Hypothetical Relationships Between the San Joaquin Kit Fox, California Grizzly Bear, and Gray Wolf On the Pre-European California Landscape

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Abstract

Predator dynamics and other community-level interactions more than 200 years ago within California's Central Valley would likely have been emphatically different with grizzly bears and wolves as an important part of the landscape. With the advent of European settlement of California, the ecosystem was drastically altered. The removal of wolves and grizzly bears from the Central Valley may have had a negative effect on the San Joaquin kit fox. Cascading effects with negative results like the ones described here are likely commonplace when top-down ecosystems are altered by human activities.

About the Author

Howard Clark is an accomplished wildlife ecologist and biologist with eleven years of professional wildlife and research experience. He earned his MS degree in Biology from CSU Fresno in 2001. His work as a researcher has focused on the fauna and ecosystems of Northern, Central, and Southern California, and the Mojave Desert provinces and includes extensive baseline mammalian inventories, conduct surveys focused on rare animals, habitat assessment, land retirement and restoration, radio telemetry, and long-term ecological studies on several endangered species. He has conducted studies for a variety of private and public agency projects, including surveys for endangered species along canals, range-wide presence/absence surveys, and scent dog detection work for endangered foxes. He is currently employed by H. T. Harvey & Associates as a mammalogist in Fresno, California.

The interspecific interactions between mammalian carnivores are typically limited to interference competition and predation (Cypher and Spencer 1998; Palomares and Caro 1999). These interactions have important implications on carnivore competition (Linnell and Strand 2000). For example, spotted hyenas (*Crocuta crocuta*) kill golden jackals (*Canis aureus*) and brown hyenas (*Hyaena brunnea*) when competing for resources (Palomares and Caro 1999). Spotted hyenas and lions (*Panthera leo*) limit the density of African wild dogs (*Lycaon pictus*) through interference competition (Creel and Creel 1996). These types of interspecific interactions are common within communities of North America, Africa, and Europe, although the behavioral factors of these interactions are poorly understood (Palomares and Caro 1999).

Comparatively, interspecific cooperative hunting and other beneficial associations between mammalian carnivores are just as poorly understood (Packer and Ruttan 1988). A notable example includes hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*; Hawkins 1907, Cahalane 1950). Badgers and coyotes have been observed on many occasions helping each other prey upon ground squirrels (*Spermophilus spp*.; Kiliaan et al. 1991; Minta et al. 1992). Hunting methods include a double rushing of a squirrel colony, where confused squirrels are easily captured by both the coyote and the badger, and opportunistic capturing of escaping squirrels by the coyote as the badger excavates the burrow, akin to the coyote using the badger as a hunting tool. In the last instance, the benefit to the badger is not immediately obvious. Perhaps having an alert predator in the area provides warning of approaching danger, or squirrels, sensing a coyote outside of the burrow, may choose to remain underground and eventually become prey for the badger. However, coyote-badger associations are most likely phoretic rather than a form of social symbiosis (Kiliaan et al. 1991). Cooperative or opportunistic foraging between badgers and swift foxes (*Vulpes velox*) have also been recorded (Ausband and Ausband 2006).

Other interspecific associations between mammalian carnivores have been described elsewhere. In one case, a Tibetan fox (*V. ferrilata*) closely followed the movements of a brown bear (*Ursus arctos*) that was excavating pikas (*Ochotona curzoniae*; Harris and Loggers 2004). The fox directly benefited from the bear's activities by capturing pikas disturbed but not captured by the bear. Przewalski (1883) recorded a similar situation whereby four Tibetan foxes were observed searching for rodents near a bear excavating a burrow complex.

At other times fox-bear interactions suggest scavenging behavior on the part of the fox. Red foxes (*V. vulpes*) have been observed patiently waiting for an opportunity to partake in feeding on carrion when a brown bear was already present at the carcass (Murie 1987). In another instance, a red fox found a bear cache and relocated a portion of it to a new cache nearby. Eventually a brown bear arrived at the original cache and ate a part of it, then followed the fox's scent to the newly hidden cache and ate what was left (Murie 1987). Arctic foxes (*V. lagopus*) are known to follow polar bears (*U. maritimus*) on pack ice and wolves (*C. lupus*) on the mainland to scavenge remains of kills (Chesemore 1968).

