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Can rare positive interactions become common when large carnivores consume livestock?

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Abstract. Livestock populations in protected areas are viewed negatively because of their interaction with native ungulates through direct competition for food resources. However, livestock and native prey can also interact indirectly through their shared predator. Indirect interactions between two prey species occur when one prey modifies either the functional or numerical responses of a shared predator. This interaction is often manifested as negative effects (apparent competition) on one or both prey species through increased predation risk. But indirect interactions can also yield positive effects on a focal prey if the shared predator modifies its functional response toward increased consumption of an abundant and higher-quality alternative prey. Such a phenomenon between two prey species is underappreciated and overlooked in nature. Positive indirect effects can be expected to occur in livestock-dominated wildlife reserves containing large carnivores. We searched for such positive effects in *Acacia–Zizhypus* forests of India's Gir sanctuary where livestock (*Bubalus bubalis* and *Bos indicus*) and a coexisting native prey (chital deer, *Axis axis*) are consumed by Asiatic lions (*Panthera leo persica*). Chital vigilance was higher in areas with low livestock density than in areas with high livestock density. This positive indirect effect occurred because lion predation rates on livestock were twice as great where livestock were abundant than where livestock density was low. Positive indirect interactions mediated by shared predators may be more common than generally thought with rather major consequences for ecological understanding and conservation. We encourage further studies to understand outcomes of indirect interactions on long-term predator–prey dynamics in livestock-dominated protected areas.

Key words: chital; indirect interactions; lion; livestock; native prey; predation risk; shared predator; vigilance.

INTRODUCTION

Conservation managers and ecologists frequently view livestock populations and their associated human settlements as impediments to the maintenance of protected areas. Ungulate livestock, for example, limit regeneration of native plant communities (Adams 1975, Belsky and Blumenthal 1997). As direct competitors for forage, livestock typically cause reduced body condition, reproductive rate, and survival in native ungulate species (Chaikina and Ruckstuhl 2006). Native ungulates often alter their behavior in the presence of livestock, resulting in reduced foraging benefits (Kie 1996, Mattiello et al. 2002, Brown et al. 2010). When large carnivores are included with livestock, intensified predator effects induced by livestock subsidies may lead to loss of native prey (DeCesare et al. 2010), and to increased costs for conservation (e.g., to compensate farmers for livestock depredation; Mishra 1997, Bagchi et al. 2003, Treves and Karanth 2003, Bagchi and Mishra 2006). Less appreciated is the understanding that the association between livestock and native prey may include positive indirect interactions via their shared predator.

Despite increased attention on the importance of indirect interactions in structuring ecological communities (Holt and Kotler 1987, Bonsall and Hassell 1997, Abrams et al. 1998, Chaneton and Bonsall 2000), empirical research rarely explores the potential for positive effects between prey sharing a common predator. We suspect that this rarity reflects an under-

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appreciation of relevant theory, as well as missed opportunities to search for positive effects in systems where they can be expected to occur, such as in livestock-dominated wildlife areas containing large carnivores.

Livestock constitute an important diet component for a variety of large carnivores, including wolves (*Canis lupus*; Vos 2000, Jethva and Jhala 2004, van Duyne et al. 2009), hyenas (*Crocuta crocuta* and *Hyaena hyaena*; Ogara et al. 2010), snow leopards (*Uncia uncia*; Bagchi and Mishra 2006), leopards (*Panthera pardus*; Ogara et al. 2010), tigers (*P. tigris*; Biswas and Sankar 2002, Bagchi et al. 2003), and lions (*P. leo*; Chellam 1993, Singh and Kamboj 1996, Patterson et al. 2004, Meena et al. 2011). The territorial behavior of these predators creates the potential for positive indirect effects among their prey (Abrams and Matsuda 1996). Thus, we make a case for a more objective evaluation of livestock coexisting with native prey both from theory and from the wealth of examples where it becomes hard to exclude their consideration. We then search for evidence of a positive interaction between livestock and native prey in the mixed *Acacia–Zizhyphus* forests of Gir sanctuary, western India, where common and abundant chital deer (*Axis axis*) are preyed on by Asiatic lions (*Panthera leo persica*) in the presence of buffalos (*Bubalus bubalis*), cattle (*Bos indicus*), and their nomadic herders.

