Predator Mediated Indirect Effects of Livestock on Native Prey

by

Sundararaj Vijayan

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Abstract

Livestock are common in many protected areas and due to their negative effects pose a considerable challenge to protected area managers attempting to conserve native ecosystems. Negative effects include resource competition with native herbivores, habitat modification, and conflicts between pastoralists and livestock-killing carnivores. A literature review on livestock in conservation areas indicates that research has predominantly focused on negative effects which are known to be major threats to the survival of many mammalian prey and predator species. However, the potential role of predator-mediated indirect interactions between native herbivores and livestock via shared predation has been overlooked or ignored in natural areas dominated by human-livestock settlements. To address this shortcoming, I investigated the role of predator-mediated effects on a native herbivore (chital deer, *Axis axis*) in a natural system containing large domestic prey (buffalo, *Bubalus bubalus*, cattle, *Bos indicus*) and their common predator (Asiatic lion, *Panthera leo persica*). I explored whether livestock alter predation risk on chitals by quantifying chital vigilance in two areas representing low and high livestock densities. Chital vigilance was lower in the area where livestock were abundant, suggesting a positive effect of livestock on native prey in lowering predation risk. This positive effect was mediated through a higher predation rate on livestock by lions in the area with dense livestock. Second, using Isodar analysis I found that at lower densities chitals preferentially occupy areas with livestock as a means of managing predation risk while accepting higher than expected resource competition; at higher densities, chitals preferentially occupy areas without livestock, trading off access to food and managing predation risk in larger conspecific groups. My study thus suggests wild prey can manage risk while co-existing with livestock. Indirect positive interactions via livestock represent a potentially valuable tool to aid in the conservation of a threatened native prey species maintained at low population levels for an endangered native predator in the system. Conservation biologists and managers should anticipate that a variety of indirect interactions come into play in systems where livestock coexist in natural predator-prey ecosystems.

Preface:

Publications arising from this thesis

Chapter III: Vijayan, S., McLaren, B.E., Morris, D.W., and Goyal, S.P. Can rare positive interactions become common when large carnivores consume livestock? Ecology: in press.

Chapter IV: Vijayan, S., Morris, D.W., and McLaren, B.E. Prey habitat selection under shared predation: Tradeoffs between risk and competition? Oikos: in press.

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Chapter I

Introduction

1.1 Livestock in Protected Areas

Globally it is now common for agricultural lands to encroach the boundaries of wildlife reserves, but many natural areas around the world (especially in Asia, Africa and South America) actually encompass human settlements with dense livestock populations. The presence of livestock in natural habitats is considered a major issue in the preservation of native flora and fauna (Prins 1992, Prins 2000, Madhusudan 2004, Mishra et al. 2004, Chaikina and Ruckstuhl 2006). Conservation and livestock management efforts are usually aimed at minimizing interspecific competition for food resources (exploitative competition) or contact (interference competition) with sympatric native herbivores. When large carnivores are included in the management domain, conservation efforts turn towards minimizing human-carnivore conflicts and public persecution of predators is often the result (Ogada et al. 2003, Woodroffe et al. 2005, Inskip and Zimmermann, 2009). These management approaches may not be completely effective when indirect interactions between the domestic and native prey (mediated by their shared predator) influence and shape the net native prey-predator dynamics or behavior in the system. This thesis considers this case in detail.

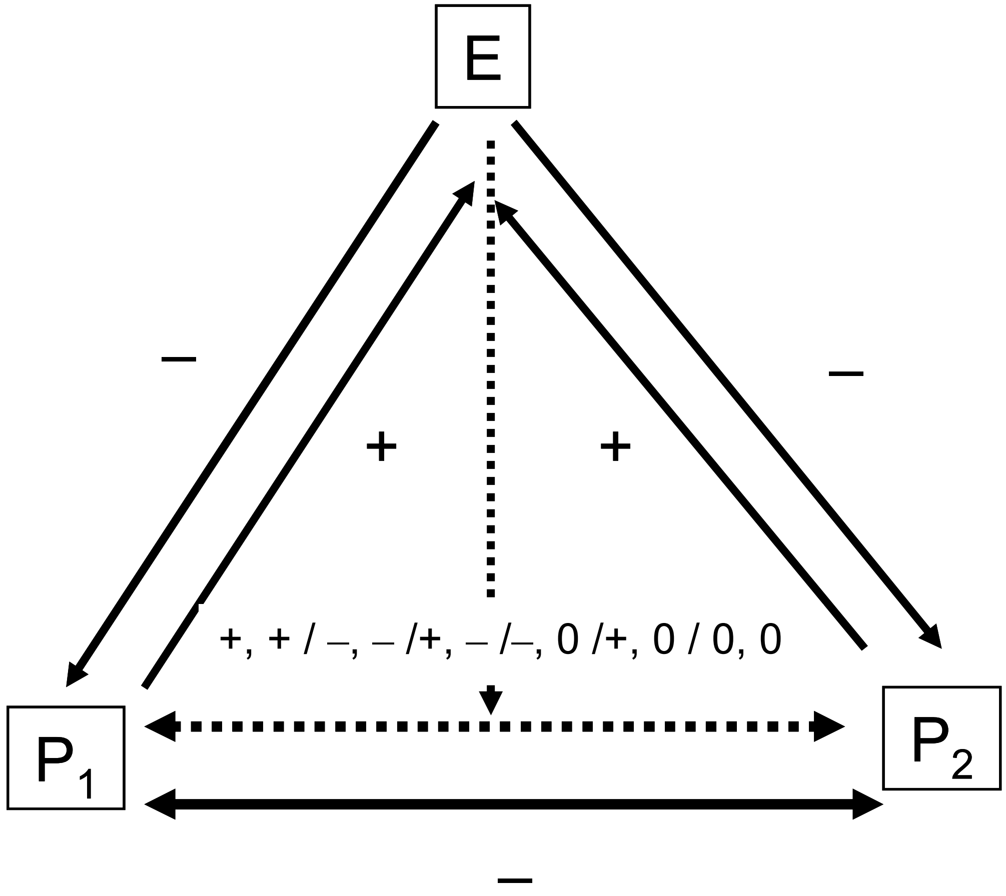
1.2 Shared Predation and Indirect Interactions

Shared predation is a common phenomenon in ecological communities where generalist predators are interlinked with prey through complex interactions (Strauss 1991). Shared predation can cause suites of symmetrical and asymmetrical indirect interactions between two prey types (Fig. 1.1). When two or more prey species coexist, each can depress the other's abundance equally and indirectly by increasing the abundance of a shared natural enemy, often referred to as apparent competition (a −,− interaction; Holt 1977, Holt and Lawton 1993). The interaction can also emerge through a functional response where the per capita rate of prey consumption changes with the density of the prey (Solomon 1949, Holling 1959).

Prey consumption rates are a function of search time (finding the prey), handling time (capture, feeding and digestion), and prey diversity. As the total foraging time is limited, the time handling one prey item is typically not available for searching or attacking another prey. When two prey species are present, each can benefit (a +, + interaction, apparent mutualism) because predation is shared between them (Holt 1977). This is likely to occur when the functional response is saturated because predator foraging-time is fixed, or when the predator’s numerical/aggregating response is limited by outside influences (Holt and Lawton 1994, Holt and Kotler 1987).

Many enemy-mediated interactions between two prey species may also involve strong asymmetrical and non-reciprocal interactions (+, −, or 0, −), which may be much more common than revealed by field research (Chaneton and Bonsall 2000). Differences between two prey types in morphology (body size, nutritional value and vulnerability) and behavior (anti-predator defenses and escape) should lead to asymmetrical interactions via their shared predators. A shared enemy may show increased consumption of susceptible and profitable prey if the second prey is less vulnerable (strong anti-predator defenses) and difficult to kill and consume (Schmidt and Whelan 1998). Such differences between prey species may be prominent in natural systems where domestic prey coexists with native prey species, and where livestock form an important part of a predator's diet. Domestic prey (e.g. large bodied livestock such as cattle and buffalo) often differ considerably from sympatric native prey species in density, body mass, social structure, vulnerability, natural anti-predator defenses, and predator preference. These differences are likely to affect a predator's prey encounter rate, search time, attack/kill rate and total prey consumption.

Figure 1.1: Schematic representation of direct and indirect interactions (Holt 1977, 1984) between two prey species (P_1 and P_2) and their common natural enemy (E). Direct effects (solid lines) between the common enemy and prey represent trophic interactions (effect on prey population dynamics caused by direct mortality). Solid lines between the two prey species represent resource competition. Possible indirect interactions between the two prey species via their shared enemy (+, +/ –, –/ +, –/ –, 0/ +, 0/0, 0) are represented by the dashed line. The sign and magnitude of the indirect interaction depends on whether the two prey species compete or not, and whether the competitive interaction is overwhelmed by predation.



1.3 Shared Predation and Habitat Selection

Habitat choices made by individuals are often influenced by interactions with individuals of other species (Svärdson 1949, Fretwell and Lucas 1969, Rosenzweig 1981, and many others). Predation risk and competition for resources are both important factors influencing population regulation and habitat selection (McNamara and Houston 1987, Sinclair and Arcese 1995) and can interactively structure prey communities (Kotler and Holt 1989). The presence of livestock in natural areas offers a particularly interesting example of a complex of such interactions because livestock can compete for resources with native herbivores and can also influence the risk of predation from shared predators. Predation risk and competition for resources can both influence native prey's habitat selection thus affecting its fitness. Organisms should behave in ways that maximize their fitness (MacArthur and Pianka 1966, Mitchell and Valone 1990) and density-dependent habitat selection is one such behavioral response to competition and hostile interactions (MacArthur 1972, Rosenzweig 1981, 1985, Kotler and Brown 1999, Morris et al. 2000). Thus, co-existence with livestock might require native prey individuals to select habitat by simultaneously managing competition for resources and predation risk.

1.4 Thesis Objectives and Outline:

The central objective of this thesis is to evaluate the role of indirect effects of domestic prey on native prey. I begin by summarizing the vast literature on ecological interactions between large-bodied livestock and native prey and discuss the possible indirect interactions that are often missed or ignored in these studies. I then assess how the presence of a resident livestock population affects predation risk and habitat selection by a sympatric native deer species via their shared predator in Gir National Park and Sanctuary, Gujarat, India (Fig. 1.2).

The thesis consists of three main chapters:

Chapter 2: *Domestic and Native Prey in Protected Areas: Potential for Indirect Interactions*.

Human-livestock settlements form an integral part of the ecosystem in many conservation areas around the world. Research concerning domestic prey in such systems mainly concentrates on resource competition with native herbivores, the negative effects of livestock on vegetation, and human-wildlife conflict in settlements where carnivores consume livestock. My review of the current literature on domestic prey in natural areas demonstrates that indirect ecological interactions between native and domestic prey via their shared predator have been mostly ignored. I present a case study from Gir National Park and Sanctuary illustrating long-term trends in a native prey population which are likely influenced by indirect interactions in the system. I describe how such interactions can be studied and conclude with management recommendations.

Chapter 3. *Can rare positive interactions become common when large carnivores consume livestock?*

I provide the context of, and evidence for, a positive indirect interaction between livestock and native prey in the Gir system. Predation risk on native prey, measured by vigilance behavior, was lower in an area with high livestock density than in one with low livestock density. This positive effect on native prey was mediated through density-dependent predation on livestock. The chapter concludes with a discussion of the possible role of positive interactions in nature conservation.

Chapter 4. *Prey habitat selection under shared predation: Tradeoffs between risk and competition?*

The presence of livestock can influence native herbivores in at least two ways: first it can reduce the forage biomass by resource competition, and second, it can affect predation risk by acting as a preferred alternative prey for their common predator. Using the theory of density-dependent habitat selection (Isodars, Morris 1988), and information on habitat and resource abundance (vegetation structure, available forage biomass), I document that habitat selection by chitals in Gir represents a tradeoff between predation risk and competition for food resources. This study confirms that competition and predation risk structure prey communities through interactions with prey behavior and dynamics.

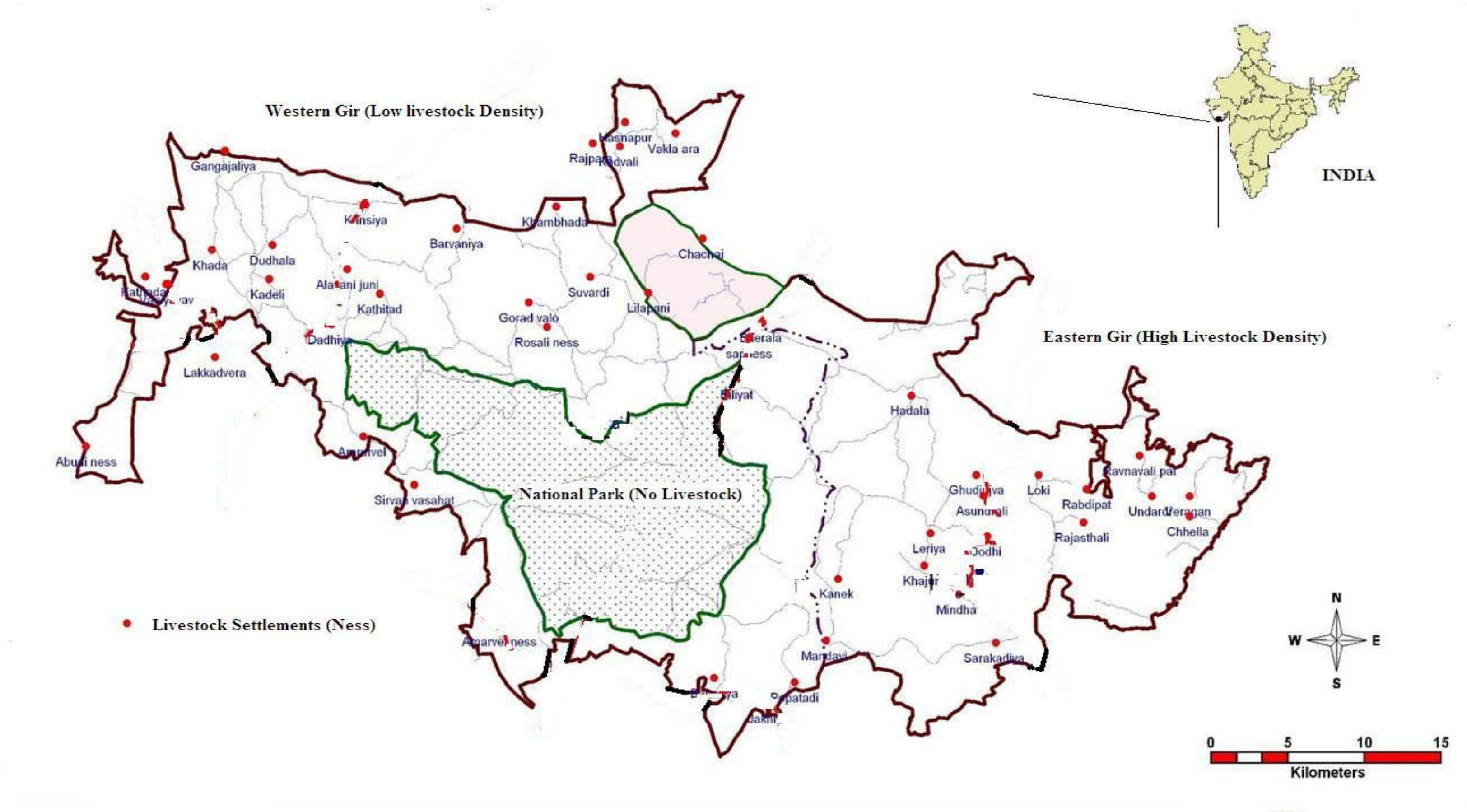
1.5 Study Area Description:

Gir National Park and Sanctuary (commonly referred as Gir protected area, ~1450 km^2, 21° 20′ to 21° 40′ N; 70° 30′ to 71° 15′ E) is the largest tract of dry deciduous forest in western India. It is a semi-arid area with average annual rainfall of 900-1000 mm and a temperature range from lows of 8° C in winter to highs of 45° C in summer (Singh and Kamboj 1996). Vegetation is typically dry deciduous forest (mixed teak and *Acacia*) and open thorny *Acacia-Zizhyphus* woodlands (Champion and Seth 1968, Khan et al. 1995). The region supports 38 species of mammals, 32 species of reptiles, more than 300 species of birds, 450 flowering plant species, and more than 2000 species of insects (Singh and Kamboj 1996).