Swift foxes and red foxes have also benefited from scavenging wolf kills (Cypher 2003). Many swift foxes have been killed due to scavenging carcasses poisoned to control coyotes and wolves (Bunker 1940). The scavenging behavior of the swift fox may indicate an evolved relationship with wolves and grizzly bears in that swift foxes directly benefit from carrion left behind by these two

larger carnivores. The post-glacial and historic distribution of the grizzly bear overlapped that of the swift fox, allowing for this relationship to occur (Jonkel 1987, Schwartz et al. 2003). Here, I hypothesize that the San Joaquin kit fox (*V. macrotis mutica*) may have had a beneficial associative relationship with the California grizzly bear (*U. a. colusus*) and the California gray wolf (*C. l. furlongi*) in pre-European California.

Early descriptions of the pre-European Central Valley of California include large expanses of native California prairie with areas of alkali sink habitats; vernal pools and swales; and regions of tule marshes and lakes, riparian forests, and river systems (Preston 1981; Schoenherr 1992; Barbour et al. 1997). Within the native California prairie were large herds of tule elk (*Cervus elaphus nannodes*), pronghorn (*Antilocapra americana*), and perhaps mule deer (*Odocoileus hemionus*; Schmidt 1991, Schoenherr 1992; Clark 2004; Wilbur 2004). Although the proposed "Serengeti" description of North America has been called into question (Kay 1998), California may have been a minor exception (Holing 1988). Large herds of ungulates supported the California condor (*Gymnogyps californianus*) and larger carnivores, including wolves and grizzly bears (Schoenherr 1992; Wilbur 2004).

Predator-prey dynamics and other community-level interactions more than 200 years ago would likely have been emphatically different with grizzly bears and wolves as an important part of the landscape. Wolves were present in the Central Valley until the 1800s, and although their population demographics were unknown, they were probably extirpated from all parts of California by the mid-1920s (Schmidt 1991; Beidleman 2006). Wolves and grizzly bears may have competed for ungulate prey (Kuzyk et al. 2001), and abandoned or cached kills were probably a major food source for other animals including California condors (Wilmers et al. 2003; Wilbur 2004).

The California grizzly was a chaparral and grassland bear, and commonly over-wintered at elevations well below the snow line (Grinnell 1938; Hall 1939; Schoenherr 1992; Storer and Tevis 1996; Snyder 2003). The San Joaquin kit fox also inhabited these same grasslands of the Central Valley (Grinnell et al. 1937; Kelly et al. 2005). Schoenherr (1992) wrote that the California grizzly may have been generally unsuccessful in capturing tule elk and pronghorn; however, Schwartz et al. (2003) stated that grizzly bears are effective predators, and various large ungulates, including elk calves, are important seasonal food items. It is likely that the San Joaquin kit fox was able to benefit from the kills of wolves and grizzly bears as the swift fox did. Grizzly bears may have also excavated the burrowing systems of ground squirrels, with kit foxes capturing escaped squirrels, similar to the Tibetan fox-brown bear dynamic.

However, with the advent of European settlement of California's Central Valley, the ecosystem was drastically altered. By 1875, pronghorn were rare in the Central Valley, and tule elk were reduced to 145 animals by 1904 (Schoenherr 1992). The last of the wolves were trapped in the Providence Mountains in 1922 and in Lassen County in 1924 (Grinnell et al. 1937; Ingles 1963; Schoenherr 1992). The last grizzly bear was killed in 1922 (Grinnell et al. 1937; Schoenherr 1992). The impact of the extirpation of the grizzly bear and the wolf on the native California prairie is speculative at best (Schmidt 1991). The interactions between the large ungulates, grizzly bears, wolves, coyotes, and kit foxes will most likely remain unknown, as researchers are only able to tentatively hypothesize how the ecosystem dynamics

of a pre-European California landscape functioned.

Predator-driven ecosystems of the past may have been much different than the systems of today (Kay 1998). When top predators are removed from an ecosystem, as occurred in California, a mesopredator release may take place; that is, other predators from lower trophic levels increase in numbers and an ecological shift ensues on the landscape (Soulé et al. 1988; Crooks and Soulé 1999). A direct effect of this release is that the demographic success of these mesopredator species can be devastating for less adaptable, rarer species (Garrott et al. 1993). For example, the removal of the grizzly bear and wolf from the Greater Yellowstone Ecosystem has allowed a cascading effect of ecological events that led to a population explosion of the moose (*Alces alces*) during the past 150 years (Berger et al. 2001). The moose subsequently altered the riparian vegetation structure (by ungulate herbivory), and as a result, a reduction of avian neotropical migrants was observed in the impacted riparian communities (Berger et al. 2001).

