of *Canis* taxa adjacent to the red wolf population and permit an influx of larger body-sized canids into the Recovery Area. Sterilisation of coyotes within the Recovery Area provides red wolves a reproductive advantage against a numerically superior coyote populations, while allowing individual red wolves to naturally displace coyotes (Gese and Terletzky 2015). However, the ability of individual red wolves to competitively exclude coyotes would be eroded if management strategies facilitated the creation of a larger hybridised population capable of immigrating into the Recovery Area.

A more balanced treatment of hybridisation than the one provided by Way (2014) is needed for red wolf recovery. We suggested in Hinton et al. (2013) that studies of phenotypic variation would be a powerful approach to detect and understand genetically meaningful variation that could be used to develop practical management of hybridisation. Therefore, we caution against generalising the conservation benefits of red wolf and coyote hybridisation with optimistic speculation until such benefits are demonstrated empirically.

Better protection and enhancement of the reintroduced red wolf population

In Hinton et al. (2013), we suggested a robust assessment of red wolf demographics to begin developing strategies to address human-caused mortality in red wolves. Indeed, a recent assessment of the wild red wolf population in eastern North Carolina reported that the probability of a red wolf death via gunshot has increased from ~15% during 1990 to ~60% by 2013 (Hinton et al., unpublished). Most of red wolf deaths via gunshot occurred during fall and winter hunting seasons. These results corroborated earlier observations reported by the US Fish and Wildlife Service's Red Wolf Recovery Programme that the wild population was experiencing increasing red wolf deaths during fall and winter hunting seasons (United States Fish and Wildlife Service 2007). Red wolves are being mistaken for coyotes in some cases, and likely intentionally shot in others. Regardless, red wolf deaths are occurring during the time of year when most sports hunters are afield. On the surface, this suggests that protection of red wolves is warranted, but the issue is more complex than it seems because by default protection of red wolves would require protection of coyotes.

Although we agree with Way (2014) that better protection and management of all *Canis* taxa will strengthen red wolf recovery efforts, we believe his stance on protecting coyotes under the Endangered Species Act as a simple and inexpensive long-term solution is currently unrealistic. Coyotes are more directly affected by the Animal Damage Control Act of 1931, which authorised the eradication of a predator species considered a threat to agricultural and ranching interests (Hawthorne 2004, Bacon 2013). Coyote control was a priority when the Animal Damage Control Act 1931 was passed and remains a primary objective of the U.S. Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS) and Wildlife Services (Hawthorne 2004, Bacon 2013). Coyotes are often targeted during predator control programmes because of the threat to livestock (Knowlton et al. 1999, Bromley and Gese 2001, Mastro et al. 2011), game species (Kilgo et al. 2010, Mastro et al. 2011, Robinson et al. 2014), and public health and safety (Gompper 2002, Draheim et al. 2013). Therefore, suggestions to protect coyotes would justifiably be viewed with reservation by state and federal agencies responsible for managing a diversity of wildlife species and public interests. This is not to say that enacting protection for canids should not or cannot be done, but rather that it is not as simple and inexpensive as Way (2014) suggests.

Coyotes are not protected wildlife under federal law, but federal statutes and hunting regulations can affect coyote management and hunting activities. As noted by Way (2014), several conservation groups sued the North Carolina Wildlife Resources Commission in an attempt to reduce human killing of red wolves within the five counties encompassing the Recovery Area (Boyle 2014). The lawsuit resulted in an initial court-approved ban of coyote hunting within the Recovery Area (Boyle 2014) followed by a court-approved settlement agreement that banned night-time hunting of coyotes and requires permitting and reporting for coyote hunting during the day (Boyle 2014). The settlement agreement is a management policy designed at reducing human killing of red wolves and eliminating factors causing a decline of the wild red wolf population.

