ECOLOGY OF THE SNOW LEOPARD AND THE HIMALAYAN TAHR IN SAGARMATHA (MT. EVEREST) NATIONAL PARK, NEPAL

By

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SUMMARY

Foraging theory, the confluence of the ecology and evolution embedded within Darwin's theory of natural selection, strives to understand patterns and processes in individuals, populations and communities, through behavioral decisions of individual animals. I use tools and concepts of foraging theory in combination with the conventional wildlife techniques to seek patterns and report on the distribution and abundance of the endangered snow leopard *Uncia uncia* and the Himalayan tahr *Hemitragus jemlahicus*, in the Mt. Everest region, Nepal. Anti-predator behavior of prey may reveal the abundance and whereabouts of predators. While predators may be elusive, their prey is more readily observed. I use the vigilance behavior of Himalayan tahr to infer indirectly the status of their predator, the snow leopard. I confirm that snow leopards have returned to Mt. Everest following their disappearance some 40 years ago, in response to the increasing population of Himalayan tahr. Himalayan tahr vigilance behavior correlates tightly with the abundance and distribution of snow leopard signs. I suggest behavioral indicators provided by prey offer a valuable tool for studying and monitoring stealthy and rare carnivores.

I model and extend two concepts central to foraging theory involving predation risk. I consider how animals should select their habitats under predation risk and once within a selected habitat how foraging animals should partition time between competing fitness enhancing activities. In the former, with predation risk as an additional factor, I show the habitat selection theory still applies but there are new and interesting wrinkles brought on by conflicting tradeoffs of food and safety and non-linearities in the isodars (number of individuals in habitat 2 as a function of those in habitat 1 such that fitness is equal across habitats). In the later, I develop a game theory model of group-size and vigilance that includes the documented ways by which group membership can influence predation risk and the value of vigilance. I suggest that group size effect on vigilance behavior is contingent upon the strength of interacting effects of many eyes, dilution and predation-attraction effects.

In the spirit of examining ecological theories, I track the growing claim that top predators structure communities from historical perspectives. Furthermore, I examine a few major ecological paradigms in the context of their relevance to conservation.

CHAPTER ONE

1. OBSERVING ECOLOGY IN SEARCH OF PATTERNS AND PROCESSES

The precursor to modern ecology lies in the study of natural history that flourished in the European countries after the industrial revolution in the nineteenth century. With the global expansion of European colonialism, the naturalists' universe expanded. Their collections and writings rose sufficiently to permit those with analytical minds to ponder over such questions as "why do some species range throughout entire hemispheres, while others have small, isolated distributions?" A century earlier, E. Haeckel (quoted in Mayr 1997) defined ecology as the study of all those complex interactions referred to by Darwin (1859) as the conditions of the struggle for existence. Although the "struggle for existence" description of Darwin sets the stage to study competition for niche space among species, ecology did not flourish until the 1920s. Ecology made great strides with empirical studies by C. S. Elton and D. Lack, and concurrent theoretical work using mathematical approaches pioneered by V. Volterra and A. J. Lotka, among others.

G. E. Hutchinson and R. H. MacArthur continued and accelerated the pace by combining empirical observations with analytical (mostly mathematical) approaches (Kingsland 1995). The triumphs of Hutchinson-MacArthur school (see Hutchinson 1957, MacArthur 1972) and its followers was the recognition that even with tremendous complexity and a myriad of ecological interactions, natural communities were dynamic systems, organized by regular and understandable forces. Soon suit of intra- and interspecific relationships came under scrutiny, many of which could be reduced to elegantly simple models. Fundamental to these models was the notion that ecological systems exist in some sort of stable equilibrium, and that if they are perturbed they behave in a predictable ways, either returning to their previous equilibrium or finding a new state. Ecologists shifted from description of the natural world to explanation, analysis and even prediction of ecological phenomena (McIntosh 1985, Kingsland 1995). The idea of equilibrium, rooted in the theory of evolution by natural selection, set the stage for ecologists to elevate the science of ecology.

"Study nature, not books!" advised the great 19th century naturalist Louis Agassiz, but one must do both to synthesize something substantial. Observations of patterns start with natural history as exemplified by Darwin himself. But patterns may not be obvious unless seen through the lens of ecological theories and evolutionary ecology. Several modern field biologists have shown that natural history study in light of population ecology and evolutionary biology can tell us much about individual animals, their distributions and their behavior (Schaller 1972, 1977; Sinclair and Arcese 1995).

Two of my chapters are intentionally concerned with natural history. They seek pattern and report on the distribution and abundance of two large mammal species – prey and predator. Chapter Two deals with the distribution and abundance of the Himalayan tahr *Hemitragus jemlahicus* (hereafter tahr) in Sagarmatha (Mt. Everest) National Park, the world's highest National Park, in Nepal. The population of tahr reached a nadir in the 1960's, but with the establishment of the park their population has increased substantially. Perhaps the burgeoning population of tahr triggered the return of the snow leopard *Uncia uncia* to the park from Tibet after the absence of almost forty years (Chapter Three). I use "mud and boots” wildlife field techniques (e.g. sign survey), the wildlife biology of the 1950s and 1960s, to study these animals.

In the 1950s, science emerged from the Second World War with a new paradigm, systems analysis. Odum’s (1953) textbook with a systems approach educated more than one generation of biologists. He emphasized ecological processes as factors that govern equilibria, a non-evolutionary approach (O’Neill 2001). Such Ecosystem approaches have taught us a lot about ecological processes such as nutrient cycling and global warming. But, how profitable is it to take a non-evolutionary stance to understand underlying patterns in communities and ecosystems? At local scales, the approach may suffice (O’Neill 2001). Traditional ecologists indeed worked to elucidate local mechanism (e.g. keystone predation: Paine 1966) to explain community structure. The current consensus, however, recognizes the roles of regional and historical processes as determinants of local community structure. And, incorporating these processes requires integrating evolution into ecological studies (Ricklefs and Schluter 1993, Holt 2005). Without evolution, biology becomes a compendium of sundry facts, some of them interesting or curious, but devoid of a meaningful picture. As Dobzhansky (1973) opined “Nothing in biology makes sense except in the light of evolution”.

The equilibrium worldview relies on biotic forces and interactions to produce natural systems as elegant and finely tuned systems. As understood in the era of modern synthesis, such a view brought many contributions to both ecology and conservation. In 1971, UNESCO started its research program, the Man and Biosphere, with the expectation of negative biotic feedbacks producing a stable and “harmonious” equilibrium. The “balance of nature" concept is still a relevant and helpful tool for framing conservation goals and agendas to laymen and politicians.

In ecological frontiers, this world view left several important legacies. One of the influential ones relevant to my study was foraging theory (Emlen 1966, MacArthur and Pianka 1966). In a word, foraging theory recognizes that because behaviors are adaptive, organisms are considered to make foraging decisions that tend to maximize fitness, i.e. per capita population growth rate.

I use tools and concepts of foraging theory to understand patterns of distribution and abundance of snow leopards and their prey, tahr (Chapter Four). In a nutshell, behavioral responses, such as vigilance behavior, allow us to study rare predators indirectly through their prey. I use the foraging and vigilance behaviors of tahr to infer indirectly the status and whereabouts of snow leopards. Tahr vigilance behavior correlates tightly with the abundance and distribution of snow leopard sign. In sum, I show that the presence of predators can be revealed from fear responses of prey.

In line with Chapter Four and in the spirit of balancing empiricism with theory, Chapters Five and Six model and extend two concepts central to forging theory. I consider how animals should select their habitats under predation risk (Chapter Five) and once within a selected habitat how should a foraging animal partition time between competing fitness enhancing activities (Chapter Six). In my model of habitat selection under predation risk, I extend standard models of population growth and habitat selection to include the effects of predation risk, concluding that because most predators follow Type II functional response, habitat selection under predation risk (Type II functional response) depicts nature more realistically. It extends the theory of density-dependent habitat selection based on the ideal free distribution. Under the ideal free distribution, at equilibrium individuals distribute themselves between habitats such that their fitness is equivalent across habitats (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 1987). With predation risk as an additional factor, the theory still applies but there are new and interesting wrinkles brought on by conflicting tradeoffs of food and safety, non-linearities in the isodars (number of individuals in habitat 2 as a function of those in habitat 1 such that fitness is equal across habitats), and predictable ambiguities in the identification of "best" or "preferred" habitat.

The 1960s was the period when the expression "evolutionary biology" gained the currency (Wilson 1994). Specialists were less concerned about knowing everything about their organisms but focused more on the search for general principles. The quest for generality and clear "Laws" in ecology has always been a Siren's call for ecologists. Sometimes this is dismissed as "physics envy" - ecologists seeking simplicity in the otherwise messy, complex and un-replicated worlds of nature. But, general principles may exist and may simply be messily manifested in nature. Regardless, this search heightened under MacArthur's influence (MacArthur and Pianka 1966, MacArthur and Wilson 1967, MacArthur 1972) who introduced the qualitative genre of ecological modeling in ecology, distinguishing between alternatives only in a qualitative sense, but without quantitative predictions.

Today, the Optimization Research Program (Mitchell and Valone 1990, Brown 1998, 2001) represents this ecological legacy, with a distinct flavor of an evolutionary approach. This worldview places an emphasis on using the ecology and evolution embedded within

Darwin’s theory of natural selection to understand individuals, populations, and communities, framed within the logic of game theory rather than population genetics (Brown 1998, 2001). Following this tradition, I develop a game theory model of group-size and vigilance that includes the documented ways by which group membership can influence predation risk and the value of vigilance. The model helps to evaluate and clarify some of the discrepancies in prior theoretical and empirical studies of vigilance and group size (Chapter Six). With the well established view “vigilance and group size should be tightly linked”, many studies have documented a negative relationship between group size and the rates of scanning by individuals (Elgar 1989, Quenette 1990, Roberts 1996). However, some studies have found either no effect or the opposite effect of group size on vigilance (Treves 2000, Beauchamp 2003). I incorporate the many eyes, dilution and predator attraction effects and show how group size affects vigilance behavior. The response of vigilance to group-size becomes contingent upon the strength of the interacting effects, particularly the predator-attraction effect.