Shared predation and indirect interactions between two prey

Shared predation is common in ecological communities and has a major influence on prey abundance and coexistence (Holt 1977, Sih et al. 1985, Holt and Lawton 1994). This influence is defined by enemy meditated indirect interactions, often in the form of apparent competition (–, – interaction, where "–" represents a negative effect on one prey) where the predator's feeding rate on one prey species is enhanced by the presence of additional species (Holt 1977, Holt and Kotler 1987). An alternative is apparent mutualism (+, + interaction, where "+" represents a positive effect on one prey), whereby both prey species benefit because predation is shared between them as time spent eating one prey is not available for eating the other and predators do not increase numerically and aggregate (despotic predators), or increase their foraging efforts by staying longer in resource patches (Holt and Kotler 1987). This reciprocal positive interaction can also be reinforced if prey switching occurs, typical of a Type III functional response for a predator that focuses on the more common prey (Abrams 1987). Reciprocal positive or negative interactions depend on the predator's functional (attack and kill rates) and numerical (and aggregation) responses. When generalist predators feed on multiple prey items with no preference among them, the indirect interaction among prey species will depend purely on their abundance (Tschanz et al. 2007). If two prey species are equally abundant and preferred, and if the behavior of the predator is fixed in regards to time spent feeding, then the interaction between prey that share a predator becomes (+, +). This apparent mutualism can revert to a (–, –) interaction when predators aggregate or spend more time in richer patches (high densities of both prey) and less time in poorer patches, resulting in higher predation rates for both prey (Holt and Kotler 1987).

Many enemy-mediated interactions may exhibit a third possibility of non-reciprocal (0, – or 0, +, where 0 represents no effect on one prey) or asymmetrical (–, +) interaction, due to difference in prey profitability (body size and vulnerability) and their abundance for the shared predator (Chaneton and Bonsall 2000). These effects between two prey species are likely to occur in domestic-prey-dominated protected areas containing large carnivores (Table 1). Domestic ungulates (e.g., livestock: cattle and buffalos) are typically larger than native ungulates, as a result of selective breeding for milk and meat production, and differ from wild stock in anti-predator behavior (e.g., lower vigilance, flight response, aggression, and tenacity) and morphological character (Mignon-Grasteau et al. 2005). They also occur in highly clumped distributions with larger group sizes (high densities). Consequently, livestock may be more optimal prey choices for carnivores that consume large-bodied prey more frequently than expected based on their availability and abundance (De Pienaar 1969, Hayward and Kerley 2005). Predators' preference for one prey species lowers the attack rate on the secondary prey (Abrams and Matsuda 1996). If the predator's functional response saturates on the preferred prey, and if its density is limited by factors other than rates of prey consumption, then the indirect interaction between prey species can be positive, a phenomenon for which field examples are rare (Abrams and Matsuda 1996, Chaneton and Bonsall 2000).

Positive interactions between livestock and native prey

Positive indirect interactions should be common in any system where predators switch prey, consume the more profitable prey species, or possess a saturating functional response (Abrams and Matsuda 1996). The key requirement for such effects between shared prey species is that the numerical response by predators should not overpower their functional response. The probability of these effects will be enhanced in a system containing large carnivores whose population is maintained at some fixed density (weak or no numerical response) either by processes such as territoriality, interference behavior, conflict mortality, and dispersal, or by external control (e.g., management). Large generalist predators (e.g., lions, tigers) consume more than one type of prey and their consumption rate for a particular prey is likely to be influenced by presence of an alternative prey. The multi-prey extension of Holling's disc equation (Murdoch 1973, Chesson 1989) provides a simplified departure point to assess a

TABLE 1. A simplistic summary of potential indirect interactions (following Holt and Kotler 1987, Holt and Lawton 1994, Chaneton and Bonsall 2000), between native and domestic prey sharing a predator, and a partial list of possible characteristics and responses of predator and prey that create them, as well as their possible role in native prey conservation.

