January 1, 1986

Community-level effects of coyote population reduction

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ABSTRACT: Predator control in the United States is directed primarily at the coyote (Canis latrans). Control programs are constructed to relieve predation losses to livestock. Although a variety of nonlethal control techniques are being used to some degree, lethal control methods continue to be a major part of modern predator control programs.

Toxicants have played a major role in past coyote population reduction programs. Traditional toxicants included strychnine, thallium sulfate, sodium cyanide, and sodium fluorooacetate (compound 1080). The use of toxicants on federal lands was banned by presidential order in 1972; this ban was revoked in 1982. Toxicants may play a larger role in predator control programs if the U.S. Environmental Protection Agency approves registration of any old or new materials for that purpose.

There appears to be an inverse relationship between population levels of coyotes and red foxes (Vulpes vulpes), gray wolves (C. lupus), or other carnivores. When large-scale coyote population reduction programs were successful, red foxes and other medium and large mammalian predators tended to increase. Experimental work and observations on coyote and red fox interactions have shown that coyotes exclude foxes from coyote-occupied habitats. Thus a single-species population reduction program, with toxicants or other means, impacts other members of the medium and large mammalian carnivore guild. The resulting change may impact prey species, because of species-specific prey preferences and foraging tactics, but this is poorly documented.

This paper reviews historical trends of populations of North American canids and recent work on interspecific interactions of canids. In addition, it examines three ecological mechanisms that may be major factors leading to canid competition.

KEY WORDS: community ecology, coyote, Canis latrans, red fox, Vulpes vulpes, gray wolf, Canis lupus, vertebrate pest control, predation, predacides, sodium fluorooacetate, compound 1080, competition

Predator damage prevention and control in the United States is directed primarily at the coyote (Canis latrans) [1]. Control programs are constructed to relieve predation losses to livestock, particularly sheep [1–18], cattle [1,10,16,19], and goats [20,21]. Although a variety of nonlethal control techniques, including modified husbandry practices, guard dogs, electric fencing, and aversive conditioning, are being researched or used to some degree [1,16,22–28], lethal
control methods (shooting, trapping, snaring, denning, toxicants) continue to be a major part of modern predator control programs [1,16,25,26,29–34].

Toxicants were used extensively in predator damage control programs in the United States through 1971 [1,16,23,29,35–37]. Traditional toxicants have included thallium sulfate, strychnine, sodium fluoroacetate (compound 1080), and sodium cyanide [1,35,37]. The use of these predacides on federal lands was prohibited in 1972 with Executive Order No. 11643 [38,39]. Immediately following this action, the U.S. Environmental Protection Agency (EPA) cancelled federal registration of all predacides and prohibited their interstate shipment [40]. Modifications of the executive order in 1975 and 1976 permitted the use of sodium cyanide in a mechanical delivery device known as the M-44 [41,42]. In 1982 the original executive order was revoked [43]. The use of toxic chemicals is now permitted in federal programs and on federal lands, subject to state and federal regulations and registration with the EPA. In 1984, sodium cyanide (used with the M-44 device) and sodium nitrate (burned with charcoal to produce carbon monoxide and used as a fumigant) were the only compounds federally registered for control of coyotes [44].

Future use of toxicants for coyote control is difficult to predict, but there are strong indications that toxicant use may increase over the levels used since 1972. There is pressure from the agriculture and livestock communities to reestablish the use of some toxicants, particularly compound 1080 [1,16,45,46]. Research is being conducted on new types of toxicants and on new or improved methods of using traditional toxicants [18,47–54]. And finally, the EPA has ruled that it will consider applications for registration of compound 1080 as a predacide [55,56].

The intent of this paper is as follows: (1) document historical trends in North American canid distributions; (2) review the evidence for the impact of coyote control (chiefly with toxicants) on coyote populations; (3) examine the known and potential community-level effects of coyote population reduction, especially as it affects foxes and other carnivores; and (4) discuss the ecological factors involved in canid interactions.

