HUNTING ASSOCIATIONS BETWEEN BADGERS (*TAXIDEA TAXUS*) AND COYOTES (*CANIS LATRANS*)

Steven C. Minta, Kathryn A. Minta, and Dale F. Lott

Department of Wildlife and Fisheries Biology,
University of California, Davis, CA 95616

Current address of S.C.M.: Division of Biological Sciences,
University of Montana, Missoula, MT 59812

Coyotes (*Canis latrans*) associating with badgers (*Taxidea taxus*) appeared to hunt Uinta ground squirrels (*Spermophilus armatus*) more effectively than lone coyotes. Coyotes with badgers consumed prey at higher rates ($P = 0.09$) and had an expanded habitat base and lower locomotion costs. Badgers with coyotes spent more time below ground and active ($P = 0.02$), and probably had decreased locomotion and excavation costs. Overall, prey vulnerability appeared to increase when both carnivores hunted in partnership. Complementary morphological adaptations and predatory strategies, interspecific tolerance, and behavioral flexibility allowed them to form temporary hunting associations. The following ecological circumstances may have increased the likelihood of this interaction in our study area: relatively high densities of predators and prey; relatively long-lived predator populations; a vegetative structure that impeded solitary hunting by coyotes; a high connectivity of prey burrows that decreased hunting success of badgers; an absence of interaction with humans; a stressful physical environment.

Key words: *Taxidea taxus, Canis latrans,* hunting association, predator interaction

In most models, predator guilds are structured by competition for resources (Hairston et al., 1960; Rosenzweig, 1966; Schoener, 1983). However, Native American folklore includes tales of badger-coyote (*Taxidea taxus-Canis latrans*) hunting associations (Dobie, 1950; Goodwin, 1939; Ramsey, 1977), and early settlers, naturalists, and scientists also reported such associations (Aughey, 1884; Dobie, 1950; Hawkins, 1907; Seton, 1929). Recent scientific reports of this association are scant and based on few observations (Cahalane, 1950; Robinson and Cummings, 1947; Young and Jackson, 1951). We have observed many such associations on the National Elk Refuge in northwestern Wyoming.

The badger is an 8-kg mustelid, morphologically specialized for digging after prey. Ground-dwelling sciurids escape predators in long, deep, or interconnected tunnels (King, 1984; Slade and Balph, 1974; Stromberg, 1975). Badgers trap them in dead-end tunnels by excavating soil (Lampe, 1976; Minta, 1990). On the National Elk Refuge, Uinta ground squirrels (*Spermophilus armatus*) were semicolonial with many interconnected tunnels. Badgers minimized escape of ground squirrels by plugging burrows and running back and forth to induce the squirrel to remain below ground (Knopf and Balph, 1969; Lampe, 1976; Minta, 1990).

The coyote, a 13-kg canid, captures rodents by pouncing and chasing; therefore, ground squirrels are accessible only while above ground. Coyotes ambush squirrels grazing too far from tunnel entrances. In our study area, brush interfered with coyote search, pursuit, and capture. A coyote associating with a hunting badger waited nearby for the badger to flush squirrels from their burrows. A squirrel detecting the coyote sentinel might remain below, giving the badger continued opportunity to capture it.

If these associations were mutualistic, overall benefits will increase relative to costs for both participants. If commensalistic, net benefits will increase relatively for one participant, but not change for the other. If parasitic, net benefits will increase relatively for one participant and decrease for the other, compared to solitary hunting.

MATERIALS AND METHODS

The observations were part of a 3-year study (1982–1985) of the ecology of badgers on the National Elk Refuge (Minta, 1990). Most observations were within a 30-km^2 area of flat to steep rolling topography (mean elev. = 2,050 m) closed to the public. The climate was markedly seasonal with long, cold winters. The mean annual temperature was 0°C (Minta, 1990) and the mean annual snowfall was 3 m, which accounts for ca. 60% of the 61.5-cm average precipitation. The plant community was dominated by mixtures of low brush (big sagebrush, *Artemesia,* and rabbitbrush, *Chrysothamnus*) and various endemic and introduced grasses that supported high densities of a single rodent herbivore, the Uinta ground squirrel.

