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THE MESOPREDATOR RELEASE HYPOTHESIS: INTEGRATING LANDBIRD MANAGEMENT WITH ECOLOGICAL THEORY

CHRISTOPHER M. ROGERS AND STEPHEN B. HEARD

Abstract. The mesopredator release hypothesis explains long-term population declines of ground- and shrub-nesting North American landbirds by suggesting that the extirpation of top predators from North America has released populations of medium-sized, mammalian nest predators. A perspective from theoretical ecology concerned with food web regulation suggests that mesopredator release following top predator removal (an example of a top-down trophic cascade) is most likely in food webs characterized by (1) efficient predation with prey held well below resource limitation, (2) lack of extensive omnivory, and (3) either low diversity of top predators, or all top predators removed together. These conditions are generally met by the landbird-mesopredator-top predator system. Empirical studies of these phenomena suggest that terrestrial mesopredator populations can in fact be released by loss of a top predator, and that addition of a top predator can significantly increase nest success of ground-nesting birds through a reduction of mesopredator populations. However intriguing these findings may be, experimental confirmation of mesopredator release and its effects on landbirds are still lacking. Because of its large size, relatively well-known predator history, and long-term data base on avian populations, the Savannah River Site would be an ideal location for conducting top predator removal and/or exclosure experiments. Results will be informative for land managers concerned with maintaining viable landbird populations.

Key words: ecological theory, management, mesopredator release, Song Sparrow, top predator.

Land managers concerned with maintaining wildlife species diversity typically rely on input from task-oriented wildlife biologists that provide data on selected game and/or nongame species. Only rarely do land managers receive input from theoretical ecologists, who typically are concerned with elucidating general principles of how individuals, populations and ecosystems function. In this paper we describe a profitable union of management science and theoretical ecology. The approach focuses on empirical and theoretical studies of food web regulation and the significance of that regulation for managing viable landbird communities.

Nest predation is the most important source of nest mortality among North American landbirds (Ricklefs 1969), and may be a main cause of population declines suggested for many landbird species (Böhning-Gaese et al. 1993, Robinson et al. 1995). Although for some Neotropical migrants declines may not be due to high nest predation, ground- and low shrub-nesting nesting species as a whole (representing a variety of migratory strategies) have shown widespread, long-term population declines (1966–1994) in eastern North America (Böhning-Gaese et al. 1993; see Peterjohn et al. 1995 for an alternative view). Arboreal-nesting species have not shown consistent declines in the same region and time interval (Böhning-Gaese et al. 1993). These facts suggest an important role for terrestrial mammals in driving declines of ground- and low shrub-nesting species. The mesopredator release hypothesis (hereafter, MRH) suggests that the historical reduction of top predators in North America (e.g., the cougar, *Felis concolor,* bobcat, *Lynx rufus,* gray wolf, *Canis lupus,* and in some areas the coyote, *C. latrans*) has resulted in "mesopredator release," a population explosion of medium-sized omnivores that are frequent nest predators (e.g., the raccoon, *Procyon lotor,* Virginia opossum, *Didelphis virginiana,* and striped skunk, *Mephitis mephitis*). According to the MRH, the historical increase in nest predation by mesopredators has caused declines in ground-nesting landbirds.

Testing the MRH has major implications for managing viable populations of landbirds. For example, would introducing a top predator into a large nature reserve (with unacceptably high mesopredator population density) necessarily increase landbird population density and/or species diversity? We assess the MRH and prospects for its application in management from two perspectives. First we consider theoretical ecology concerned with food web structure and regulation, with special reference to why or why not top terrestrial carnivores might successfully regulate mesopredator abundance and landbird nest success. Second, we examine studies of landbird-mesopredator-top predator relationships, to learn directly whether such interactions might be occurring in nature. The major conclusion is that top predators can, and probably do, influence mesopredators and songbirds as predicted by the hypothesis, but definitive experiments in terrestrial ecosystems are still lacking. Therefore, we close with a brief discussion of why the Savannah River Site (SRS) in South

Carolina offers a good opportunity to fill this gap in our knowledge.