Historical Trends in Canid Distribution

Hall [57] recognized eight species of wild canids in North America (Table 1). The current distribution of these animals in North America is much different than it was in historical times, and has been summarized elsewhere [57–65]. Briefly, more than 200 years ago, gray wolves (Canis lupus) had a very broad distribution, probably occupying the major part of the continent except for the southeastern coastal plain. Coyotes were confined to open plains and more arid regions, mainly

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2 On 18 July 1985 the U.S. Environmental Protection Agency approved the use of compound 1080 in “livestock protection” collars to be worn by sheep, goats, and other livestock. When a coyote bites the throat of its prey, it should puncture a rubber reservoir in the collar, which contains a lethal dose of compound 1080. The coyote swallows the poison as it asphyxiates its prey.
TABLE 1—Wild canids of North America, with descriptive physical parameters.

<table>
<thead>
<tr>
<th>Name</th>
<th>Total Length, mm</th>
<th>Tail Length, mm</th>
<th>Hind Foot Length, mm</th>
<th>Weight, kg</th>
<th>Length of Skull, mm</th>
<th>Reference</th>
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<tbody>
<tr>
<td><em>Canis lupus</em></td>
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<td><em>Canis latrans</em></td>
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<tr>
<td><em>Canis rufus</em></td>
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<tr>
<td>Arctic fox</td>
<td>1100</td>
<td>420</td>
<td>160</td>
<td>1.4–3.2</td>
<td>120</td>
<td>57, 142</td>
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<tr>
<td><em>Alopex lagopus</em></td>
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<tr>
<td>Red fox</td>
<td>900–1030</td>
<td>340–400</td>
<td>145–170</td>
<td>3–7</td>
<td>130–150</td>
<td>57, 60, 97</td>
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<tr>
<td><em>Vulpes vulpes</em></td>
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<tr>
<td>Kit fox&lt;sup&gt;a&lt;/sup&gt;</td>
<td>600–800</td>
<td>225–300</td>
<td>110–130</td>
<td>2–3.5</td>
<td>100–115</td>
<td>57, 60, 143</td>
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<tr>
<td><em>Vulpes velox</em></td>
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<tr>
<td>Gray fox</td>
<td>800–1125</td>
<td>275–445</td>
<td>100–150</td>
<td>3–6</td>
<td>110–130</td>
<td>57, 60, 144, 145</td>
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<tr>
<td><em>Urocyon cinereoargenteus</em></td>
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<tr>
<td>Island gray fox</td>
<td>590–790</td>
<td>110–290</td>
<td>100–160</td>
<td>2–3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>92–105</td>
<td>57</td>
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<tr>
<td><em>Urocyon littoralis</em></td>
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<sup>a</sup> Hall [57] recognizes *Vulpes macrotus* as a subspecies of *V. velox*.

<sup>b</sup> Estimated.
in the western half of the continent. Their eastern distribution seemed to follow the prairie peninsula through the midwestern states. Red foxes (*Vulpes vulpes*) were present in the northern portions of the continent, while gray foxes (*Urocyon cinereoargenteus*) occupied the southern hardwood forests and coastal regions. Kit foxes (*V. velox*) occurred in the arid western states. Occupying the southeastern states were red wolves (*C. rufus*). Finally, arctic foxes (*Alopex lagopus*) occurred in the arctic biome, while the island gray fox (*U. littoralis*) occurred only on islands off the coast of southern California.

Over the past 200 years, human activities, particularly in agriculture, livestock production, and forestry, have had a profound influence on wildlife and habitats [66–69]. These activities have also influenced canid distribution and abundance patterns. Hall [57] speculated that

\[ \ldots \text{on the Midgrass and Shortgrass prairies of the High Plains, wolves were abundant as long as natural mortality in the bison herds provided most of the wolves' food. When the wolf population declined, the coyote population increased. When the coyote population decreased in the 1900s, the red fox moved westward and now lives where few or none did two or three decades ago. (p. 938)} \]

Nowak and Paradiso [70] concluded that the eastward expansion of coyotes could be attributed to "\ldots the creation of favorable habitat through the breaking up of the forests by settlement, and human elimination of the wolves (*C. rufus* and *C. lupus*) that might have competed with the coyote'" (p. 951). Gier [63] felt that the west and northwest extensions of coyote range "\ldots followed reduction of gray wolves, coupled with provision of a special, although temporary, food supply of horse flesh, and the opening of forested areas, by logging and burning \ldots,’’ while the east and northeast extension followed removal of gray wolves and "\ldots return of millions of acres to pastures and brushland \ldots’’" (p. 248). Currently, gray wolves are practically extirpated below the 48th parallel, but above it their populations are fairly stable [59]. Coyotes have expanded their range into every state, province, territory, and country north of Panama [65,71]. Red foxes have moved south and west, expanding their range, while the range of the kit fox has probably been reduced, although this fox is still found in the arid western plains [57]. There are a number of regions, particularly in the northern portion of the continent, where populations of gray wolves, coyotes, and red foxes overlap.