Unita ground squirrels accounted for the majority of the badger's annual prey biomass (Minta, 1990) and of the coyote's seasonal prey biomass from May through July (Weaver, 1977). They hibernated below ground from August to April. Camenzind (1978) estimated a minimum pre-whelping coyote density of 0.5/km^2 and post-whelping density of 1.5/km^2 in this area in 1971–1973. Post-dispersal density of badgers in autumn was a minimum of 2/km^2 in 1984 (Minta and Mangel, 1989).

In the research design, a badger-coyote association was a sampling unit. Sampling was confined to those of 42 badgers with implanted radiotransmitters that interacted with coyotes. With random sampling, observations of experimental (sampling) units would be independent, but our observations were not. We believe that the mobility of coyotes and telemetered badgers over four annual cycles (26 months of field time) may have approached randomized sampling. Therefore, descriptive statistics will be followed by qualified inferential statistics. Test of two proportions as Poisson variates follows Fleiss (1981); *t*-test for unequal sample sizes follows Mendenhall and Scheaffer (1973) after satisfying Bartlett's test for homogeneity of variances at $P = 0.05$ level; the Kolmogorov-Smirnov test follows the computation of Siegel (1956).

Badgers and coyotes were considered to be hunting in association when either's attention was focused on the other's activity with apparent intent to hunt ground squirrels. Intent was defined to be the first initiation by either of a predatory sequence (Lampe, 1976 for badgers; Wells and Bekoff, 1982 for coyotes). After the first predatory action, the association was considered ongoing if the members of the pair were in proximity and seemed to respond to each others' activities, including solitary behaviors (e.g., resting, dozing, rolling). The association ended when the badger remained below ground or repelled the coyote, or when the coyote lost interest.

We used two types of indices of the association's costs and benefits to each species: first we compared rates of prey capture and activity budgets of each species hunting alone and hunting in an association. Then we recorded each species' response to the other's presence assuming that behavior that initiates or maintains the association is evidence that the net outcome for the behaving animal is neutral or positive, while behavior that tends to avoid or terminate the association is evidence that the net outcome is negative.

RESULTS

A coyote's available hunting habitat increased greatly while hunting with badgers. Relative to open habitat, within brushy habitat (with higher densities of squirrels—Minta, 1990) far more coyotes hunted with badgers than hunted alone. Associated coyotes saved energy and (possibly) time via decreased searching, stalking, and chasing. They mostly waited for the opportunity to quickly scramble and capture a squirrel.

During the several weeks following the emergence of juvenile squirrels in June, badgers sought out burrows containing squirrel litters (Knopf and Balph, 1969; Minta, 1990; J. O. Murie, in litt.) and associated coyotes captured many more squirrels. Associated coyotes captured more prey than solitary coyotes; 26 solitary coyotes observed for 41.3 h, ($\bar{X} = 1.59$ h, $SD = 1.15$) captured 0.55 squirrels/h compared to 71 coyotes hunting with badgers observed for 86.6 h ($\bar{X} = 1.22$ h, $SD = 0.87$) capturing 0.74 squirrels/h, a 34% increase in capture rate. If we assume these associations represent a random sample of hunting episodes, then a conservative test of the two capture rates marginally supports the hypothesis of increased capture rates ($Z = 1.34$, $P = 0.09$, one-tailed).

Predation rates of badgers could not be similarly assessed because squirrels mostly were caught and eaten below ground. However, badgers hunting alone spent far more time aboveground than badgers hunting with coyotes. Seven solitary badgers resurfaced 61% more often during 74 excavations than the same seven badgers associated with coyotes during 31 excavations. If we assume that these excavations and associations are a random sample of hunting episodes, then there is a difference in the number of resurfacings per excavation ($t = 2.43$, $d.f. = 103$, $P = 0.02$, two-tailed). We interpret the increased time below ground as a direct benefit if that time was spent in consumption, or a decrease in costs if that time was spent more efficiently pursuing prey. Comparisons of older, more skilled badgers versus younger, less efficient badgers supports this interpretation. Younger badgers resurfaced more often to check nearby tunnels and dug more exploratory holes (Minta, 1990). In addition, coyotes clearly did not inhibit badgers from surfacing (see below). Soil excavation is costly (Lampe, 1976), so small decreases in digging would save substantial energy. Additional potential benefits are discussed below.