TOP-DOWN EFFECTS IN ECOLOGICAL SYSTEMS

The MRH is a specific case of a more general hypothesis of top-down control in ecological communities. By "top-down control," we mean that the effects of predators on their prey directly or indirectly play a major role in structuring ecological communities. The notion of strong top-down effects in natural communities dates back to Darwin (1859), who noted that preventing mowing or browsing of turf increased biomass but lowered diversity. Early laboratory experiments (Gause 1934, Huffaker and Kennett 1956) showed that predators could control prey densities in the simplest systems, but the importance of predation in structuring natural communities remains controversial.

In an influential paper, Hairston et al. (1960) argued that most natural communities were structured by top-down effects. Predators, being limited only by competition for their herbivore prey, reduce herbivores to low densities; herbivores as a result have little impact on plants, which are limited by competition instead. The Hairston et al. model was constructed for a 3-trophic level community, but Fretwell (1977) and Oksanen et al. (1981) generalized it for any number of trophic levels: of n trophic levels, production at level n (the top) should be limited by competition, level n-1 by predation from level n, level n-2 by competition, and so on alternately down the food chain. When a top predator is removed, the pattern of regulation at each trophic level should shift accordingly (e.g., Peacock 1982). The MRH assumes top-down regulation such that top predators (n) limit the abundance of mesopredators (n-1) and prevent mesopredators from limiting landbirds (n-2). When top predators are removed mesopredators (which are now the top level n') increase sufficiently to depress landbird densities (now n'-1).

While the Hairston et al. model assumes both that top predators limit prey at level n-1 and that prey production at n-1 limits top predators, only the first assumption is necessary for top-down effects to be strong on a particular species. In fact, the top-down effects of a predator on one species of prey are likely to be strongest when the predator has abundant alternative prey (e.g., Caughley et al. 1980, Terborgh 1992).

The idea of strong top-down structuring in natural communities has been controversial (Hunter and Price 1992, Power 1992, Strong 1992). In some communities predators control prey densities (e.g., Estes et al. 1978, Caughley et al. 1980, Schoener and Spiller 1987, Dial and Roughgarden 1995), but in others they do not (Jackson and Kaufmann 1987). In many cases predator effects are felt only in some microhabitats (Hacker and Bertness 1995, Robson 1996) or by only some prey species (Morin 1984, Sinclair 1995, Johnson et al. 1996; review in Pimm 1980). Frequently, predator activity will remove one prey species, but another, less vulnerable species will replace it and total productivity may be unchanged (Paine 1980, Black and Hairston 1988, Crowder et al. 1988, Strong 1992). Even strong predator effects do not guarantee that top-down effects will propagate further down the food chain (McQueen et al. 1989). Removal of the top predator may release its prey, but an effect on the next trophic level requires that the released prey can be an effective regulator of its prey in turn.

Clear cases are known where effects of predator manipulation extend down through three or more trophic levels ("trophic cascades;" e.g., Edson 1985, Spiller and Schoener 1990, Dial and Roughgarden 1995, Morin 1995, Robson 1996; citations in Brett and Goldman 1997), but this result is not universal and may even be unusual (Strong 1992). Some theoretical models predict temporal variation in top-down vs. bottom-up regulation (Bartell et al. 1988), and careful experimental approaches often find simultaneous influences of both predators (top-down) and resources (bottom-up) at a given trophic level. Bottom-up control may be more important near the base of a food chain, with top-down effects more important at higher trophic levels (McQueen et al. 1986, 1989; Brett and Goldman 1997).

TOP-DOWN EFFECTS AND MESOPREDATOR RELEASE

Because top-down effects are not universally strong, recent treatments have taken a pluralistic approach (McQueen et al. 1986, Hunter and Price 1992), asking in which ecological circumstances top-down effects on a particular trophic level might be more or less intense. In assessing the mesopredator release hypothesis, then, we can look to ecological theory for insight into whether strong top-down effects might be expected for the top predator/mesopredator/landbird system. Little integration of the MRH and trophic cascade literatures has occurred as yet. While a few MRH papers mention examples of top-down control from other systems (Terborgh and Winter 1980, Soulé et al. 1988), none to our knowledge cite any theoretical background. Similarly, none among 25 papers examined on top-down effects in theory or in other systems refers to the mesopredator release-landbird decline idea. It is possible that data on the MRH can illuminate trophic cascades, and general consideration of trophic cascades can illuminate the MRH.