The removal of wolves and grizzly bears from the Central Valley of California may have had a similar negative effect on the San Joaquin kit fox. First, with the demise of two top predators, the coyote population likely would have increased (Goldman 1930; Schoenherr 1992, Cohn 1998). Second, with the rapid loss of native grassland habitat due to agriculture and development and the additive pressure of an increasing coyote population, the San Joaquin kit fox experienced a drastic population decrease, so that by 1970, they were nearing extinction.

Today, coyotes are the main predator of the San Joaquin kit fox (Ralls and White 1995; Cypher and Spencer 1998). This was most likely not the case when wolves occupied the Central Valley. Other researchers have shown that coyotes and wolves usually cannot tolerate each other where their home ranges overlap and competitive exclusion of coyotes by wolves occurs (Carbyn 1982; Cohn 1998). However, this is not always the case, especially when food sources are not limited (Paquet 1991; 1992). In contrast, California wolves probably did not interact with the San Joaquin kit fox directly. However, kit foxes benefited from wolf presence in two ways: (1) kit foxes likely received supplemental food resources from wolf caches and scavenged wolf kills (Wilmers et al. 2003), and (2) competitive interactions between kit foxes and coyotes were reduced due to the antagonistic interactions between wolves and coyotes (Fuller and Keith 1981). However, interference competition and predation between kit foxes and coyotes occurred often enough for kit foxes to evolve spatial partitioning mechanisms to avoid coyotes, like the use of year-round denning systems. Today, with wolves removed from the Central Valley ecosystem, coyote populations increased significantly, adding a confounding competitive pressure on the San Joaquin kit fox (Cohn 1998; Nelson et al. 2007).

Cascading effects like the ones described here are most likely commonplace where top-down ecosystems are drastically altered by anthropogenic-sourced activities. This is especially true if beneficial associative relationships co-evolved among carnivore species. San Joaquin kit fox declines may have begun much sooner than previously believed. Other species, besides the kit fox, may have also experienced negative ecological impacts with the removal of top predators. For example, California is significant geographically in regard to the Pacific Flyway (Bellrose 1980). With coyotes kept at low numbers by wolves, a lower predation level on many species of ducks and geese

by coyotes may have occurred (Goldman 1930). California was no doubt a much different place 200 years ago, and current conservation measures are necessary to preserve what biodiversity is left.

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Literature Cited

Ausband, D. E., and E. A. Ausband. 2006. Observations of interactions between swift fox and American badger. *The Prairie Naturalist* 38:63-64.

Barbour, M., B. Pavlik, F. Drysdale, and S. Lindstrom. 1997. California's Changing Landscapes. Diversity and Conservation of California Vegetation. California Native Plant Society, Sacramento, California, USA.

Beidleman, R. G. 2006. California's frontier naturalists. University of California Press, Berkeley, USA.

Bellrose, F. C. 1980. Ducks, Geese, and Swans of North America. Third edition. Stackpole Books, Harrisburg, Pennsylvania, USA.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11:947-960.

Bunker, C. D. 1940. The kit fox. *Science* 92:35-36.

Cahalane, V. H. 1950. Badger-coyote "Partnerships." Journal of Mammalogy 31:354-355.

Chesemore, D. L. 1968. Notes on the food habits of arctic foxes in northern Alaska. Canadian Journal of Zoology 46:1127-1130.

Clark, H. O., Jr. 2004. Occurrence of California mule deer in the southern San Joaquin Valley, California. Transactions of the Western Section of the Wildlife Society 40:127-128.

Cohn, J. 1998. A dog-eat-dog world? BioScience 48:430-434.

Creel, S., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. Conservation Biology 10:526-538.

Crooks, K. R., and M. E Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.

Cypher, B. L. 2003. Foxes (Vulpes species, Urocyon species, and Alopex lagopus). Pages 511-546 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America. Biology, Management, and Conservation. Second edition. The John Hopkins University Press, Balimore, Maryland, USA.

Cypher, B. L., and K. A. Spencer. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79:204-214.

Fuller, T. K., and L. B. Keith. 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. Journal of Mammalogy 62:403-405.

