

Coyote Abundance, Sheep Predation, and Wild Prey Correlates Illuminate Mediterranean Trophic Dynamics

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ABSTRACT Sheep predation by coyotes (*Canis latrans*) is a major problem for sheep producers in North America. Solutions are facilitated by a basic understanding of the trophic dynamic context of this problem, one that likely varies geographically in important qualitative ways. Little is known about vertebrate trophic dynamics in Mediterranean ecosystems, where prey are diverse and their biomass is strongly influenced multi-annually by variable rainfall. We used long-term data sets from north-coastal California, USA, to investigate whether wild prey fluctuations caused immediate negative effects on sheep predation via a reduction in the coyote functional response or delayed positive effects on sheep predation via a numerical response by coyote predators. Because we could not measure prey biomass directly, we used variables associated with lower trophic levels (e.g., annual plant productivity, vole abundance, rainfall) as proxies for wild prey biomass. Coyote population growth rate was positively correlated with lower-trophic-level variables of the previous year, suggesting a numerical response, and sheep (ad F + lambs) predation was positively correlated with coyote abundance in the current year. Sheep predation also was negatively correlated with lower-trophic-level variables of the current year, suggesting an immediate buffering effect of wild prey on sheep predation. Together, coyote abundance and lower-trophic-level variables explained 47% of the multi-annual variation in sheep kills. The negative pathway between lower-trophic-level variables and sheep predation was stronger than the positive pathway, possibly due to the erratic nature of multi-annual fluctuations in lower-trophic-level variables, which could prevent the numerical response from reaching its full potential. Monthly analyses revealed a type III functional response of coyotes to lambs, which is expected to enhance buffering effects of wild prey on sheep predation. Our findings suggest the dominant effect of wild prey biomass on sheep predation by coyotes in this Mediterranean-type community is as a buffer. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2404–2411; 2007)

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Coyotes (*Canis latrans*) are the most important predator on domestic sheep in North America and have a major economic impact on the sheep industry (Wagner 1988). Nonlethal and lethal predation control methods are currently employed in localized areas where sheep are grazed (Wagner and Conover 1999). These approaches, which do not appreciably reduce coyote population density, have been met with inconsistent or limited success (Knowlton et al. 1999). Consequently, much research has attempted to understand the ecological context of sheep predation with an eye toward improving the efficacy of predator management (Knowlton et al. 1999; Sacks et al. 1999a, b; Blejwas et al. 2002). Predation intensity is a highly stochastic process at the local scale, varying due to many factors such as preferences of the particular individual coyotes with territories overlapping sheep. However, it is clear from multiregional-scale studies that coyote density is also positively correlated with predation intensity on average (Roy and Dorrance 1985, Knowlton et al. 1999). Thus, it is important to understand demographic and behavioral processes associated with sheep predation, as well as how these fit into the broader trophic-dynamic context of the ecosystem.

Classical theory of trophic dynamics assumes equilibrium conditions (Holt 1977, Holt and Lawton 1994, Abrams and Matsuda 1996) and, therefore, may be inadequate for circumstances where perpetual disturbance prevents equilibrium. For example, in Mediterranean environments, short-

term fluctuations in rainfall and primary productivity may cause prey biomass to change rapidly over periods of time too short for predator numerical responses to equilibrate (i.e., for abundance to reach temporarily high carrying capacities). Such short-term fluctuations in prey biomass would not be expected to dampen functional responses, however, which depend primarily on concurrent prey abundance. Thus, such disturbance can be expected to act against apparent competition and to favor positive indirect effects between prey.

Empirically, predator-mediated interactions between prey have been largely unexplored among terrestrial vertebrates, especially in temperate climates. Short-term studies in north-coastal California, USA, suggest that the high annual variability in sheep kills resulted from multiple causes, including variability in success and seasonal timing in removing (related to predation management) particular coyotes responsible for most sheep predation in any given year (Sacks et al. 1999a, b). However, individual coyote kill rates on sheep varied considerably over space and time (Blejwas et al. 2002, Sacks and Neale 2002), indicating that factors other than presence or absence of particular coyotes affected sheep predation rates. In particular, coyotes preyed on sheep and wild prey species proportional to the abundance of these prey in their territory, suggesting that an increase in a subset of prey is likely to decrease predation on remaining prey (Sacks and Neale 2002). For similar reasons, it seems likely that an increase in coyote abundance would lead to an increase in predation on all prey. Although predation on sheep appears to be restricted to breeding

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coyotes (Sacks et al. 1999b, Blejwas et al. 2002), increases in abundance of nonbreeding coyotes could lead to increased sheep predation by breeders due to increased intraspecific competition for alternative prey. Thus, wild prey are likely to affect sheep predation via both numerical and functional responses of coyotes.

