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

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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.

Species differ in their habitat specialization and preference in a way that is often influenced by interactions with other species (Svärdson 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 (>300 kg). 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 km²) reduces the standing crop of food resources for chital (density $\sim 45-50$ km²) 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).

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

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

and

$$\frac{1}{N_N}\frac{dN_N}{dt} = r_N\left(\frac{K_N - N_N}{K_N}\right) - Pa_N \quad (2)$$

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 Eq. 1 and 2 equal to one another,

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

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 (Eq. 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.

Methods

Study area

The dry deciduous forests of Gir National Park and Sanctuary, western India have an approximate area of 1500 km² (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 km²). The peripheral Sanctuary is approximately five times the size of the National Park (~1250 km² and 260 km² 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 4-km line transects (Burnham et al. 1980, Khan et al. 1995, Khan 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 h), and again during evening (between 16:00 to 17:00 h), when chital are active and easily visible. Distance travelled was measured by a calibrated

pedometer and hand-held global positioning system. 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 (1.25×1.25 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.
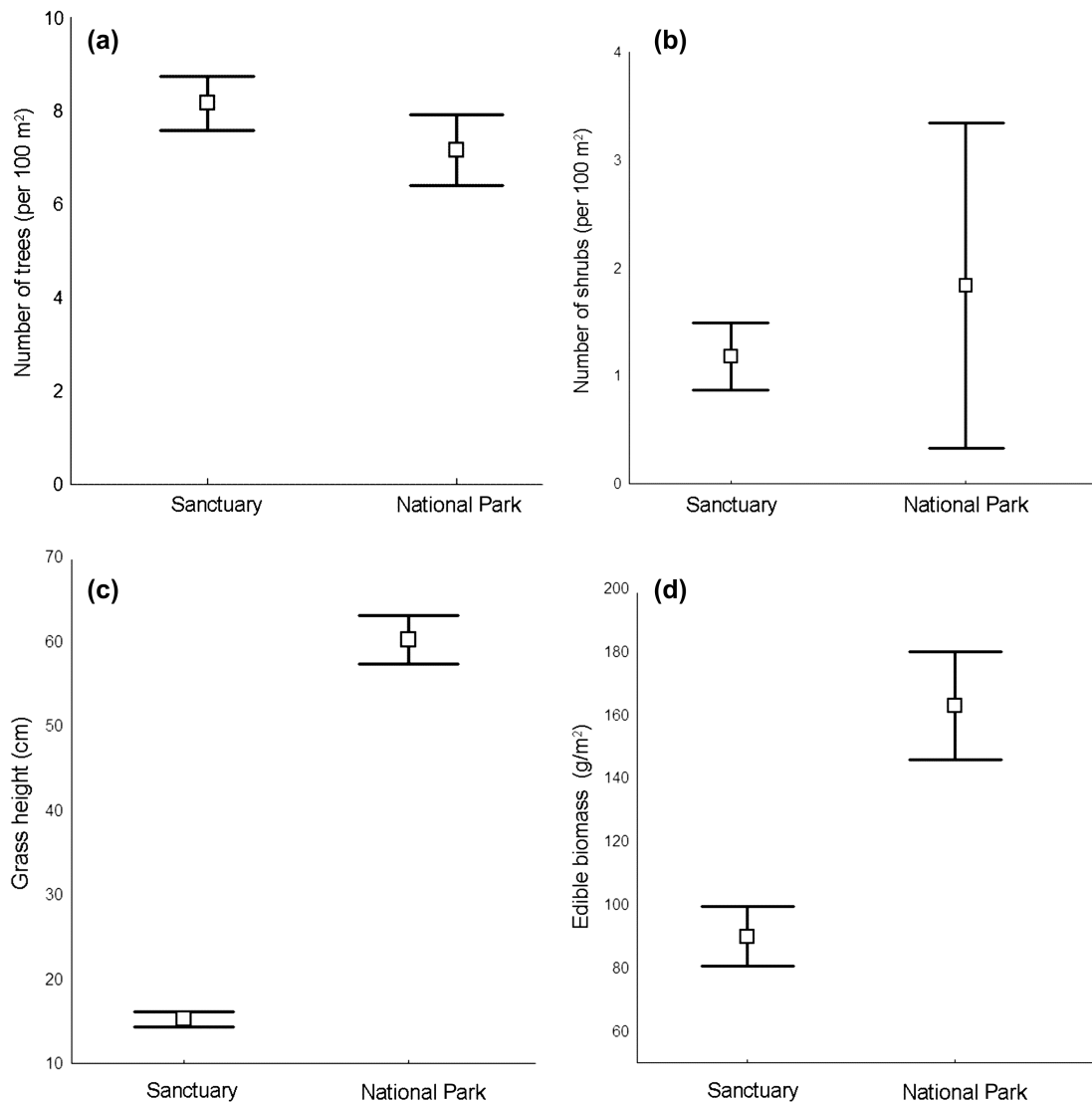

Figure 1. Comparisons of vegetation structure in Gir's Sanctuary and National Park. (a) tree density (p = 0.29), (b) shrub density (p = 0.60), (c) grass height (p < 0.001), and (d) edible biomass (p < 0.001). Error bars represent mean ± 1 SE.

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 ver. 7.0 (Statsoft, OK, USA).

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 ± SE) 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 ± SE) in the Sanctuary = 15.2 ± 0.8; in the National Park = 60.2 ± 2.8; Fig. 1). There were no differences in tree (p = 0.29) and shrub densities (p = 0.60) between the two areas.