The study area is divided into two management units, namely a Sanctuary and a National Park (Fig 1.2). The central part is the National Park, which extends over an area of approximately 260 km^2. This area is densely wooded and has a high vegetation biomass. The National Park is surrounded by the much larger Sanctuary region (~1200 km^2), which supports more than 50 settlements and *nesses* (hamlets) of relocated villages and tribal *Maldharis* (pastoralists) with their resident livestock population (~25,000). The Gir Sanctuary and National Park is also surrounded by 97 additional villages within a 5 km radius. Associated with these villages are approximately 100,000 more livestock which occasionally enter the Sanctuary to graze (Singh and Gibson 2011).

Figure 1.2. A map of Gir National Park and Sanctuary, Gujarat State, India.

(Source: GIS Cell, Wildlife Division, Gir National Park and Sanctuary)



1.6 *Maldharis* Tribesmen, Settlement Villages and Livestock in Gir Forest:

The "*Maldhari*" tribes are pastoralists settled in the Gir forest for several decades (Berwick 1971, 1976, Casimir 2001). They form the most important human component of the Gir ecosystem and are often viewed as direct competitors of lions for the Gir territory. The *Maldharis* livestock compete for food resources and space with native herbivores (Berwick 1976). Excessive grazing pressure on Gir's vegetation caused a major decline of biodiversity during the 1960s (Berwick 1971, Joslin 1973). In order to deal with this crisis, managers launched the "Gir Lion Sanctuary Project" in 1972: several *Maldhari* families were resettled and the core area was declared a National Park. During this period, the livestock population in Gir fell from 25,000 to 12,500 animals. The Gir Lion Sanctuary Project was abandoned in 1982. There are presently 50 tribal settlements and 14 fringe forest settlements with approximately 25,000 livestock within Gir.

Livestock (*Bubalus bubalis* and *Bos indicus*) are managed by herders and graze the forested areas of the Sanctuary throughout the year. The eastern part of Gir has higher densities of settlements and livestock and correspondingly experiences a higher grazing pressure than the western part (Khan 1994, 1995, Khan et al. 1996).

1.7 Chital Deer (*Axis axis*) and other prey herbivores

The chital is a medium sized deer (~45 to 65 kg) and is one of the most widely distributed cervids on the Indian subcontinent (Schaller 1967, Fuchs 1977, Mishra 1982). Chitals occur in a wide variety of forest types ranging from dry deciduous to tropical evergreen forests. Chitals have been categorized as generalist or intermediate/mixed feeders consuming forbs, grass and woody plants (Rodgers 1988, Hofmann, 1985). Chitals are common in Gir with an estimated population of 50,000 to 60,000 animals, and comprise up to 80-90 % of the total native herbivore density (Singh and Gibson 2011, Dave and Jhala 2011) and approximately 80% of wild ungulate biomass.

The other prey species in the system include: Sambar deer (*Rusa unicolor*), nilgai (blue bull, *Boselaphus tragocamelus*), chausingha (four horned antelope, *Tetracerus quadricornis*), chinkara (*Gazella gazella*), wild pig (*Sus scrofa*), porcupine (*Hystrix indica*), common langur (*Semnopithecus entellus*), and peafowl (*Pavo cristatus*; Singh and Kamboj 1996). Sambar deer (150 kg) and nilgai antelope (180 kg) represent optimal prey sizes for lions (Hayward and Kerley 2005) but occur at very low densities and are absent in some parts of Gir (~2 km^{-2} and <1 km^{-2} for sambar and nilgai respectively). All prey herbivores in Gir are resident throughout the year with very low seasonal variation (Khan et al. 1996)

1.8 Asiatic Lion (*Panthera leo persica*) and other carnivores

The critically endangered Asiatic lion's (130-230 kg) historic distribution ranged across much of south west Asia (O'Brien et al. 1987, Nowell and Jackson 1996). Gir National park and Sanctuary and its surrounding region now supports the last free-ranging population of this unique subspecies (O'Brien et al. 1987) [411 animals including 105 lions found in satellite populations; Singh and Gibson 2011]. The lion population in Gir show an consistent increase with increase in prey population since 1970's, however, the lion population the park area has been growing at a declining rate from late 1990 to 2010 (~250 to 300 animals), suggesting a carrying capacity for the system. Further evidence of carrying capacity or saturation in Gir system arises from the fact that lions started dispersing out of the protected area since the mid 1980s forming several satellite populations (Meena 2010). The lion population in these areas have increased more than 25 fold (4 animals in 1984 to 120 in 2010; Meena 2010, Meena 2011, Singh and Gibson 2011). The territory sizes of adult male and female lions in Gir region ranges from approximately 70 – 150 km^{-2} and 60 – 80 km^{-2} respectively (Joslin 1973, Chellam 1993, Meena 2008).

The major prey item for lions in the system are chital deer, livestock and sambar deer (normally restricted to western and National park areas). Livestock biomass today (4,600 kg km^{-2}) greatly exceeds that of wild herbivores (2,931 kg km^{-2}) in the Gir protected area (Singh and Gibson 2011). Though recent studies suggest that the lion's diet in Gir is shifting toward increased consumption of wild herbivores in relation to their abundance, livestock still constitutes approximately 33 to 40 % of total prey biomass consumed by lions overall (Meena 2008, Meena et al. 2011). Lion dependence on livestock is especially high (>50 % of lion diet, Chellam 1993, Meena *unpublished*) in the eastern part of the Sanctuary, where livestock occur at a higher density (20 to 34 km^{-2}) than in the western part (6 to 11 km^{-2}, Meena et al. 2011, Meena 2008). Local lion densities and pride sizes are known to be higher in areas with livestock (Jhala et al. 2006, Meena 2008) and lion populations in the periphery of the Gir protected area and outside its boundaries depend largely on livestock (>70 % of diet; Meena 2011). On average, lions kill approximately 2,300 buffalos and cattle annually in and around the Gir forests. Predation on sambar deer, which occurs at very low density in the Gir system, is restricted to western and central parts of Gir forest (generally absent in most of the eastern Gir), and constitute about 6 % of the lion's diet in terms of biomass (Meena et al. 2011).

The other dominant predator in the system is the leopard (*Panthera pardus*), typically concentrated in densely vegetated core areas of the (livestock-free) National Park and pasto-agricultural landscapes dominating the peripheral areas of Gir.

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Chapter II

Domestic and Native Prey in Protected Areas: Potential for Indirect Interactions

Abstract

In many parts of the world protected areas harbor permanent livestock populations that are often freely ranging with native herbivores. Livestock are typically considered an undesirable ecosystem component and pose a challenge to park managers and biologists who wish to maintain the species interactions and diversity of the natural system. Studies dealing with livestock in protected areas have focused on interactions such as competition for food resources with native herbivores, habitat degradation, and human-carnivore conflicts caused by livestock depredation. The negative effects of such interactions are a major threat to the survival of many mammalian prey and predator species. The role of indirect interactions between native and domestic prey via their common enemy has received comparatively little attention and poses a significant knowledge gap in understanding the net impacts of domestic prey on native herbivores. I describe a case study of Gir protected area in which I illustrate the possible role of shared predation and resulting indirect interactions in understanding the general patterns of chital distribution, which could not be previously explained by resource competition alone. A broader understanding of both direct and indirect interactions involving livestock, native herbivores and their predators will aid in better management of conservation areas dominated by human-livestock settlements.

Domestic and Native Prey in Protected Areas: Potential for Indirect Interactions

2.1 Introduction

Conservation areas around the world contain human settlements with livestock populations which depend upon forest resources for their survival (Das 2008). Persistence of these settlements is sometimes tolerated even though it is often controversial and highly debated among wildlife biologists, park managers and policy makers. For example, more than half of India's livestock population of approximately 270 million animals grazes in the nation's wildlife parks that comprise less than 5% of India's total geographical area (Mishra et al. 2004, Kothari et al. 1989, Madhusudan and Karanth 2002, Das 2008). Two thirds of Indian wildlife parks harbor permanent livestock populations in the form of tribal or forest settlements (Mishra 1997; Madhusudan and Raman 2003). One fourth of all parks sustain high densities of cattle (~ 50 per km^2, Mehra and Mathur 2003), with some parks maintaining as high as 1500 animals per km^2 (Kothari et al 1989). Livestock greatly outnumbers native ungulates in many natural areas in India (Mishra 1997).

Livestock grazing has a variety of negative effects on native flora and fauna (Prins 1992, Van Der Wal 2003, Bagchi and Ritchie 2010). Livestock can compete for food resources with native ungulates and can detrimentally modify vegetation structure, diversity and nutritional quality of forage (Mishra and Rawat 1998; Prins 2000; Bagchi et al. 2003, 2004; Madhusudan 2004, Mishra et al. 2004; Bagchi and Mishra 2006). When large carnivores are part of a native ecosystem, and especially where they are protected by government efforts, attention shifts to human-carnivore conflict resulting from livestock depredation (Ogada et al. 2003, Woodroffe et al. 2005, Inskip and

Zimmermann, 2009). The International Union for Conservation of Nature and Natural Resources (IUCN) Red List of threatened species lists livestock as one of the important threats to mammalian diversity throughout the protected areas of the world (IUCN 2011). Although these important livestock-induced interactions on native herbivores and carnivores have serious long-term implications for conservation, the possibility of indirect interactions via shared predation has been largely ignored in mainstream research.

The interactions between livestock and native prey involving their common predator are often complex and might have comparable or greater impacts than competition for shared resources. Livestock can, for example, alter both the behavior and abundance of native herbivores via changes in the behavior and abundance of their common predator(s). This co-existence of livestock with wild prey, in theory, can produce either positive or negative effects via “apparent mutualism” or “apparent competition” (Holt 1977, Holt and Kotler 1987, Abrams and Matsuda 1996) as well as other interactions (Chaneton and Bonsall 2000, DeCesare et al. 2009) [please see Table 3.1 for suite of possible indirect interactions, Chapter 3, Vijayan et al. *in press*]

The objective of this review is to describe broadly the interactions created when livestock occupy conservation areas. I begin by documenting the extent of protected areas and the number of mammalian species threatened by the presence of ungulate domestic prey in different regions of the world. I then summarize the focus of published scientific work involving livestock in conservation areas. I describe a case study to illustrate the importance of missed or ignored indirect interactions between livestock and native prey, stressing the importance of indirect interactions with wild herbivores. I finish with a commentary on the importance of missed knowledge on such systems.

2.2 Literature Search

I searched the United Nations list of protected areas to document the global extent of protected areas harboring livestock (Category IV, IUCN-UNEP [WCMC], Chape et al. 2003). Category IV areas are managed mainly for habitat and species conservation through human intervention. I then searched the IUCN Red List to determine the number of mammalian species threatened by livestock and human settlements in terrestrial habitats (I list my IUCN search criteria in Appendix I). I categorized the threats to native mammalian species as follows: (1) competition for resources, (2) habitat modification, (3) human-wildlife conflicts, and (4) disease transmission. I also searched the peer-reviewed scientific literature assessing livestock in conservation (online database search engine Thomas Reuters Web of Knowledge (version 1). I used the following subject heading terms and key words: "domestic prey*wildlife," "livestock*wildlife," "livestock*interactions," "livestock*native prey" and "domestic prey*native prey" (full details are provided in Appendix II). I omitted studies that referred to livestock or domestic prey only incidentally. I categorized the remaining studies by their research focus and findings as follows: (1) competition for resources, (2) habitat modification, (3) human-wildlife conflicts, (4) other disturbances, (5) habitat selection, and (6) indirect effects.

2.3 Domestic Prey in Protected Areas

Globally, 16.1 % of protected areas fall into Category IV where human settlements and livestock form an integral part of the natural system (Table 2.1). Higher occurrences in this category are found in Southern Asia, West and Central Africa, and Central America (respectively, 50.5 %, 34.1 %, and 26.6 % of protected areas in these regions).

Table 2.1: Number and extent of Category IV Protected Areas (data from Chape et al. 2003). Numbers in parentheses are percentages. Category IV deals with particular habitat/species management as priority which may require regular and active interventions (Dudley 2008).