Ecologists now know that predation matters (Brown et al. 1999)! The period from the 1960's through the early 1970’s was indeed the heyday of competition as the principal factor structuring natural communities (e.g. Cody and Diamond 1975). Later, the ubiquity of competition as the dominant factor structuring natural communities was questioned. The increasing use of field experiments in the 1970s and 1980s led to a growing consensus regarding the importance of predation relative to competition (Sih et al. 1985). Although this was a much delayed response following the first incontrovertible evidence of the keystone role of predators in regulating the diversity of the prey community (Paine 1966), ecologists have since amassed a plethora of evidence demonstrating that predators can have tremendous influences on the structure and dynamics of ecological populations and communities.

I argue that such insights into the role of predation have been made possible by examining predation from the perspectives of foraging theory, the Optimization Research Program, and present techniques of community and evolutionary ecology (Chapter Seven). Today the frequent top-down governance of ecosystems by large carnivores is viewed as a useful generalization to guide management. Top predators are thus both the targets of and the means for conservation at the landscape scale.

The subsequent decades after the 1970s witnessed an increase in number of ecologists and their abilities to collect, store and analyze quantitative data. While ecologists learned much about communities and ecosystems, they often concluded with how messy they are. “Laws and models in (community) ecology are too contingent to be widely applicable”, suggested Lawton (1999, 2000). Traditionally ecologists had worked at small spatial scales and tried to minimize the amount of disturbance and heterogeneity that affected sampling designs (traditional community ecology means “experimental, highly reductionist and intensely local in focus”: Lawton 2000). But the relationships that appear clean at small spatial scales and short temporal scales become fuzzier and often break down as spatial and temporal scales increase. This is because disturbances of all sorts creep into observations. Ecological processes and the patterns they produce change as the scale in space or time changes, and these changes are often nonlinear (Wiens 1989, Levin 1992). Increasingly, ecologists have begun to realize that the disturbance itself may be a key factor, like competition or predation, in certain cases, structuring communities (Connell 1978). Is it then disturbance (and heterogeneity), not equilibrium, that generates biodiversity?

The emphasis on disturbance revived an old debate over the importance of density dependent and density independent factors in regulating animals' abundance and therefore community structure (Sinclair 1989). These intertwined debates regarding population regulation, the extent to which systems are equilibrial or disequilibrial, and the importance of disturbance indicate a level of uncertainty or confusion in ecology.

Unresolved debates in ecology, however, had and will continue to have significant implications for conservation. One approach is to ignore uncertainty in all of its forms. For example, there may be times when a deterministic model suffices for conservation (Caughley 1994). Studies (>40 years) of two large mammal species in the Serengeti, the African buffalo and the wildebeest (Mduma et al. 1999), have identified the density dependent factors sufficient for population regulation. Mduma et al. (1999) identified a synergistic interaction of lack of food and disease. Animal populations can be regulated via top-down processes through predation (Chapter Seven). Just when each process occurs has been the subject of some controversy. In many cases a synergistic interaction of food and predators likely determines the abundance of species. In the Ecology of Fear, food (competition) and safety (predation) blur the distinction between "bottom-up" and "top-down". Food and safety become flip sides of the same coin, and it is the tradeoffs and interactions involved in acquiring food and avoiding predation that structure the communities and determines patterns of distribution.

Among all of these messy developments within ecology and despite weaknesses in the architecture of a science, science has helped manage nature, but the challenge is to determine why ecology sometimes fails to match needs of managers and assists at other times. Managers may expect too much of paradigmatic blueprints, while ecologists believe them too much (Chapter Eight). The problems may be exacerbated because ecologists who create theory often are ignorant of what park managers, conservation planners, and forest rangers need at local scales.

In Chapter Eight, I discuss some of these issues and examine a few major ecological paradigms, e.g. the theory of island biogeography (MacArthur and Wilson 1967), in the context of their relevance to conservation. In fact, one of the most important contributions of the equilibrial thinking in ecology is the theory of island biogeography- the elegant idea that ecological communities on oceanic islands are shaped by two fundamental processes: immigration of new species from mainland sources, and the local extinction of populations on islands. The island biogeography theory in subsequent decades has heavily influenced conservation actions, particularly in designing nature reserves and national parks around the globe. The third legacy of that era was a model for determining maximum sustainable yield (with the fusion of ecology and resource economy), the concept that a population is held at a constant level by harvesting individuals that would normally be added to the population, allowing it to continue to be productive. But, living off the interest of “natural capital” has proven harder in practice than in theory!

Pluralism is what many suggest (Mayr 1997, Lawton 1999, May 1999, Holt 2005) as a way forward in ecology. To date, (community) ecology at most offers relatively few fuzzy generalizations as “general laws” (Lawton 1999, Simberloff 2004). Some of these, for example, the frequent top-down governance of ecosystems by large carnivores (Chapter Seven) have been gleaned from excellent scientific research and may be enormously useful in management. Ecology may develop clusters of such laws or rather fuzzy generalizations, tailored for particular settings with a metalaw that allows us to know which local laws apply to which situation (Holt 2005). Clearly, much remains to be learned. The very realization that nature may be complex should lure ecologists to seek for generality. Imagine that everything is completely known and that science has nothing more to discover: what a nightmare!

References

Beauchamp, G. 2003. Group-size effects on vigilance: a search for mechanisms. *Behavioural Processes* 63: 111-121.

Brown, J.S. 1998. Game theory and habitat selection. In: *Game Theory and Animal Behavior*, eds. L.A. Dugatkin and H.K. Reeves, pp. 188-220. Oxford University Press: Oxford.

Brown, J.S., Laundre, J.W. and Gurung, M. 1999. The ecology of fear: Optimal foraging, game theory and trophic interactions. *J. Mammal.* 80: 385-399.

Brown, J.S. 2001. Ngongas and ecology: on having a worldview. *Oikos* 94: 6-16.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63: 215-244.

Cody, M.L. and Diamond, J.M. 1975. *Ecology and evolution of communities.* Cambridge, Mass, Beldnap.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection* (1st edn). Murray, London.

Dobzhansky, T. 1973. Nothing in Biology Makes Sense Except in the Light of Evolution. *American Biology Teacher* 35: 125-129.

Elgar, M.A. 1989. Predator vigilance and group size in mammals and birds. *Biol. Rev*. 64: 3-33.

Emlen, J.M. 1966. The role of time and energy in food preference. *Am. Nat.* 100: 611-617.

Fretwell, S.D. and Lucas, H.L. Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19: 16-36.

Holt, R.D. 2005. On the integration of community ecology and evolutionary biology: historical perspectives, and current prospects. In: *Ecological Paradigms Lost: Routes of Theory Change*, eds. B. Beisner and K. Cuddington, pp. 235-271. Academic Press.

Hutchinson, G. E. 1957. "Concluding remarks, Cold Spring Harbor Symposium." *Quant. Biol.* 22: 415-427.

Kingsland, S. 1995. *Modeling Nature: Episodes in the History of Population Ecology* (2nd edition). The University of Chicago Press.

Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84: 177-192.

Lawton, J. H. 2000. *Community ecology in a changing world*. Ecology Institute, Oldendorf/Luhe.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

MacArthur, R.H and Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press: Princeton.

MacArthur, R.H. 1972. *Geographical Ecology*. Princeton University Press: Princeton.

MacArthur, R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. A*m. Nat.* 100: 603-609.

Mayr, E. 1997. *This is biology: the science of the living world*. The Belknap press of Harvard University Press.

McIntosh, R. P. 1985. *The background of ecology: concept and theory*. Cambridge University Press: Cambridge.

Mduma, S.A.R., Sinclair, A.R.E. and Hilborn, R. 1999. Food regulates the Serengeti wildebeest population: a 40-year record. *J. Anim. Ecol.* 68: 1101-1122.

Mitchell, W.A. and Valone, T.J. 1990. The optimization research program: studying adaptations by their function. *Quar. Rev. Biol*. 65: 43-52.

Morris, D.W. 1987. Spatial scale and the cost of density-dependent habitat selection. *Evol. Ecol*. 1: 379-388.

O'Neill, R. V. 2001. Is it time to burry the ecosystem concept? *Ecology* 82: 3275-3284.

Odum, E. P. 1953. *Fundamentals of Ecology*. Philadelphia: Saunders.

Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65-75.

Quenette, P.-Y. 1990. Functions of vigilance in mammals: a review. *Acta Oecol*. 11: 801-818.

Ricklefs, R.E. and Schluter, D. 1993. *Species Diversity in ecological communities: historical and geographical perspectives*. The University of Chicago Press: Chicago.

Roberts, G. 1996. Why individual vigilance declines as group size increases. *Anim. Behav.* 51: 1077-1086.

Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology* 62: 327-335.

Schaller, G.B. 1972. The Serengeti lion. Chicago: University of Chicago Press.

Schaller, G.B. 1997. *Mountain Monarchs: Wild Sheep and Goats of the Himalayas*. University of Chicago Press: Chicago.

Sih, A., Crowley, P., McPeek, M., Petranka, J., and Strohmeier, K. 1985. Predation, competition, and prey communities: A Review of Field Experiments. *Ann. Rev. Ecol. Syst.* 16: 269-311.