The duration of partnerships was extremely variable. We timed 214 associations totaling 184.4 h ($\bar{X} = 0.86$ h, $SD = 1.09$). There are disproportionately more short and long associations than expected from a random process (Fig. 1) for several reasons; female badgers in natal den areas always, and females with mobile offspring frequently, rebuffed coyotes. Male badgers attentive to females during the breeding season sometimes suddenly rebuffed coyotes.

We could locate badgers (and accompanying coyotes) via telemetry at distances beyond their sensory ranges, but coyotes readily ended an association upon detecting us. We judged our influence to be the cause of breakup when, immediately before a breakup, a coyote's attention shifted from coordinating complex predatory tasks with the badger and it oriented toward us (these occasions are noted on Fig. 1). Thus, we expect the duration of associations in which the observer was likely detected ($\bar{X} = 0.54$ h, $SD = 0.77$, $n = 127$) to be less than those that we did not break up ($\bar{X} = 1.32$ h, $SD = 1.31$, $n = 87$; Fig. 1). If we assume that these associations represent a random sample of hunting episodes, then we reject the null hypothesis and conclude that undetected associations persist longer (Kolmogorov-Smirnov, $\chi^2 = 27.67$, $P < 0.0001$, $d.f. = 2$).

The greater the portion of time the badger spent actively hunting (searching, exploratory digging, excavating), the longer an undisturbed association endured. Badgers usually ended the association by not reemerging from a burrow; they rarely did so by agonistic behavior. The coyotes' posture and behavior, correlated with telemetry from the badger, suggested that coyotes could hear badger activity below ground. After badger activity apparently ceased, coyotes usually left within 0.5 h. Because some coyotes had uniquely identifiable markings, we occasionally observed recurring associations over periods of weeks. Percentage of coyotes hunting with a badger were: single coyotes, 90.6% of recorded episodes; coyote pairs, 8.8%; trios, 0.7%.

A coyote and badger were typically within 10 m while hunting within a set of burrows and within 50 m while searching for squirrels aboveground and moving between burrow systems. Coyotes were extremely alert and focused their attention over a wider visual and auditory range than did badgers. Coyotes encouraged badgers to move and search by mock pursuit and by scrambling