A number of ecological factors have been suggested to influence the likelihood of strong top-down effects in a particular system (Hunter and Price 1992, Power 1992). Here we consider how some of these factors weigh for or against the plausibility of landbird decline via mesopredator release, and ask what is needed to learn in order to support or reject the MRH. The general message is that careful consideration of theoretical context can help guide research programs.

PREDATOR EFFICIENCY

Inefficient predators are unlikely to regulate their prey (Power 1992; an efficient predator is one that can, when common, exploit its prey at a very high rate and drive it to very low densities). Predators may be inefficient if aggressive behavior causes strong interference among predator individuals (Hassell 1978, Loyn et al. 1983); if prey have effective chemical, physical, or behavioral defenses or if such defenses are inducible (Farrell et al. 1991, Dini et al. 1993, Polis and Strong 1996, Zangerl and Rutledge 1996); or if predators are limited by scarce resources other than the prey in question (Connell 1961) or have a life stage limited by such a resource (Mittelbach et al. 1988, Polis and Strong 1996). In contrast, predators are likely to be particularly efficient if their densities are kept high by an abundance of alternative prey (e.g., Caughley et al. 1980).

The MRH assumes that both the top predator-mesopredator link and, following mesopredator release, the mesopredator-landbird link are characterized by efficient predation. This certainly appears true for mesopredator-landbird interactions. Most mesopredators eat eggs and nestlings opportunistically, and are limited by more abundant prey (Leach and Frazier 1953, Terborgh and Winter 1980, Sieving 1992, Vickery et al. 1992). While birds do show some behavioral defenses against nest predation (e.g., Berg 1996), measured nest predation rates are generally high (Ricklefs 1969) and can exceed 90% (range 11–99% [mean 48%] for 125 temperate landbird estimates reported or reviewed by Brawn and Robinson 1996 and Martin 1993). We doubt that defense against mesopredators or interference among mesopredators have strong effects on mesopredator-landbird interactions, especially because the main mesopredators in eastern North America (raccoon, striped skunk, and opossum) are not strongly territorial (McManus 1974, Lotze and Anderson 1979, Wade-Smith and Verts 1982). Top predators are generally very efficient predators on mesopredators, because they will take many alternative prey and possibly can drive mesopredator densities quite low without becoming food-limited (Soulé et al. 1988, Terborgh 1992).

SCOPE FOR EXPANSION AFTER PREDATOR RELEASE

The trophic cascade concept predicts that removal of a predator (at trophic level *n*) results in prey (*n*-1) expanding from a density set by predation to a new, higher density set by resources (Peacock 1982). However, the latter density may not be much higher than the former. If it is not, we should not expect strong top-down effects on level *n*-2 (Soranno et al. 1993). In the mesopredator-landbird example, however, mesopredator increases after top predator extirpation have been substantial (Terborgh 1992, Sovada et al. 1995), although we do not know whether this will be universally true. Similarly, suppression of nest predators may decrease nest predation rates, but if other sources of mortality compensate, the decrease in predation may have little effect on bird densities.

INTERACTION AMONG NONADJACENT TROPHIC LEVELS

The prediction that the removal of trophic level *n* should depress species at *n*-2 (via release of level *n*-1) depends on a view of food chains where all interactions are between species at adjacent trophic levels. Nonadjacent levels may interact through nutrient release by predation (Vanni and Layne 1997), or through modification of shared habitat (Power 1992). However, the most common kind of interaction between nonadjacent trophic levels is doubtless omnivory (we use this term in its food-web sense: consumption of prey from more than one trophic level; Pimm 1982). Clear trophic cascades are expected only when consumers can be easily assigned to distinct trophic levels, and this may be uncommon (Power 1992, Strong 1992, Polis and Strong 1996; but see Hairston and Hairston 1997). With strong omnivory, predicting responses to predator removal becomes more complex. For instance, if species A eats B eats C, but A also eats substantial numbers of C, it is unclear whether removing A should cause an increase or decrease in C, for which the easing of predation by A may be outweighed by increased predation by a released population of B. Spiller and Schoener (1990) removed lizards in a lizard-spider-herbivorous insect-sea grape food chain, and found that damage to plants by midges decreased (in a typical trophic cascade) but homopteran damage actually increased. They attributed this result to omnivory by lizards, which consume both spiders and homopterans but not midges. In the mesopredator-landbird system, top predators such as coyotes and wolves take nest contents (Leach and Frazier 1953, Sovada et al. 1995 for prairie ducks) as well as larger prey, but it seems likely that they have their strongest effect via mesopredator densities rather than direct predation. The same is true for peregrine falcons in a peregrine-crow-seabird food chain (Paine et al. 1990).