Indirect interactions (native, domestic prey)	Effect via shared predator	Characteristics		Potential for native prey conservation
		Predator	Prey	
−,− (reciprocal negative interaction), apparent competition	both prey negatively affect each other	increase in functional and numerical response or aggregation in patch toward both prey types	vulnerability, large or equal body size of domestic prey, both prey densities low (poor environments)	higher attack rate on native prey, native prey population will decline
0, – (asymmetrical non-reciprocal interactions)	presence of domestic prey does not affect the native prey	increase in functional and numerical response toward domestic prey, but no changes toward native prey	vulnerability, large or equal body size, and high densities of domestic prey	no change in attack rates on native prey, native prey population stable
0, 0	both prey do not affect each other	functional response equal, no numeric response, no preference for any particular prey type	rich environments with high densities of both prey, equal vulnerability and body size	no change in attack rates on native prey, native prey population stable
+,– (asymmetrical interactions)	presence of domestic prey positively affects the native prey	predators despotic or no numeric response and selectively take domestic prey in the patch	vulnerability, large body size, and high densities of domestic prey, native prey common or rare	lower attack rate on native prey, native prey population will increase
+,+ (reciprocal positive interaction), apparent mutualism	both prey positively affect each other	predators despotic or no numeric response, forage for fixed period of time, no preference among prey types and leave patch independent of prey densities	vulnerability, large body size, and high density of domestic prey maintained by animal husbandry activities	lower attack rate on native prey, native prey population will increase

Note: The symbol "–" represents a negative effect on one prey, "+" represents a positive effect on one prey, and 0 represents no effect on one prey.

generalist predator's consumption of a focal prey (F_1) in the presence of an alternative prey species ($F_1 = a_1N_1/[1 + a_1N_1h_1 + a_2N_2h_2]$), where N_1 and N_2 represent, respectively, the number of native and alternative prey (i.e., domestic prey), a_i is the attack rate and h_i represents the handling time for each prey type. This simple model assumes that the predator's consumption of native prey is a function of the availability of domestic prey. Predator preference for a prey should increase with prey profitability (i.e., large body size) and vulnerability, and the number of domestic prey consumed by the predator will often increase where they are more abundant. This is especially true for large-carnivore systems where large-bodied domestic prey may represent an optimum prey size (sensu Hayward and Kerley 2005). Efficiencies associated with search, capture, and consumption of preferred prey reduces the time available for encountering secondary prey (Chesson 1989). If total foraging time is fixed because predator density is controlled independent of prey population size, then consumption of native prey per unit time will decline as the density of preferable domestic prey increases. In addition, native prey frequently possess anti-predator behavioral strategies that further limit the attack rate of the predator.

Measuring predator attack rates on native prey (or the number consumed) is difficult in natural field conditions. Fortunately, for behaviorally sophisticated animals, such as large mammalian herbivores, the measurement of vigilance can be used to gauge predation risk as a function of attack rate, especially in large-carnivore fear-driven systems (Brown et al. 1999).

Vigilance behavior is the primary adaptive response to perceived predation risk for many ungulates (Elgar 1989, Hunter and Skinner 1998, Caro 2005), and native prey vigilance should be higher than vigilance in domestic prey (sensu Mignon-Grasteau et al. 2005). Time spent vigilant reduces opportunities for efficient foraging, and prey animals typically modify their vigilance behavior according to the predation risk and activity of their predators (Scheel 1993, Laundre et al. 2001). In locations where predation risk is perceived to be higher, foraging ungulates spend a significantly greater proportion of their time vigilant (Hunter and Skinner 1998). We thus expect native prey to spend less time vigilant where increased abundance of domestic prey dilutes risks for native prey species.