Predictions about whether coyote prey should ultimately experience positive or negative predation-mediated effects are complex and likely depend on timescale. On the one hand, coyotes are territorial, such that their density, especially of breeders, is regulated in part by spacing behavior (Knowlton and Stoddart 1983), which should tend to favor positive indirect effects (Abrams and Matsuda 1996). As with other canids (Packard and Mech 1983, Lindstrom 1989), established coyote territories typically do not contract in response to annual increases in prey density, which means that the density of breeding coyotes is somewhat decoupled from multi-annual variation in prey biomass, in the short term. On the other hand, the size of coyote territories varies spatially depending on average prey density (Knowlton and Stoddart 1983), suggesting that long-term norms in prey biomass do affect coyote territory size and, hence, density of breeders. Indeed, observations in other canids indicate that when prey biomass increases consistently over several consecutive years, territory-size inertia does not endure (Packard and Mech 1983). This suggests that protracted droughts, for example, may lead to eventual reduction of breeding density. Numerical responses of nonbreeding components of coyote populations may be considerably more sensitive than breeding components to multi-annual fluctuations in prey biomass (Mills and Knowlton 1991). Using annual and monthly data for 20 years (1976–1995), our objectives were to test for and quantify 1) positive correlations between wild prey variables and coyote abundance the following year, 2) positive correlations between coyote abundance and sheep predation, 3) negative correlations between wild prey variables and sheep predation, and 4) to investigate forms of functional responses of coyotes to sheep as this can also affect whether predator-mediated effects are ultimately positive or negative (Holt 1977, Abrams and Matsuda 1996).

STUDY AREA

We used long-term data on coyote predation on domestic sheep on a year-round sheep ranch in north-coastal California (the Hopland Research and Extension Center [HREC]) as a model system. The use of this canid–livestock system had several practical advantages. First, the annual number of sheep killed by coyotes at HREC has varied considerably since the 1970s (Scrivner et al. 1985, Neale et al. 1998), providing an ample opportunity to investigate potential causes. Second, a parvo virus epizootic (Thomas et al. 1984, Coolahan 1990) and a 6-year drought occurred during the 20-year study period, providing 2 natural experiments as well. Third, we knew abundance of sheep and predation rates were determined directly from sheep carcasses, which enabled quantification of predation rates

with greater accuracy than is typically feasible with wild prey. Finally, although domesticated, sheep were ranched on the site for several decades, such that this prey was a naturalized component of the coyote prey base (Sacks and Neale 2002).

The HREC was located in the mountains of the North Coast Range, Mendocino County, California (39°00'N, 123°05'W) in a Mediterranean climate zone, characterized by hot, dry summers and mild, wet winters. Average annual precipitation was approximately 100 cm and fell mostly as rain between November and February. Major vegetation types were annual grassland, chaparral, oak (*Quercus* spp.) woodland, and mixed evergreen–deciduous forest, described in detail by Murphy and Heady (1983). The HREC has been used for research on sheep production since 1951. Flocks of 900–1,500 adult females were rotated among 32 fenced pastures averaging approximately 30 ha each. The addition of lambs roughly doubled the existing sheep population between November and May (the lambing season) of each year. The number of sheep killed annually by coyotes at HREC varied considerably (Scrivner et al. 1985, Neale et al. 1998). We used only the portion of HREC containing lambing pastures (approx. 10 km²) because this is where sheep kill data were most reliable.