Region	Number of Protected Areas	Number of Category IV Protected Areas	Total Protected Area (km^2)	Area Under Category IV (km^2)
World	**102,102**	**27,641 (27)**	**18,763,403**	**3,022,515 (16.1)**
Antarctica	126	23 (18.0)	70,294	461 (0.7)
Australia and New Zealand	8,724	1,230 (14.1)	1,187,320	77,640 (6.5)
Caribbean	953	203 (21.3)	69,470	9,672 (13.9)
Central America	145,322	12,643 (8.7)	762	203 (26.6)
Europe	43,018	16,797 (39.0)	750,225	90,023 (12)
Eastern and Southern Africa	4,852	463 (9.5)	1,967,242	2,61,122 (13.3)
North America	13,369	1,323 (9.9)	4,552,905	737,151 (16.2)

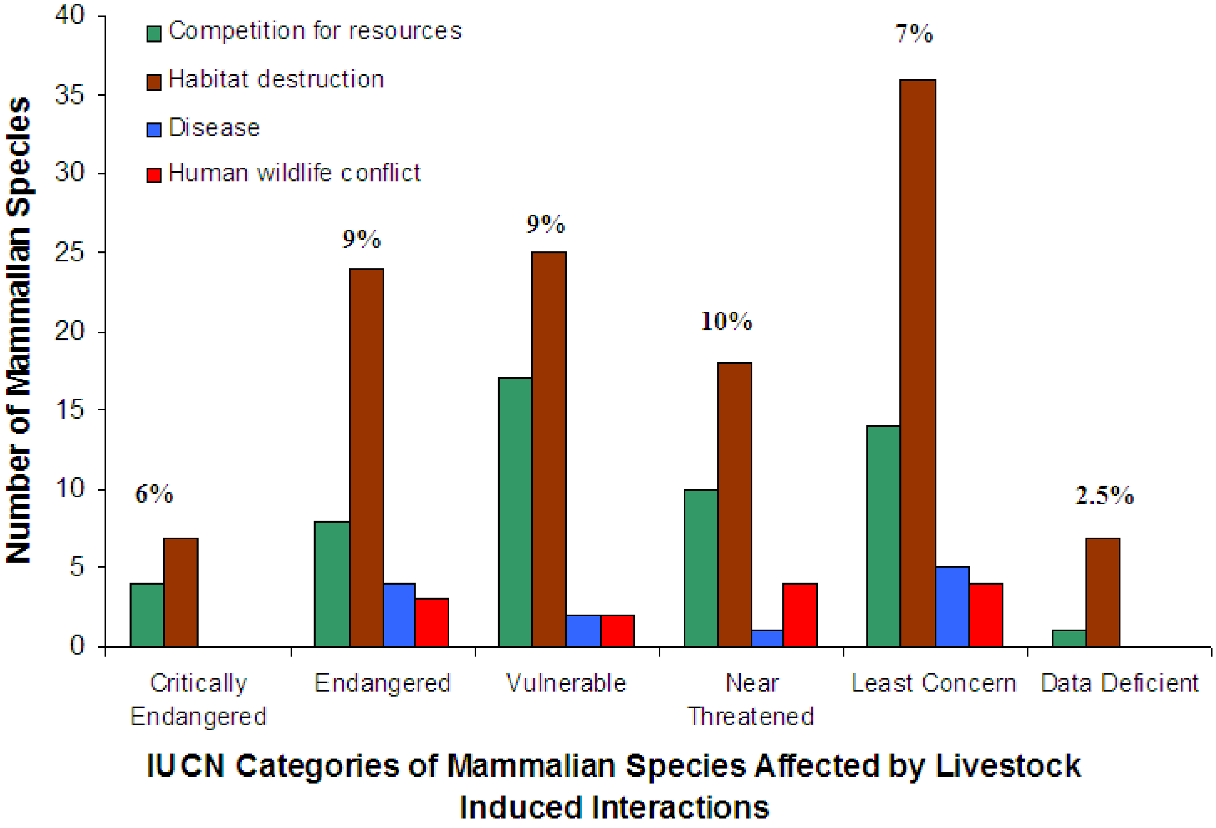
North Africa	1,133	277 (24.4)	1,272,840	77,079 (6.1)
West and Central Africa	2,605	146 (5.6)	1,125,926	384,079 (34.1)
N.Eurasia	17,724	5,267 (29.6)	1,816,735	874,110 (4.81)
Pacific	321	68 (21.2)	20,489	1,104 (5.4)
South America	2,749	382 (13.8)	4,137,180	102,258 (2.6)
South Asia	1,477	658 (44.5)	308,826	155,831 (50.5)
Southeast Asia	2,656	198 (7.5)	759,788	118,882 (15.6)
East Asia	1,031,813	120,469 (11.6)	2,098	325 (15.5)

2.4 Mammalian Species Affected by Livestock

The IUCN Red List documents 580 mammal species threatened by ungulate livestock. Excluding species for which the negative effect is largely human-induced destruction of habitat (by clearing and burning to maintain pastures) reduces the number to 196 species. This list likely under-represents threats to mammals by livestock because the status of more than 15% of Earth's 5488 mammalian species is not properly documented (IUCN 2011). Overall, livestock pose a threat to approximately 6 % of Critically Endangered, 9 % of Endangered, 9 % of Vulnerable and 10 % of Near Threatened mammalian species listed in Red List threat categories (Fig 2.1).

The highest frequency of threats from livestock occurs by habitat destruction (60 %) and competition for food resources (28 %, Fig 2.1). Overall, ninety species of large ungulates (> 5 kg) are threatened by livestock populations through competition for food and habitat degradation. Out of this list, sixty ungulate species fall under IUCN's major threatened categories (critically endangered, vulnerable, endangered and near threatened) which requires considerable management intervention. The presence of livestock also threatens carnivore populations in conservation areas, albeit indirectly. Twenty-one large (> 5 kg) carnivore species are threatened by human–carnivore conflicts associated with livestock predation. Habitat degradation by and for the livestock sector is particularly relevant for conservation because habitat destruction is considered to be a main cause for mammalian decline in many developing countries (IUCN 2007). Overall, IUCN lists habitat loss as the most important threat to mammals in all natural areas, affecting ~ 2,000 species or 37 % of mammalian species.

Figure 2.1: IUCN Red List threat categories of mammalian species as affected by livestock induced interactions (IUCN, 2011, accessed 20 July 2011). Percentage values at the top of the bars represent the proportion of mammals affected in the ways listed relative to the totals for each threat category.



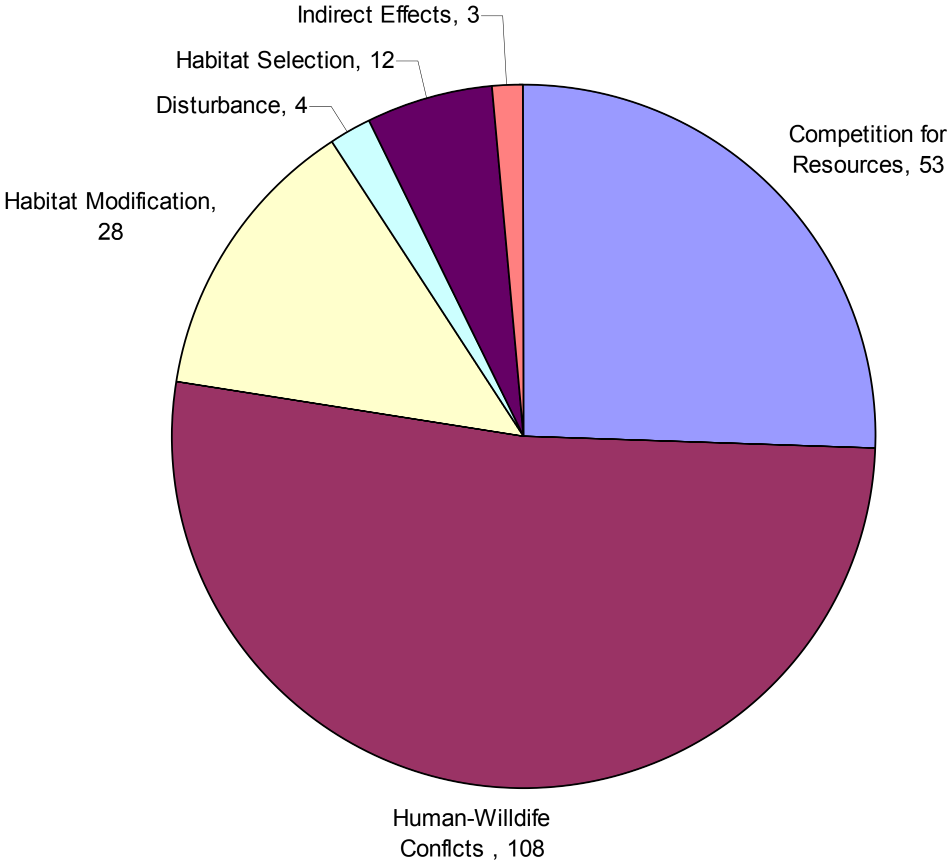
2.5 Livestock as Focus of Research in Ecological Studies: Survey of published information

The presence of livestock in natural systems has received considerable attention in ecological research around the world, including at least 208 published articles since 1970 (Appendix II). Description of human-wildlife conflicts (~52 % of all studies), competition for resources (~25 %), and habitat destruction (~13 %) were more prevalent than all other interactions in research studies involving livestock (Fig. 2.2). Other effects of livestock included changes in native prey and predator habitat use (i.e. avoidance behavior, 5 %), and disturbance caused by human presence (~2 %). However, only eight studies among the 208 reviewed concluded that resource competition with livestock caused declines in native prey densities. Some studies document historical positive trends in native herbivore populations after reduced livestock density or complete removal (Khan et al. 1996, Mishra et al. 2004, Madhusudan 2004, Dave and Jhala 2011). Emphasis on the negative impacts of wildlife is particularly clear where long-term population declines (1977 to 2009) of many native African ungulates have been documented in the Masai Mara nature reserve (Ogutu et al. 2011). The declines were linked to human induced land-use changes, including increased settlement and livestock grazing.

Although published studies show overwhelmingly negative effects of livestock on wildlife, there were some contrasting results. A study in Uganda showed that pastoral ranches supported higher densities of several wild ungulates (Impala, *Aepyceros melampus*, zebra, *Equus quagga*, bushbuck, *Tragelaphus scriptus,* and waterbuck *Kobus ellipsiprymnus*) compared to protected areas because livestock grazing improved grass production (Rannestad et al. 2006). Positive effects of wild herbivores on cattle have also been observed. During the wet season, cattle benefited from nutritious higher-quality forage facilitated by wild herbivores (medium size ungulates >20 kg, mainly from *Equus burchelli* and *E. grevyi*) grazing in a savanna ecosystem in Kenya (Odadi et al. 2011).

When livestock coexist with native carnivores, studies focus primarily on aspects of human-carnivore conflicts emerging from carnivore attacks on livestock and humans (Patterson et al. 1994, Saberwal et al. 1994, Karanth and Madhusudan 2002, Treves and Karanth 2003, Ogada et al. 2003, Woodroffe et al. 2005). Resolution of the conflict is crucial because many critically endangered species, especially large carnivores, are targets for persecution and retaliatory killings (Ogada et al. 2003).

Figure 2.2: Research focus (number of publications, total n=208) on interactions involving livestock/domestic prey in conservations areas.



2.6 Gir Protected Areas: A Case Study on the Role of Livestock in Native Prey and Predator Conservation

The dry deciduous forests of Gir National Park and Sanctuary (~ 1200 km^2), western India, form a critical system to protect because they contain a source population of rare and endangered Asiatic lions (*Panthera leo persica*). Approximately 25,000 livestock in 54 permanent tribal and forest settlements graze year-round in forested areas of the Sanctuary that they share with native ungulate herbivores, primarily chital deer (*Axis axis*). In the middle of the twentieth century, when the region faced regular drought periods, many nomadic pastoralists from far-off places brought their cattle to Gir for grazing during the dry season. Very high levels of grazing occurred during the 1960s when tribal "*Maldhari*" settlements reached a maximum of 137 settlements (with approximately25,000 animals) and when livestock belonging to the surrounding peripheral villages, and to nomadic pastoralists, also grazed in Gir (~120,000 additional animals, Joslin 1972, Berwick 1974).

The protected area managers gradually relocated many tribal settlements and banned grazing by the peripheral livestock populations in the early 1970s. The core area was declared a National Park (~250 km^2) and livestock grazing was eliminated there by 1974. The livestock population in the Sanctuary was reduced to approximately 12,000 animals by the late 1970s (Fig. 2.3). The population of wild herbivores increased substantially from approximately 6,500 animals in 1974 (Berwick 1974) to ~65,000 animals in 2010 (Singh and Gibson 2011). The chital deer (*Axis axis*), a dominant prey species in the system, increased from 4000 individuals to approximately 50,000 during the same period (Fig. 2.3). In general, increases in chital densities are attributed to recovery of vegetation and forage biomass with release from resource competition previously created by livestock (Khan et al. 1996, Singh and Gibson 2011, Dave and Jhala 2011). Long-term population trends for livestock in the Sanctuary also illustrate a recovery to the prevalent levels in the 1970s (Fig. 2.3). Presumably tracking the prey population (Singh and Gibson 2011), the lion population increased from 180 in 1974 to 267 in 1990 (an increase of 48 % @ 3 % per year); then increased at a lower rate (14.6 % @ 0.7 % per year) from 1990 to 2010 (Fig. 2.3). Thus, since the 1990s the population of lions may be closer to carrying capacity, limited by territoriality and other social interactions. This is further supported by the fact that lions were first observed dispersing outside the park once they reached population above 200 animals in mid 1980s. The lion population outside the protected area has increased from 4 animals in the 1980s to 105 animals in 2010 (a 25 fold increase) compared to 30 % increase in the park for the same period.

Chital density in eastern and western Gir do not vary with livestock density, which ranged in 2010 from ~ 6 to 11 per km^2 in western Gir (~ 750 km^2) to ~ 20 to 34 per km^2 in eastern Gir (~ 450 km^2) (Vijayan et al. in press, chapter 3, Dave and Jhala 2011). Overall similar chital densities in different livestock stocking areas (Fig.2.4) is then counter-intuitive to the suggestion that grazing livestock were limiting chitals in the Gir system. Jhala (2011) also conclude that livestock reduction in the protected area does not alone explain chital population growth over the last four decades. We suspect the role of shared predation by lions in the Gir system may provide insights into chital population.