We tested the prediction with a common and abundant native prey, chitals, encountering Asiatic lions in Gir sanctuary, Gujarat State, western India (~1150 km^2; 21°20′ to 21°40′ N; 70°30′ to 71°15′ E). Tribal settlements ("Ness") have existed in the Gir sanctuary for the past 500 years (Abdi 1993), and nomadic herders, or Maldharis, along with their livestock, have been an integral part of the Gir ecosystem since 1880 (Berwick 1976, Casimir 2001). Adult buffalo (mean body mass 300–400 kg) and cattle (150–200 kg) are herded by Maldharis and settlement villagers every day between early morning and late evening. The livestock graze sympatrically with chitals (mean body mass 40 kg) in Gir sanctuary, and both species are eaten by lions (Chellam 1993, Meena et al. 2011). Lions are generalists and opportunistic hunters and kill prey of various sizes, but their preferred prey size of 350 kg (Hayward and Kerley 2005) matches the size of the domestic prey available in Gir sanctuary. Despite the abundance of wild prey (especially chitals) in Gir forests, livestock constitutes an important part of the overall diet of lions (33–40% of total biomass consumed; Meena et al. 2011), and lion dependence on livestock is greater in areas (eastern Gir) containing high livestock density (Meena 2008). The western (low livestock density) and eastern (high livestock density) areas of Gir sanctuary support approximately 7800 (~11 individuals/km^2) and 11 000 (~ 24 individuals/km^2) buffalo and cattle, respectively (Park Office, Junagadh, Gujarat State, *personal communication*), and are separated by a distance of approximately 90 km. If preference by lions for livestock increases with livestock density, then vigilance in chitals should be reduced in areas where lions encounter and kill more livestock. Thus, we compared chital vigilance in two similar open *Acacia-Zizhypus* forests (~450 km^2) where we predict lower vigilance by chitals in eastern Gir (high livestock density) relative to western Gir. We also evaluated the domestic prey's anti-predator behavior in response to lion predation in both areas to understand its role in influencing the indirect interactions between lions and the chitals.

Measuring native and domestic prey behavior

We selected only open *Acacia–Zizhyphus* habitats (patch area $\geq$ 0.5 km^2) for chital observations during the dry season (January to June 2009). We observed randomized focal groups of chitals within 5–6 km of settlements, a distance that approximates livestock grazing distances. We divided the habitats surrounding settlements into several numbered 1.25 × 1.25 km grids that we selected at random. Once a chital group was sighted, we selected only one foraging adult female (focal animal) for detailed behavioral observation to minimize pseudo-replication within groups (Altmann 1974). We recorded all observations with a camouflaged Sony Handy Cam (DCR-DVD 610, 40× optical zoom; Sony Corporation, Tokyo, Japan) mounted on a tripod. Observers dressed in army camouflage suits and concealed themselves in surrounding vegetation. All recordings were conducted when chitals were active in early morning (05:30 to 08:30) and evening (16:00 to 19:30; Schaller 1967, Miura 1981). We avoided recording near forest roads, water holes, or other areas dominated by human activity (i.e., agriculture fields, tourist areas). Chital home ranges are generally small (~2–3 km^2; Mishra 1982, Mishra and Wemmer 1987), so we were able to obtain independent observations by not recording in the same blocks of forests where a group was previously encountered.