Simberloff, D. 2004 Community Ecology: Is It Time to Move On? *Am. Nat*. 163: 787-799.

Sinclair, A.R.E. and Arcese, P. 1995. *Serengeti II: Dynamics, Management and Conservation of an Ecosystem.* Chicago University Press: Chicago.

Sinclair, A.R.E. 1989. Population regulation in animals. In: The contribution of ecology to an understanding of the natural world, ed. J.M. Cherret, pp 197-241. Blackwell, Oxford.

Treves, A. 2000. Theory and method in studies of vigilance and aggregation. *Anim. Behav*. 60: 711-722.

Wiens, J.A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3: 385-397.

Wilson, E. O. 1994. *Naturalist*. Island Press.

CHAPTER TWO

2. POPULATION STATUS, DISTRIBUTION AND GROUP STRUCTURE OF HIMALAYAN TAHR IN SAGARMATHA NATIONAL PARK, NEPAL

2.1 INTRODUCTION AND OBJECTIVES

During the 1960s the endangered Himalayan tahr *Hemitragus jemlahicus* (hereafter tahr) reached a low population level in what is now Sagarmatha (Mt. Everest) National Park (27°45' - 28°07' N; 86°28' - 87°07' E). Low population abundance may have been due to poaching and other anthropogenic disturbances from the advent of tourism, following the first ascent of Mt Everest in 1953. In 1976, to better reconcile the opportunities for tourism development with conservation, Sagarmatha (area of 1,148 km^2) was declared a National Park. Since then, strict rules and regulations were enforced within the park boundary, all sorts of wildlife hunting banned, and goats removed from the park to better improve grazing grounds for wildlife species (Sherpa 1985, 1987). By the late 1980s, populations of tahr were burgeoning in the region (Fleming, *undated*), but the onset of the millennium witnessed poor reproductive success (Lovari et al., in press). My objectives in this study were to 1) assess population sizes and distributions of tahr in major valleys of Sagarmatha, and 2) examine their population structure.

Himalayan tahr are prey species of the snow leopard *Uncia uncia* in central Himalaya (Schaller 1973, 1977, Jackson and Ahlborn 1989). Tahr also constitute potential prey for other predators such as the common leopard *Panthera pardus* and dhole *Cuan alpinus*

(Schaller 1977). Maintenance of the healthy tahr populations is thus a prerequisite to maintain these last remaining predators in the Himalaya. Although formerly widespread as far as Europe, at present tahr form a fragmented "bathtub ring" along the southern flank of the Himalaya in Nepal, India and a small remote part of the Qomolangma in Tibet, China (Schaller 1977, Green 1979, Shackleton 1997). The presence of tahr in Bhutan is equivocal. Although Holmes (1970) reported that they occurred in the country, no mention of the species was made in the latest comprehensive IUCN report (Shackleton 1997). (Introduced populations of tahr presently inhabit New Zealand, Table Mountain of South Africa, California, USA and Ontario in Canada).

In Nepal, loss of habitat is increasingly an important cause for the decline of tahr, as well as localized hunting, as settlers cleared tillable land between cliff systems and hunted off isolated populations (Schaller 1977, Shackleton 1997). Consequently, the erstwhile continuous distribution of tahr has been disrupted and their populations exposed to anthropogenic disturbances (Green 1979, Bjonness 1980, Bauer 1990), all resulting in dwindling numbers of tahr. Although several studies have focused on introduced populations of tahr in New Zealand (Caughley 1970, 1971, Forsyth 2000, Forsyth and Tustin 2000), only general surveys of tahr (e.g. Green 1979, Gurung 1995) have been made in their native range in the Himalaya. Schaller (1973, 1977) describes their behavior repertoires in some detail.

Over a decade ago, Lovari (1992) concluded that Sagarmatha National Park (hereafter Sagarmatha) was home to *ca*. 350 tahr. Since then no study has been done on tahr populations. Tahr have spread to several alpine and sub-alpine valleys in Sagarmatha, but 6we know very little about their distributions and abundances in these valleys. Such information is vital for management, particularly in light of snow leopards' return to the region after four decades of absence (Ale and Boesi 2005).

2.2 METHODS

2.2.1 Study area

The upper part of Sagarmatha National Park, locally known as Khumbu, comprises three watersheds- Imja, Dudhkosi and Bhotekosi. For my purpose of tahr study, I recognized four major valleys along these rivers - Gokyo, Namche, Phortse and Thame (Figure 1). The park was established in 1976 to conserve tahr and musk deer (Heinen and Yonzon 1994), with protection largely carried out by a battalion of the Nepal army (400 soldiers) to check illegal activities such as poaching in this Natural World Heritage Site (criterion III). My study area, the upper reaches of the park (*ca*. 86 km^2), where tahr are most common (Figure 2), reveal two distinct vegetation habitats: scrubland and forest. Forest (open forest) at the height of 3,000 m to 4,000 m a.s.l. is dominated by *Pinus wallichiana*, *Abies* spp. and *Betula utilis*. These patches of open forests grade higher up into the alpine and subalpine grassland/scrubland zones (4,000-5,000 m a.s.l.) with thick mats of *Juniperus* spp. and *Rhododendron* spp. For the ease of discussion, I call this tahr habitat above tree line as "scrubland" (see Buffa et al. 1998, for vegetation detail). I further divide (vegetation) habitat (scrubland vs. forest) into three terrain types: cliff, broken and rolling.

Wildlife species occurring in the park are game birds of such species as Impeyan pheasant *Lophophorus imejanus*, Tibetan snow cock *Tetraogallus tibetanus* and blood pheasant *Ithaginus cruentus*, and several small mammal species (e.g. the pika *Ochotona* *himalayana*), as well as such carnivores as the Himalayan weasel *Mustela sibirica*, the hill fox *Vulpes vulpes*, the golden jackal *Canis aureus* and the snow leopard (Lovari et al. in press).

Figure 1: Sagarmatha (Mt. Everest) National Park, Nepal

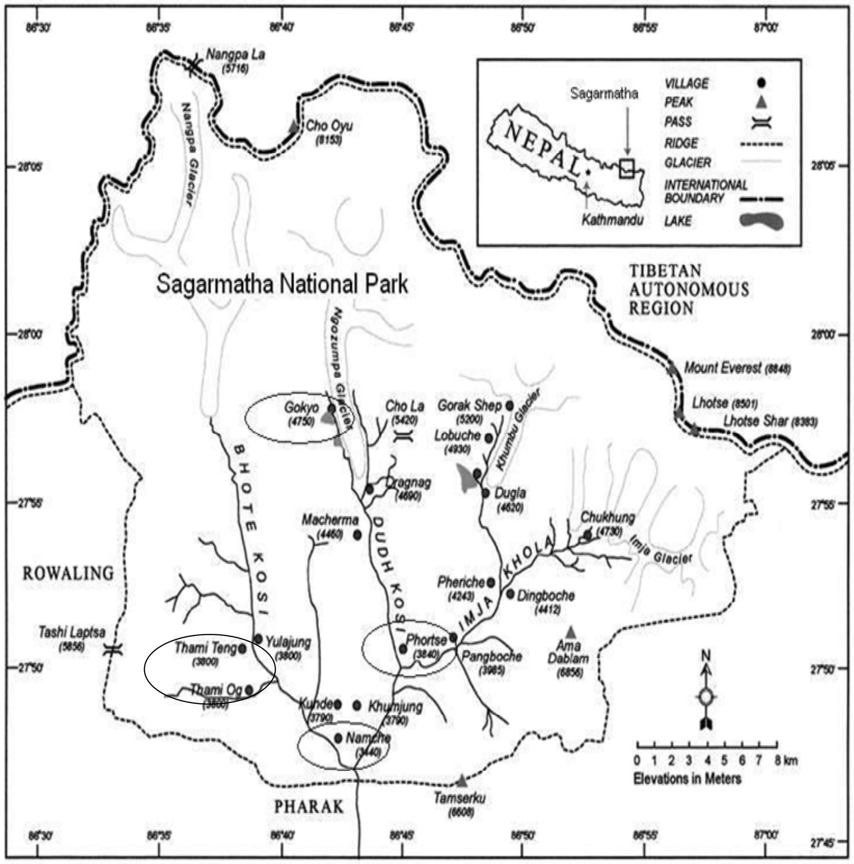
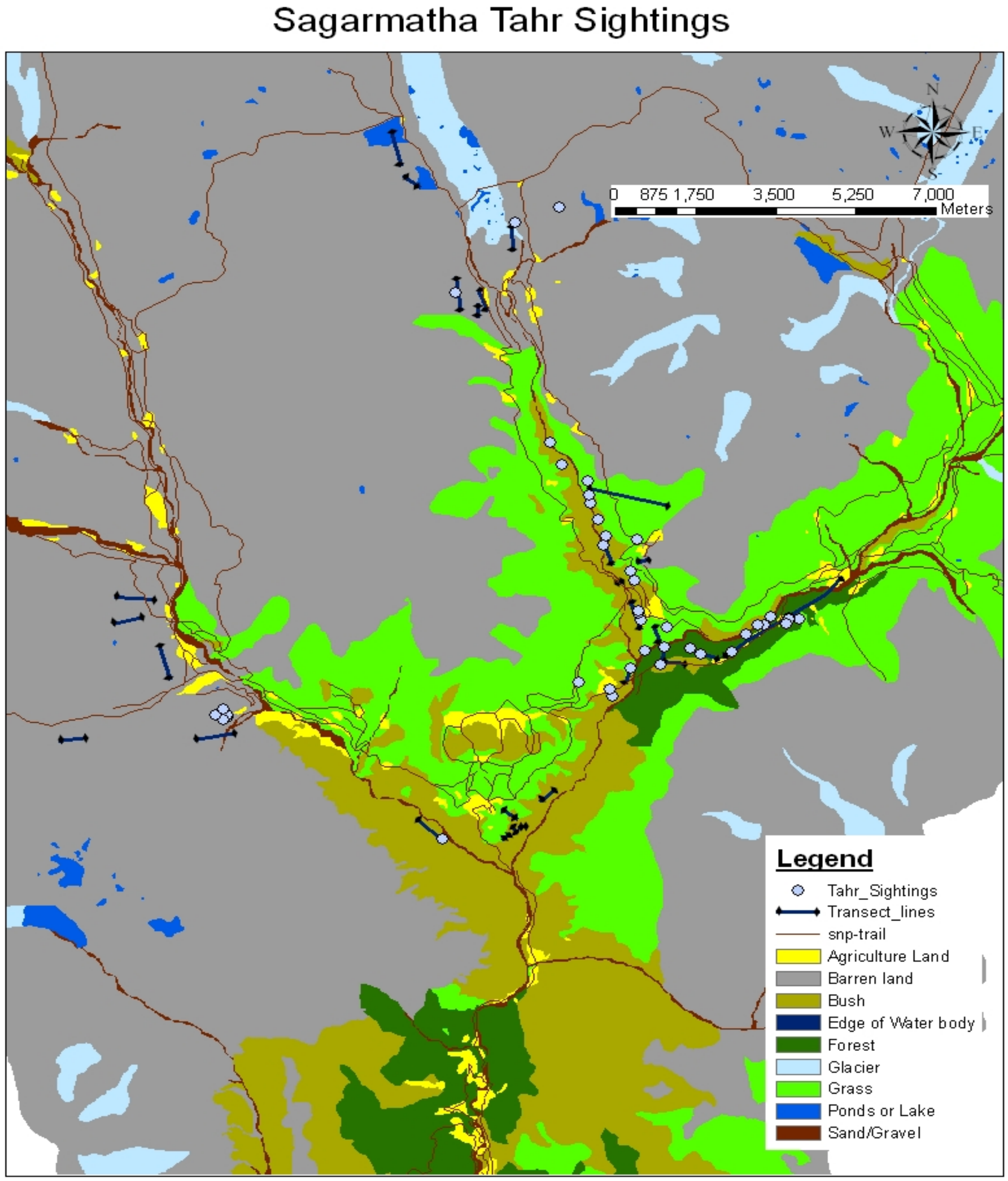