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. 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. 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 ± SE) in the Sanctuary = 8.5 ± 0.9; in the National Park = 12.9 ± 1.9; Fig. 3).

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), 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 (Eq. 3). This interpretation holds even if the maximum reproductive rate is greater in the National Park than in the Sanctuary
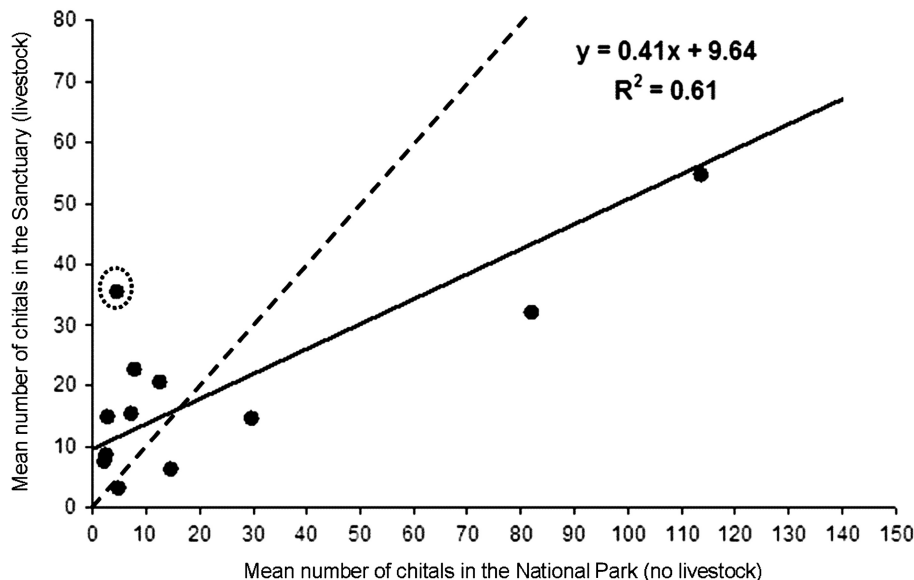

Figure 2. The chital habitat isodar in Gir National Park and Sanctuary (western India). Each data point represents the mean number of chitals counted along a 2 km transect in adjacent pairs of Sanctuary and National Park habitats. The dashed circle outlines one possible outlier with higher than expected 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.
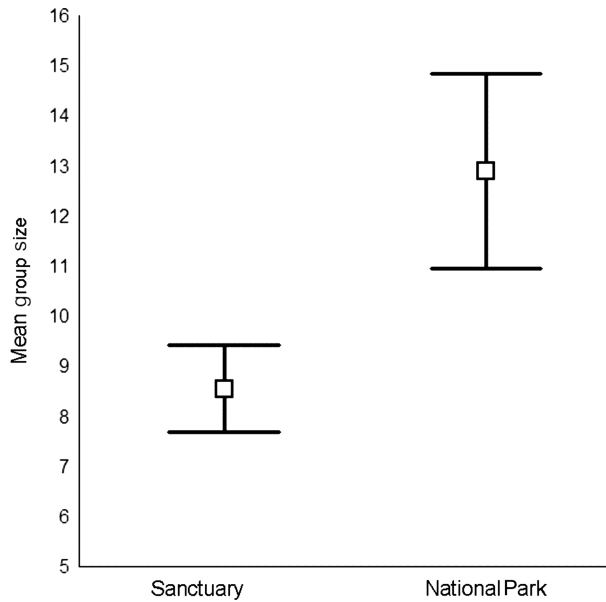
Figure 3. Mean chital group size in the Sanctuary (with livestock) and National Park (without livestock) of Gir National Park and Sanctuary, western Indian. Error bar represent mean ± 1 SE.

($r_N > r_S$). 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). 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.

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
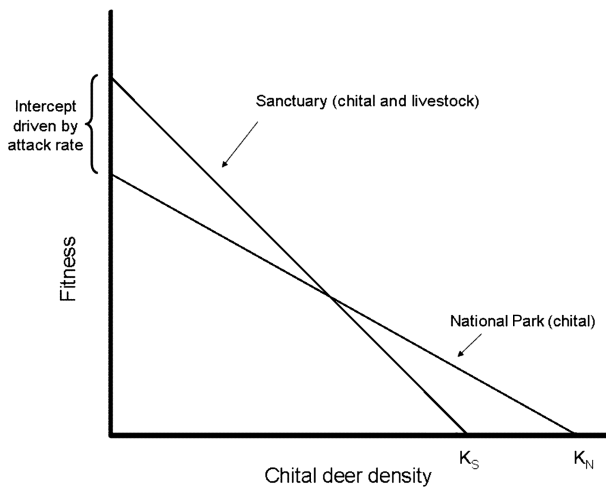

Figure 4. A representative "crossover" model of population regulation of chital deer in two habitats (Sanctuary and National Park) plotted as fitness–density graphs. K_S and K_N are the respective carrying capacities of Sanctuary and National Park habitats at equilibrium. The fitness intercept (ordinate) reflects differences in attack rates by predators living in the two habitats.

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 ($K_S/K_N < 1$, Eq. 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).

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 tradeoff 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 (Brown and Kotler 2004). Such tradeoffs are typical when individual

foragers allocate time to alternative foraging patches (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 (Hobbs et al. 1996, Fortin et al. 2004), and is likely to also increase encounters with predators (Ale and Brown 2007, 2009). 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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