We recorded behavior in each of the 61 foraging groups ($n = 22$ and 39 groups, respectively, for low and high livestock density areas) for five minutes or until the focal animal moved away from, or spotted, the observer. We always selected the focal animal from the central part of the group to reduce any confounding effect of an animal's spatial position (Elgar 1989, Caro 2005). We also estimated the distance to the focal animal's nearest neighbor (two classes; near, <5 m; distant, >5 m) to test for effects of neighboring animals on a focal animal's vigilance (Blumstein 1996). We classified behavior into three main categories: (1) vigilant, focal animal standing with its head raised above shoulder height with ears pointed and attentive toward a specific direction; (2) feeding, head down or looking for resources; (3) other, social interactions, grooming, or lying down. We alternated observations between the low and high livestock density areas to remove any temporal bias and completed our assessment by recording the total number of individuals and sex ratio of all groups.

We also estimated livestock vigilance similarly in areas of high ($n = 9$) and low density ($n = 14$, where n is the number of livestock groups examined). We selected grids at random and searched the open habitats for grazing animals. After encountering a group we selected a focal adult female buffalo and recorded its behavior with the same protocol used for chitals. We chose the animal farthest from herders in order to reduce the effect of humans.

Prey and predator population estimates

We estimated population density and mean group size of chitals in the high and low livestock density areas with vehicular-based road transects (Hirst 1969, Berwick 1974). We monitored transects during early morning (06:00 to 08:00) and again in the evening (16:30 to 18:30). Observers sat in an open vehicle (traveling at 15–20 km/h) and counted the number of individuals in any chital group within 50 m of both sides of the road. We calculated average density estimates for each transect separately using the methods described by Khan (1994) and Khan et al. (1996) for the Gir system (Distance v.5.0; Thomas et al. 2010).

We obtained lion density estimates from recent surveys in Gir (Jhala et al. 2006, Meena 2008; 16 lions/100 km^2 and 12 lions/100 km^2 in the high and low livestock density areas, respectively). The lion popula-

TABLE 2. Comparisons of western and eastern Gir sanctuary, western India.

Area	Habitat variables (*Acacia–Zizhyphus* forest) Tree density (no./100 m^2)	Shrub density (no./100 m^2)	Biomass (g/m^2)	Density Livestock (no./km^2)	Lions† (no./100 km^2)	Chital deer (no./km^2)	Livestock killed (no./yr)
Eastern Gir (high livestock density)	5.4 (0.3)	0.1 (0.07)	50.9 (8.3)	24	16	58.7 (9.9)	192*
Western Gir (low livestock density)	4.3 (0.8)	0.4 (0.2)	61.2 (18.7)	11	12	49.1 (10.7)	94*

Note: Values are means with SE in parentheses.
Sources: Jhala et al. (2006); V. Meena, *unpublished data.*
* $P < 0.05$ (chi-square test).

tion has been more or less constant since the early 1980s (~250 adult animals; Singh 1997, Pati and Vijayan 2002, Gujarat State Forest Department 2010). This stable population suggests that the lion densities inside the park are likely influenced by the processes of territoriality, conflict mortality, and dispersal. Subsequently, their dispersal for new territories has resulted in several "satellite" populations outside the park boundary (~120 animals; Meena 2010, Singh and Gibson 2011). We were concerned that predation risk to chitals might be modified by the presence of leopards, for which we lack population estimates. However, mark–recapture estimates from forest authorities, and our own observations, suggest that leopards are concentrated in the central and outer areas of Gir, and are uniformly low across the open habitats of *Acacia–Zizhyphus* (Pati et al. 2004, Khan et al. 2007).

We obtained annual livestock kill statistics by settlement from 2006 to 2009 from park managers. Forest authorities compensate the Maldharis and settlement villagers in Gir for livestock depredation by carnivores and kill statistics are well documented.

Vegetation structure and edible ground biomass

We were concerned that vigilance might vary with local habitat, so we measured tree and shrub densities that can alter sight lines and conceal predators. When we finished recording the behavior of the focal animal we quantified tree (2–6 m tall) and shrub (50–200 cm tall) density within 50 m of the animal's position by counting stems in four randomly located 10 × 10 m plots. To determine if food density influenced vigilance behavior (Elgar 1989, sensu Beauchamp 2009), we estimated uneaten biomass next to the area where the focal animal had foraged by collecting and weighing (nearest g) all edible items on the ground (grass, acacia pods, and *Zizhyphus* berries) in four 1 × 1 m plots.