Similar efforts by environmental organisations and ecologists to reform federal wildlife control have facilitated a shift in emphasis by USDA's Wildlife Services from widespread, non-targeted lethal control to an increased use of non-lethal control methods combined with lethal control targeted to individual animals (Knowlton et al. 1999, Mitchell et al. 2004, Shivik 2004, 2006, Feldman 2007, Bergstrom et al. 2014). Indeed, red wolf recovery has benefitted from these techniques and uses a similar combination of lethal euthanasia and non-lethal sterilisation techniques adopted by the USDA to better manage coyote depredation of domestic livestock (Bromley and Gese 2001, Gese and Terletzky 2015). Changes in legislation to protect coyotes and hybrids under the Endangered Species Act may force the United States Fish and Wildlife Service to abandon their ability to control hybridisation via sterilisation and euthanasia. Additionally, extending complete protection to coyotes and hybrids will expend time and effort to deal with political backlash from special interest groups. Instead, we suggest designing effective coyote management programmes within the Recovery Area that involve cooperation with the North Carolina Wildlife Resources Commission and United States Fish and Wildlife Service, environmental organisations, local communities and private citizens. This approach will benefit site-specific recovery of wild red wolves and protect necessary strategies used by the United States Fish and Wildlife Service and North Carolina Wildlife Resources Commission to manage coyote populations. Establishing flexible approaches to managing coyote populations using both lethal and non-lethal methods will contribute to broader recovery strategies for other potential reintroduction sites by addressing wildlife laws affecting red wolves and coyotes, as well as refining regulations and strategies used to manage coyotes.

Conclusions

Successful recovery of red wolves will require the elimination of factors that initially caused the decline of the species. Human-caused mortality facilitated the complete extirpation of red wolves and continues to limit the growth of an ecologically functional population in eastern North Carolina (Hinton et al., unpublished). We agree with Way (2014) that the red wolf population in eastern North Carolina needs better protection and we appreciate Way's (2014) commentary on strategies to achieve that goal. Reducing human-caused mortality of red wolves during fall and winter hunting seasons will require increased regulation of coyote hunting. A large part of conservation work is changing human behaviours that are detrimental to endangered and threatened species. Effective permitting and reporting for coyote hunting in the Recovery Area is an essential step to begin changing human behaviour responsible for the primary source of red wolf deaths.

Our primary concern with Way's (2014) approach to improving red wolf recovery in eastern North Carolina was that his recommendations neglect to incorporate potential negative effects in developing management strategies. For instance, Way's (2014) suggestion to implement protection of canids outside the Recovery Area to allow hybridisation to occur as a natural process does not benefit red wolf recovery. In Hinton et al. (2013), we advocated that management should promote ecological and evolutionary processes, but those processes should result in a healthy, growing red wolf population rather than a hybrid swarm. Political and financial capital for red wolf recovery should not be expended to protect "wolf-like" canids in areas outside the Recovery Area. It would be more practical to use the limited space to extend the Recovery Area and increase the number of red wolves on the landscape.

The purpose of Hinton et al. (2013) and our response to Way (2014) was to provide a summary review to highlight how inbreeding, hybridisation and human-caused mortality hampered red wolf recovery. Effective management of red wolves will require ongoing studies to understand how they respond to changing landscapes. As illustrated by Way (2014), developing strategies to recover red wolves is fraught with potential political, social and ecological problems. Indeed, attempts to reform wildlife agencies justifiably require strong evidence derived through science to combat entrenched rhetoric. Therefore, incorporating the best empirical science available to predict outcomes and tradeoffs of alternative management strategies to address issues of inbreeding, hybridisation and human-caused mortality is necessary to implement effective policy to successfully restore red wolves to their historic range.

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References

Bacon, T. 2013. The implementation of the Animal Damage Control Act: A comment on Wildlife Services' methods of predatory animal control. *Journal of the National Association of Administrative Law Judiciary* 32:361-401.

Benson, J.F., Patterson, B.R. and Wheeldon, T.J. 2012. Spatial genetic and morphologic structure of wolves and coyotes in relation to environmental heterogeneity in a *Canis* hybrid zone. *Molecular Ecology* 21:5934-5954.

Bergstrom, B.J., Arias, L.C., Davidson, A.D., Ferguson, A.W., Randa, L.A. and Sheffield, S.R. 2014. License to kill: reforming federal wildlife control to restore biodiversity and ecosystem function. *Conservation Letters* 7:131-142.