Figure 2: Distribution of tahr in Sagarmatha National Park



2.2.2 Tahr counts and classification

The survey was conducted in the autumns of 2004 and 2005, and the summer of 2006. In 2004 (October-November: 58 full days), I enumerated tahr in two valleys, Namche (15 km^2) and Phortse (18.3 km^2). The 2005 survey (August-November: 111 days) survey covered Namche, Phortse and two additional valleys, Gokyo (33.2 km^2) and Thame (20 km^2), when I extensively traversed total tahr habitats of *ca*. 86 km^2 on foot, accompanied by one or two local trackers. Walks were replicated in 2006 (May and June: 32 days). I located tahr from a number of suitable vantage points in periods of good visibility, scanning opposite slopes of the mountain with the aid of 8X21 binocular (Schaller 1977, 1998). Once spotted, I used 15-60X variable spotting scopes to count and classify them into 1) young (<1 year old), 2) yearling (1-<2 years), 3) adult female (≥2 years) and 4) adult males. The adult males were further classified into class I (2-<3 years), class II (3-4 years), class III (≥5-7 years, blond), class IV (>7-9 years, pale brown), and class V (≥9 years, dark brown), based on mane length/color, horn length/shape, and body size (S. Lovari *pers. com*).

Because I spent several days in each valley (average 50 full days or 600 hours per valley or *ca*. 7 hours per km^2), I recognized distinct herds (total 11) with fixed numbers of individuals. Members of a herd (sub-population) frequent the same locality, but at times are broken into smaller groups (Schaller 1973). I counted all tahr in a herd or group (total count method), spending a week in a valley and then moving to another valley (Figure 2). The total count reveals population sizes (a minimum number known alive) and population structure. I use second method to analyze structure, which is to add all tahr seen daily in the area (Schaller 1973). I made all observations myself to eliminate possible inter-observer bias.

2.2.3 Tahr faecal pellet transects

I systematically quantified pellets of tahr along randomly selected fecal pellet (hereafter pellet) transects to assess the relative abundance of tahr in four valleys. Indirect methods, which are usually based on pellet counts (Bailey and Putman 1981, Marques et al. 2001), give an estimate of the overall animal abundance. In extensive open ground areas, both direct and indirect count methods can be used, although the former are generally more effective and widely used. In woodland areas, however, direct methods are often not feasible or they are potentially biased (Ratcliffe 1987) and indirect methods are preferred. Here, I used indirect method to independently corroborate population sizes of tahr obtained from direct count method. Gregarious tahr leave their pellets in groups, therefore locating and counting pellets (pellet groups) was not difficult. I established 50 m long transect (at least 200 m apart from one another), six in each habitat type (scrubland and open forest) in each valley except in Gokyo. As Gokyo offers no distinct forests, I established only six transects in scrubland habitat. In total, I conducted 42 transects in my study area. I carefully counted all tahr pellets in a circular plot (with 3 m radius) placed at intervals of 10 m along transect. Altogether I sampled 210 plots.

2.3 RESULTS

I counted 277 tahr in four valleys of Sagarmatha in 2005 (repeated total count): Gokyo exhibited the least abundance of tahr and Phortse the greatest (Table 1), in eleven herds (broken into as many as 29 groups) across all valleys.

Table 1: Distribution of tahr across valleys

Valley	Class I	Class II	Dark brown	Pale brown	Blond	Un-known	Total Male	Female	Yearling	Young	Total
Gokyo	2	1	2	5	3	2	15	9	4	3	31
Namche	2	3	3	2	4	6	20	38	8	9	75
Phortse	4	1	10	12	5	4	36	58	9	22	125
Thame	0	0	4	4	5	3	16	18	3	9	46
Total	8	5	19	23	17	15	87	123	24	43	277

Tahr densities ranged from *ca.* 1 animal/km^2 in Gokyo to as high as 7 animals/km^2 in Phortse (Figure 3), results that matched closely with pellet abundance along transects (Figure 4). Tahr pellets were least abundant in Gokyo and most abundant in Phortse ($F_{(2,207)}=12.35$, $p<0.001$). Tahr used scrubland (70%) more than open forest ($\chi^2=60.9$, $p<0.001$, *d.f.*$= 1$, $n=257$, pooled data 2004 - 2006). Average group size was higher in forest than in scrubland (Mann-Whitney test $U=7963$, $p<0.01$). They equally frequented different types of terrains (cliffs, broken and rolling).

Figure 3: Tahr densities across valleys based on total counts (total animals=277)

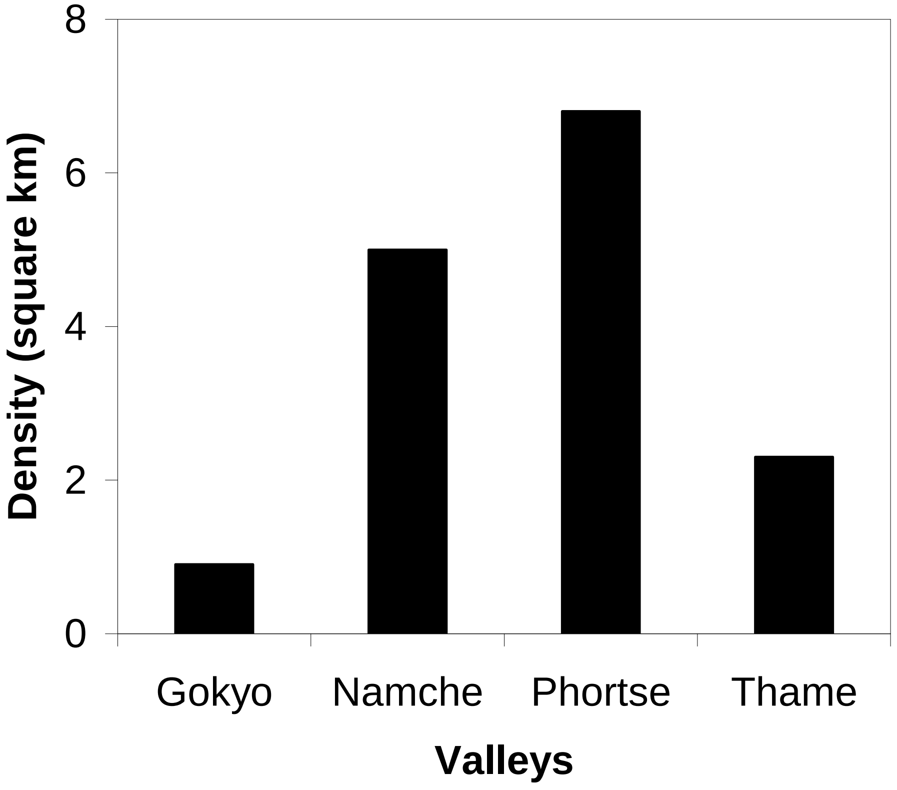
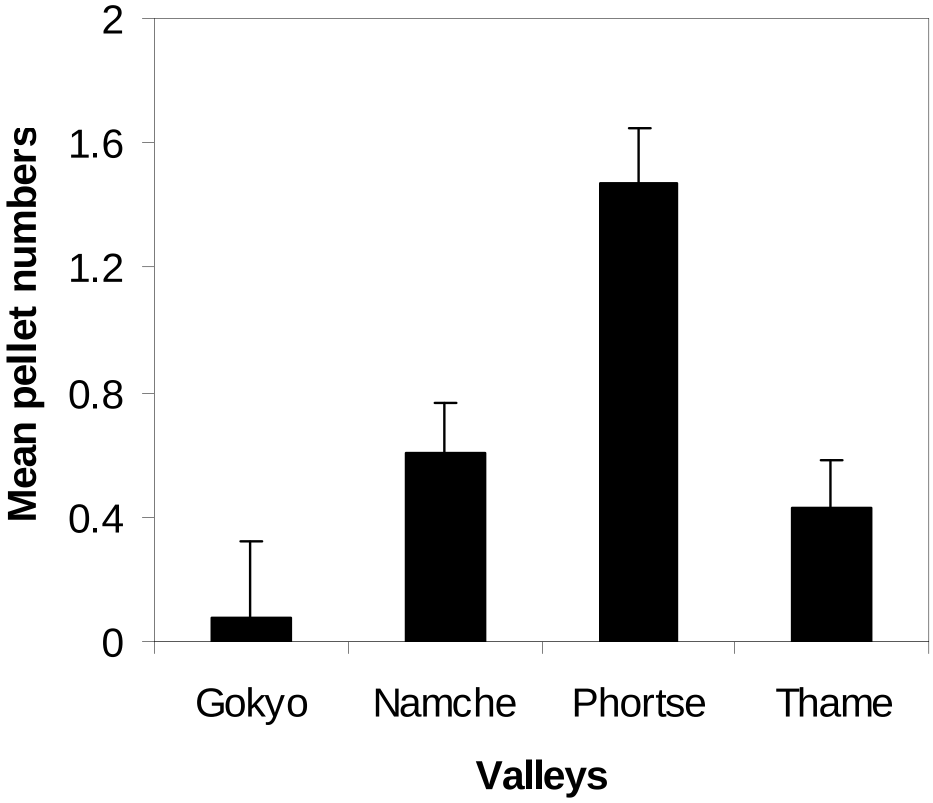