DATA ANALYSIS

We searched for any underlying differences in food biomass and the densities of trees and shrubs that might influence vigilance behavior between the high and low livestock density areas with a multivariate analysis of variance. We calculated a focal animal's vigilance as the arcsine square-root transformation (Zar 1999) of the amount of time spent vigilant, divided by total duration of the recording. We then searched for differences in chital density, chital group size, vigilance, and average livestock kills per settlement between high and low livestock density areas with one-way analyses of variance. We tested whether lion predation rates on livestock increased with livestock density using linear regression and further evaluated overall differences between sites in the average number of livestock killed annually by lions with respect to the total livestock available using a chi-square test. Where appropriate, we report mean values and their standard errors. Analyses were performed with Statistica v 7.0 (Statsoft, Tulsa, Oklahoma, USA).

RESULTS

Habitat and native prey densities

Tree and shrub density and uneaten forage biomass did not differ between high and low livestock density areas (Wilks' $\lambda = 0.89$, $F_{3,57} = 2.12$, $P = 0.10$; Table 2). Chital density was similar in both areas ($P = 0.55$; Table 2). Group size also did not differ ($P = 0.67$; low livestock density area, 5.8 ± 0.8 individuals [mean ± SE]; high livestock density area, 6.2 ± 0.6 individuals).

Native and domestic prey vigilance behavior

Chitals were significantly more vigilant in the low livestock density area ($F_{1,59} = 21.05$, $P < 0.001$; Fig. 1). The actual proportion of time (from back-transformed data) spent vigilant by foraging chitals in the low and high livestock density area was 0.20 ± 0.03 and 0.07 ± 0.01, respectively. There was no significant effect of nearest neighbor distance on focal animal vigilance ($P = 0.59$). There was also no relationship between vigilance rates and forage biomass availability ($r^2 < 0.01$, $P = 0.41$).

There was also no difference in vigilance of livestock between high and low livestock density areas ($P = 0.41$, Fig. 1). The majority of livestock failed to display any vigilance behavior (13 of 23 focal animals).

Livestock kills by lions

The annual livestock kill by lions was positively correlated with livestock density across different settlements in Gir sanctuary ($r^2 = 0.34$, $P < 0.001$; Fig. 2).

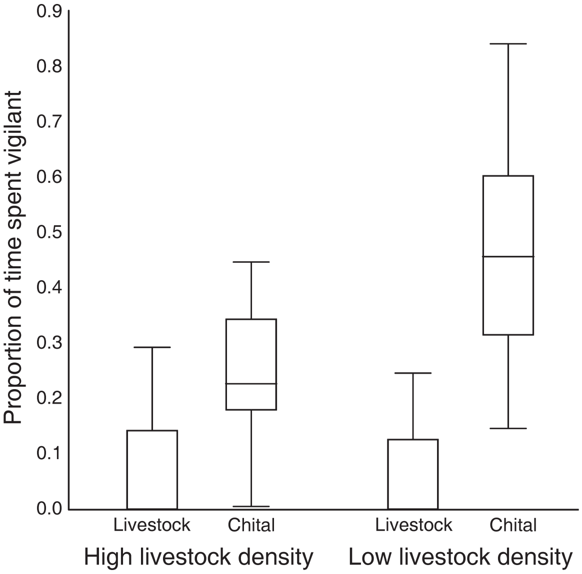

FIG. 1. Proportion of time (arcsine square-root transformed) spent vigilant by chitals and livestock with high and low livestock density in Gir sanctuary, western India. The figure illustrates the median (lines), 25% to 75% quartiles (boxes), and ranges (whiskers).