**Impacts of Coyote Control on Coyote Populations**

Over four million coyotes have been destroyed by federal animal damage (ADC) programs since 1916 [31,80]. Pearson [81] estimated that only one quarter of the coyotes harvested in the 17 western states in 1974 were attributed to the federal ADC program (71 572 coyotes); the majority of coyotes were taken by private hunters and trappers (223 884 coyotes). The U.S. Fish and Wildlife Service (FWS) [7] has estimated the fall coyote population of the 17 western
states at 1,592,000. They concluded, "This is more than five times the total 1974 coyote harvest, and more than 22 times the 1974 ADC coyote take. Thus, the ADC program annually may take about four percent of the westwide fall coyote population" (p. 76). They admit, however, that since the federal control program involves only about 11% of the area in the west, "... removal from local populations is substantially greater" (p. 76). Simulation models of coyote populations have indicated that, because of density-dependent responses in mortality and natality rates, it is difficult to suppress coyote populations for an extended period of time [80]. Connolly [80] concluded, "During this century millions of coyotes have been destroyed in the western United States, yet a large and healthy coyote population remains" (p. 328).

Nevertheless, predator control practices have been credited with at least temporary coyote population reductions in central Texas [16,46,58,72], New Mexico [73,74] (however, see Ref 36), Wyoming [1,35,36,63,77–79], Montana [1,35,36,63], Idaho [1,35,36], Utah [1,35,36,63], Colorado [63], Nevada [63], South Dakota [16], and North Dakota [63,75,76]. Documentation of population reductions is usually based on the correlation of some coyote population index with the utilization or intensity of control, or it is based on an expert’s opinion. The data most often cited are from the FWS Division of Wildlife Service records [1,35,36] and use the number of coyotes taken per man–year as an index to coyote populations in different states (Fig. 1). The primary assumption with this index is that "... the more coyotes there are, the more that will be taken per man–year of control effort" [1, p. 76]. Problems with this index have been discussed elsewhere [1,35,36]. The data indicate a general decline in coyote density as 1080 use increased, at least in the northern states. This decline was not evident in southern states [35,36]. Since the 1972 ban on predacides, a new, standardized coyote population index based on coyote visitation to lines of scented tracking stations [82–84] has not shown a dramatic increase in coyote population levels [1]. Whether this is a real phenomenon or an indication of the inadequacy of the index itself is not known [1, p. 77]. It is recognized that coyote control can eliminate local populations [1,72,85], and that blanket predator control can be effective at reducing predator densities [86,87]. There are few who would doubt that coyote control can depress coyote populations [e.g., 88]; the main unknowns are the amount and type of effort required to achieve a particular level of control and the persistence of a control pulse before coyote populations return to pre–control levels.

To summarize, although there have been major changes in distribution patterns (and presumably abundances) of coyotes because of land–use changes, there is evidence that coyote populations can be reduced with intensive coyote control, especially when compound 1080 is used (although not necessarily, as discussed in Ref 88). The next question deals with the community–level effects of reducing coyote populations. The discussion that follows addresses the effects of coyote control on foxes and other carnivores, on large mammals, and on small mammals and birds, as well as other potential community effects.
FIG. 1—Annual coyote population trends using indices based on coyotes-killed-per-man-year of effort for the years 1930 through 1970 (from Ref 1, based on data presented in Refs 35 and 36). The indices indicate a general reduction in coyote populations following the introduction of compound 1080 as a predacide in these four northern states.