Figure 4: Abundance of tahr across valleys based on pellet counts along transects (plots=240)



I sighted and classified a total of 163 groups of tahr (422 individuals)- cumulative counts (see "second method" in section 2.2.2)- in four valleys in 2005 (Table 2). Population structures derived from two methods, i.e. (1) the known numbers from repeated total counts and (2) all tahr seen daily in each part of the study area showed close match (Tables 2, 3). Tahr exhibited the average group size of 8.7 (*SE*=0.6, range 2-46) (Table 2). This was consistent from 2004 to 2006 (overall mean group size 8.5, *SE*=0.01, range 1-46, pooled data) (Table 3).

Table 2: Population structure of tahr based on known tahr and all animals tallied in 2005

	Known animals (n=277, 11 herds)		All tallied (n=422, 163 groups)	
Himalayan tahr	Number	%	Number	%
Male Class I	8	2.9	18	1.3
Male Class II	5	1.8	25	1.8
Class III (blond)	19	6.9	49	3.4
Class IV (pale brown)	23	8.3	63	4.4
Class V (dark brown)	17	6.1	53	3.7
Unknown Male	15	5.4	148	10.4
Total Male	87	31.4	356	25
Female	123	44.4	770	54.1
Yearling	24	8.7	115	8.1
Young	43	15.5	181	12.7
Total	277	100	1422	100

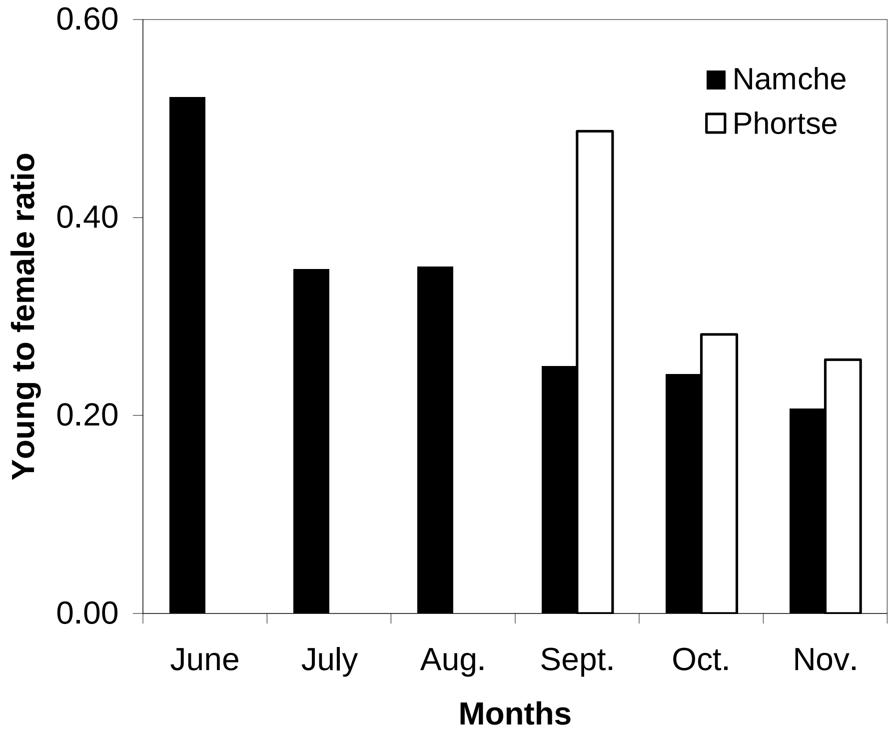
Table 3: Population structure of tahr: known numbers in 2005 vs. all tallied from 2004 to 2006

	Known animals in 2005 (n=277, 11 herds)		All tallied in 2004-2006 (n=2432, 285 groups)	
Himalayan tahr	Number	%	Number	%
Male Class I	8	2.9	45	1.9
Male Class II	5	1.8	69	2.8
Class III (blond)	19	6.9	75	3.1
Class IV (pale brown)	23	8.3	86	3.5
Class V (dark brown)	17	6.1	72	3.0
Unknown Male	15	5.4	257	10.6
Total Male	87	31.4	604	24.8
Female	123	44.4	1273	52.3
Yearling	24	8.7	198	8.1
Young	43	15.5	287	11.8
Unidentified (all)	0		70	2.9
Total	277	100	2432	100

Adult females outnumbered males (e.g. male to female ratio 0.7 in October 2005-cumulative data, all valleys). Male to female ratio, however, changed by the rutting season (November). For example, in Namche in 2004 this ratio changed from 0.2 (26 females vs. 6 males) in September to 1.2 by November when more males (31) joined the group.

The 2005 total counts revealed low young to female ratio, i.e. 0.3 (Table 2), in October and November. Only 30% females had young. The ratio of yearling to female (0.2) indicated that only 50% of the young survived to the following year. For Namche and Phortse, there was a decline in young to female ratios from *ca*. 0.5 in summer (birth season) to *ca*. 0.2 in late autumn (rutting season) (Figure 5).

Figure 5: Changes in young to female ratios of tahr in Sagarmatha in 2005



2.4 DISCUSSION

Exterminated in some areas and decimated throughout their range, tahr nevertheless remain the most numerous and widespread large ungulate in the southern range of the Himalaya (Schaller 1977, Shackleton 1997). In Nepal, Schaller (1977) mapped 14 tahr populations, but he visited only one population in upper Bhotekoshi, east Nepal. Baur (1989) estimated some 1,300-1,800 tahr occur inside protected areas (no density mentioned, no basis given as to how he arrived at this figure). Many more tahr populations undoubtedly exist throughout Nepal.

My estimate of tahr of 277 individuals in Sagarmatha is a minimum number in my study area of *ca.* 86 km^2 because a few tahr herds were no doubt overlooked, especially in very rugged terrains between Namche and Phortse. Heaps of fresh spoor in rugged and sparsely forested ravines below Namche and grassy slopes around Pheriche (4,700 m), Marulung (4,200 m) and slopes of Renojo La pass (>5,200 m) provided evidence of a few additional herds. In the entire Sagarmatha National Park, with some 160 km^2 potential tahr habitat (Ale et al. in prep), *ca.* 400 tahr may exist, a figure that is not substantially different from what Lovari (1992) estimated over a decade ago. This indicates that the tahr population has not been growing in Sagarmatha recently. No data exist, but anecdotal reports indicate that tahr numbers were on rise since the park was gazetted in 1976 (Heinen and Yonzon 1994, Green 1993). No comparative study is available from the Himalayas on population growth rates of tahr, but surveys in New Zealand indicate that they are prolific breeders in absence of predation and hunting. Systematic counts at 14 sites in southern Alps, New Zealand, from 1978-1979 to 1991-1996, revealed a six-fold increase in the mean abundance of tahr (Forsyth and Hickling 1998). That in Sagarmatha no substantial increment in tahr population size has occurred since the 1990s suggests that one or more limiting factors may have been impacting tahr populations.

Tahr occupy all major valleys of Sagarmatha, i.e. Gokyo, Namche, Phortse and Thame, although with differential abundance. Rugged and precipitous terrains of Phortse support more tahr ($7/km^2$) than any other valleys, followed by Namche (Figures 3 and 4). Cliffs may serve as escape habitat for tahr where they may retreat in times of danger (see Schaller 1973, 1977). Thame and Gokyo with relatively rolling terrain flanked by broad hills are sparsely populated by tahr, Gokyo being the least populated valley ($1/km^2$).