BUFFERING BY DIVERSITY

Strong (1992) argued that trophic cascades should be confined to low-diversity systems or systems where a few species can have disproportionate effects on community structure. In more diverse systems, Strong suggested that top-down control will be buffered and weak because in complex food webs consumption effects are spread over many predators for each prey, and many prey for each predator. At any trophic level, then, removing one species only will allow another to increase and substitute in function: predator for predator, prey for prey, or producer for producer. Many clear trophic cascades indeed are found in low-diversity systems or in highly specialized food chains (Strong 1992, Gómez and Zamora 1994). Furthermore, replacement of one species by another (among either predators or prey) is an extremely common response to predator manipulation (Paine 1980, Loyn et al. 1983, Black and Hairston 1988, Crowder et al. 1988, Strong 1992).

The diversity issue raises two major questions for the MRH. First, can different top predators substitute for one another? Historically, in most regions of North America all mammalian top predators were probably extirpated more or less together, and so substitution of one top predator for another is unlikely to have buffered effects on mesopredators. However, some areas have recently reacquired top predators as coyotes have undergone a major range expansion. The effect on landbirds of wolf or large cat reintroductions may depend on the presence or absence of coyotes and on how these alternative top predators interact. Second, does increased predation from released mesopredators simply replace consumption by other species? For instance, raccoon abundance may have increased because of top predator extirpation, but there might be no net effect on landbirds if predation by raccoons simply removes eggs that would have been taken by snakes anyway.

EQUILIBRIUM OR NON-EQUILIBRIUM COMMUNITIES

Trophic cascade theory is an equilibrium theory, and it envisages communities where species abundances are relatively stable and locally regulated by density-dependent predation or competition. When populations are perturbed away from equilibria, strong top-down effects will not be expected. Landbird densities are certainly perturbed by disturbances (Rogers et al. 1991), and many landbird populations are probably decoupled from local regulation by source-sink relationships (e.g. Rogers 1994, Brawn and Robinson 1996, Smith et al. 1996, Rogers et al. 1997). If these effects are strong, then testing the MRH may mean analyzing population trend data on broad spatial scales (to remove source-sink effects), while removing disturbance effects statistically.

EVIDENCE FOR TROPHIC CASCADES IN TERRESTRIAL ECOSYSTEMS: LANDBIRDS, MESOPREDATORS, AND TOP PREDATORS

The above perspective from theoretical ecology suggests that top-down trophic cascades are possible for the landbird-mesopredator system. We next review the sparse evidence from empirical studies for their existence. The two main concepts underlying the MRH have their historical roots in John Terborgh's original discussion of extinction-prone species in the Neotropics (Terborgh 1974). Terborgh noted that after the Chagres River was dammed to form part of the Panama Canal around 1914, forming Barro Colorado Island (BCI) in Lake Gatun, a number of ground-dwelling landbirds subsequently became extinct, ostensibly because large carnivores themselves died out. Extinction of top predators may have in turn led to high "released" mesopredator populations, and subsequent low avian nest success. A recommendation was made for maintaining complete ecosystems (all trophic levels, including top predators) in order to preserve maximum biodiversity. Terborgh and Winter (1980) more explicitly discussed these trophic relationships for BCI, suggesting that its high population densities of nest-destroying mesopredators (coatimundi, *Nasua narica,* collared peccary, *Tayassu tajacu,* nine-banded armadillo, *Dasypus novemcinctus*), released from regulation by the extinction of top predators (Harpy Eagle, *Harpia harpyja,* cougar, and jaguar, *Felis onca*), in large part caused extinction of 15–18 species of ground-nesting landbirds. Further partial support for this neotropical trophic cascade came from comparing coatimundi density between Cocha Cashu, Peru, a forest site where large felids are common, and BCI. Coatimundi density was at least 20 times greater at BCI than Cocha Cashu (Terborgh 1992). Sieving (1992) consistently found higher predation rates on ground- and shrub-borne artificial nests at BCI than in nearby mainland forest.