Correcting for the total number of livestock available in western and eastern areas, lions killed more livestock annually in the high livestock density area than in the low livestock density area ($\chi^2 = 5.17$, df $= 1$, $P = 0.02$, Table 2). Lions kill almost four times the number of livestock per settlement per year in the high livestock density area than in the low livestock density area ($F_{1,42} = 22.35$, $P < 0.001$; low livestock density area, 2.3 ± 0.8 kills per settlement per year; high livestock density area, 8.1 ± 0.8 kills per settlement per year).

DISCUSSION

Though lion density is higher in eastern Gir, the density of livestock, the annual number of livestock killed, and livestock kill rates in eastern Gir are also higher. An indirect, positive effect on chital fitness is thereby mediated by lower lion attack rates on chitals and expressed as lower vigilance in chitals, wherever livestock densities are higher. The ecological relevance of this positive effect on predation risk, expressed by vigilance and other anti-predator behaviors, is high. For many large herbivores, being vigilant in a continuous landscape of fear is a costly trade-off between obtaining food and keeping safe from predators (Sih 1980, Lima 1998, Brown et al. 1999, Luttbeg and Kerby 2005, Preisser et al. 2005).

Previous comparisons of body-condition scores confirm our assumption that less time spent on vigilance can enhance foraging opportunities. Chitals in high livestock density areas were in better condition than in low livestock density areas (Jhala et al. 2004). Differences in condition are often assumed to reflect differences in resource availability. This difference may now be explained, not by differences in resource availability, but by differences in the landscape of fear which influence forage intake (sensu Brown et al. 1999, Laundre et al. 2001). The interpretation is supported by the fact that the chital vigilance rates were not related to available ground biomass in the system.

Although we found a significant indirect positive effect of domestic prey on chital vigilance behavior, we did not detect differences in chital population densities between the high and low livestock areas. It thus appears that area-dependent differences in condition do not translate directly to higher fitness and ultimately to higher regional densities. We suspect that this rather perplexing result is related to costs and trade-offs in density-dependent habitat selection. One possible explanation is that the chital in both the western and eastern areas of Gir disperse into the central area (National Park, 250 km^2), where there are no settlements or livestock grazing, in a way that equalizes density. Such a process could most likely be maintained if the central area is a sink caused by cues of habitat quality that are misleading indicators of fitness ("ecological trap," e.g., chitals select habitat according to high resource abundance and cover even though predation rates are also high in the absence of domestic prey).

The behavior of alternative prey species may often be important in determining the overall relationship among prey species via their predators and in defining the landscape of fear. Livestock in Gir were indifferent to predation risk even though lion kill rate increased with livestock density. If native prey respond adaptively to differences in fear, why not domestic prey? We suggest

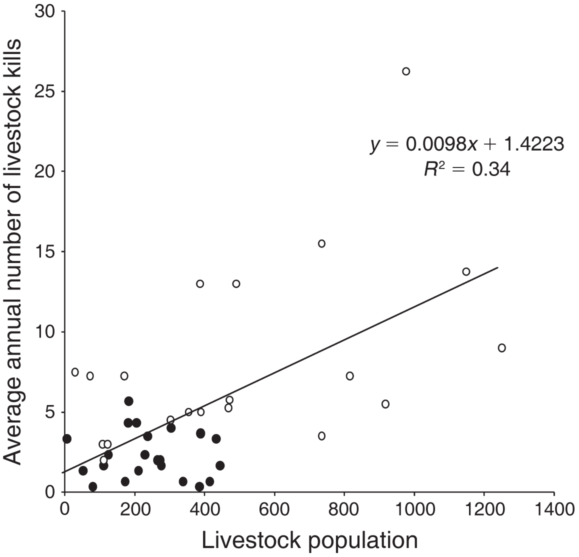

FIG. 2. Average annual number of livestock killed by lions, by settlement, and size of livestock population in Gir Sanctuary, western India (2006–2009). Solid circles represent kills in each settlement in western Gir; open circles represent kills in each settlement in eastern Gir.