Since Burrard's (1925) hunting account, tahr have been known to traverse the steepest precipices. Studies in east Nepal (Kang Chu area; Schaller 1973), central Nepal (Langtang National Park; Green 1979) and in west Nepal (Annapurna Conservation Area; Gurung 1995) indicate that tahr occupy various habitat types from open alpine and subalpine grassland (scrubland) to dense forests. However, precipitous cliffs break the continuity of all these habitats. Schaller (1973) wrote, "Tahr frequented all habitats in my area, although the conifer-rhododendron belt appeared to be used mainly in transit…the animals certainly were not adverse to open terrain". Despite their reputation as high-alpine dwellers, tahr in New Zealand live in a variety of habitats (Forsyth and Tustin 2000).

In Sagarmatha, tahr preferred alpine/sub-alpine scrubland more than open (conifer) forest, perhaps in response to predation pressure in open forest (snow leopards preferred open forest with cliff faces in Sagarmatha (Chapters Three and Four). Tahr in New Zealand, in contrast, preferred scrubland to open forest in response to systematic helicopter shooting (culling) program (Forsyth and Tustin 2000). I found no significant difference in tahr using different terrains (cliff, broken and rolling) in Sagarmatha ($\chi^2=0.042$, $n=257$), although I usually encountered them in rolling hill close to precipitous terrain. This cliff-hugging behavior of tahr restricted their distribution. Such patchy distribution of tahr was evident in Gokyo and Thame valleys with expanses of hills with few cliffs. In contrast, Namche and Phortse valleys are more precipitous where both tahr and snow leopards are higher in abundance. Tahr grazed in steep rolling to gentle terrain, but bedded in nearby cliffs as their abundant pellets indicated. The best tahr habitat in Sagarmatha can be described as cliff faces broken by ledges supporting grasses, forbs and shrub mats at higher altitudes (mean 3863 m, $SE=0.9$, range 3260 m-4800 m, $n=191$) and patches of pine/birch forest at lower altitude (mean 3621 m, $SE=1.4$, range 3300 m-4031 m, $n=66$). In these mountains, steep hill slopes and undulating terrains are often characteristically interrupted by abrupt cliffs which act as oasis for these cliff-huggers whose presence is often very predictive in these enclaves.

I recognized eleven distinct herds in Sagarmatha: three each in Gokyo and Thame, four in Namche, and five in Phortse. These herds at times broke into as many as 29 groups, a group being defined as two or more individuals separated at least by 200 m of terrain from each other (Schaller 1973). Members of a herd often joined and separated in various combinations. In the course of a single day a herd may divide into several groups, perhaps in response to a number of factors, such as distribution and abundance of food, and encounters with predators (see Brown et al. 1999). For example, in Thame one herd of 14 was scattered into 4 groups on 31 October 2005 after a snow leopard visited their slopes. Sometimes groups remained scattered for several weeks and even months. A group of 21 tahr in Namche separated from its main herd for three months (May through August in 2005 and also in 2006).

From 2004 to 2006, tahr groups ranged in size from 1-46, with an average of *ca*. 8 (Tables 2 and 3). Lovari (1992), in the early 1990s, documented considerably smaller group size in Sagarmatha (Phortse/Pangboche median 5, range 1-53, *n*=9; and Namche 4, range 1-53, range 1-7, *n*=7). The average group size of tahr in Sagarmatha may have increased over the decade. Interestingly, such adaptation coincided with the return of snow leopards to the region (Ale and Boesi 2005). Annapurna (13.8, range 1-57, *n*=134) and Langtang (15, largest group 77) exhibited much larger groups of tahr. Among others, this apparent difference in average group size in different localities may be attributed to the degree of habitat ruggedness that characterizes particular localities. This in turn influences distribution and abundance of food and predation pressure. Sagarmatha supports smaller group sizes of tahr than that of Langtang and Annaupuna, perhaps because the former is more rugged than the later two areas. Schaller (1973) reported that Nilgiri tahr (average group size 23) fed on rolling grassland near cliffs, a habitat that provided an adequate food supply, thereby promoting cohesiveness among herd members. Himalayan tahr with the average group size of 6.5 (in Kang Chu), on the other hand, spent much of their time along narrow ledges where large groups would be at a disadvantage. Explanation of the different group sizes based on habitat features, however, requires caution, as factors other than habitat may be involved. For instance, in Himachal Pradesh, western Himalaya (India), herds of tahr were very small (~ = 1.7, *n* = 7) because hunting pressure severely reduced populations (Gaston et al. 1983). The largest (mixed) herd (46) I consistently recorded in Sagarmatha from 2004 to 2006 was smaller than that reported from Annapurna (57) and Langtang (77). Kang Chu, with severe hunting, had only 23 in its largest herd (Schaller 1973). The overall density of tahr in Sagarmatha (*ca*. 3.4/km^2) was much lower than that documented from elsewhere. Gurung (1995) reported tahr at the density of 7.7/km^2 in parts of Annapurna with no hunting. In the absence of hunting or natural predation, food can be the principle factor liming the size of populations. In Langtang area of Langtang National Park, local density of tahr reached as high as 24/km^2 (Green 1979: 170 in 7 km^2), where tahr were neither hunted nor was their habitat grazed by livestock. On the other hand, Yala, with ten times more domestic sheep and eight times more cattle than Langtang, supported low tahr density (6/km^2). In the absence of hunting in parts of New Zealand, tahr attain densities of >30/km^2 (Tustin and Challies 1978) but with regular hunting their population maintained a density of *ca.* 5/km^2.

In Sagarmatha, the park banned hunting of tahr and any other wildlife species in 1976, but allowed grazing by local livestock (yak and yak/cattle crossbreed). In the absence of hunting, it is plausible that current low tahr density in Sagarmatha can be attributed to predation by recently colonizing snow leopards. The impact of novel predators on prey populations can be substantial. Tahr constitute 40% of the snow leopard diet in Sagarmatha (Lovari et al. in prep.), and they behaviorally respond to the presence of snow leopards (Chapter Four). The effect of predation on tahr population structure is already evident (see below). The returning snow leopards (Chapter Three) may already be impacting tahr population in Sagarmatha.

The reproductive success of tahr, as expressed by the ratio of young to adult female, was poor (<0.4) in 2005. This was even lower (<0.3) in 2004. The proportion of females seen with a calf at the end of birth season is used as a proxy of birth rate (e.g. elk *Cervus elaphus* L.: Eberhardt et al. 1996; White-eared kob *Kobus kob leucotis* A. Smith: Fryxell 1987; moose *Alces alces* L.: Laurian et al. 2000). Such count-based methods that are widely used to monitor population levels in the field (Schaller 1998, Smart et al. 2004), however, may not be very reliable in closed habitats (see Bonenfant et al. 2005). No closed habitats (dense forests) exist in my study area where tahr occur. The young to female ratios of tahr in Annapurna (Gurung 1995) and Kang Chu (Schaller 1973) were within a normal range (0.5-0.6) for stable populations of ungulates (*ca*. 0.7 for growing populations). The young to female ratios of tahr in Pangboche/Phortse and Namche in 1991 and 1992 (Lovari 1992) were within normal range. The observed low young to female ratios in Sagarmatha may be a recent event. In 2005, ratios from the birth season (June-July) to the reproductive period (November-December) dropped from *ca*. 0.5 to 0.2, indicating that in these years young were apparently born in fair numbers but they decreased greatly between early summer and late autumn. As no disease has been reported from the region, predation should be responsible for young mortality. Young mortality due to predation can be high in ungulates (64% in some species: Bergerud 1988), and predators may affect prey population sizes and structure through mortality (*cf.* Terborgh et al. 2001, Sinclair et al. 2003).

Apparently, adult females outnumbered males in populations of tahr in Sagarmatha, in contrast to most ungulate species which show 1:1 ratio. The observation on low male to female ratio is not surprising outside the rutting season, because of bias in sightings (males wander widely while females are localized in small home ranges: Schaller 1973, 1977). The male to female ratio of tahr populations in Annapurna was 0.6 (Gurung 1995). As the rutting season advanced, male to female ratio increased favoring males (1.2 in Namche, at the end of November, i.e. the rutting month, in 2004) when males from neighboring areas may have joined the female groups.

Is predation by snow leopards responsible for the low reproductive success of tahr population in Sagarmatha? This may be a possible scenario. Manor and Saltz (2004) convincingly showed that recruitment of gazelles (expressed as Kid to female ratios) were lower in areas with more free-roaming dogs, threatening gazelle populations in southern coastal plain of Israel. Recruitment in ungulates is considered the primary determinant in their dynamics (Gaillard et al. 1998). A variety of factors impact recruitment in ungulates, of which predation appears to be dominant (Linnell et al. 1995). Unlike other caprins (sheep and goats and their relatives) with short synchronized births, the birthing season for tahr seems to stretch over a period of almost 4 months, from June to September, which may make their young exposed to predation. Synchronous births reduce predation rates on newborns by swamping predators with a surfeit of vulnerable prey (*cf*. Schaller 1998, Estes 1976), but I have no data to support this claim on tahr population in Sagarmatha. A regular, multiple year monitoring of tahr population in Sagarmatha is recommended to better understand tahr population dynamics.

References

Ale, S. B. and Boesi, R. 2005. Snow leopard sightings on the top of the world. *Cat News* 43: 19-21.

Bailey, R.E. and Putman, R.J. 1981. Estimation of fallow deer (*Dama dama*) populations from fecal accumulation. *J. Appl. Ecol.* 18: 697-702.

Bauer, J.J. 1990. The analysis of plant-herbivore interactions between ungulates and vegetation on alpine grasslands in the Himalayan region of Nepal. *Vegetatio* 90: 15-34.