Two additional studies supporting the MRH bear mention. Soulé et al. (1988) found higher landbird species diversity in California chaparral

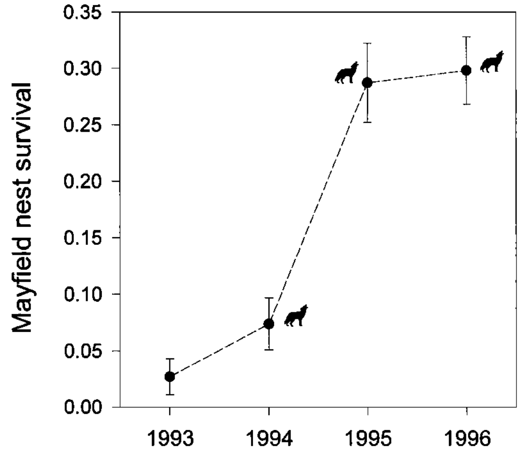

FIGURE 1. Annual increases in the Mayfield estimator of nest survival (mean ± SE, after Mayfield 1975 and Hensler and Nichols 1981) at Lux Arbor, southwest Michigan, 1993–96. Years when coyotes were detected (by sightings of adults, dens found, and scat counts) at Lux Arbor are indicated by the stylized coyote symbol. Sample sizes were 20, 25, 26, and 35 nests per year for 1993–1996, respectively. Using the program CONTRAST and the Bonferroni adjustment of the critical P-value for a posteriori contrasts, 1993 differed significantly from 1994–1996 pooled, but 1993 and 1994 were not significantly different. Thus nest survival did not increase beyond pre-coyote levels until coyotes had been present about 1 year at Lux Arbor.

fragments with coyotes than in otherwise similar fragments without coyotes. In an entirely different ecosystem, Sovada et al. (1995) demonstrated higher nest success of prairie ducks in areas where coyotes are the main canid than in areas where the red fox (*Vulpes fulva*), a major predator of duck nests, is the main canid. Coyotes, which rarely prey on duck nests, were assumed to depress the abundance of red foxes (Sovada et al. 1995).

Finally, results from a four-year "natural experiment" with Song Sparrows (*Melospiza melodia*, a ground-nesting landbird) in the agricultural landscape of southwestern Michigan support the MRH (Rogers and Caro 1998). Coyotes were absent from the Lux Arbor Reserve (650 ha of fields, woodlots, and lake borders) in 1993 and present in 1994, 1995 and 1996. Over this interval, Mayfield nest survival increased, and the relative frequency of nest predation decreased (Fig. 1). Coyotes may have reduced nest predation in 1994–1996 by depressing the abundance of raccoons, apparently the main nest predator in the study area. Coyotes are well-known to prey upon raccoons (Andrews and Boggess 1978, Clark et al. 1989, Hasbrouck et al. 1992), and an inverse relationship between coyote population density and raccoon population density has been observed (Sargeant et al. 1993). In an experiment with artificial nests in the same Michigan landscape, mesopredator abundance and predation rate on ground nests were positively related, as predicted by the MRH (Rogers and Caro 1998).

ADVANTAGES OF TESTING THE MESOPREDATOR RELEASE HYPOTHESIS AT THE SAVANNAH RIVER SITE: INTEGRATING LANDBIRD MANAGEMENT WITH ECOLOGICAL THEORY

This final section considers how the SRS would be useful as an experimental and observational site to further our understanding of the trophic role of top mammalian predators and how that role influences landbird population viability. A land manager seeking that understanding might ask four different questions concerned with the possible outcomes of maintaining populations of top predators in a given nature reserve. This final section attempts to answer these anticipated questions, integrating the present main theoretical findings with the utility of using SRS as a model ecosystem.

WILL A TOP PREDATOR REDUCE MESOPREDATOR POPULATIONS IN A GIVEN RESERVE TO THE POINT WHERE GROUND-NESTING LANDBIRDS WOULD BENEFIT?