Figure 2.3: Chital, livestock and lion population sizes in the Gir protected area from 1970 to 2010. Data sources: Joslin (1973), Berwick (1974, 1976), Khan and Vohra (1992), Khan (1994, 1995), Chellam (1993), Pathak (2002), Singh and Gibson (2011).

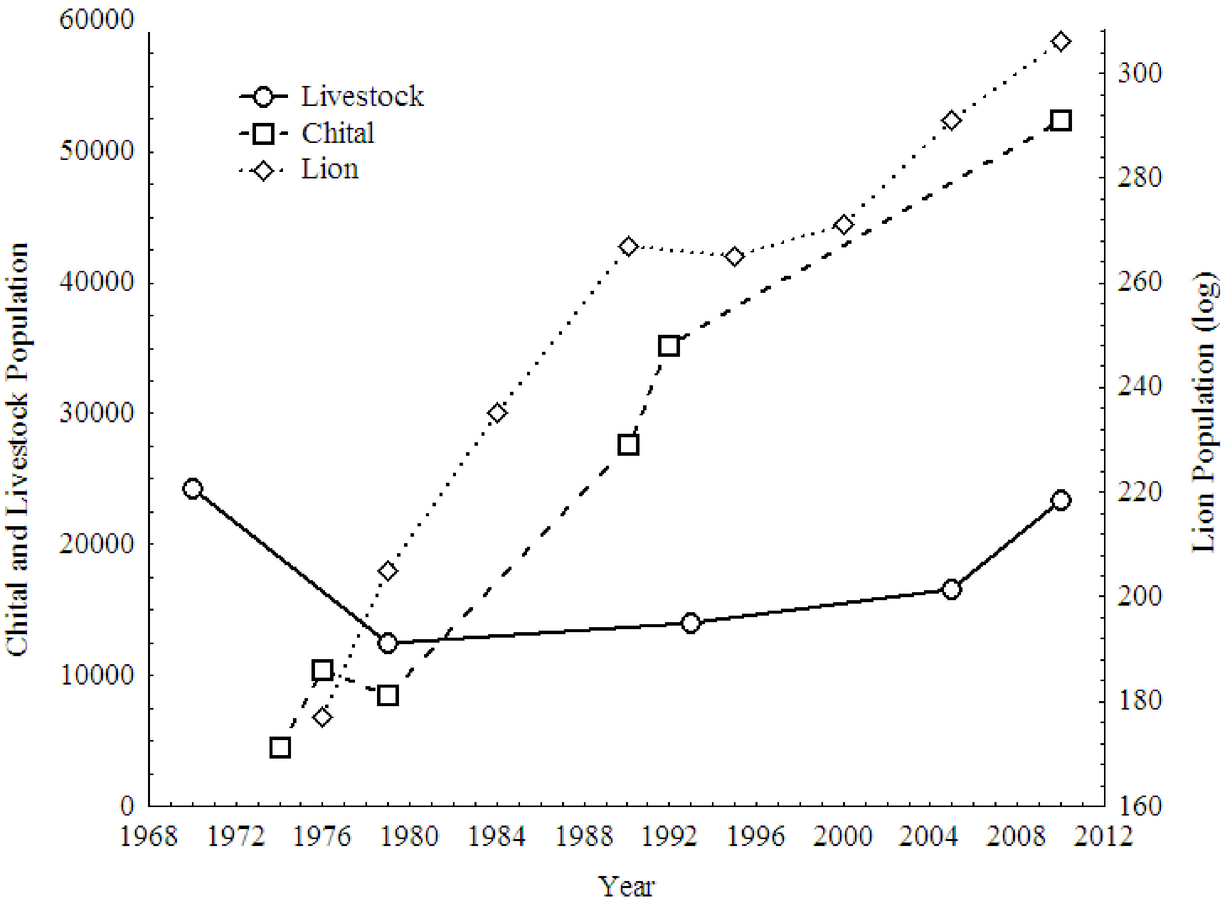
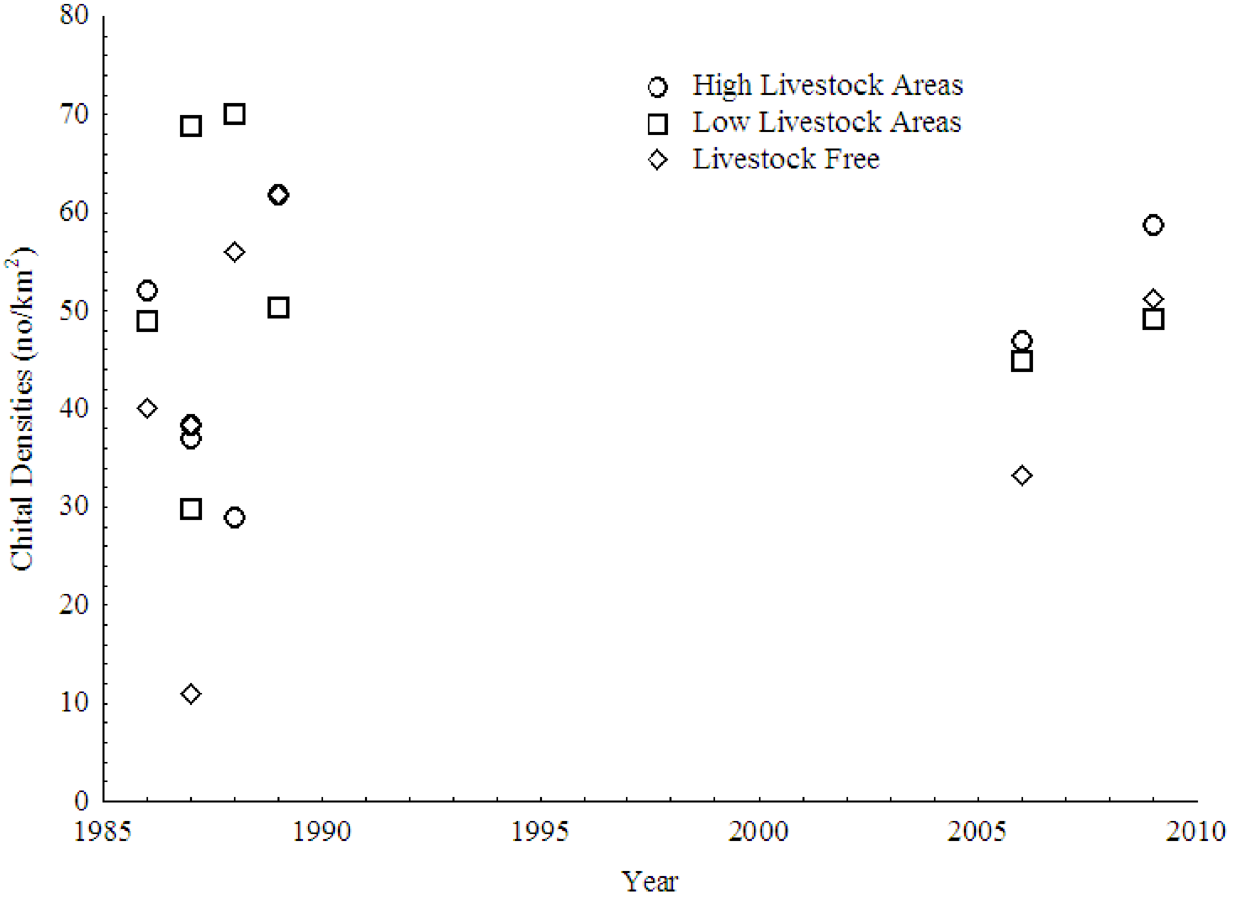


Figure 2.4: Chital population densities (per km^2) in high, low and livestock free areas (1987 to 2010) for the Gir National Park and Sanctuary. Data sources: Khan (1997), Chellam (1993), Vijayan (2009, unpublished), Dave and Jhala (2011).



2.7 Can Shared Predation Play A Role In The Gir System?

Prey size is an important attribute of large carnivore's diet preference. Lions preferentially consume large-bodied prey disproportionate to their abundance (De Piennar 1969, Hayward and Kerley 2005); in this regard it is not surprising that livestock continue to form an important diet component in Gir. Chitals, even though abundant in Gir, may not represent an optimal prey size for lions (Vijayan et al. 2012 in press, chapter 3). Another large wild prey comparable to livestock in body size, sambar deer (*Rusa unicolor,* 300 kg), occurs at very low densities in Gir (~2 per km^2) and is absent in many areas (especially in eastern Gir). Yet it constitutes a measurable percentage of the lion's diet (6% in terms of biomass) in low livestock and National park areas.

Lion preference and foraging strategy seems to be dynamic with respect to livestock density in Gir. Though the lions' diet in Gir has shifted toward wild herbivores during recent years, the overall livestock kill in and around the protected area has also increased from approximately 1,700 annually during the period from 1986 to 2000 to 2,300 animals in the period from 2000 to 2010 (Singh and Gibson, 2011). Within the protected area, livestock still form an important component of the lion diet overall (~40 % in prey biomass) and lions kill a higher proportion of livestock where ever livestock are more abundant (Chellam 1993, Meena 2008, Jhala et al. 2009, Singh and Gibson 2011). Past studies on lion dietary patterns confirm our assumption that livestock constitutes a relatively higher proportion of lion's diet compared to the common and abundant chital deer in areas wherever the livestock are available in higher densities in the park and the surroundings areas (Joslin, 1973, Chellam 1993, Jhala et al. 2009, Meena 2008, Table 2.2). Chellam (1993) found the proportion of livestock in lion's diet to be positively correlated with livestock abundance in different areas of park suggesting preference for livestock as optimal prey in the system.

Regarding the variability in livestock density throughout the protected area, and the argument that livestock is a preferred prey item, livestock become a candidate for illustrating top-down positive indirect effects on wild prey in the Gir system. The chitals are likely to experience relatively low predation risk in areas where lions encounter high livestock densities. Based on the total lion population in high livestock areas (~ 72 lions and 192 kills annually), the per capita lion consumption of livestock (0.007 livestock/day) is higher than in the low livestock areas (~90 lions and 92 kills, 0.002 livestock/day) [Lion population calculated from Jhala et al. 2006, Meena 2008; 16 per 100 km^2 and 12 per 100 km^2 in the high and low livestock density areas, respectively, Livestock kills obtained from park office, Junagadh]. This difference in per capita attack rate is likely to widen if pride size is controlled in both areas, as lions form bigger pride sizes in high livestock areas (Jhala et al. 2006, Meena 2008). The weak numerical response typically associated with large carnivores may protect resident prey such as chitals (Khan et al.1996) from intense predation rates (*sensu* Fryxell and Lundberg 1998, Fryxell and Lundberg 1994). The presence of a sympatric large bodied livestock prey is likely to benefit the smaller chital deer via an indirect positive effect [a possible (–, +) or (0, +) interaction] by reducing the per capita attack rates of lions on chitals. The presence of vulnerable livestock in high numbers is likely to dilute the attack rate on chitals.

Table 2.2: Lion dietary pattern based on chital and livestock abundance in and around Gir protected area.

Year	Area	Livestock abundance	Chital abundance	Proportion of livestock in lion diet	Proportion of Chital in lion diet	Study reference
1973	Park	Overall High, ~25,000 animals 82 % of all prey available	Low 4000 animals	High, ~ 83 %	~15%	Joslin (1973)†
1987	Park	Overall High ~15000 animals + influx of migrant livestock (several thousand)	High 47000 animals (48 km^2)	High ~88 %	Low 15 %	Chellam (1993) †
1986/ 1987	Park	High livestock areas (20 km^2)	High (52 km^2)	~70%	~39 %	Chellam (1993) †
		Low livestock areas (8 km^2)	High (49 km^2)	~48%	~42 %	

		Absent in National Park (0 km^2)	High (40 km^2)	NA	NA	
1989	Park	High livestock areas (20 km^2)	High (52 km^2)	~46%	~38 %	Chellam (1993) †
		Low livestock areas (8 km^2)	High (49 km^2)	~32%	~59 %	
		Absent in National Park (0 km^2)	High (40 km^2)	~13%	~50 %	
1987	Outside	High (~100,000 in villages)	Low	~76 %	~14%	Chellam (1993) †
2002-2006	Park	Overall high (24000)	High (50 km^2)	~20% (36 %* in terms of biomass, (50 % * in terms of biomass, Jhala et al	~32% (32 % in terms of biomass)	Meena et al (2011) †* Meena 2008† Jhala et al 2009*

				2009 > 50 % in high livestock areas (Meena, *unpublished*)		
2002-2006	Outside	High	Low	76 %	NA	Meena et al 2011[@]

† dietary findings based on % occurrences in scats,* based on biomass contribution to diet,[@] based on kill data

2.8 Management Implication and Future Direction

Conservation policies have focused on maintenance of natural diversity in protected areas. There is general consensus among managers, researchers, and policy makers to remove or eliminate livestock from protected areas (Osofsky et al. 2005, Das 2008). My review of published information on interactions between wildlife and livestock confirms the general bias toward prominent negative effects related to resource competition, habitat modification or human-wildlife conflicts. My review indicates a dearth of studies assessing predator-mediated indirect interactions between native ungulate and domestic prey in human-dominated landscapes.

It is difficult to generalize how livestock interact with native ungulates because pastoral systems vary across different parts of the world. Spatio-temporal variation between native and domestic prey, their relative densities and accessibility, the level at which they are guarded by herders, and their response to a shared predator can all influence the impacts of indirect interactions. For example, modern ranch systems where the livestock are often maintained separately from wildlife in a fenced environment differ from traditional uncontrolled grazing in protected areas containing permanent human settlements where native prey are sympatric to livestock. These difference in prey association as well as differences in availability of livestock prey item for the shared predator is likely to result in asymmetrical outcomes via indirect interactions. Further, the detection of impacts of indirect interactions on a focal prey species can be complicated by a mixture of direct and indirect effects such as predation and competition for shared resources. Behavioral disruptions due to shared predation and resulting indirect interactions may play a strong role in structuring long term dynamics between the two prey types. Indirect interactions via a common enemy influences predation risk or kill rates for one or more prey species. Predators apart from being a direct agent of mortality also have non-lethal effects on their prey species (Preisser et al. 2005). Negative interactions can cause declines in native prey densities (*sensu* DeCesare et al. 2010, Garrott et al. 2009), but where positive interactions occur, managers can apply them toward conservation of rare and endangered native species. Careful behavioral observations coupled with definitive experiments may be necessary to guide insights on interactions mediated by shared resource competition and their common predators (*sensu* Morris et al. 2009, Ale and Brown 2009, Caro 2007, Berger-Tal et al. 2011). Mammals often respond to natural and anthropogenic disturbances by producing distinct behavioral responses (i.e. foraging trade offs, vigilance levels, group formation, association with other sympatric species etc) before the onset of detectable disruptions of critical demographic processes, so monitoring behavioral responses may provide early warning for conservation managers (Clemmons and Buchholz 1997) in livestock systems. Indirect interactions influenced by shared predators should be evaluated in conjunction with other interactions between native and domestic prey species in livestock-wildlife systems. A broader perspective will help biologists and managers to better understand the dynamics and processes that structure ecological communities in human-livestock dominated conservation areas. Further, by studying the indirect interaction in natural systems, one may be able to infer mechanisms of habitat selection or ecological separation between species that may not be fully explained by other interactions (i.e. competition, predation).