Community-Level Effects of Coyote Control

Effects on Foxes and Other Carnivores

There is a great deal of evidence that suggests that certain canid species have a suppressing effect on other canid species. Johnson and Sargeant [75] have reviewed the changes in canid abundance and distribution in the Prairie Pothole region of North Dakota. They conclude the following [75, p. 41]:

The mechanisms whereby large canids suppress populations of smaller canids are largely unknown but in instance after instance, coyotes have fared poorly in wolf-dominated areas and red foxes have fared poorly in coyote-dominated areas. What is known about the relationships among these three species suggests that the degree of tolerance is much higher between species of greatest size difference. Wolves are more tolerant of foxes than they are of coyotes . . . . Confusing the issue is that, at times and in certain situations, smaller canids may actually benefit from the larger canids by feeding on the remains of prey left by the larger species . . . . Direct killing of small species by larger species occurs, but there is insufficient evidence to suggest that killing is the principle mechanism for suppression.

Gray wolves kill coyotes when the opportunity presents itself [29,89–91], and
there appears to be an inverse relationship between gray wolf and coyote population densities [89,91]. Mech [90] described the history of coyotes and gray wolves on Isle Royale in Lake Superior. Coyotes had been present on the island ever since the early 1900s, but after the arrival of wolves, they became very scarce. Since 1958, no coyotes have been found on Isle Royale. This relationship probably aided the rapid expansion of coyote populations following the elimination of gray wolves below the 48th parallel.

A similar relationship exists between coyotes and red foxes. Coyotes kill red foxes, especially trapped red foxes [29,63,92–96], although it is unlikely that this is a significant source of mortality for foxes [63,94,97,98]. There is strong evidence that, mortality factors aside, coyotes exclude or displace red foxes from coyote-occupied habitats [36,63,75,79,94–96,99,100]. (However, see Ref 101, p. 710). This observation leads to the prediction that reductions in coyote populations can result in increased red fox populations. Red fox population indices tend to increase following coyote population reduction [1,36,75,76,79]. Population indices of other large carnivorous mammals, including bobcats (Lynx rufus) [36,73,74,77–79,102], badgers (Taxidea taxus) [36,77–79], and kit foxes [36,77–79,103] also have been found to increase following coyote population reduction. Wagner notes, "The implication seems to be that interspecific population regulatory processes exist between these species in the same trophic level, with perhaps the larger Canids the more aggressive, dominant forms" [Ref 36, p. 40]. However, Voigt and Earle [94] reviewed evidence that red fox populations may limit coyote numbers, and Gier [63] noted a single ravine in Kansas inhabited by coyotes, red foxes, and gray foxes "... with no evidence of agonistic reactions between them" (p. 261). Interactions between species of canids (arctic fox-red fox [104,105], kit fox-red fox coyote [106], coyote-kit fox [107], and coyote-red fox [75,76,108–110]) have been discussed as management concerns or as systems to be exploited to fulfill management goals (for example, red foxes as biological control agents for arctic foxes occupying islands).

**Effects on Large Mammals**

The impact of coyote predation on populations of large mammals, particularly ungulates, is a point of controversy. In a comprehensive review, Connolly [111] found 16 studies in which coyotes were reported to have a limiting or regulatory influence on specific North American ungulate populations, and at least 12 studies in which coyotes had no apparent effect. In areas where coyotes have an impact on ungulate populations, a release in predation pressure may enable the ungulate population to increase in either abundance or in distribution. Clearly, it would be difficult to predict significant community-level influences resulting from such a population increase; any change would be highly dependent upon the strength and duration of the reduced predator pressure, and on the compensatory nature of other mortality factors. Since red foxes rarely kill ungulates [60,62], replacement of coyotes by foxes would not replace pre-existing predation mortality.
Effects on Small Mammals and Birds