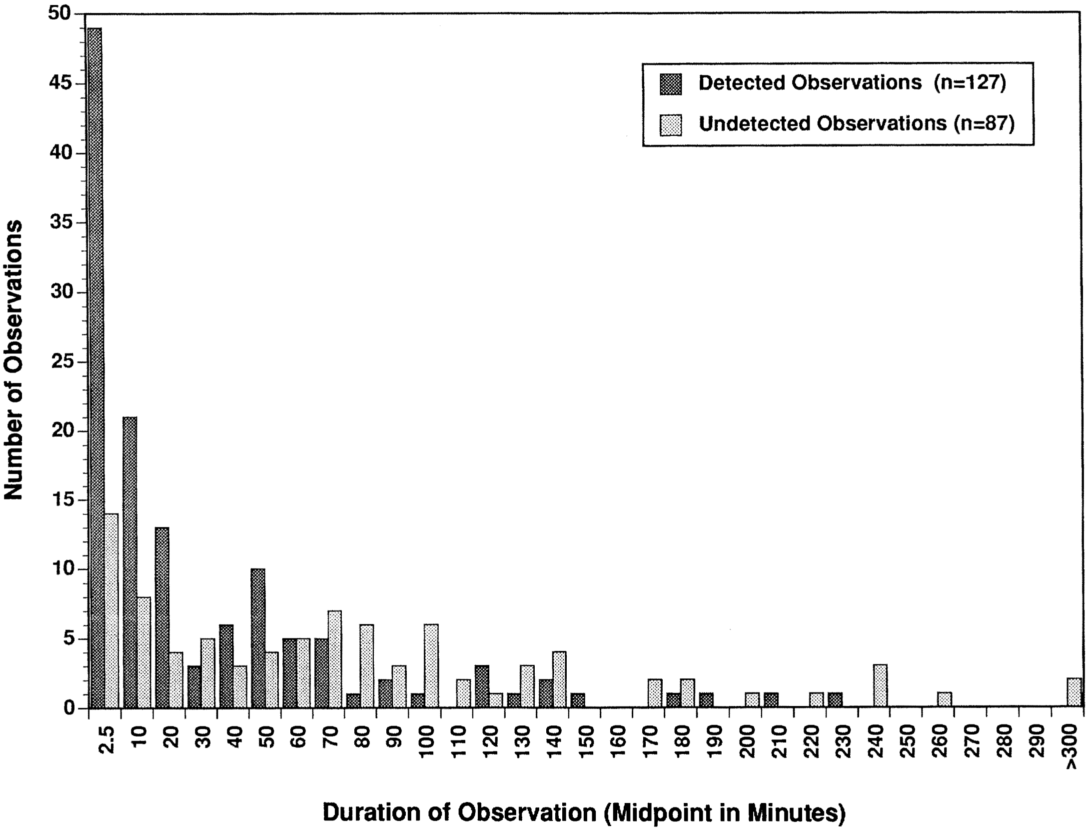

FIG. 1.—Frequency distribution of timed observations of badger-coyote hunting associations. Duration of associations are grouped into 10-min intervals (midpoint) except the first interval, which is 0 to 5 min, and the last interval, which is 300–410 min. We categorized observations as "detected" when a member of an association exhibited behavior indicating awareness of the observer's presence. Otherwise, the observation was classified as "undetected."

around a specific site; by leading or by soliciting play (e.g., play-bow, play-dance, face-pawing—Bekoff, 1974).

The short-legged badgers prop their head and body for long-range scanning. By this and other indices, badgers reduced long-range scanning during the associations. Associated badgers may have benefited from the coyotes' wider-ranging vigilance and information gathering capacities. The exception was "double-rushing," an occasional, apparently spontaneous tactic. In dense patches of squirrels, the badger and coyote would simultaneously rush the area, scattering squirrels so they were more easily caught aboveground or trapped in a shallow or unconnected tunnel.

Young and weak badgers can fall prey to a group of coyotes (Rathbun et al., 1980), but the virtual immunity from mutual predation among adults of both species may preadapt these two species to the rapid and radical behavioral transitions necessary for the hunting associations. Both predators preying on a single species in our area may have eased learning-effective interaction and enhanced predatory effectiveness.

The badgers' behavior indicated the association with coyotes was either neutral or positive for them. Associated badgers often tolerated coyotes within 1 m and physical contact was seen about once every 2 h of observation. Most contact was inadvertent or brief, but there were at least 36 episodes of sustained nasal-nasal contact, or body contact while resting near each other or during activity or play initiation by the coyote. Badgers and coyotes played together longer than 10 s four times. Food was never shared, though coyotes took captured squirrels from badgers six times; five times from lactating females. Badgers almost always consumed prey without surfacing (Lampe, 1976; Minta, 1990); however, the five females providing for a natal den each lost a squirrel to a coyote that induced her to drop it or snatched it from her mouth. The absence of direct contention eliminated immediate physical competition and agonism.

Discussion

From trophic equivalence and strict carnivory we expect severe competitive interaction—the opposite of mutualism (Hairston et al., 1960; Rosenzweig, 1966; Schoener, 1983). Thus, individual interactions within a hunting association would likely be manifested as commensalism or parasitism. Our direct and indirect evidence of net benefits and costs for two interacting predators are limited because badgers usually hunted below ground where they could not be observed. However, coyotes and badgers have complementary morphological adaptations and predatory strategies for combined pursuit of ground-dwelling squirrels, and the association benefits at least one, perhaps both, species.

Badger-coyote associations are only observed in certain circumstances. Thompson (1979) observed no interactions in two central-Oregon study areas, but ca. 45 interactions on Malheur National Wildlife Refuge in southeastern Oregon. The refuge study area was less disturbed, badger density was higher, and badgers were more observable (S. E. Thompson, pers. comm.).

In our study area, squirrels lived semicolonially at high densities. Their burrow connectivity (Stromberg, 1975) increased their escape routes. Tunnels dug by hunting badgers contributed to this connectivity. Moreover, the root structure of sagebrush inhibited rapid and efficient excavation, and the mixture and density of brush species decreased the effectiveness of solitary hunting by coyotes. Consequently, fewer of the many squirrels present were vulnerable to a coyote or badger hunting alone than to a hunting pair. The relatively high densities of long-lived resident badgers and coyotes (Minta, 1990; Tzilkowski, 1979) increased chances of contact, tolerance, and prolonged behavioral reinforcement necessary for joint hunting.