Bohling, J.H. and Waits, L.P. 2015. Factors influencing red wolf-coyote hybridization in eastern North Carolina, USA. *Biological Conservation* 184:108-116.

Bohling, J.H. and Waits, L.P. 2011. Assessing the prevalence of hybridization between sympatric *Canis* species surrounding the red wolf (*Canis rufus*) recovery area in North Carolina. *Molecular Ecology* 20:2142-2156.

Boyle, T.W. 2014. Red Wolf Coalition, *et al*., Defendants. In the United States District Court for the Eastern District of North Carolina. Northern Division. No. 2:13-CV-60-BO.

Bromley, C. and Gese, E.M. 2001. Surgical sterilization as a method of reducing coyote predation on domestic sheep. *Journal of Wildlife Management* 65:510-519.

Brzeski, K.E., Rabon Jr., D.R., Chamberlain, M.J., Waits, L.P. and Taylor, S.S. 2014. Inbreeding and inbreeding depression in endangered red wolves (*Canis rufus*). *Molecular Ecology* 23:4241-4255.

Carely, C.J. 2000. The Red Wolf (*Canis rufus*) Recovery Program: things they didn't tell me in graduate school. Pp. 125-141 in J.R.Choate (ed.), *Reflections of a naturalist: papers honoring Professor Eugene D. Fleharty*. Fort Hays State University, Hays, Kansas, USA.

Charlesworth, D. and Charlesworth, B. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237-268.

Charlesworth, D. and Willis, J.H. 2009. The genetics of inbreeding depression. *Nature Reviews Genetics* 10:783-789.

Creel, S. 2006. Recovery of the Florida panther – genetic rescue, demographic rescue, or both? Response to Pimm et al. (2006). *Animal Conservation* 9:125-126.

DeBow, T.M., Webster, W.D. and Sumner, P.W. 1998. Range expansion of the coyote, *Canis latrans* (Carnivora: Canidae), into North Carolina; with comments on some management implications. *Journal of the Elisha Mitchell Scientific Society* 114:113-118.

Dellinger, J.A., Proctor, C., Steury, T.D., Kelly, M.J. and Vaughan, M.R. 2013. Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biological Conservation* 157:324-330.

Draheim, M.M., Patterson, K.W., Rockwood, L.L., Guagnano, G.A. and Parsons, E.C.M. 2013. Attitudes of college undergraduates towards coyotes (*Canis latrans*) in an urban landscape: Management and public outreach implications. *Animals* 3:1-18.

Feldman, J.W. 2007. Public opinion, the Leopold Report, and the reform of federal predator control policy. *Human-Wildlife Conflicts* 1:112-124.

Gese, E.M. and Terletzky, P.A. 2015. Using the "placeholder" concept to reduce genetic introgression of an endangered carnivore. *Biological Conservation* 192:11-19.

Gipson, P.S. 1976. Melanistic *Canis* in Arkansas. *Southwestern Naturalist* 21:124-26.

Gompper, M.E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of north-eastern North America by coyotes. *BioScience* 52:185-190.

Hawthorne, D.W. 2004. The history of federal and cooperative animal damage control. *Sheep & Goat Research Journal* 19:13-15.

Hedrick, P.W. and Fredrickson, R. 2010. Genetic rescue guidelines with examples from Mexican wolves and Florida panthers. *Conservation Genetics* 11:615-626.

Hedrick, P.W. and Kalinowski, S.T. 2000. Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics* 31:139-162.

Hinton, J.W. 2014. Red wolf (*Canis rufus*) and coyote (*Canis latrans*) ecology and interactions in northeastern North Carolina. Ph.D. Dissertation, University of Georgia. Athens, Georgia, USA.

Hinton, J.W. and Chamberlain, M.J. 2014. Morphometrics of *Canis* taxa in eastern North Carolina. *Journal of Mammalogy* 95:855-861.

Hinton, J.W., Chamberlain, M.J. and Rabon Jr., D.R. 2013. Red wolf (*Canis rufus*) recovery: A review with suggestions for future research. *Animals* 3:722-744.

Hinton, J.W., Brzeski, K.E., Rabon Jr., D.R. and Chamberlain, M.J. In press. Effects of anthropogenic-caused mortality on red wolf breeding pairs: Implications for red wolf recovery. *Oryx*.