Bergerud, A.T. 1988. Caribou, wolves and man. *Trends Ecol. Evol.* 3: 68-72.

Bjonness, I.M. 1980. Animal husbandry and grazing, a conservation and management problem in Sagarmatha National Park. *Norsk Geogr. Tidskr.* 33: 59-76.

Bonenfant C., Gaillard J.M., Klein F. et al. 2005. Can we use the young: female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. *J. Appl. Ecol.* 42: 361-370.

Brown, J.S., Laundre, J.W. and Gurung M. 1999. The ecology of fear: Optimal foraging, game theory and trophic interactions. *J. Mammal.* 80: 385-399.

Buffa, G., Ferrari, C. and Lovari, S. 1998. The upper Subalpine vegetation of Sagarmatha National Park (Khumbu Himal Area, Nepal) and its relationship with Himalayan tahr, musk deer and domestic yak. In: *Top of the World Environmental Research: Mount Everest-Himalayan Ecosystem (Ecovision World Monograph Series)-An outline*, eds. R. Baudo, G. Tartari and M. Munawar, pp. 167-175. Backhuys Publishers, The Netherlands.

Burrard, G. 1925. *Big game hunting in the Himalayas and Tibet*. London: H. Jenkins.

Caughley, G. 1970. Liberation, dispersal and distribution of Himalayan tahr in New Zealand. *N. Z. J. Sci.* 13: 220-239.

Caughley, G. 1971. The season of births for northern-hemisphere ungulates in New Zealand. *Mammalia* 25: 204-219.

Eberhardt, L.E. 1996. Growth of an isolated elk population. *J. Wildl. Manage.* 60: 369-373.

Estes, R. 1976. The significance of breeding synchrony in the wildebeest. *East Afr. Wildl. J.* 14: 135-152.

Fleming, R.L. Jr., *undated*. The natural history of the Everest area. A summary. Background paper for heart of Himalayas. *Conserv. Progr.*: 1-30.

Forsyth, D.M. and Tustin, K.G. 2000. Advances in New Zealand mammalogy 1990-2000: Himalayan tahr. *J. Roy. Soc. N.Z.* 31: 251-261.

Forsyth, D.M. 2000. Habitat selection and coexistence of the Alpine chamaois and Himalayan tahr in the eastern Southern Alps, New Zealand. *J. Zool. Lond.* 252: 215-225.

Forsyth, D.M. and Hickling, G.J. 1998: Increasing Himalayan tahr and decreasing chamois densities in the eastern Southern Alps, New Zealand: evidence for interspecific competition. *Oecologia* 113: 377-382.

Fryxell, J.M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. *Oecologia* 72: 83-91

Gaillard, J.M. and Festa-Bianchet, M., Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* 13: 58-63.

Gaston, A. J., Garson, P. J. and Hunter, M. L. Jr. 1983. The Status and Conservation of Forest Wildlife in Himachal Pradesh, Western Himalayas. *Biol. Conserv.* 27: 291-314

Green, M.J.B. 1979. Tahr in a Nepal National Park. *Oryx* 14: 140-144.

Green, M.J.B. 1993. *Nature reserves of the Himalaya and the mountains of Central Asia*. IUCN, Cambridge and Gland.

Gurung, J.B. 1995. *Population, habitat selection and conservation Himalayan tahr in Annapurna sanctuary, Nepal*. M.Sc. thesis. Agricultural university of Norway.

Heinen, J.T. and Yonzon, P.B. 1994. A Review of Conservation Issues and Programs in Nepal: from a single species focus towards bio-diversity protection. *Mountain Research and Development* 14: 61-76.

Holmes, J.R.S. 1970. A note on Himalayan tahr. *J. Bambay Nat. Hist. Soc.* 67: 103-105.

Jackson, R. and Ahlborn, G. 1989. Snow leopards (Panthera uncia) in Nepal- home range and movements. *National Geographic Research* 5: 161-175.

Laurian C. 2000. Effects of intensive harvesting on moose reproduction. *J. Appl. Ecol.* 37: 515-531.

Linnell, J.D.C., Aanes, R. and Andersen, R. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* 1: 209-223.

Lovari, S. 1992. Observations on the Himalayan tahr and other ungulates of the Sagarmatha National Park, Khumbu Himal, Nepal. *Oecologia Montana* 1: 51-52.

Lovari, S., Ale, S. B. and Boesi, R. *in press*. Notes on the large mammal community of Sagarmatha National Park (Nepal) In: *Proceedings of International Karakorum Conference*. Islamabad 2005.

Manor, R. and Saltz, D. 2004. The impact of free-roaming dogs on gazelle kid/female ratio in a fragmented area. *Biol. Conserv.* 119: 231–236.

Marques, F.F.C., Buckland, S.T., Goffin, D., Dixon, C.E. etc. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *J. Appl. Ecol.* 38: 349-363

Ratcliffe, P.R. 1987. Red deer population changes and the independent assessment of population size. *Symposia of the Zoological Society of London* 58: 153–165.

Schaller, G.B. 1973. Observations on Himalayan tahr. *J. Bombay Nat. Hist. Soc.* 70: 1-24.

Schaller, G.B. 1997. *Mountain Monarchs: Wild Sheep and Goats of the Himalayas*. University of Chicago Press: Chicago.

Schaller, G.B. 1998. Wildlife of the Tibetan Steppe. The University of Chicago Press: Chicago.

Shackleton, D.M. 1997. *Wild sheep and goats and their relatives. Status survey and conservation action plan for Caprinae.* IUCN, Gland, Switzerland and Cambridge, UK. 390 pp.

Sherpa, L.N. 1987. *A proposal for forest research and management in Sagarmatha (Mt. Everest) National Park, Nepal.* Working Paper No. 8. East-West Center, Hawaii. 47 pp.

Sherpa, M.N. 1985. *Conservation for survival: a conservation strategy for resource self-sufficiency in the Khumbu region of Nepal,* M.Sc. thesis. University of Manitoba, Canada.

Sinclair, A.R.E. and Arcese, P. 1995. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology* 76: 882-891.

Smart, J.C.R., Ward, A.I. and White P.C.L. 2004. Monitoring woodland deer populations in the UK: an imprecise science. *Mamm. Rev.* 34: 99-114.

Terborgh J. et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294: 1923- 1925.

Tustin, K.G. and Challies, C.N. 1978: The effects of hunting on the numbers and group sizes of Himalayan thar (Hemitragus jemlahicus) in Carneys Creek, Rangitata catchment. *NZ J. Ecol.* 1: 153-157.

CHAPTER THREE

3. STATUS, DISTRIBUTION AND ABUNDANCE OF SNOW LEOPARDS IN SAGARMATHA NATIONAL PARK, NEPAL

3.1 INTRODUCTION AND OBJECTIVES

Snow leopards *Uncia uncia* disappeared from the Everest region in the 1960s (Fleming, *undated*). Tourism has flourished since the first ascent of Mt. Everest in 1953, bringing both prosperity and adverse ecological impacts to the region (Sherpa 1985, 1987, Brower 1991). In 1976, the Everest region (area of 1,148 km^2) became Sagarmatha (Mt. Everest) National Park (hereafter Sagarmatha). By the late 1980s, Ahlborn and Jackson (1987) reported the presence of transient snow leopards, visiting from adjacent Tibet, in the Gokyo region of Sagarmatha. With almost three decades of effective protection, the virtual cessation of hunting and the higher abundance of Himalayan tahr *Hemitragus jemlahicus* (hereafter tahr), musk deer *Moschus chrysogaster* and game birds in Sagarmatha in contrast to the abundance of animals before 1976 (Green 1993), one would expect a possible return of snow leopards from Tibet (China). Have they really made a come back to this world heritage site? Apart from anecdotal claims of visitors having “spotted” a snow leopard, we know very little about the status of snow leopards in Sagarmatha. The objectives of this study were 1) to examine distribution and abundance of snow leopards in the major valleys of Sagarmatha, and 2) to assess their habitat use patterns.

For management purposes, information on local megafauna such as the snow leopard is crucial not only for the overall management of the park, but also to expedite the current trans-boundary landscape conservation efforts in Nepal and its neighboring countries (India and China). Because no protected areas in Nepal are large enough to contain viable populations of snow leopards and other large predators, the establishment of trans-frontier conservation areas at the landscape level with neighboring countries may facilitate genetic exchanges between individuals, ensuring their long-term survival (Jackson and Ahlborn 1990, Green 1993). Qomolongma Nature Preserve (Tibet, China), and Langtang, Makalu-Barun and Sagarmatha National Parks in Nepal form the largest trans-frontier conservation area covering approx. 40,000 km^2 in the Himalaya. In the adjacent Qomolongma, snow leopards occur "widely but sparsely" (Jackson et al. 1994), but we know virtually nothing about the distribution and abundance of snow leopards in the southern slopes of Mt. Everest.

Assessing distribution, abundance and habitat use patterns of cryptic, rare carnivores can be problematic. For elusive felids, field signs such as feces and pugmrks (tracks) may often provide the only practical means by which to monitor density and abundance. Signs of large predators infer not only their habitat use patterns (see Schaller 1977, 1998), but signs may provide an index of abundance that may be used to compare abundance between areas in space or to monitor trends in one location over time (Wilson and Delahay 2001). Index values can be used to estimate population size when it is possible to calibrate them with estimates derived from a formal estimate method carried out in parallel. For snow leopards, attempts have been made to correlate sign density (all sign types) and cat density (Ahlborn and Jackson 1988, Jackson and Hunter 1996). Other studies have used tracks to identify different individuals and population abundance, e.g. Smallwood and Fitzhugh (1993) and Grigione et al. (1999) for mountain lions *Puma concolor*, and Stander (1997) for common leopard *Panthera pardus*. Here I use such indirect method of sign search to study snow leopards in Sagarmatha.