Even if badger-coyote associations are common, they may go unnoticed. We often disrupted associations (Jordan and Burghardt, 1986). Our implanted badgers, and coyotes in general, were much more wary and secretive in the part of our study area where they were trapped, shot, or harassed. Coyote behavior and social organization are particularly sensitive to exploitation regimes and human disturbance (Andelt, 1985; Bowen, 1981). Camenzind (1978; pers. comm.), Bekoff and Wells (1986; pers. comm.), and Weaver (1977; pers. comm.) rarely saw badger-coyote interactions on neighboring study sites where the coyotes were exploited and disturbed more (Tzilkowski, 1979), and most observations were made in more open habitats or sagebrush-grassland and grassland where badger densities were lower.

Are the coyote-badger hunting associations mutualism, commensalism, or parasitism? Associated badgers and coyotes displayed reduced agonism and behaved in ways that maintained their association. Thus, our behavioral index suggests that the association had a positive outcome for both. Thompson (1982) generalized that organisms that have a high probability of encounter, a low probability of antagonistic interactions (e.g., competition), and endure high levels of physical stress have a higher probability of mutualism. Our subjects were in a stressful abiotic environment, with low diversity of terrestrial fauna, and high probability of encounter due to prey distribution and population densities of predators and prey. Mutualisms also are more likely in species with rich social behavior (Thompson, 1982), which the coyote has.

The badger-coyote association probably is neither cooperation nor reciprocal altruism. Cooperation traditionally is restricted to the intraspecific level because each participant potentially shares genes. Conner (1986) introduced the term pseudo-reciprocity for interactions in which the return benefit for a beneficent act is a byproduct or incidental effect of egoistic behavior by the recipient of the beneficent act. We do not believe either reciprocal altruism or pseudo-reciprocity is applicable to the badgers and coyotes, because there was no investment (beneficent act performed) by either participant in the mutualism. All behavior appeared to be directed toward individual prey capture or facilitating interspecific toleration.

The associated badger and coyote were most likely expressing a nonevolved mutualism that took the form of a short-term, two-species social system that benefited both. The coyotes' association-initiating behavior probably evolved as a result of their intraspecific social plasticity. Both species probably drew upon a behavioral repertoire evolved in the context of intraspecific interactions to establish a functional, if limited, two-species social system. Learning could occur if each species is capable of associating the other with prior hunting success (stimulus-stimulus paradigm—Bolles, 1975).

Alternatively, since we lacked critical data to firmly resolve the benefits received by badgers, the coyotes might have "parasitized" badgers (T. Schoener, pers. comm.). Similarly, if the net energetic impact on the badger was neutral instead of negative, the interaction was commensalism. In either case, the badger may have tolerated the coyote to avoid a greater cost of repelling it. However, if the coyotes were parasitizing the badgers, they would have imposed the association over the badgers' resistance, and the badgers could have ended the association by simply being inactive underground for a brief period (<0.5 h).

ACKNOWLEDGMENTS

We thank T. W. Schoener, N. Willits, M. G. Hornocker, P. Wilson, and K. Wilson for advice and assistance. We are grateful to T. W. Schoener, J. O. Murie, R. A. Powell, O. J. Schmitz, and an anonymous referee for improving an earlier draft of this paper. Without the extraordinary cooperation of the United States National Elk Refuge staff, the study could not have been conducted. Data collection and preparation of this manuscript was supported by grants from the National Science Foundation (Doctoral Dissertation Grant BSR-8320495), American Museum of Natural History, Max McGraw Wildlife Foundation, Sigma Xi, New York Zoological Society, Grand Teton Natural History Association, Jastro-Shields Scholarship (University of California), and federal funds administered through the University of California Agricultural Experiment Station Hatch Project no. 3915.

LITERATURE CITED

ANDELT, W. F. 1985. Behavioral ecology of coyotes in South Texas. Wildlife Monographs, 94:1–45.

AUGHEY, S. 1884. Curious companionship of the coyote and the badger. The American Naturalist, 18: 644–645.

BEKOFF, M. 1974. Social play in coyotes, wolves, and dogs. BioScience, 24:225–230.

BEDOFF, M., AND M. C. WELLS. 1986. Social ecology and behavior of coyotes. Advances in the Study of Behavior, 16:251–338.

BOLLES, R. C. 1975. Learning theory. Holt, Rinehardt and Winston, New York, 416 pp.