Johnson, W.E., Onorato, D.P., Roelke, M.E., Land, E.D., Cunningham, M., Belden, R.C., McBride, R., Jansen, D., Lotz, M., Shindle, D., Howard, J., Wildt, D.E., Penfold, L.M., Hostetler, J.A., Oli, M.K. and O'Brien, S.J. 2010. Genetic restoration of the Florida panther. *Science* 329:1641-1645.

Kilgo, J.C., Ray, H.S., Ruth, C. and Miller, K.V. 2010. Can coyotes affect deer populations in southeastern North America? *Journal of Wildlife Management* 74:929-933.

Knowlton, F.F., Gese, E.M. and Jaeger, M.M. 1999. Coyote depredation control: An interface between biology and management. *Journal of Range Management* 52:398-412.

Kyle, C.J., Johnson, A.R., Patterson, B.R., Wilson, P.J. and White, B.N. 2008. The conspecific nature of eastern and red wolves: conservation and management implications. *Conservation Genetics* 9:699-701.

Mastro, L.L. 2011. Life history and ecology of coyotes in the Mid-Atlantic states: a summary of the scientific literature. Southeastern Naturalist 10:721-730.

Mitchell, B.R., Jaeger, M.M. and Barrett, R.H. 2004. Coyote depredation management: Current methods and research needs. *Wildlife Society Bulletin* 32:1209-1218.

Nowak, R.M. 1979. North American Quaternary *Canis*. *Monograph of the Museum of Natural History, University of Kansas* 6:1-154.

Nowak, R.M. 2002. The original status of wolves in eastern North America. *Southeastern Naturalist* 1:95-130.

Phillips, M.K. and Parker, W.T. 1988. Red wolf recovery: A progress report. *Conservation Biology* 2:139-141.

Pimm, S.L., Dollar, L. and Bass Jr., O.L. 2006. The genetic rescue of the Florida panther. *Animal Conservation* 9:115-122.

Rabon Jr., D.R. and Waddell, W. 2010. Effects of inbreeding on reproductive success, performance, litter size, and survival in captive red wolves (*Canis rufus*). *Zoo Biology* 29:36-49.

Robinson, K.F., Diefenbach, D.R., Fuller, A.K., Hurst, J.E. and Rosenberry, C.S. 2014. Can managers compensate for coyote predation of white-tailed deer? *Journal of Wildlife Management* 78:571-579.

Rutledge, L.Y., Wilson, P.J., Kyle, C.J., Wheeldon, T.J., Patterson, B.R. and White, B.N. 2009. How the gray wolf got its color. *Science* 325:33-34.

Rutledge, L.Y., White, B.N., Row, J.R. and Patterson, B.R. 2012. Intense harvesting of eastern wolves facilitated hybridization with coyotes. Ecology and Evolution 2:19-33.

Shivik, J.A. 2004. Non-lethal alternatives for predation management. *Sheep and Goat Research Journal* 19:64-71.

Shivik, J.A. 2006. Tools for the edge: What's new for conserving carnivores? *BioScience* 56:253-259.

Sparkman, A.M., Waits, L.P. and Murray, D.L. 2011. Social and demographic effects of anthropogenic mortality: a test of the compensatory mortality hypothesis in the red wolf. PLoS One 6:e20868.

United States Fish and Wildlife Service 2007. Red wolf 5-year status review: summary and evaluation. United States Fish and Wildlife Service, Manteo, North Carolina, USA.

Way, J.G. 2014. Strategies for red wolf recovery and management. *Canid Biology & Conservation* 17:9-15.

Wilson, P.J., Grewal, S., Lawford, I.D., Heal, J.N.M., Granacki, A.G., Pennock, D., Theberge, J.B., Theberge, M.T., Voight, D.R., Waddell, W., Chambers, R.E., Paquet, P.C., Goulet, G., Cluff, D. and White, B.N. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. *Canadian Journal of Zoology* 78:2156-2166.

Biographical sketches

Joseph Hinton's research interests lie in understanding how selective pressures operating on key traits influence the abundance and distribution of wildlife populations.

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