One of the main theoretical findings of the present report was that increasing landbird nest success (and possibly, but not necessarily, population density) is likely if a top predator is efficient, i.e., if predation reduces a prey population below its level of resource limitation. In the eastern North American top predator-landbird-mesopredator system, the top predator most likely to be maintained as a viable population is the coyote. Studies supporting coyote predation upon raccoons, a frequently common mesopredator, were cited above. In addition, in central Iowa, remains of radio-collared adult male raccoons have been found following coyote predation (W. Clark, personal communication). Efficient predation on mesopredators by coyotes is likely if coyote density is maintained by abundant alternative prey, such as voles and winter- and auto-killed deer. This is a plausible scenario for many nature reserves, given the frequently high abundance of these prey types in many regions of North America. A local reduction in mesopredator density of only 1–2 raccoons per 30 pairs of breeding landbirds would seem a priori to be sufficient to increase landbird nest density significantly, but this estimate needs empirical testing.

How might the SRS function in tests for efficient predation on mesopredators? The above considerations do not take into account the role of non-mammalian nest predators, such as snakes, which are major nest predators in many parts of North America, including SRS. Data are urgently needed on the effects of top predators on landbirds in terrestrial ecosystems with and without snakes. A particularly useful study would test for such effects in the SRS and a comparably-sized reserve lacking snakes.

An important related point is that "efficient predation" on mesopredators by a top carnivore need not involve a trophic relationship sensu stricto. Adult female raccoons travelling with young of the year during the nesting season of many North American landbirds (April–July) should avoid areas of high coyote density to reduce predation risk to their young, a significant investment in fitness. Indeed, raccoons avoid food-rich areas experimentally marked with coyote urine in Iowa (C. M. Rogers, unpubl. data), and tame raccoons show strong avoidance of areas with coyotes present (without having seen coyotes), also in Iowa (W. J. Fitzgerald, pers. comm.).

WILL TOP PREDATORS CONSUME LANDBIRD NEST CONTENTS AS WELL AS REDUCE MESOPREDATOR ABUNDANCE?

A second main theoretical finding was that landbird density might not be increased if an introduced top predator is omnivorous, i.e., a top predator feeds at multiple trophic levels and reduces landbird density as well as mesopredator density. Continuing to reason about using coyotes as top predators in a given nature reserve, this canid is known to prey upon ground-nesting landbird nest contents, including the incubating female, but such predation is rare (Rogers et al. 1997). Thus some omnivory is likely, but would probably be insignificant (the main prey items of North American coyotes were discussed above; see also Andrews and Boggess 1978, Parker 1995).

IS A GIVEN RESERVE LARGE ENOUGH TO SUPPORT A VIABLE POPULATION OF TOP PREDATORS?

The large size of SRS can permit evaluation of the role of top predators in "reserves" of differing size. This might be achieved by subdivision of available space into geographically separated research areas (large, medium, and small). Such information would be of interest to land managers concerned with maximizing wildlife species diversity in nature reserves of different areas. A likely size effect is that small areas with low habitat diversity support lower population density of top predators than larger areas, which can be expected to have higher habitat diversity. Additional factors potentially related to reserve size also can be addressed, such as the effect of proximity to developed areas.

WHAT EFFECT WILL A TOP PREDATOR HAVE ON AVIAN SPECIES DIVERSITY?

Significant numbers of top predators are long gone from SRS, and there is a historical data base including censuses of landbird abundance and species diversity from the 1950s to the present (gathered by Eugene Odum and colleagues; see Meyers and Odum *this volume*), providing an effective "top predators absent" data base. A more recent background data set on nesting success of landbirds at SRS is also available (Sargent et al. 1997). Coyotes are just now reaching South Carolina as they continue their eastward range expansion from the Great Plains (Parker 1995). They are present at SRS now, and might build up high densities there in the near future (as they have done since 1993 in southwestern Michigan). Sidney Gauthreaux and his colleagues (pers. comm.) are conducting standardized landbird censuses at SRS, and, when continued, this research can provide "top predators present" population and community data. Thus, an informative natural experiment could be completed in the foreseeable future.

Note that the dependent variable of ultimate interest to wildlife biologists and managers is bird species diversity, not nesting success; however, the two probably are closely related. To illustrate, bird communities typically show a log-normal distribution of species, which includes rare and uncommon species in addition to common and abundant species. Rare and possibly also uncommon species might be preserved in a small- to medium-sized nature reserve by the presence of a top predator that facilitates success of a small number of nests through a depression of mesopredators. Such an effect was suggested by the data of Soulé et al (1988), who found higher bird species diversity in chaparral fragments with coyotes than without them.

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