METHODS

Data Sets

A standardized index of coyote abundance was calculated for 1976–1995. This index used both scent stations and coyote removals corresponding to the availability of data. Scent-station and removal indices of coyote abundance have been used together previously and found to be highly correlated (Windberg et al. 1997). The index was expressed in standard deviations of the mean calculated separately for each of 3 periods: 1976–1981, 1982–1986, and 1987–1995. During the first period, coyote numbers were indexed using scent station surveys, conducted annually at 2 sites in Mendocino County (Linhart and Knowlton 1975; R. D. Roughton and M. W. Sweeney, United States Department of the Interior, unpublished report). We log-transformed scent station data before standardization to minimize any effects of multiple scent-station visitations by individuals. During the second period, we used annual numbers of coyotes removed by United States Department of Agriculture/Wildlife Services (USDA/WS) control specialists in Mendocino County. The amount of capture effort was relatively constant during this period, when 7 full-time specialists were employed year-round, during which time an annual average of 318.6 coyotes (SD = 54.8) was removed from Mendocino County (Coolahan 1990; J. Schuler, USDA/WS, personal communication). During the third, and longest, period numbers of trappers varied annually, but monthly data on both effort and numbers of coyotes were available. To exclude unwanted effects of variable capture effort, we regressed numbers of coyotes removed during April–June on person-hours of effort and we used the ratios of observed-to-expected (i.e., based on the regression) numbers. The

average monthly number of person-hours during this period was 594 (SD = 320), during which time an average of 27.4 coyotes (SD = 13.4) was removed per month (H. Jones, USDA/WS, unpublished data). To obtain the most representative demographic sample of the population, we focused on data from the spring and early summer period when breeding coyotes, rarely caught during most of the year, are least able to evade capture efforts (Sacks et al. 1999a).

We used lower-trophic-level variables as proxies for wild prey biomass because the diet of coyotes in the study area was diverse (principally 9 rodent and lagomorph species and black-tailed deer [*Odocoileus hemionus*]) and heterogeneously distributed, precluding direct quantification of total prey biomass (Neale and Sacks 2001, Sacks and Neale 2002). We used rainfall and annual herbaceous plant productivity for this purpose, taking advantage of the close association between rainfall and, more proximately, plant productivity with mammalian herbivore biomass in the region (Dasmann and Dasmann 1963, Garsd and Howard 1981, Heske et al. 1997, Cypher et al. 2000). We also used data on California vole (*Microtus californicus*) abundance, although voles composed only 10% of the estimated biomass consumed by coyotes on the study area (Neale and Sacks 2001).

We defined annual rainfall as the cumulative amount falling from the previous July through June. We estimated plant productivity annually in May (reflecting wet-season growth) through above ground clippings and expressed it as dry biomass per unit area (Pitt and Heady 1978, Garsd and Howard 1981). The vole abundance index was the number of captures from 2 plots on HREC, as described by Garsd and Howard (1981). Sheep predation by coyotes was recorded by shepherds throughout the study period. Shepherds surveyed pastures daily for dead sheep and used characteristic canine punctures and other evidence to diagnose coyote-killed sheep (Scrivner et al. 1985, Sacks et al. 1999b).

Numerical Response of Coyotes to the Prey Base

To test the prediction that coyote abundance was correlated to lower-trophic-level variables over time, we had to address 2 problems: 1) dependence of coyote abundance in a given year on that of previous years (i.e., temporal autocorrelation in the dependent variable) and 2) selection of independent variable(s), i.e., specific lower-trophic-level variables. Population abundance of coyotes in one year is not independent of the population abundance in the previous year, resulting in temporal autocorrelation. To ensure that temporal autocorrelation in the coyote index would not bias calculation of the test statistic (i.e., F -ratio), we used coyote growth rate, indexed as $\ln(\text{coyote abundance in yr } t / \text{coyote abundance in yr } t - 1)$, instead of coyote abundance, as the dependent variable. We regressed coyote population growth rate on lower-trophic-level variables (see below) in year $t - 1$ to allow for coyote gestation and neonatal growth. We excluded 4 years (1981–1984) from this analysis due to a parvo virus epizootic, which presumably reduced coyote

abundance irrespectively of the wild prey base (Thomas et al. 1984, Coolahan 1990, Cypher et al. 2000).

The above analysis was useful for qualitatively assessing the statistical evidence for a numerical response. To assess the strength of a numerical response for the purposes of relating it to sheep predation, we calculated a β -weight (i.e., standardized coeff.) for the effect of lower-trophic-level variables on coyote abundance (not growth rate). We included the 4 parvo virus years for this purpose because such factors affect the realized strength of the numerical response.