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Chapter III

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

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 towards increased consumption of an abundant and higher-quality alternative prey. Such phenomenon between two prey species is under-appreciated 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 (chitals, *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.

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

3.1 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, Treves and Karanth 2003, Bagchi et al. 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, Abrams et al. 1998, Bonsall and Hassell 1997, 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-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.

3.2 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 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), 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, +) 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 3.1). 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 Kerely 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).

TABLE 3.1. A simplistic summary of potential indirect interactions (following Holt and Lawton 1994, Holt and Kotler 1987, 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. The sign of interactions, (0, –, +) represents no effect, negative effect and positive effect respectively for one prey type.

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 towards 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	Presence of domestic prey does not affect the native	Increase in functional and numerical response towards domestic prey, but no changes	Vulnerability, large or equal body size and high densities of domestic prey	No change in attack rates on native prey, native prey

non reciprocal interactions)	prey	towards 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	Both prey positively affect each other	Predators despotic or no numeric response, forage for fixed period of time, no	Vulnerability, large body size, and high density of domestic prey maintained by	Lower attack rate on native prey, native prey population will

interaction)	preference among prey types	animal husbandry activities	increase
Apparent mutualism	and leave patch independent of prey densities		

3.3 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 generalist predator's consumption of a focal prey (F_1) in the presence of an alternative prey species ($F_1 = a_1 N_1 / [1 + a_1 N_1 h_1 + a_2 N_2 h_2]$), 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 Kerely 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 (Hunter and Skinner 1998, Elgar 1989, 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 (~ 1,150 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 generalist 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 to 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 8000 (~11 per km^2) and 11,000 (~ 24 per km^2) buffalo and cattle respectively (source: Park office, Junagadh, Gujarat State), 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.

3.4 Methods

Measuring Native and Domestic Prey Behavior

We selected only open *Acacia-Zizhyphus* habitats (patch area ≥ 0.5 km^2) for chital observations during the dry season (January to June 2009). We observed randomized focal groups of chitals within five to six kilometers of settlements, a distance that approximates livestock grazing distances. We divided the habitats surrounding settlements into several numbered 1.25 x 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 X optical zoom) 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 (5:30 to 8:30) 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 to 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, for low and high livestock density areas, respectively) 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 towards 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). 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 (Berwick 1974, Hirst 1969). We monitored transects during early morning (6:00 to 8:00) and again in the evening (16:30 to 18:30). Observers sat in an open vehicle (traveling at 15-20 kph) 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 program v.5.0, Thomas et al. 2010).

We obtained lion density estimates from recent surveys in Gir (Jhala et al. 2006, Meena 2008; 16 per 100 km^2 and 12 per 100 km^2 in the high and low livestock density areas, respectively). The lion population has been more-or-less constant since the early 1980s (~250 adult animals; Singh, 1997, Pati and Vijayan 2002, Gujarat State Forest Department report of 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; Singh and Gibson 2011, Meena 2010). 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 multi-variate 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, OK, USA).

3.5 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 3.2). Chital density was similar in both areas ($P = 0.55$, Table 3.2). Group size also did not differ ($P = 0.67$; low livestock density area: 5.8 ± 0.8; high livestock density area: 6.2 ± 0.6).

Table 3.2. Comparisons of western and eastern Gir sanctuary, western India.

Area	**Habitat Variables (*Acacia-Zizhyphus* forest) Mean (S.E.):**	**Average Livestock Density (per km^2)**	**Lion Density† (per 100 km^2)**	**Chital Deer Density (per km^2) Mean (S.E.)**	**Mean Annual Livestock Killed**
Eastern Gir (High Livestock Density)	Number of trees(100m^2): 5.4(0.3) Number of shrubs(100m^2):0.1(0.07) Biomass(g/m^2): 50.9(8.3)	24	16	58.7(9.9)	192*
Western Gir (Low Livestock Density)	Number of trees (100m^2): 4.3(0.8) Number of shrubs (100m^2): 0.4(0.2) Biomass(g/m^2):61.2(18.7)	11	12	49.1(10.7)	94*

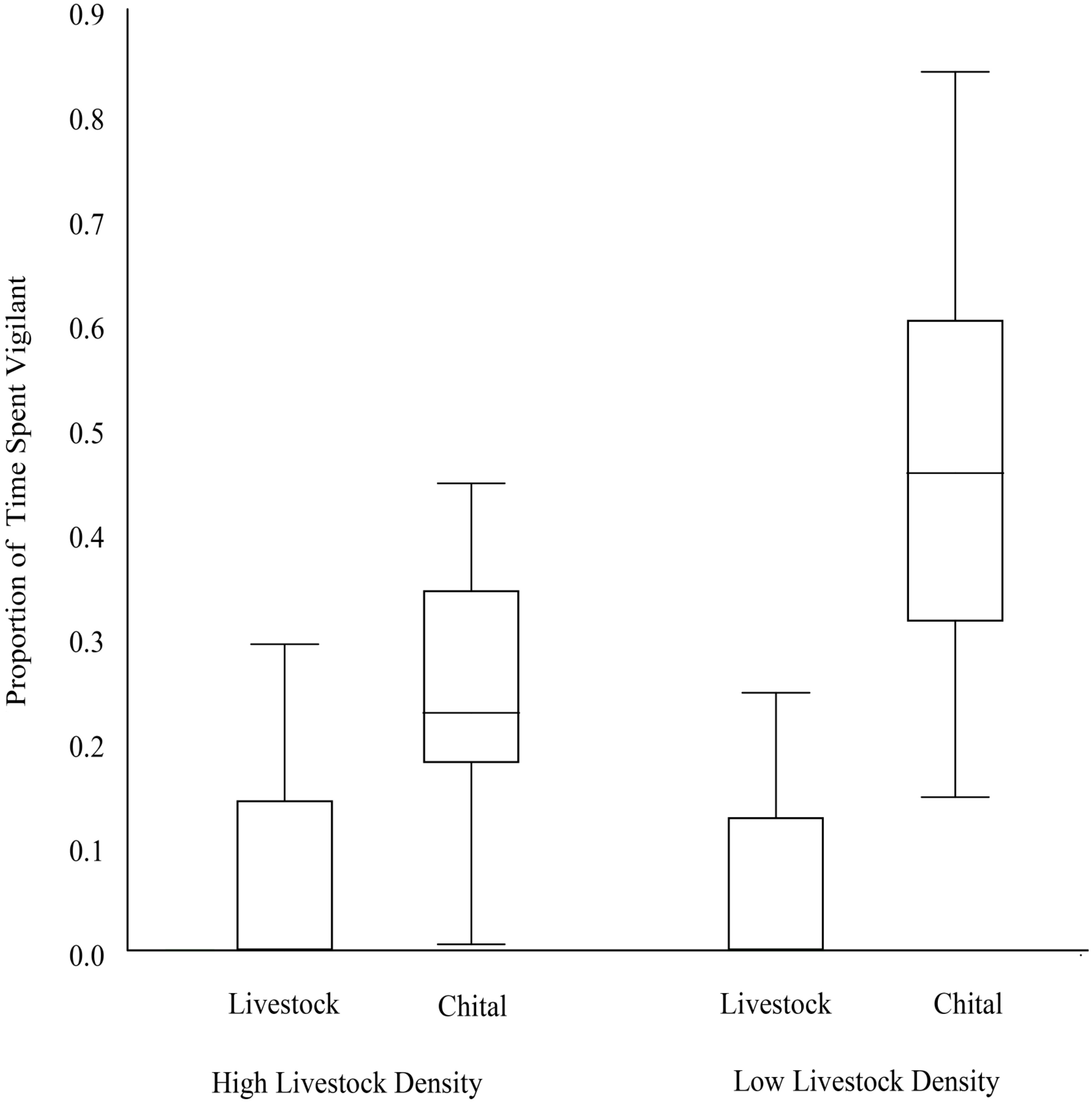
“*”*denotes a significant difference (Chi-square test),* “†” *source: Jhala et al. 2006, Meena unpublished data.*

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. 3.1). 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 no difference in vigilance of livestock between high and low livestock density areas ($P = 0.41$, Fig. 3.1). The majority of livestock failed to display any vigilance behavior (13 of 23 focal animals).

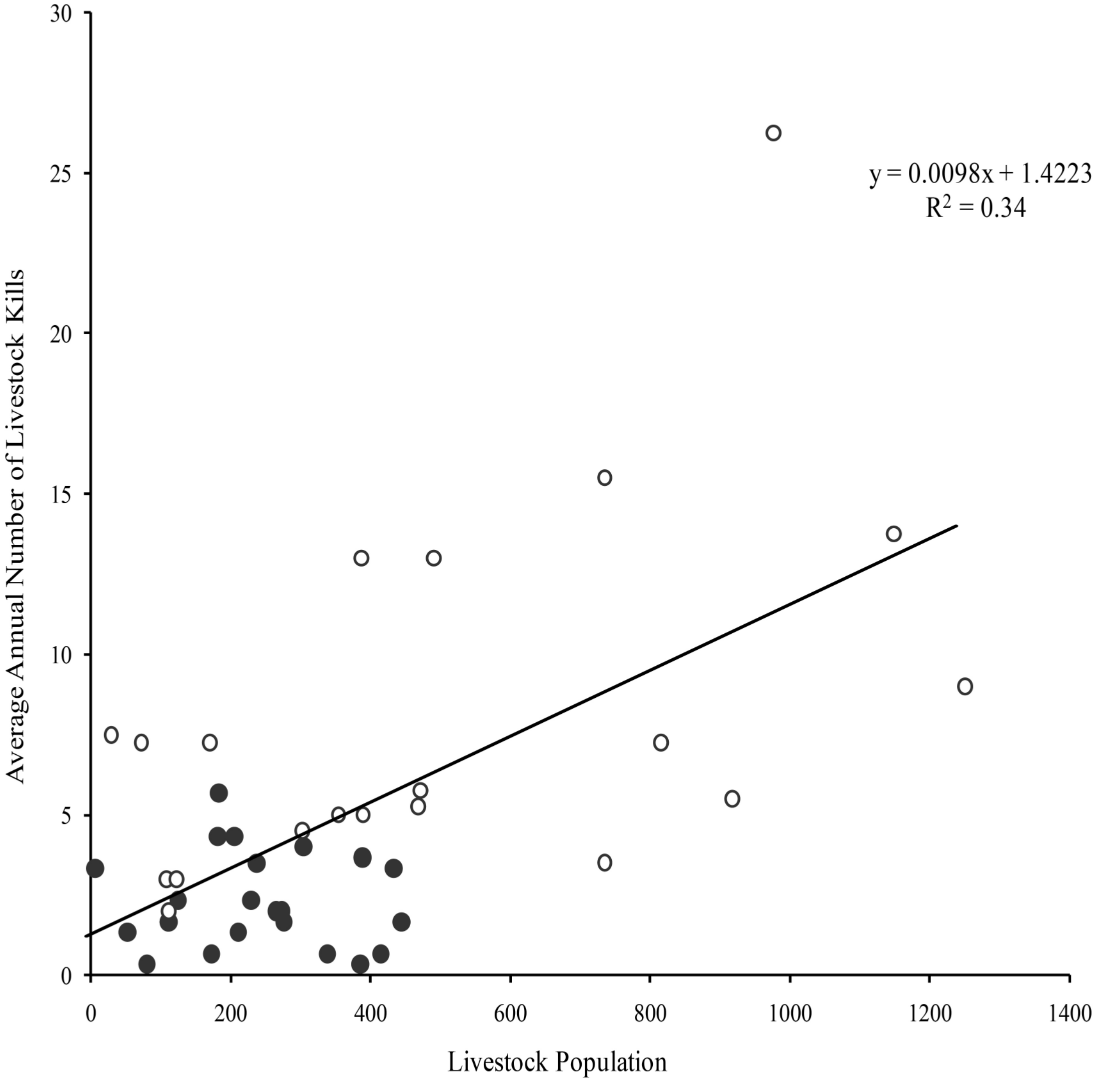
FIGURE. 3.1. Proportion of time (arcsine square-root transformed) spent vigilant by chitals and livestock with high and low livestock density in Gir sanctuary, western India. The figure illustrates the median (lines), 25 % to 75% quartiles (boxes), and ranges (whiskers).



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. 3.2). 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 (X^2 = 5.17, df = 1, P = 0.02, Table 3.2). 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).

FIGURE. 3.2 Average annual number of livestock killed by lions by settlement and size of livestock population in Gir Sanctuary, western India (2006-2009). Filled circles represent kills by settlement in western Gir; open circles represent kills by settlement in eastern Gir.



3.6 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, Preisser et al. 2005, Luttbeg and Kerby 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 deer 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., 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 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.

3.7 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 3.1). 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 1970's) in the system (Joslin, 1973, Berwick 1974). The present annual livestock depredation inside the park area is about 300 animals (out of approximately 2,200 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 towards large predators by the *Maldhari* tribesman and local villagers

(Srivastav 1997, Varma 2009). Regular compensation for livestock kills by park management has also helped to reduce antagonistic attitudes among the settlers towards 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 long term response of native herbivore (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.

3.8 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 non-native 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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CHAPTER IV

Prey habitat selection under shared predation: Tradeoffs between risk and competition?