Whether vertebrate predators can regulate small mammal populations has been debated for many years [112,113]. In some instances, vertebrate predators can increase the amplitude of fluctuations and extend the time of recovery period in prey population oscillations; however, impact on prey populations is reduced or nonexistent during periods of peak numbers [112]. If coyotes play a major role in regulating small mammal populations, then coyote removal may have community–level effects. Small mammals have real impacts on ecosystems, especially on soil and nutrient dynamics, vegetation production and composition, energy flow rates and pathways, and on other small mammals [113–119]. Small mammals commonly are preyed upon by a diverse assemblage of predators, and while we know that different species of predators have unique food preferences and foraging tactics [75,120–122], we do not understand the effects on prey populations of removing a single predator from this assemblage. Field experiments involving vertebrate predator removal [reviewed in Ref 123, pp. 34–42] often had at least temporary effects on prey populations; however, in these experiments, many predator species were removed from the experimental plots instead of a single predator species. Erlinge et al [113] concluded that an assemblage of nine vertebrate predator species regulated a population of voles (Microtus agrestis), while Guthery and Beasom [124] reported that removal of seven vertebrate predator species had no discernible effects on rodent populations. Wagner [36] felt that coyotes in Utah were responsible for hastening and deepening the decline of black-tailed jackrabbit (Lepus californicus) population oscillations, but had minimal impact on rabbit numbers when rabbits were at high densities. The overall conclusion appears to be one of equivocality regarding the impact of coyote removal on small mammal populations.

Evidence of significant impacts of coyote removal on bird populations is also rare, but an outstanding exception is the work of Sargeant and his colleagues [75,76,108–110]. They document changes in the canid predator assemblage in North Dakota over the past 100 years and conclude that coyote population reduction in the early 1900s was one of the principle causes for increases in the red fox population. Increased red fox densities have led to increased predation on ground-nesting dabbling ducks, most notably mallards (Anas platyrhynchos).

Although predation by foxes does not jeopardize the survival of any midcontinent duck species, it does affect annual production, population composition, and may, when coupled with other mortality factors, be sufficient to hold populations at much lower levels than would otherwise occur” [Ref 108, p. 36].

Using a simulation model, Johnson and Sargeant [75] demonstrated that red foxes are most likely responsible for the unbalanced sex ratio (excess males) in midcontinent mallard populations. This clearly demonstrates a community–level effect of coyote population reduction, with increased red fox populations and foxes impacting a prey species.
Other Potential Community-Level Effects

Since little is known about some of the more obvious effects of coyote population reduction on communities (for example, effects on other carnivores), it is not surprising that almost nothing is known about more subtle effects, such as effects on vegetation composition. Coyotes are omnivorous, and sometimes include a large proportion of fruit and other seeds in their diet [29,63]. Their importance as both predators and dispersers of these seeds [125] is not understood. In addition, coyotes probably disperse seeds of plant parts which get tangled in their fur. Regarding Opuntia spp. in the southwest United States, Young [29] speculated that “... there is reason to suspect many cholla cactus of our arid Southwest have been planted not by the ‘hand of man,’ but by the ‘body of the coyote’” (p. 142). It is possible that coyotes can influence community dynamics through direct impacts on vegetation, but the extent or degree of these effects is unknown. The impact of coyote removal on the population dynamics of canid parasites also is unknown.

Ecological Factors Involved in Canid Interactions

This review of canid interactions indicates that there is a strong negative interaction between gray wolves, coyotes, and red foxes. It seems proper to call this interaction competition [126], and the competition appears to be of the interference type. The next question thus arises: If competition is the process leading to these interactions, what limiting resource are these species competing for? Detailed descriptions of the morphology, food habits, behavior, and ecology of coyotes, wolves, and foxes are given by Bekoff [65], Paradiso and Nowak [59], and Samuel and Nelson [65], respectively. The general body shapes of these canids are similar, although they differ in size and weight (Table 1). Generally, the larger the animal is, the larger the home range size.