Regarding the second problem (i.e., selection of independent variables), we employed a hierarchical regression procedure (Tabachnick and Fidell 1989) to select the best subset of lower-trophic-level variables among plant productivity, vole abundance, and rainfall. This procedure is similar to a stepwise regression analysis except that in hierarchical regression the order in which variables are entered into the model is determined based on theoretical knowledge about the causal relationship of variables rather than biologically arbitrary criteria. We entered plant productivity into the prey model first. We selected plant productivity over rainfall because of its more direct relationship to wild prey abundance and over vole abundance because of its expected relationship to the abundance of all prey species. That is, voles, a single species, composed only a small portion of the coyote diet (Neale and Sacks 2001) and probably did not correlate as strongly as plant productivity with the abundance of other prey species (Garsd and Howard 1981). The choice of second and third variables was arbitrary. Results presented here used vole abundance as the second variable and rainfall as the third variable, although results were not affected qualitatively by which variable we entered second.

Effects of Coyote Abundance and Alternative Prey on Sheep Predation

To test the predictions that 1) numbers of sheep killed by coyotes were inversely correlated with lower-trophic-level variables and 2) numbers of sheep killed by coyotes were positively correlated with coyote abundance, we used hierarchical regression analyses of lower-trophic-level variables on sheep kills as described above to select a subset of lower-trophic-level variables along with coyote abundance in a standard multiple regression analysis. We tested hypotheses for lambs, adult females, and total sheep using log-transformed (for normality of residuals) numbers of sheep killed by coyotes on coyote abundance and lower-trophic-level variables. Annual lamb abundance varied slightly but was not correlated with sheep kills, lamb kills, or female kills ($P \geq 0.12$) and therefore we excluded it from analyses. We also excluded adult female abundance, which was even less variable among years.

Monthly Analyses and Functional Responses

We used months of lambing seasons (Nov–May), 1976–1995, as sample units for monthly analyses. In contrast to the annual data for which lamb abundance varied little, in

the monthly data, lamb abundance varied considerably. Therefore, we conducted an analysis of covariance (ANCOVA), with lamb abundance as the covariate, to determine whether the lamb-kill rate differed due to annual coyote abundance, annual wild prey abundance (i.e., lower-trophic-level variables), or an interaction of the two. We classified each month with respect to whether it belonged to a higher- or lower-than-average coyote abundance year and prey abundance year (based on lower-trophic-level variables). First, we used a test for homogeneity of regression (Tabachnick and Fidell 1989) to test for interaction among lamb abundance (the covariate) and each of lower-trophic-level variables and coyote abundance; significant interaction would imply differences in slopes of lamb kill rate as a function of lamb abundance. If we found no difference, we could perform an ANCOVA to determine effects of coyote abundance, lower-trophic-level variables, and their interaction on lamb kill rate as a function of lamb abundance. Such an effect would indicate differences in the magnitudes of functional responses. An assumption of these analyses was that lamb-kill rate was linearly related to lamb abundance, which would have been violated in the case of a nonlinear functional response. However, log-transformation of numbers of lambs killed, which we did prior to analysis, was sufficient to approximately linearize this relationship (as well as to equilibrate variance in residuals).

Although the functional response is typically expressed quantitatively as the number of prey killed per unit time per predator (as a function of abundance of the prey), we did not know the number of coyotes having access to sheep in any given month and therefore we expressed the relationship without respect to coyote abundance. As long as coyote abundance did not vary systematically with lamb abundance, which is almost certainly the case, this procedure should have provided a reasonable qualitative representation of the functional response. We conducted statistical analyses with SYSTAT (version 5.0, Evanston, IL).

RESULTS

Numerical Response and Wild Prey Variables

Coyote abundance varied over the 20-year period, with low points corresponding to the parvo virus epidemic and the drought (Fig. 1). Our index of coyote abundance was highly correlated with an independently derived index of coyote abundance in central California ($r = 0.88$; Cypher et al. 2000), supporting its validity. Vole abundance was correlated with plant productivity ($r = 0.65$, $P = 0.002$), which, in turn, was correlated with rainfall ($r = 0.64$, $P = 0.002$). Based on the hierarchical regression, coyote population growth rate was correlated with plant productivity (sq semipartial correlation coeff. $sr^2 = 0.29$, $F_{1,13} = 5.22$, $P = 0.04$). Addition of rainfall ($sr^2 = 0.02$) or vole abundance ($sr^2 = 0.04$) did not improve the fit of the model ($P > 0.10$). Based on the regression of coyote abundance on plant productivity the previous year, the standard coefficient (β) was estimated at 0.25, which implies that an increase in plant productivity of one standard deviation of its normal

variability corresponds to 25% of a standard deviation's increase (i.e., $\beta = 0.25$) in coyote abundance.