Abstract

An individual's choice of habitat should optimize amongst conflicting demands in a way that maximizes its fitness. Habitat selection by one species will often be influenced by presence and abundance of competitors that interact directly and indirectly with each other (such as through shared predators). The optimal habitat choice will thus depend on competition for resources by other species that can also modify predation risk. It may be possible to disentangle these two effects with careful analysis of density-dependent habitat selection by a focal prey species. We tested this conjecture by calculating habitat isodars (graphs of density assuming ideal habitat selection) of chital deer living in two adjoining dry-forest habitats in Gir National Park and Sanctuary, western India. The habitats differed only in presence (Sanctuary) and absence (National Park) of domestic prey (cattle and buffalo). Both species are preyed on by Asiatic lions. The habitat isodar revealed at low densities, that chital live in small groups and prefer habitat co-occupied by livestock that reduce food resources, but also reduce predation risk. At higher densities, chital form larger groups and switch their preference toward risky habitat without livestock. The switch in chital habitat use is consistent with theories predicting that prey species should trade off safety in favor of food as population density increases.

Prey habitat selection under shared predation: Tradeoffs between risk and competition?

4.1 Introduction

Species differ in their habitat specialization and preference in a way that is often influenced by interactions with other species (Svärdsson 1949, Fretwell and Lucas 1969, Rosenzweig 1985, Morris 1988). Habitat selection reduces intra- and inter-specific competition and other hostile interactions (MacArthur 1972, Rosenzweig, 1981, 1985, Kotler and Brown 1999, Morris et al. 2000) that frequently interact to influence the structure of ecological communities (Kotler and Holt 1989). A sympatric competing prey species, for example, can reduce resource abundance and attract predators to a focal species' habitat. If the competing species is more profitable for predators than is the focal species, then predation risk is likely to increase for both species through the predator's numerical (Holt 1977) and functional responses (Holt and Kotler 1987). The ecological outcome from this form of shared predation is especially important in systems with fierce predators where non-lethal risk has major effects on prey distribution and abundance (Lima 1998, Preisser et al. 2005).

The presence of livestock in natural habitats is a particularly interesting example of the consequences of shared predation because livestock often compete with native herbivores for food (Chaikina and Ruckstuhl 2006) and can also increase predation risk if they attract or support higher predator densities (apparent competition, Holt 1977). But it is also possible, even likely, that preferred prey species can reduce predation risk on less preferred prey (e.g., positive indirect effects, Abrams and Matsuda, 1996). Less preferred prey might then choose to live in areas supporting the highest density of their competitor.

In order to test this idea, we studied habitat selection by an abundant native herbivore competing with large-bodied domestic herbivores that share a common large predator. Chital deer (*Axis axis,* 45 kg) occupy adjoining mixed-teak (*Tectona grandis* – *Acacia*) habitat in Gir National Park and Sanctuary, western India. The two areas differ only in presence (Sanctuary) and absence (National Park) of domesticated cattle and buffalo (>300kg). Chital are preyed on by Asiatic lions (*Panthera leo persica*) that also consume substantial numbers of livestock (~33 to 40 % of total biomass consumed, Meena 2008, Meena et al. 2011). The lions kill more livestock where they encounter them in higher densities (Meena 2008, Vijayan et al., in press). Livestock are excluded from the adjacent National Park areas where chital are the lion's dominant prey (Meena et al. 2011).

Continuous grazing by livestock (density ~ 11 km^2) reduces the standing crop of food resources for chital (density ~45 − 50 km^2) in the Sanctuary relative to the National Park that has higher vegetation biomass and plant density (Khan et al. 1995, Dave and Jhala 2011). Thus, we use Gir as a model system in which we evaluate the concurrent effects of competition and shared predation on habitat selection. We used isodar theory (Morris 1987, 1988) to understand chital deer habitat selection faced with the choice of habitats differing in food resources as well as predation risk. Isodars provide the evolutionary solution to habitat choice and thereby link animal behavior to the pattern of abundance at the landscape scale (Morris 1988).

4.2 An isodar model for two prey sharing a common predator

The process of habitat selection often requires individuals to choose and occupy non-random sets of available habitats that differ in growth potential and mortality risks (Morris 2003). The Sanctuary and National Park habitats at Gir differ quantitatively (food biomass) and qualitatively (different suites of prey species). Both differences can be assessed by isodars (regressions of density between pairs of habitats assuming ideal habitat selectors, Morris 1987, 1988).

We base our isodar on a model developed by Morris (2005) for a single prey and predator system. We generalize that model by extending Lotka-Volterra equations to the two prey species such that the per capita growth rates of chital in the Sanctuary and National Park are given by

$$\frac{1}{N_S}\frac{dN_S}{dt} = r_S\left(\frac{K_S - N_S - \alpha L}{K_S}\right) - Pa_S$$

(1)
and

$$\frac{1}{N_N}\frac{dN_N}{dt} = r_N\left(\frac{K_N - N_N}{K_N}\right) - Pa_N$$

(2)

respectively where N_S and N_N refer to chital abundance in the Sanctuary and National Park, L is the (constant) abundance of livestock in the Sanctuary, r is intrinsic rate of increase for chital subscripted for each habitat, K is chital carrying capacity in the two habitats, α is the competition coefficient measuring the resource-depressing effect of livestock on chital, P is the (constant) number of predators and a is the per capita linear attack rate of lions on chital. Our assumption about constant livestock density appears valid because livestock population size is restricted by the owners' management decisions. Our assumption about constant predator density also appears valid for Gir where the lion population is limited by territoriality and dispersal away from Gir (Singh 1997, Venkataraman 2010)

Solving for N_S by setting equations (1) and (2) equal to one another,

$$N_S = \left\{ \frac{K_S}{r_S} \left[(r_S - r_N) + P(a_N - a_S) \right] - K_S \alpha L \right\} + \frac{K_S}{K_N} \frac{r_N}{r_S} (N_N) . \tag{3}$$

Equation (3) represents the chital isodar, the set of densities such that the expected fitness of a chital is the same in both the National Park and Sanctuary. This model can yield a positive intercept only if 1, the maximum per capita growth rate in the Sanctuary exceeds that in the National Park $(r_S > r_N)$; and/or 2, the predator attack rate is greater in the National Park than in the Sanctuary $(a_N > a_S)$; and 3, if these effects are greater than the reduction in density caused by competition with livestock $(K_S \alpha L)$. The isodar slope, however, depends only on the ratios of *K* and *r* respectively.

For chital in Gir, we anticipate a surplus of resources at low density such that both habitats yield similar maximum growth rates. Thus, a significant positive intercept should occur only if predator attack rates are higher in the National Park than in the Sanctuary. If our assumption that maximum growth rates are similar holds, then the slope of the isodar will be determined primarily by the ratio of carrying capacities. The slope will thereby be less than unity only if the carrying capacity for chital deer is greater in the National Park than in the Sanctuary (equation 3).

We used a three-step process to test the model in the field. First, we estimated chital densities along transects bisecting the Sanctuary and National Park to create data for the chital isodar. Second, we measured chital group sizes as an indicator of predation risk in both areas (*sensu* Lima and Dill, 1990, Brown et al. 1999). Additionally, we also used chital foraging vigilance in areas with low versus high densities of livestock to verify that predation risk varies with the presence and absence of livestock (Vijayan et al., in press). Third, we quantified forage biomass and habitat structure (fruits, seeds, and herbaceous and woody cover) to estimate relative carrying capacities and habitat-mediated predation risk in these two habitats.

4.3 Methods

Study area

The dry deciduous forests of Gir National Park and Sanctuary, western India have an approximate area of 1500 km^2 (21° 20′ to 21° 40′ N & 70° 30′ to 71° 15′ E). The chital (~45 kg) is the most widely distributed and abundant cervid in Gir, with an estimated population size of 50,000 to 60,000 animals (density ~ 45 per km^2). The peripheral Sanctuary is approximately five times the size of the National Park (~1250 km^2 and 260 km^2 respectively). The Sanctuary contains human settlements and livestock (buffalo and cattle, ~ 18,000 animals), which are excluded from the National Park. The main predators in the system are Asiatic lions (*Panthera leo persica*) and leopards (*Panthera pardus*). We conducted our study in the western part of Gir forest which encompasses both Sanctuary and National Park in adjacent habitats.

Chital census

We estimated chital numbers along 12 replicates of four-kilometre line transects (Burnham et al. 1980, Khan et al. 1995, 1997). One half (2 km) of each perpendicular transect traversed the presence (Sanctuary) and absence of livestock (National Park). There are no fences between the two adjacent habitats (the boundary is marked only by stone pillars) which allows free movement of wildlife between them. We located transects such that it would be unlikely for any animals to use more than one (minimum distance between adjacent transects = 2.5 to 3 km). SV and two field assistants walked the paired transect early in the morning (between 05.30 to 06.30 hrs), and again during evening (between 16.00 to 17.00 hrs), when chital are active and easily visible. Distance travelled was measured by a calibrated pedometer and hand-held global positioning system (Garmin GPS 72). All chital deer encounters (number of chital and group size) within approximately 50 m on both sides of the transect were recorded for both areas. We replicated the census during Gir's two dry seasons (February and May).

Habitat characteristics

Though we selected similar mixed-teak forest for the isodar transects, we estimated cover and food abundance in each habitat in order to verify our assumption that the National Park area is quantitatively superior to the Sanctuary. We used a GIS map of Gir to divide the Sanctuary and National Park area into blocks (1.25 x 1.25 km) along the transect lines. These blocks were numbered and randomly selected for habitat evaluation. In the selected blocks, we randomly located (by blind twist of a compass dial) four 10 × 10 m plots separated by 50 m. We quantified tree (>2 m tall) and shrub (50 –200 cm tall) density by counting the number of each in every plot. We evaluated differences in food resources influencing available biomass and potential carrying capacity by estimating edible ground biomass based on chital food habits (Schaller 1967) in four randomly selected 1 × 1 m plots. We clipped herbaceous biomass in the plots, sorted it for edible contents (grass, browse, acacia pods, and *Zizhyphus* berries) and weighed it using a calibrated electronic scale. We measured mean standing grass height in each plot as an additional estimate of habitat cover.

Data analysis

We used MANOVA to evaluate differences in habitat based on our measurements of tree and shrub densities, food biomass, and grass height. We then constructed the chital isodar from the mean number of chital sighted in the two habitats along each transect in both dry seasons. We could not evaluate each season separately because annual chital home ranges are small (~ 2 to 3 km^2, Mishra 1982, Mishra and Wemmer 1987); thus the same animals may have been present in both census periods. We estimated the chital isodar with geometric mean regression (Krebs 1999) and calculated the 95% confidence intervals about the slope and intercept (package "lmodel2" in R Software, R Development Core Team 2009). We completed our analysis by testing whether there were significant differences in chital group size, an indicator of predation risk, between the two habitats by one-way analysis of variance. Where appropriate, we report mean values and their standard errors. Analyses were performed with Statistica v 7.0 (Statsoft, OK, USA).

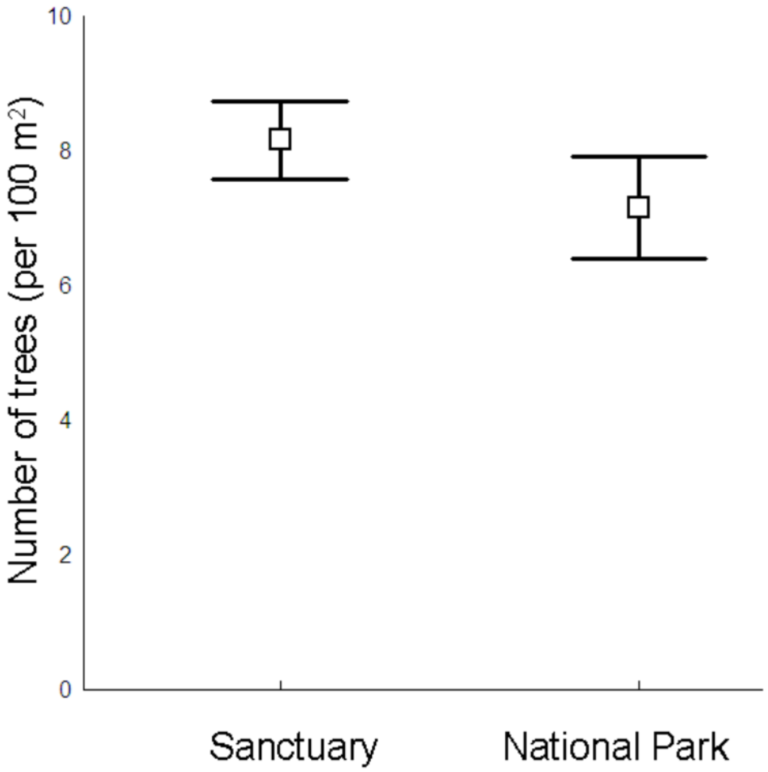
4.4 Results

Food biomass and grass height were greater in the National Park than in the Sanctuary

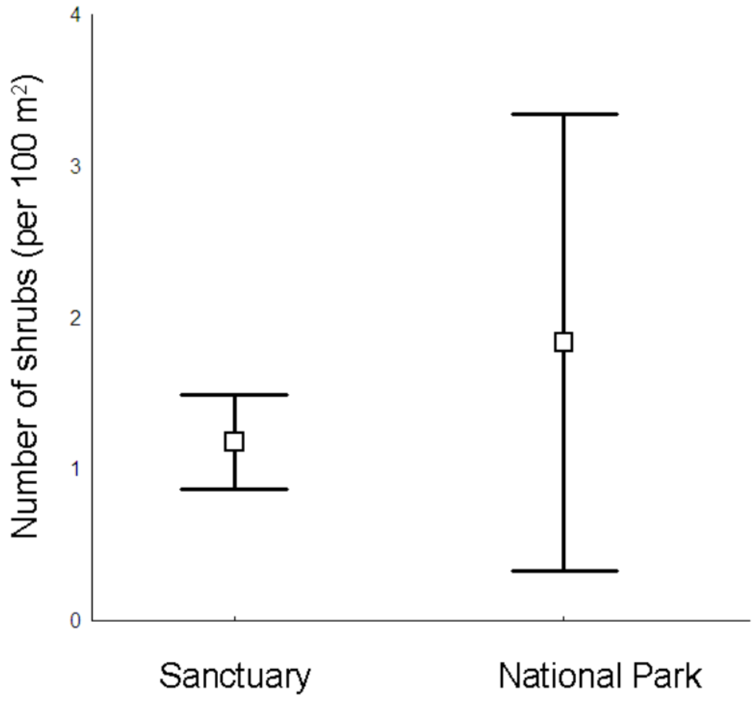
The National Park possessed significantly more biomass, and taller grass cover, than did the Sanctuary grazed by livestock (one-way MANOVA, $F_{4,\,46} = 88.5$, $p < 0.001$ for the overall model; $F_{1,\,49} = 16.7$, $p < 0.001$ for biomass; g/m^2(mean ± S.E) in the Sanctuary =89.9 ± 9.3; in the National Park =162.9 ± 16.9; $F_{1, 49} = 313.5$, $p < 0.001$, for grass height; cm(mean ± S.E) in the Sanctuary =15.2 ± 0.8; in the National Park = 60.2 ± 2.8; Fig. 4.1(c) and 4.1(d)). There were no differences in tree ($p = 0.29$, Fig. 4.1(a)) and shrub densities ($p = 0.60$, Fig. 4.1 (b)) between the two areas.