four explanations. (1) Low livestock vigilance in Gir is consistent with low levels of anti-predator behavior typical of domesticated animals elsewhere (Linnell et al. 1999, Mignon-Grasteau et al. 2005). (2) Risk may be so low, and vigilance so ineffective, as to render it useless. Although significantly different between areas, annual livestock mortality is low, equivalent to just 1.3% and 2.0% for low and high livestock density areas, respectively. (3) Livestock may face such high energetic demands that they cannot afford the "luxury" of vigilance. (4) Livestock may rely on the security of herders to provide required vigilance.

We suspect that additional general insights can be gleaned from our study in Gir. Lions at Gir form larger groups in the high livestock density area than elsewhere (Meena 2008). Group forming by both predators and their prey limits encounter rates by reducing predator search efficiency and by causing gaps in the landscape where prey is absent (Fryxell et al. 2007). In eastern Gir, large prides of lions are associated with lower predation risk for chitals.

Possible conservation applications

Positive indirect effects may have valuable implications for conservation. Large domestic prey are the most abundant and vulnerable prey in many ecosystems, and are thus likely to be the preferred choice for large carnivores. Where positive interactions are expected to occur between domestic and native prey, conservation managers may be able to use domestic prey to preserve large carnivore ecosystems and their increasingly endangered native prey. Asymmetrical (+, −) and reciprocal positive interactions (+, +) occurring between native and domestic prey can have potential use in conservation and recovery of endangered native prey populations (Table 1). Domestic prey can also help in recovery of predator populations normally limited by low native prey numbers in the system. Buffalo and cattle in Gir forest have historically supported the prey requirements for Asiatic lions when the native prey species were scarce (~6000 individuals in early 1970s) in the system (Joslin 1973, Berwick 1974). The present annual livestock depredation inside the park area is about 300 animals (out of approximately 2200 animals killed in total, inside and around the Gir forest; Singh and Gibson 2011). In terms of biomass, the livestock killed inside Gir are likely to offset chital consumption by lions by almost 10% of their total population annually.

Maintenance of the Gir ecosystem depends on the tolerant and respectful attitudes toward large predators by the Maldhari tribesman and local villagers (Srivastava 1997, Varma 2009). Regular compensation for livestock kills by park management has also helped to reduce antagonistic attitudes among the settlers toward conservation of this critical ecosystem. However, we caution that using domestic prey to conserve threatened species may be more controversial elsewhere. In a majority of areas where livestock and wildlife coexist, livestock depredation leads to bitter human–wildlife conflict, often resulting in retaliatory killings of large carnivores, and decline or local extinction of native predators (Woodroffe 2001, Ogada et al. 2003). Further, maintaining high densities of livestock can enhance resource competition with other native prey species (Chaikina and Ruckstuhl 2006). Understanding niche overlap, strength of competition (Bolnick and Preisser 2005), and the long-term response of native herbivores (Dave and Jhala 2011) is critical to management of systems with livestock. Habitat heterogeneity (Oliver et al. 2009, Gorini et al. 2011) and its complexity (i.e., availability of safe refuges and risky areas) can further influence indirect interactions through modifying predator and prey behavior.

CONCLUSION

Abrams and Matsuda (1996) argued that one should expect a mixture of both positive and negative indirect interactions between prey sharing a common predator. Asymmetry in indirect interactions is usually considered in terms of negative effects for one prey species through apparent competition, where one species is at higher risk of extinction than the other (DeCesare et al. 2010). While it is true that introduction of nonnative prey may increase predator densities and thus increase predation on native prey (Smith and Quin 1996, Courchamp et al. 2000, Courchamp and Caut 2006), it is also clear that indirect positive and non-reciprocal effects are not only possible, but may be more common than many anticipate (Chaneton and Bonsall 2000).

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