Effects of Coyote Abundance and Alternative Prey on Sheep Predation

During the 20-year study, 1,468 sheep-kills (613 ad F, 855 lambs) were documented, averaging 73.4 (SD = 30.7) sheep kills per year. Based on the hierarchical regressions, sheep kills were inversely correlated with plant productivity ($sr^2 = 0.22$, $F_{1,17} = 4.69$, $P = 0.045$). Female kills ($sr^2 = 0.16$, $F_{1,17} = 3.31$, $P = 0.087$), but not lamb kills ($sr^2 = 0.08$, $F_{1,17} = 1.47$, $P > 0.10$), were marginally inversely correlated with plant productivity. The addition of vole or rain to these models did not improve the fit ($P > 0.10$).

Based on standard multiple regressions, sheep kills were correlated with plant productivity ($\beta = -0.40$, $P = 0.04$) and coyote abundance ($\beta = 0.53$, $P = 0.008$) in the predicted directions ($R^2 = 0.47$, $F_{2,17} = 7.50$, $P = 0.005$), implying that a one standard-deviation increase in plant productivity corresponded on average to a reduction in predation of 12.3 sheep per year and a 1-standard deviation increase in coyote abundance corresponded on average to an increase in predation of 16.3 sheep per year. Coyote abundance and plant productivity (i.e., in concurrent yr) were not significantly intercorrelated ($r = 0.05$, $P = 0.83$). Because we found no subset of lower-trophic-level variables significant in the previous analysis of lamb kills, we regressed lamb kills on coyote abundance alone, which was significant ($\beta = 0.49$, $P = 0.03$). The regression of female kills on plant productivity and coyote abundance was marginally significant ($R^2 = 0.29$, $F_{2,17} = 3.48$, $P = 0.054$), although this was apparently due to coyote abundance alone (coyote abundance $\beta = 0.42$, $P = 0.055$; plant productivity $P > 0.10$).

Monthly Analyses and Functional Responses

We classified each month with respect to whether it belonged to a higher- or lower-than-average coyote-abundance year and plant-productivity year. We chose plant productivity as the defining lower-trophic-level variable based on the previous analyses. Slopes of relationships between lamb kill rate and lamb abundance (i.e., the forms of the functional responses) were not significantly different for high versus low coyote abundance or high versus low plant productivity periods, based on the test for homogeneity of regression, which produced no significant interaction terms ($F_{1,124} \leq 1.79$, $P \geq 0.18$). The ANCOVA indicated a positive correlation between monthly numbers of lambs killed and lamb abundance (i.e., functional response; $F_{1,125} = 50.08$, $P < 0.001$). In addition, an interactive effect of coyote abundance and plant productivity on the magnitude of functional response was significant ($F_{1,125} = 5.57$, $P = 0.020$). A post hoc Tukey test indicated that the functional response was lower when coyote abundance was low and plant productivity was high (average monthly no. of lambs killed = 2.5, SD = 3.1) than when coyote abundance and plant productivity both were high ($P = 0.008$) and possibly lower than when coyote abundance was high and