Figure 4.1 (a-d) Comparisons of vegetation structure in Gir's Sanctuary and National Park. a, Tree density ($p = 0.29$), b, Shrub density ($p = 0.60$), c, Grass height ($p < 0.001$), and d, Edible biomass ($p < 0.001$). Error bars represent mean ± 1 S.E.

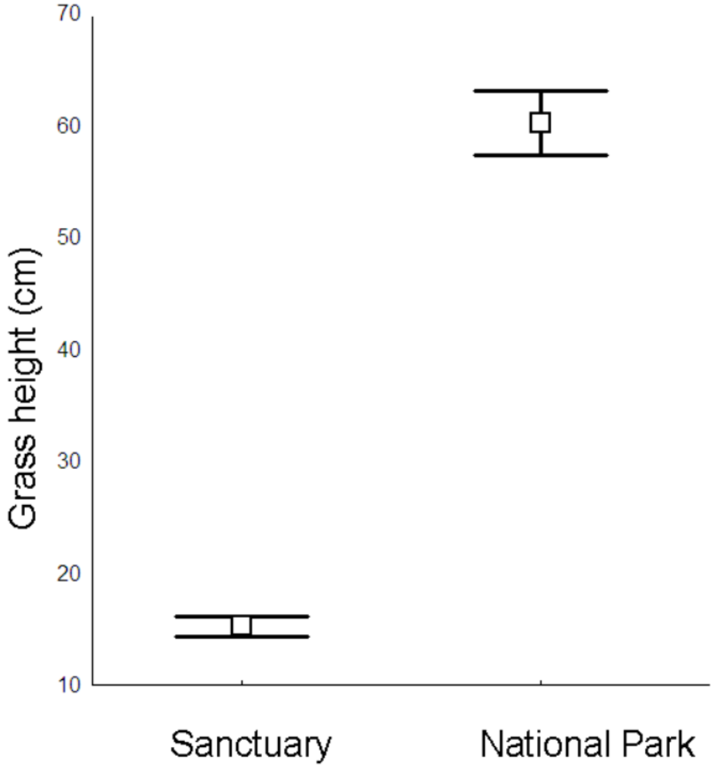
4.1 (a)



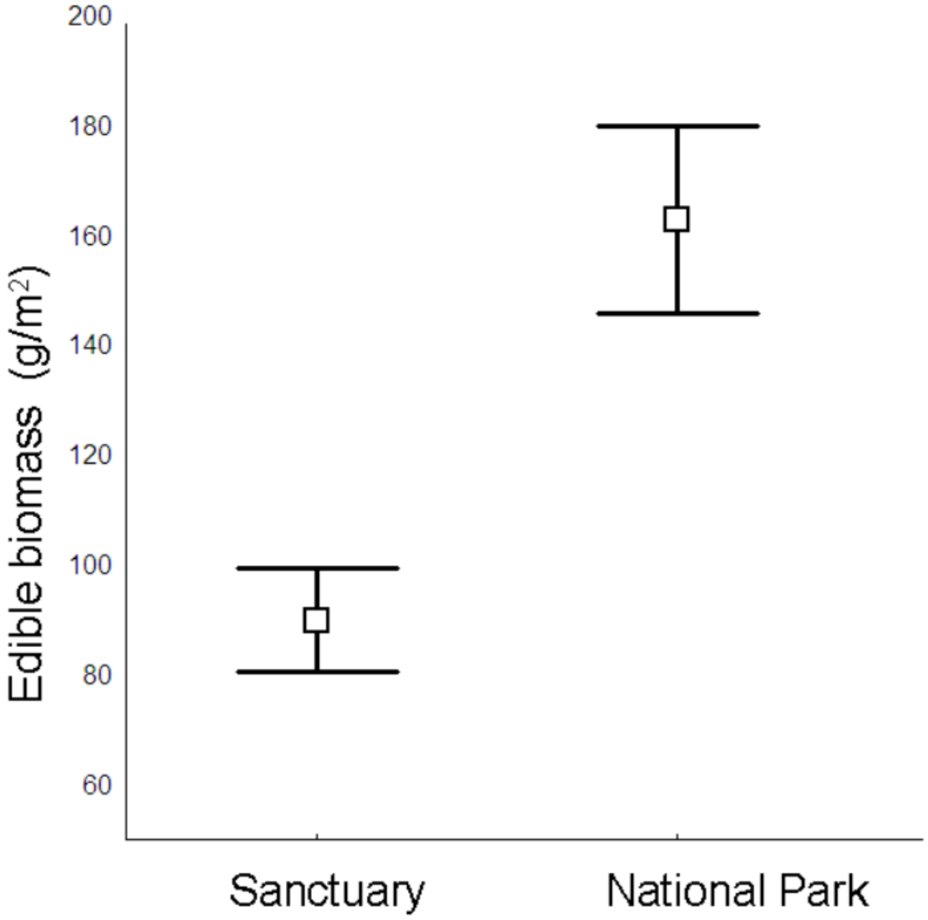
4.1(b)



4.1(c)



4.1(d)



Edible biomass (g/m²)
200
180
160
140
120
100
80
60
Sanctuary
National Park

Occupation of the Sanctuary versus the National Park depended on population density

Chital density in the Sanctuary depended on the density in the National Park (density in Sanctuary = 9.64 + 0.41 density in National Park, $F_{1,10} = 15.38$, $R^2 = 0.61$, $p < 0.001$, Fig. 4.2). Chital density in the Sanctuary exceeded that in the National Park along transects with few deer (isodar intercept greater than zero; 9.64, CI $_{0.95}$ = 4.6 – 12.9). The preference for the Sanctuary declined along transects with many deer (isodar slope less than unity; 0.41, CI $_{0.95}$ = 0.26 – 0.62). One data point with higher density in Sanctuary is likely an outlier (Fig. 4.2), but its exclusion does not significantly affect the isodar interpretation (intercept; 8.06, CI $_{0.95}$ = 4.2 –10.9, slope; 0.40, CI $_{0.95}$ = 0.28 – 0.54, $F_{1,9} = 37.20$, $R^2 = 0.78$, $p < 0.001$). The differences in density were reflected in chital group-sizes that were significantly larger in the National Park than they were in the Sanctuary ($F_{1,110} = 5.57$, $p = 0.02$; group size (mean± S.E) in the Sanctuary = 8.5 ± 0.9; in the National Park = 12.9 ± 1.9; Fig. 4.3).

Figure 4.2 The chital habitat isodar in Gir National Park and Sanctuary (western India). Each data point represents the mean number of chitals counted along a 2 km transect in adjacent pairs of Sanctuary and National Park habitats. The dashed circle outlines one possible outlier with higher than expected chital density in the Sanctuary. The hypothetical dotted line through the origin with a slope of 1.0 represents the null hypothesis of equal preference for the two habitats.

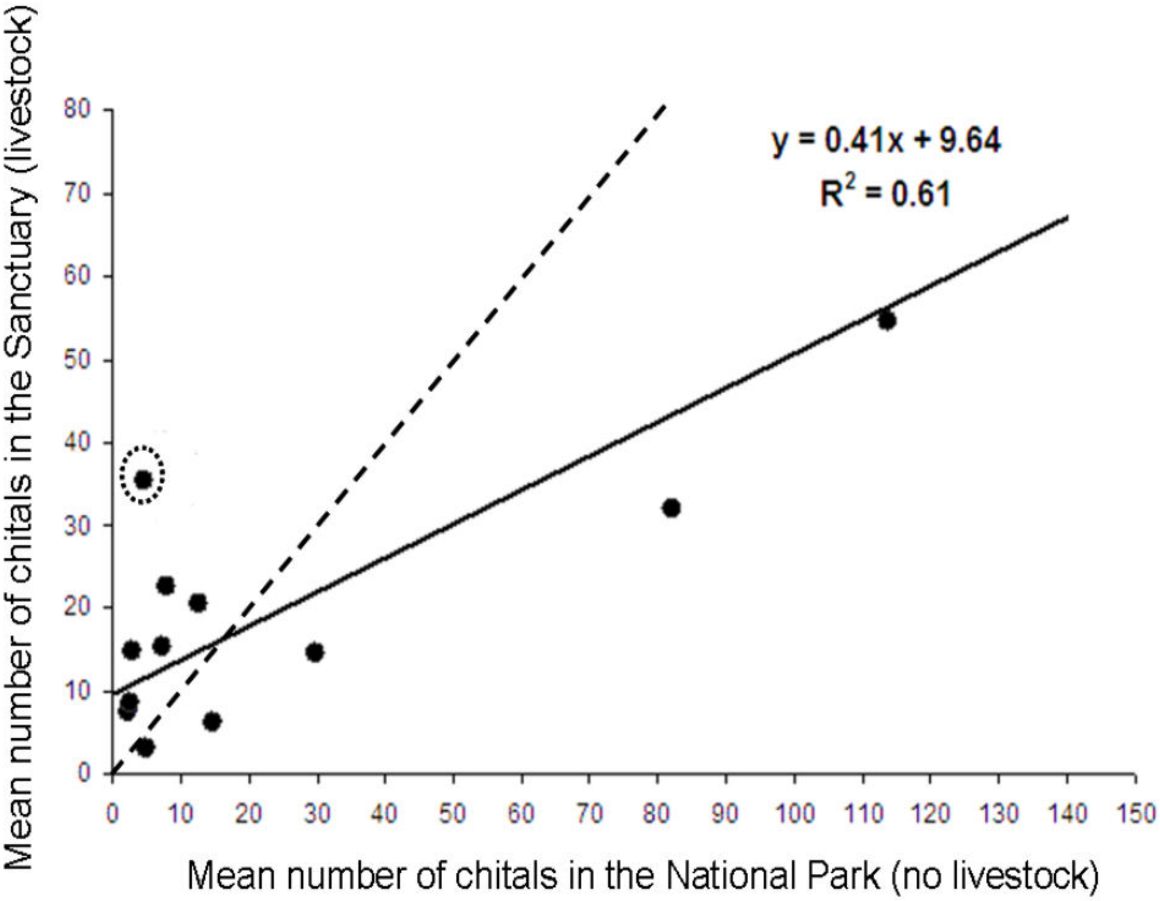
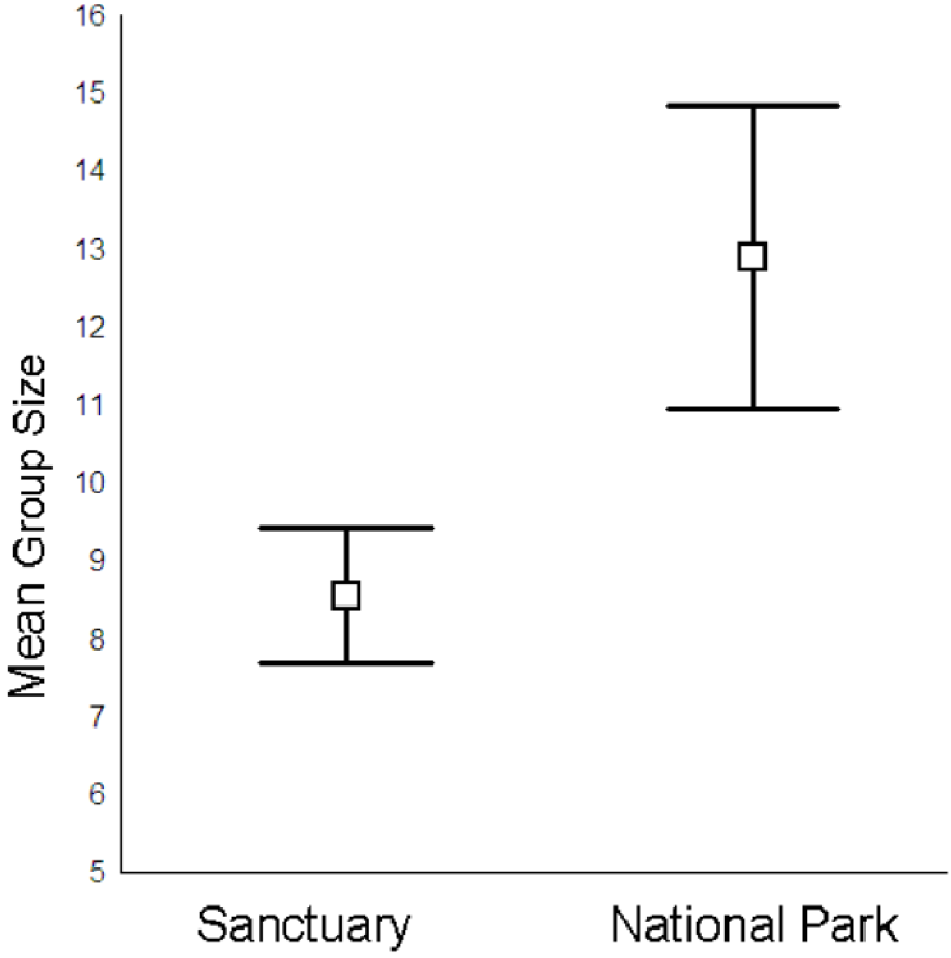


Figure 4.3 Mean chital group size in the Sanctuary (with livestock) and National Park (without livestock) of Gir National Park and Sanctuary, western India. Error bar represent mean ± 1 S.E.