BOWEN, W. D. 1981. Variation in coyote social organization: the influence of prey size. Canadian Journal of Zoology, 59:639–652.

CAHALANE, V. H. 1950. Badger-coyote "partnerships." Journal of Mammalogy, 31:354–355.

CAMENZIND, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pp. 267–296, *in* Coyotes: biology, behavior, and management (M. Bekoff, ed.). Academic Press, New York, 384 pp.

CONNOR, R. C. 1986. Pseudo-reciprocity: investing in mutualism. Animal Behaviour, 34:1562–1566.

DOBIE, J. F. 1950. The voice of the coyote. Little, Brown and Company, Boston, 386 pp.

FLEISS, J. L. 1981. Statistical methods for rates and proportions. Second ed. John Wiley & Sons, New York, 321 pp.

GOODWIN, G. 1939. Myths and tales of the White Mountain Apache. The American Folklore Society, New York, 342 pp.

HAIRSTON, N. G., F. G. SMITH, AND L. B. SLOBODKIN.

1960. Community structure, population control, and competition. The American Naturalist, 94:421–425.

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

Jordan, R. H., and G. M. Burghardt. 1986. Employing an ethogram to detect reactivity of Black bears (*Ursus americanus*) to the presence of humans. Ethology, 73:89–115.

King, J. A. 1984. Historical ventilations on a prairie dog town. Pp. 447–456, *in* The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.

Knopf, F. L., and D. F. Balph. 1969. Badgers plug burrows to confine prey. Journal of Mammalogy, 50: 635–636.

Lampe, R. P. 1976. Aspects of the predatory strategy of the North American badger, *Taxidea taxus*. Ph.D. dissert., The University of Minnesota, St. Paul, 103 pp.

Mendenhall, W., and R. L. Scheaffer. 1973. Mathematical statistics with applications. Duxbury Press, North Scituate, Massachusetts, 561 pp.

Minta, S. C. 1990. The badger, *Taxidea taxus* (Carnivora: Mustelidae): spatial-temporal analysis, dimorphic territorial polygyny, population characteristics, and human influences on ecology. Ph.D. dissert., The University of California, Davis, 317 pp.

Minta, S. C., and M. Mangel. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. Ecology, 70:1738–1751.

Ramsey, J. 1977. Coyote was going there: Indian literature of the Oregon country. The University of Washington Press, Seattle, 295 pp.

Rathbun, A. P., M. C. Wells, and M. Bekoff. 1980. Cooperative predation by coyotes on badgers. Journal of Mammalogy, 61:375–376.

Robinson, W. B., and M. W. Cummings. 1947. Notes on behavior of coyotes. Journal of Mammalogy, 28: 63–65.

Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy, 47: 602–612.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist, 122: 240–285.

Seton, E. T. 1929. Common badger of America. Pp. 286–305, *in* Lives of game animals. Doubleday, Doran and Company, Garden City, New York, 2(1):1–449.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, New York, 312 pp.

Slade, N. A., and D. F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology, 55:989–1003.

Stromberg, M. R. 1975. Habitat relationships of the black-tailed prairie dog (*Cynomys ludovicianus*): vegetation, soils, comparative burrow structure and spatial patterns. M.S. thesis, The University of Wisconsin, Madison, 175 pp.

Thompson, J. N. 1982. Interaction and coevolution. John Wiley & Sons, New York, 179 pp.

Thompson, S. E., Jr. 1979. Socio-ecology of the yellow-bellied marmot (*Marmota flaviventris*) in central Oregon. Ph.D. dissert., The University of California, Berkeley, 223 pp.

Tzilkowski, W. M. 1979. Mortality patterns of radio-marked Jackson Hole coyotes (*Canis latrans*). Ph.D. dissert., The University of Massachusetts, Amherst, 73 pp.

Weaver, J. L. 1977. Coyote-food base relationships in Jackson Hole, Wyoming. M.S. thesis, Utah State University, Logan, 88 pp.

Wells, M. C., and M. Bekoff. 1982. Predation by wild coyotes: behavioral and ecological analyses. Journal of Mammalogy, 63:118–127.

Young, S. P., and H. H. T. Jackson. 1951. The clever coyote. The University of Nebraska Press, Lincoln, 411 pp.

Submitted 15 April 1991. Accepted 29 October 1991.