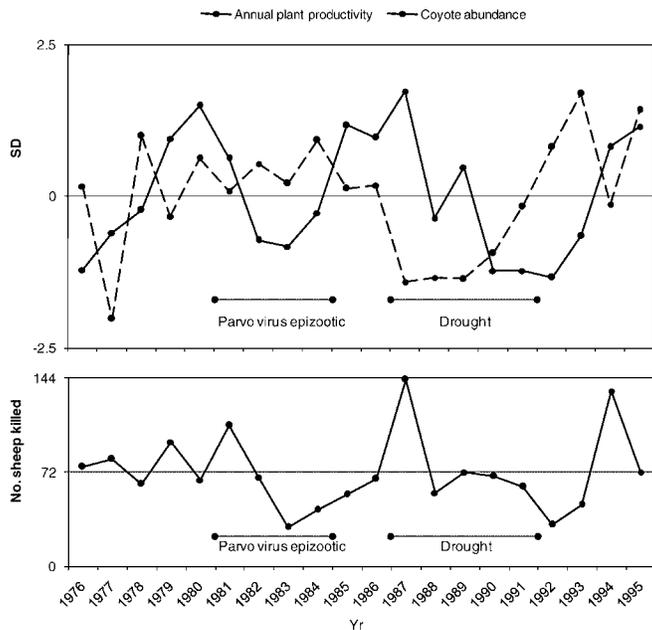


Figure 1. Coyote abundance in Mendocino County, California, USA, and annual plant productivity and sheep predation by coyotes at Hopland Research and Extension Center over 20 years (1976–1995) in relation to 2 natural perturbations.

plant productivity was low ($P = 0.080$). In the 2 groups where coyote abundance was high, there was no difference between the groups with high versus low plant productivity (monthly no. of lambs killed $\bar{x} = 6.3$, $SD = 6.1$; $P = 0.55$; Fig. 2). The form of the functional response increased disproportionately with increasing lamb abundance, consistent with a type III functional response and was most apparent in the period when coyote abundance was high (Fig. 2A).

DISCUSSION

In our study, coyote abundance tracked plant productivity, suggesting that coyotes responded numerically to their overall prey base in this Mediterranean climatic region. This was most apparent during a 6-year drought, which caused a prolonged reduction in plant productivity and wild prey (Heske et al. 1997, Cypher et al. 2000). A positive correlation between coyote growth rate and plant productivity during the drought as well as for the 20-year study, in general, suggested that coyotes responded numerically to the prey base. Other studies in warm climates provide additional evidence that coyotes respond numerically to their prey base. Two studies found a positive correlation between rainfall and coyote abundance in desert climates, where prey biomass was likely to closely correspond to rainfall (Windberg et al. 1997, Cypher et al. 2000). In southern Texas, a positive correlation between prey abundance and coyote abundance 2 years later ($r = 0.77$) occurred over 7 years (calculated from data in Windberg 1995 after excluding 3 yr of a parvo virus epizootic). In all 4 of these studies, it was impossible to assess the strength of the numerical response.

Evidence suggests the numerical response was generally weak in our study. The relationship between coyote

abundance and plant productivity was much weaker than that between coyote population growth rate and plant productivity (and between plant productivity and sheep predation). This difference may reflect inertia in the coyote population from one year to the next (e.g., due to overlapping generations), combined with the short-term nature of multi-annual fluctuations in plant productivity. Erratic changes in prey biomass from one year to the next are expected to dampen the magnitude of demographic responses by coyotes. In boreal regions, where coyotes and their staple prey cycle over a decade or so (Keith et al. 1977), coyote populations may be able to realize more of the potential of increases in their prey-limited carrying capacities.

Coyote abundance and lower-trophic-level variables potentially explained nearly half of the annual variation in sheep kills (as indicated by the R^2 value), which was considerable given the known importance of coyote removal as a stochastic variable affecting annual sheep predation (Sacks et al. 1999a, b). For example, the difference in numbers of sheep killed in 1994 and 1995 was largely attributable to the fact that one individual responsible for most predation in 1994 was removed in mid-August (10 months after the onset of lambing) and the individual responsible for most predation in 1995 was removed in early May of the year (5 months after the onset of lambing; Sacks et al. 1999b). Because individual coyotes were difficult to remove despite year-round efforts, the timing of such events in any given year was effectively random and, therefore, independent of variables we examined in this study.

Other studies investigating immediate effects of one prey's abundance on predation rates by coyotes on other prey support that alternative prey buffer predation on focal prey in the short-term. In Montana, fawn mortality was inversely correlated with microtine abundance (Hamlin et al. 1984). In Nova Scotia, where coyotes consume primarily white-tailed deer (*O. virginianus*) and snowshoe hares (*Lepus americanus*), increases in abundance or vulnerability of one prey reduced predation rates on the other (Patterson et al. 1998). Wolf predation on cattle in Minnesota also appeared to vary inversely with fawn availability (Mech et al. 1988). Prey buffering was also indicated to occur on our study area by the findings that 1) occurrence of deer remains in coyote scats was inversely correlated with the abundance of lambs and 2) breeding coyotes preyed on sheep and wild prey species proportional to the abundance of these prey in their territories (Sacks and Neale 2002).