Food resources are a popular area to look for overlap in the utilization of limiting resources. Food habits overlap broadly in some instances, but there are some general trends. Red foxes feed on fruits, insects, mice and other small rodents, birds, rabbits, and hares. Deer carcasses are an important food source in the winter, along with other carrion. Coyotes feed on fruit, insects, mice and other small rodents, rabbits, hares, birds, and ungulates. Carrion also plays an important role when live prey is scarce. Gray wolves feed on larger animals, including beaver (Castor canadensis), snowshoe hares (Lepus americanus), deer (Odocoileus spp.), moose (Alces alces), elk (Cervus elaphus), and caribou (Rangifer tarandus). Overlap between coyote and gray wolf diets is low. Green and Flinders [127] looked at the diets of sympatric red foxes and coyotes in Idaho. They concluded that the diets differed from each other in both the winter and summer seasons. Red foxes and coyotes generally consumed similar food items, but in dissimilar proportions. Larger canids tend to consume larger food items [128]; as canid species increase in size differences, food types tend to become less similar. Although foods of coyotes, red foxes, and gray wolves overlap,
they consume similar food items in different proportions. However, there are times (for example, low points in rodent, hare, or ungulate cycles or when heavy snow covers food supplies) when food is definitely limiting and is an important mortality factor [Ref 90, p. 316]. These occasional periods of food shortage may encourage the development and evolution of competitive interactions that persist during periods of food abundance. Interspecific territoriality may function to establish favored and private feeding and foraging sites.

Although food is an obvious resource to turn to when attempting to find limiting factors that could explain the intensity of canid interactions, other potential reasons exist. Gray wolves are reported to use “abandoned” red fox dens [90], and both coyotes and red foxes utilize old badger dens and each other’s dens to some extent [60,63,94]. Multiple dens are commonly used within territorial boundaries, and the same den is often used from year to year [94]. It has not been demonstrated that rearing dens are ever in short supply, however. Since wolves, coyotes, and foxes all seem capable of using the abandoned dens of other species, there is the potential that den sites may be a limiting resource. The data do not exist to evaluate this possibility at this time.

Larger canids can kill smaller canids, as noted earlier. Reduced risk of predation is a potential selective force to avoid the territory of a larger sympatric canid; however, the infrequency of occurrence of hairs of other canid species appearing in food–habits analyses suggests that actual predation is rare.

The influence of parasites on the populations of their hosts is beginning to receive more deserved attention [129]. Parasitism is not only an important evolutionary selective pressure [130,131], it is also an important proximate mortality factor. Gray wolves, coyotes, red foxes, and other canids share a large ectoparasite and endoparasite fauna [132–134]. Todd et al [135] reviewed the importance of sarcoptic mange, caused by the mite Sarcoptes scabiei, on gray wolf and coyote mortality and concluded that it was an important density–dependent mortality factor. Sarcotic mange also affects red foxes [60]. Gier et al [136] suggested that if sarcotic mange is not fatal, then it probably preconditions coyotes to additional infections of other parasites. Of course, mange is only one of many deleterious conditions caused by parasites. Helminth infections, viral and bacterial diseases, fungal infections, and invasions by various disease–carrying arthropods all are factors that can increase the probability that the host may die or suffer decreased fecundity (decreased fitness). Since most species of canids are suitable hosts for similar parasite faunas, and since many of these parasites are density–dependent in their transmission (such as sarcotic mange or rabies), strong interference competition may result in lowered transmission rates of potentially fatal infections. Interspecific territoriality may function to decrease the probability of contracting a disease or parasite.

We do not know which factors are the main determinants of competitive interactions, but potential ones are food, rearing dens, and “parasite–free” areas. One hopes these issues will receive more attention in the future.
Concluding Remarks

Many of the potential community-level effects of reducing coyote populations are unknown, but a review of the literature indicates real impacts in certain areas: impacts on other canids, and at least one documented case of impacts on prairie mallards resulting from the canid interactions. In addition to the data-poor areas raised in this review, two larger and important questions still remain unanswered. First, are the community-level effects resulting from coyote population reduction "significant" [137]? And finally, should we go beyond community-level effects and look at potential effects on ecosystems [138]? Predation by coyotes on livestock will always be a management concern in areas where they coexist [139]. Although it is doubtful that any multispecies community is sufficiently well understood for us to make confident predictions about responses to disturbance [140], an understanding of community-level effects of coyote population reduction should be useful in understanding the role of coyotes in nature and in coyote and livestock management decisions.

Acknowledgments

I thank R. M. Timm, W. E. Howard, and E. Gould for reviewing portions of the manuscript, and C. A. Toft for helpful discussions regarding the impact of parasitism on community structure. This study was supported in part by a University of California at Davis (UCD) Jastro Research Scholarship, a grant from the UCD Institute of Ecology (Stebbins Cold Canyon Reserve), and a UCD Graduate Student Travel Award.

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