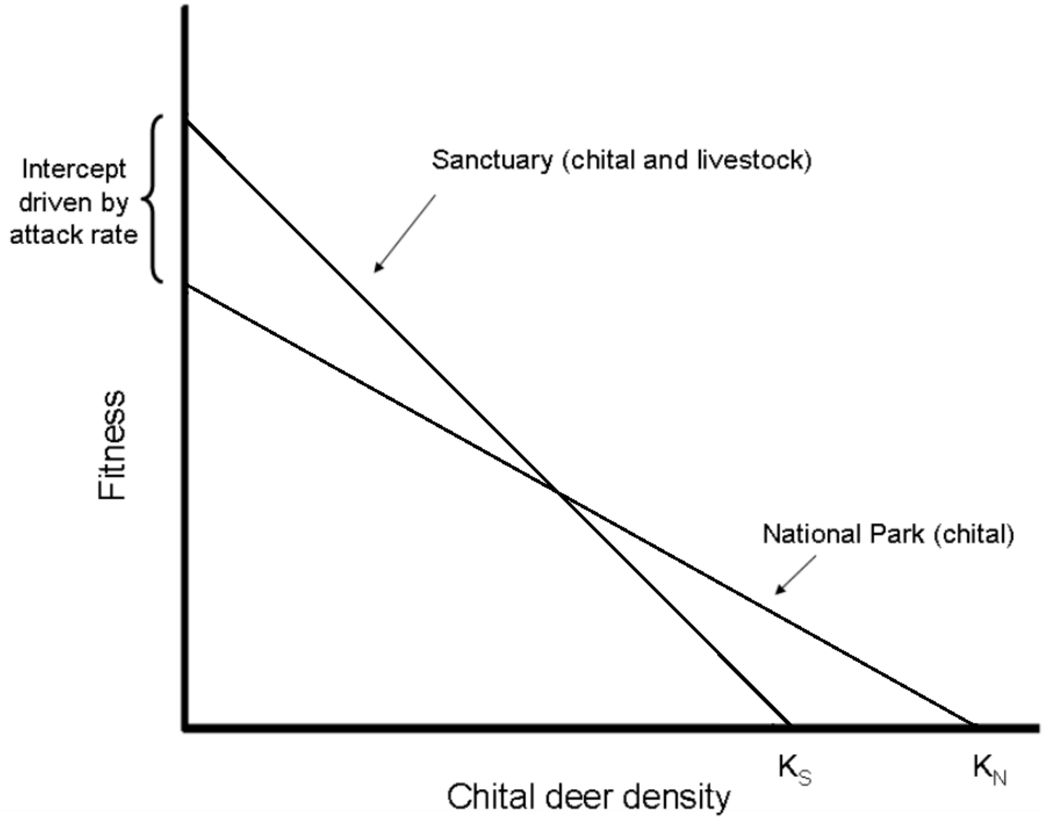


4.5 Discussion

Chitals select adjoining Sanctuary and National Park habitats in accordance with their population density. Despite the apparently higher value of the National Park, chital living along transects with low density prefer to occupy the Sanctuary. Chital habitat preference shifts toward the National Park along transects supporting higher deer densities. But their preference doesn't simply 'crossover' towards the National Park with increasing density (Fig. 4.4), chital also live in larger groups.

Cross-over regulation was originally suspected in systems where animals preferentially occupy quantitatively superior habitat at low density that has a low carrying capacity as may be caused by high predation (Morris 1988). It is commonly assumed that isodar intercepts correspond to quantitative differences and habitat quality (Morris 1988). The situation we describe in Gir is somewhat different. Chital prefer the quantitatively inferior habitat (Sanctuary) at low density then switch to the apparently more productive one at high density. This result is consistent, nevertheless, with our model for chital habitat selection in Gir if predator attack rates (and more generally predation risk) are higher in the National Park than they are in the Sanctuary (equation 3). This interpretation holds even if the maximum reproductive rate is greater in the National Park than in the Sanctuary ($r_N > r_S$). In systems such as that we explore in Gir, intrinsic habitat quality revealed by the isodar intercept emerges through differences in habitat-dependent predator attack rates (Fig. 4.4). A clear knowledge of natural history is thus necessary in order to ensure that analyses of habitat selection properly ascribe patterns in density to underlying causes of habitat preference.

Figure 4.4 A representative "crossover" model of population regulation of chital deer in two habitats (Sanctuary and National Park) plotted as fitness-density graphs. K_S and K_N are the respective carrying capacities of Sanctuary and National Park habitats at equilibrium. The fitness intercept (ordinate) reflects differences in attack rates by predators living in the two habitats.



The presence of alternative prey can lower the predation rate on another prey, especially if the alternative prey is vulnerable and easier to catch (Messier 1994, Potvin 1988). Chital vigilance is lower in areas with high stocking rates of domestic livestock than it is in areas of Gir with lower stocking rates (Vijayan et al., in press). We interpret this important observation as evidence that the preferential consumption of livestock by lions reduces predation risk on chital deer whose body size is less than optimum prey size for lions (*sensu* Hayward and Kerley 2005). The preference of low-quality sanctuary habitat at low chital density suggests that predation risk may trump competition for resources in Gir.

If we now turn our attention to the low isodar slope, it has two possible causes. The carrying capacity of the National Park may simply exceed that of the Sanctuary ($^{K_S}/_{K_N} < 1$, equation 3). This interpretation is consistent with our measurements of food biomass. The chital's habitat selection game is likely to be more intriguing. Where chital density is high, they aggregate in larger group sizes. Increasing group size may reduce predation risk while increasing competition for resources. In order to balance predation risk with competition, chital shift from the relatively safe but unproductive Sanctuary towards the rich and otherwise risky National Park. Regardless which interpretation one chooses, our results suggest that the habitat choices by chital reflect a sophisticated management of competition for food, versus predation risk, that is modulated through the combined influence of large domestic prey and human land use. Grazing by livestock in the Sanctuary, and not in the National Park, creates an asymmetry between the availability of food and predation risk on native herbivores.

Livestock likely have two important effects on chital habitat use. Firstly, their presence likely dilutes the predation risk for chitals via their shared predator. Secondly, they modulate the habitat-mediated predation risk for chitals by reducing vegetation cover and habitat complexity (Andruskiw et al. 2008). Habitat and landscape features (such as vegetation, topography, and refuge areas) influence predation risk through detection of, and escape from, predators (Lima and Dill 1990, Laundré et al. 2001, Ripple and Beschta, 2004, Thaker et al. 2011). The dense and tall grass cover in Gir's National Park present high quality ambush sites for lions and leopards, and thereby a risky habitat for deer. Meanwhile, long-term grazing by livestock in the Sanctuary offers long sight lines that facilitates predator detection and escape by small-bodied herbivores (Shrader et al. 2008, C. Iribarren, unpublished data).

Chital respond to the asymmetry in habitat by changing tactics. When density is low, they preferentially occupy safe habitat with small-groups that minimize intra-specific competition. When density is high, their balance for habitat preference shifts towards the high carrying capacity, high risk, National Park. Their preferences may also shift as they balance density and group-size dependent increases in intra-specific competition with reduced predation risk. And if they do, then the linear isodar suggests that the trade-off is also linear.

One might expect that chital living under high competition in the Sanctuary would be in poorer condition than animals living in the rich National Park. We suspect that this hypothesis is too simplistic. Although resource densities at a given chital density are greater in the Park than in the Sanctuary, it might be naive to anticipate that chital actually attain a higher foraging profit in the Park. Foraging under predation risk will often be interrupted by vigilance, and its efficiency reduced by increased apprehension (e.g., Brown and Kotler 2004). Such tradeoffs are typical when individual foragers allocate time to alternative foraging patches (e.g., Brown 1998). Although larger chital group size should offset predation risk in the National Park, this behaviour will also increase intra-specific competition for shared resources (Hobs et al. 1996, Fortin et al. 2004), and is likely to also increase encounters with predators (Ale and Brown 2009, Ale and Brown 2007). In accordance with our hypothesis, comparison of body condition scores by Jhala et al (2004) in the Gir forests revealed that chital deer in the Sanctuary were in better condition than were chitals in the resource-rich but risky National Park.

Competition and predation risk interact in their effects on the structure of prey communities (Kotler and Holt 1989). The resulting evolutionary game played between predators and their prey has important consequences not only on abundance and distribution, but also on subsequent evolution (Brown et al. 1999). Our research suggests that the tradeoffs, and their delightful density and frequency-dependent foraging games, may also apply to larger scales where individuals optimize their choice of habitat. The game is enriched by our observation that the presence of livestock in conservation areas, traditionally thought to be detrimental, is likely to have unexpected positive indirect effects on native fauna.

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Chapter V

Conclusion

Livestock populations in natural areas pose considerable challenges for park managers and biologists striving to maintain pristine natural environments for wildlife. Chapter 2 demonstrates that inter-specific interactions between native and domestic herbivores, and human-carnivore conflicts, are often the focus of ecological and management studies in areas affected by livestock. However, indirect interactions via shared predation (Holt 1977, Abrams 1987, Holt and Lawton 1994, DeCesare et al 2010) have important consequences for native prey co-existing with livestock, especially when livestock dominate prey abundance and biomass. Interactions can also be asymmetrical and can have non-reciprocal negative or positive effects for both species (Abrams et al 1998, Chaneton and Bonsall, 2000).

Chapters 3 and 4 demonstrate why it is important for park managers and biologists to document indirect effects in protected areas dominated by humans and their livestock populations. It will often be necessary to identify the full complex of indirect interactions in order to infer mechanisms of habitat selection or ecological separation between native herbivore species and livestock. Species interactions can be effective tools in management and conservation only if our understanding is complete. Chapter 3, for example, documented an unexpected indirect positive effect of livestock on native prey mediated by a large territorial predator. Such rare positive indirect effects may be much more common than previously anticipated and their ecological and conservation relevance is high. Where positive interactions occur between domestic and wild prey, attentive conservation managers may be able to carefully use domestic prey to preserve large carnivore ecosystems and their increasingly endangered wild prey. Management will be most effective if the predator population is controlled by factors other than prey density such as social interactions (territoriality) and extrinsic mortality, typical of large carnivores. Further, where negative indirect interactions such as apparent competition are detected in the system, attentive management can suggest preventative measures. Actions could involve relocation and/or spatial segregation/aggregation of livestock settlements to maintain a desired livestock density which will result in a favorable outcome for a focal native species. However, there could be another important aspect regarding the ability of optimally-sized domestic prey to yield positive interactions with other prey species. Domestic animal abundance often exceeds that of native prey and management options will be complicated by the need to conserve biodiversity of other species negatively affected by over-grazing (Chaikina and Ruckstuhl 2006). Further, indirect interactions between domestic and a focal native prey can also be driven by presence of several other suboptimal or optimal alternative prey types for a shared predator in the system. For example, in the Gir system, the importance of lower densities of two large native prey species (Sambar deer, *Rusa.unicolor*, and Nilgai, *Boselaphus tragocamelus*) cannot be ignored in the midst of positive interactions involving livestock and chital in the system. It is plausible that due to the rarity of these optimally sized native prey (due to predation and/ or competition with livestock), the lions key on livestock preferring them over suboptimal chital and allowing the latter population to increase. This may also suggest that positive interactions with native prey may be much more difficult to achieve than with domestic prey (predation rates on livestock are much less than on native prey – e.g., they are protected by their herders, and especially so at night).

In diverse prey–predator systems, both predation (top-down) and resource limitation (bottom-up) regulate herbivore populations (Sinclair et al 2003). The presence of domestic prey poses a unique challenge to native herbivores and their presence can be a mixed blessing. Livestock may dilute predation risk as chapter two demonstrates, but can also be detrimental through competition for limited food resources and habitat. Chapter 4 provides insights on how native prey balances these joint risks of predation and competition for resources through habitat choice. At lower densities chital preferably occupy quantitatively inferior livestock areas with low risk, but select resource-rich, risky habitat without livestock as their density increases. Native prey choosing livestock-free resource-rich but risky areas can lead to costly behaviors such as increased vigilance, larger group sizes and increasing intraspecific competition that affect its survival and reproduction (Brown 1998).

Livestock and its interactions with coexisting wild herbivores may be more complex than generally thought. A recent study by Odadi et al. (2011) sheds light on how wild herbivores benefit cattle by improving the quality of forage when food quantity is higher in wet season (facilitation effect). Referencing this novel discovery, du Toit (2011) encourages “bold experimentation” and steering away from “orthodoxy” in approaching inter-specific relationships between livestock and wild herbivores. I also encourage the same path in investigating the role of predator-mediated indirect interactions in livestock dominated conservation systems. The net effects of inter-specific competition plus indirect interactions via their predator are likely to be driven by relative densities of livestock, native prey and their predator(s) plus spatial and temporal variations in ecosystem productivity (forage). Careful observations on adaptive behavior (i.e. foraging, anti-predator response and habitat selection, *sensu* Morris et al 2009, Ale and Brown 2009, Caro 2007, Kotler et al 2007), coupled with definitive controlled experiments where one can manipulate densities, food resources and predation risk may be necessary to assess the fitness consequences of both resource competition/or facilitation (bottom-up process) and indirect effects of predators (top down) on native prey species. Only then we may be able to perceive the true impacts of livestock on native herbivore in the system.

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Appendices

Appendix I: Search Criteria for IUCN Red List Categories threatened by livestock

Search terms

Search by taxonomy:

CHORDATA

Search by location:

Caribbean Islands
East Asia
Europe
Mesoamerica
North Africa
North America
North Asia
Oceania
South America
Sub-Saharan Africa
West & Central Asia
(Native)

Search by systems:

Terrestrial

Match any habitat:

1. Forest

2. Savanna

3. Shrubland

4. Grassland

6. Rocky areas (eg. inland cliffs, mountain peaks)

8. Desert

Search by threat:

2.3. Livestock farming & ranching

Search by taxonomy:

MAMMAL

Webpage: http://www.iucnredlist.org/apps/redlist/static/categories_criteria_3_1

Search Results Webpage:

http://www.iucnredlist.org/apps/redlist/search/link/4dae3502-dea209cc

Date accessed: 20 July, 2011

Appendix II (Literature survey): Search Terms and Reference List from Literature Survey

Search terms:

“Domestic prey*wildlife”,

“Livestock*wildlife”, “

“Livestock*interactions”

“Livestock*native prey”, and

“Domestic prey*native prey”

General Categories: Science and technology, Social Sciences

Subject Categories: Zoology, Environmental Sciences, Biodiversity Conservation, Agriculture and Dairy Science

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