In general, the buffering effect of lower-trophic-level variables on lamb predation, as reflected by correlations in our study, appeared to be weaker than on adult sheep predation. The annual analyses revealed no significant relationship between plant productivity and lamb predation, but the monthly analyses, which provided greater statistical power, suggested that high plant productivity reduced lamb predation when coyote abundance was low. Regardless of the causes for the interactive effect on lamb predation, it is not surprising that an increase in wild prey would have a

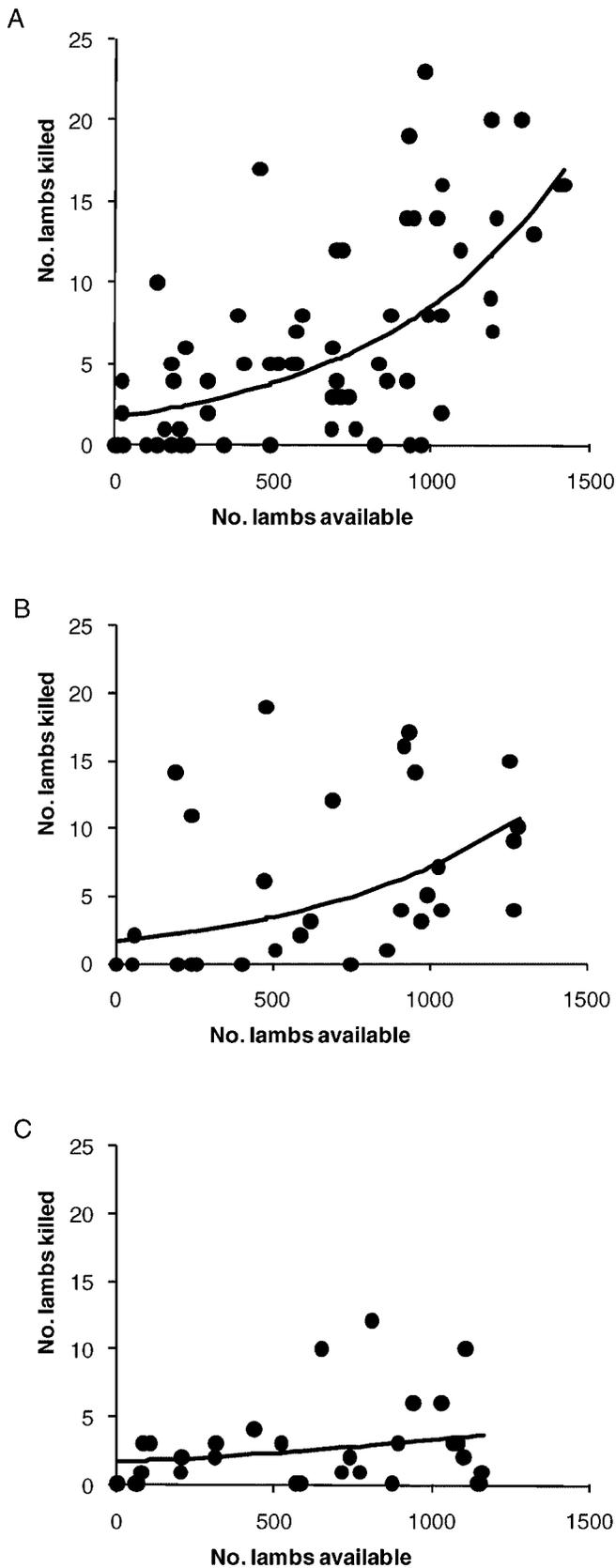


Figure 2. Relationships between monthly numbers of lambs killed and lamb abundance for years of high coyote abundance (A), low coyote abundance and low plant productivity (B), and low coyote abundance and high plant productivity (C), Hopland Research and Extension Center, California, USA (Nov–May) 1976–1995. We performed regressions on log-transformed values; we back-transformed those shown and the regression line.

generally stronger effect on adult sheep than on lamb predation given that lambs are smaller, easier to prey on, and typically killed preferentially over females by coyotes (Scrivner et al. 1985, Sacks and Neale 2002).