Garrott, R. A., P. J. White, and C. A. Vanderbilt White. 1993. Overabundance: An issue for conservation biologists? Conservation Biology 7:946-949.

Goldman, E. A. 1930. The Coyote: Archpredator. Journal of Mammalogy 11:325-335.

Grinnell, J. 1938. California's grizzly bears. Sierra Club Bulletin 23:70-81.

Grinnell, J., J. Dixon, and J. Linsdale. 1937. Kit foxes. Pages 399-420 in J. Grinnell, J. Dixon, and J. Linsdale, editors. Fur bearing animals of California. Volume 2, University of California Press, Berkeley, California, USA.

Harris, R. B., and C. O. Loggers. 2004. Status of Tibetan plateau mammals, in Yeniugou, China. Wildlife Biology 10:91-99.

Hall, E. R. 1939. The grizzly bear of California. California Fish and Game 25:237-244.

Hawkins, A. H. 1907. Coyote and badger. The Ottawa Naturalist 21:37.

Holing, D. 1988. California Wild Lands. Chronicle Books, San Francisco, California, USA.

Ingles, L. G. 1963. Status of the wolf in California. Journal of Mammalogy 44:109-110.

Jonkel, C. J. 1987. Brown Bear. Pages 456-473 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild Furbearer Management and Conservation in North America. Ministry of Natural Resources, Ontario, Canada.

Kay, C. E. 1998. Are ecosystems structured from the top-down or bottom-up: a new look at an old debate. Wildlife Society Bulletin 26:484-498.

Kelly, P. A., S. E. Phillips, and D. F. Williams. 2005. Documenting Ecological Change in Time and Space: The San Joaquin Valley of California. Pages 57-78 in E. A. Lacey, and P. Myers, editors. Mammalian Diversification: From Chromosomes to Phylogeography. University of California, Berkeley, USA.

Kiliaan, H. P., C. Mamo, and P. C. Paquet. 1991. A coyote, Canis latrans, and badger, Taxidea taxus, interaction near Cypress Hills Provincial Park, Alberta. The Canadian Field-Naturalist 105:122-123.

Kuzyk, G. W., C. Rohner, and J. Kneteman. 2001. Grizzly bear defends moose carcass from wolves in west-central Alberta. Alberta Naturalist 30:75-76.

Linnell, J. D., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions 6:169-176.

Minta, S. C., K. A. Minta, and D. F. Lott. 1992. Hunting associations between badgers (Taxidea taxus) and coyotes (Canis latrans). Journal of Mammalogy 73:814-820.

Murie, A. 1987. The grizzlies of Mount McKinley. University of Washington Press, Seattle, USA.

Nelson, J. L., B. L. Cypher, C. D. Bjurlin, and S. Creel. 2007. Effects of habitat on competition between kit foxes and coyotes. Journal of Wildlife Management 71:1467-1475.

Packer, C., and L. Ruttan. 1988. The evolution of cooperative hunting. The American Naturalist 132:159-198.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153:492-508.

Paquet, P. C. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy 72:397-401.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy 73:337-343.

Preston, W. L. 1981. Vanishing landscapes. Land and life in the Tulare lake basin. University of California Press, Berkeley, USA.

Przewalski, H. M. 1883. The third travel in central Asia. Zaisan through Khami to Tibet and on the Yellow River head. Saint Petersburg, Russian Empire. [In Russian.]

Ralls, K., and P. J. White. 1995. Predation on San Joaquin kit foxes by larger canids. Journal of Mammalogy 76:723-729.

Schmidt, R. H. 1991. Gray wolves in California: Their presence and absence. California Fish and Game 77:79-85.

Schoenherr, A. A. 1992. A natural history of California. University of California Press, Berkeley, USA.

Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly Bear (Ursus arctos). Pages 556-586 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America. Biology, Management, and Conservation. Second edition. The John Hopkins University Press, Balimore, Maryland, USA.

Snyder, S. 2003. Bear in Mind: The California Grizzly. Heyday Books, Berkeley, California, USA.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75-92.

Storer, T. I., and L. P. Tevis. 1996. California Grizzly. University of California Press, Berkeley, California , USA.

Wilbur, S. R. 2004. Condor Tales. What I learned in twelve years with the big birds. Symbios, Gresham, Oregon, USA.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. The Journal of Animal Ecology 72:909-916.