The correlation of sheep predation with coyote abundance was similar in magnitude (but opposite in sign) to that with lower-trophic-level variables. However, because only a small portion of coyote abundance could be explained by plant productivity (the previous yr), negative effects of wild prey biomass on sheep predation were apparently stronger than positive ones (Fig. 3). Based on the beta weights and standard deviations in annual numbers of sheep killed, the overall model suggests that a 1-standard deviation increase in plant productivity corresponds to an increase in sheep predation via the numerical response of 4.1 sheep per year, and a reduction in sheep predation via buffering of 12.3 sheep per year, for a net reduction in sheep predation of 8.2 sheep per year, approximately 10% of the average annual loss to coyotes.

The functional response of coyotes to lambs appeared to be type III, which also is expected to strengthen buffering effects of one prey on another (Abrams and Matsuda 1996). For example, a type III functional response can reflect prey-switching (i.e., that coyotes prey disproportionately more on alternative [wild] prey) and therefore disproportionately less on lambs, when alternate prey are abundant relative to lambs. In fact, the per-lamb rate of predation increased throughout most of the range of lamb densities. In another study reporting a type III functional response of coyotes to a prey, the functional response saturated about the point when the prey density was at its average abundance (Keith et al. 1977). The long concave portion of the type III functional response we observed would be expected to enhance the buffering effect of wild prey on lamb predation.

In conclusion, correlations we observed support the occurrence of both positive and negative indirect effects of wild prey on sheep predation. However, findings suggest that the buffering effect of wild prey on sheep predation is dominant, due to a partial decoupling of coyote density with prey density. This is in contrast to conclusions of an empirical study conducted in a boreal region where one wild prey species dominated the coyote diet (Stoddart et al. 2001). We suggest that the essential difference between the predator–prey dynamics in the Mediterranean study region and those in boreal regions, where they have been studied more extensively, is that of disturbance—erratic rainfall-driven prey fluctuations—in the former as contrasted with regular 4-year or 10-year cycles in the latter. This hypothesis comes under the more general rubric of disturbance theory (sensu Huston 1979) whereby ecological systems are kept in states of perpetual disequilibrium (with respect to resource limitation) by continuous disturbance, in this case, erratic prey fluctuations.

MANAGEMENT IMPLICATIONS

Our findings indicate that the fluctuating abundance of wild prey characteristic of the rainfall-driven community in

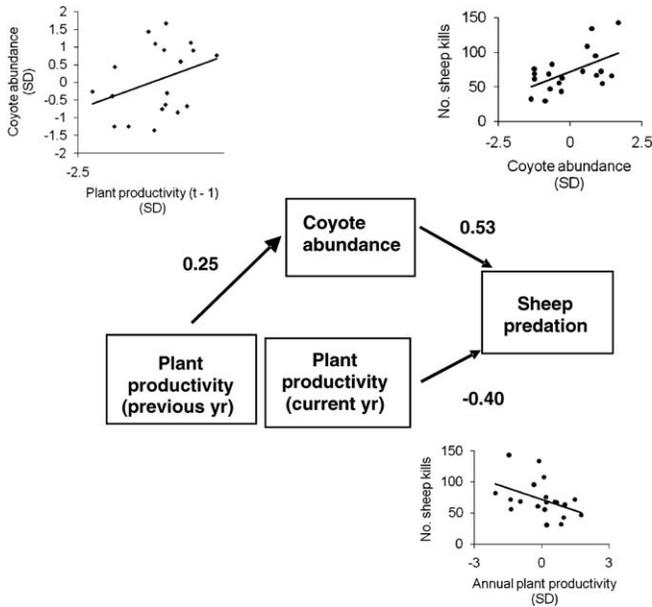


Figure 3. Observed relationships among wild prey biomass, coyote abundance, and sheep predation by coyotes, Hopland Research and Extension Center, California, USA, 1976–1995. Values are standardized regression coefficients and indicate estimates of effect strength. We calculated the strength of the positive pathway as the product of the 2 positive coefficients and it is smaller in magnitude than the negative productivity indicating a larger negative than positive effect of plant productivity on sheep predation.

north-coastal California has predictable effects on sheep predation. Knowing that lamb losses due to predation are likely to be reduced in high-rainfall winters (especially those following low-rainfall winters) but increased in low-rainfall winters (especially those following high-rainfall winters) could be useful in sheep management decisions. For example, more costly but effective means of predation management (e.g., keeping lambs in barns for longer periods) could be reserved for low-rainfall years following high-rainfall years.

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