3.2 METHODS

3.2.1 Study area

The Sagarmatha National Park (27°45’- 28°07’ N; 86°28’- 87°07’ E) lies in the Solu-Khumbu district of the northeastern region of Nepal. My survey area consists of four survey blocks 15-33 km^2 in size, a total of *ca*. 86 km^2, the survey blocks which represent the four main valleys of Sagarmatha: Gokyo (33.2 km^2), Namche (15 km^2), Phortse (18.3 km^2) and Thame (20 km^2), all lie along three watersheds- Imja, Dudhkosi and Bhotekosi (Figure 1). The park was established in 1976 to conserve tahr and musk deer, with protection carried out by park authorities in combination with a battalion of the Nepal army (400 soldiers) and local people to check such activities as hunting in this Natural World Heritage Site (criterion III).

My study area reveals two distinct vegetation habitats: scrubland and forest. Forest (open forest) at the altitude of 3,000 - 4,000 m a.s.l. is dominated by *Pinus wallichiana*, *Abies* spp. and *Betula utilis*. These patches of open forests grade higher up into the alpine and subalpine grassland/scrubland zones (4,000-5,000 m a.s.l.) with thick mats of *Juniperus* spp. and *Rhododendron* spp. For the ease of discussion, I call this habitat above tree line as “scrubland” (see Buffa et al. 1998, for vegetation detail). In addition to snow leopards, tahr and musk deer, wildlife in the park include game bird species such as Impeyan pheasant

Lophophorus imejanus, Tibetan snow cock *Tetraogallus tibetanus*, and blood pheasant *Ithaginus cruentus*, as well as several mammal species such as the pika *Ochotona himalayana*, the Himalayan weasel *Mustela sibirica*, the hill fox *Vulpes vulpes*, and the golden jackal *Canis aureus* (Lovari et al. in press).

3.2.2 Snow leopard survey

I conducted the snow leopard survey in the autumns of 2004 and 2005 and the summer of 2006. In 2004 (September-October), I searched for snow leopard signs in the Gokyo, Namche and Phortse valleys. In 2005 (August-November) and 2006 (June-July), I surveyed those three valleys as well as Thame valley, traversing extensively, on foot.

Sign transects

With modifications to meet my particular field conditions and data needs, I employed the techniques of the Snow Leopard Information Management System (SLIMS) (Jackson and Hunter 1996), a standardized approach widely used in snow leopard research. Sign surveys were conducted in all areas in Sagarmatha but the search was intensified in the four main valleys (Gokyo, Namche, Phortse and Thame) to determine the distribution and relative abundance of snow leopards. Transects were laid out in possible snow leopard routes in each valley (29 transects, mean length 652.8 m, $SE=0.33$). Most transects (Figure 6) were along landforms where snow leopard signs are likely to be found, such as ridgelines, cliff edges, or livestock trails. To minimize within-transect variability, transects were short and rarely crossed habitat boundaries. Transects were walked by a pair of observers and all signs recorded as to type and number. At each site with sign, I recorded the date, global positioning system location, elevation, slope, aspects, land ruggedness, habitat types and distance to cliff, within a radius of 20 m. Four types of signs were recorded: scrape (a characteristic heart-shaped claw raking), pug-marks (i.e. tracks), scats, and spray/urine (scent-mark, made by spraying urine usually on over-hanging rocks and cliff bases. Cliffs were defined as being surfaces of 50^0 or steeper over an area of at least 5 m width and height (McCarthy 2000).

On each transect a number of random sites (6 to 8 per km) were selected and all habitat features were recorded to allow comparisons with sign sites (McCarthy 2000). Random sites were selected using a random number table. The attributes of sign sites and random sites were used to compare use and availability. A selectivity value was assigned ranging from '-' indicating that snow leopards marked sites with these attributes less frequently than they occur (p=0.05) to '+', indicating they marked these site types more frequently than would be expected by chance alone. A selectivity value of '0' indicated marking use in proportion to availability. Sign density, expressed in sign/km of transect was calculated for each valley. I tested for differences in mean density between valleys with a chi-square test. Substrate type (rock, gravel, vegetation, snow) may influence sign deposition rates and longevity. However, in this study substrates were thought to occur in similar proportions across all valleys (*cf*. McCarthy 2000).

Incidental method

Besides collecting information along sign transects, I recorded all information whenever a snow leopard sign was encountered incidentally while locating tahr for behavioral observation (Chapter Four). I compared frequency of signs and habitat attributes of sign site, obtained using the two methods (transect method vs. incidental method).

3.3 RESULTS

Altogether, 24 transects were walked covering 13.9 km in length, in 2004. In 2005, I laid out 5 additional transects (5 km), making the total transect length 18.9 km. From 2004 to 2006, I characterized 193 snow leopard signs along transects and 252 signs encountered incidentally across four valleys (Figure 6). Scrapes (63%) were by far the most common sign type, which together with feces (21%) constituted over 80% of signs characterized.

Snow leopard sign density/km of transect was not equal across valleys, and regional differences were apparent in 2004 ($\chi2=8.4$, *d.f.=2*, $P<0.05$, adjusted for overall transect length), 2005 (Table 4, $\chi2=48.7$, *d.f.=3*, $P<0.01$), and 2006 ($\chi2=24$, *d.f.=3*, $P<0.01$).

Figure 6. Snow leopard signs in 2004 and 2005

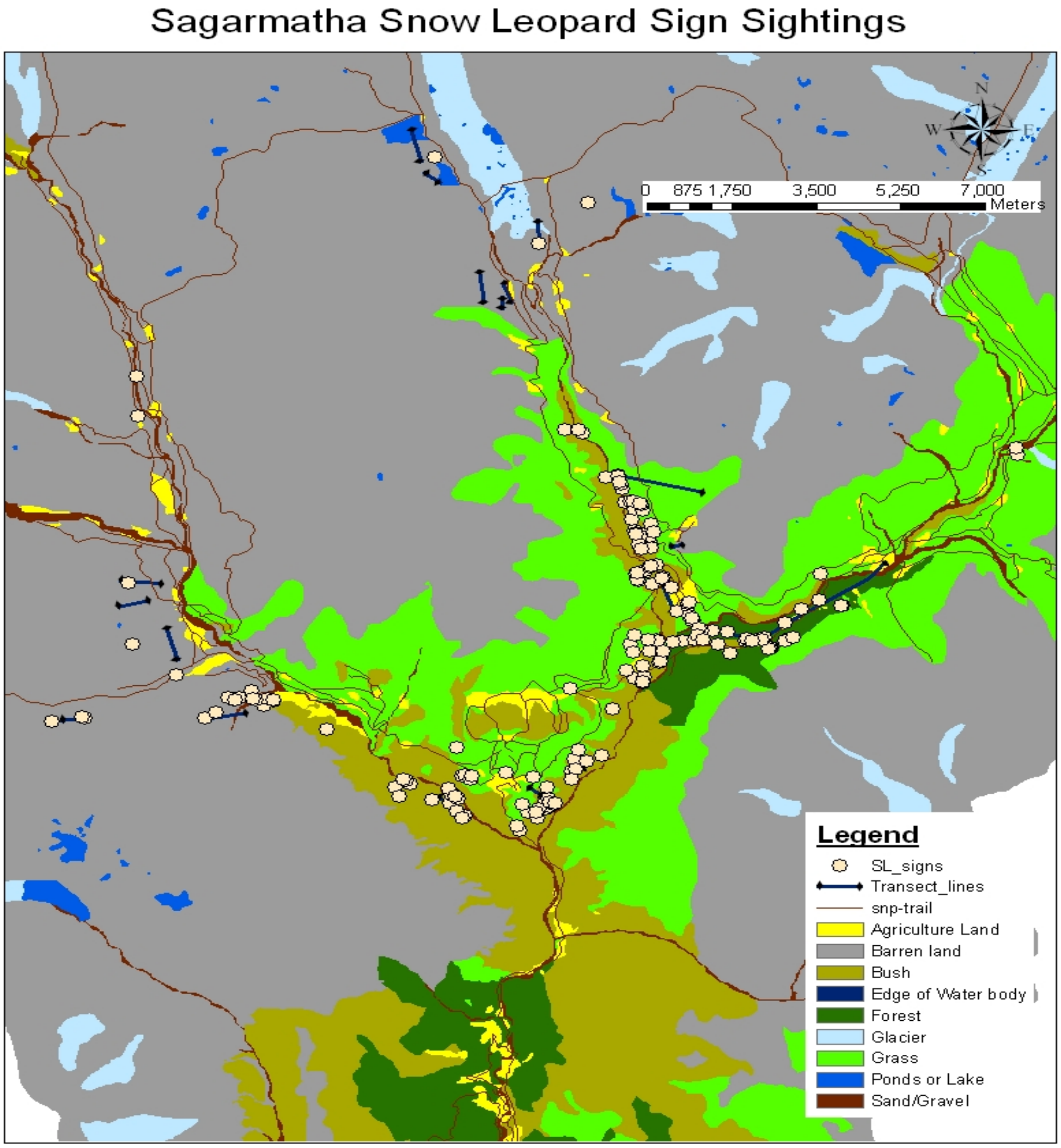


Table 4: Distribution of snow leopard sign across valleys in 2005

Valley	Transect (km)	Scrape	Feces	Pugmark	Other	Total	Mean sign (all)/km	Mean scrape/km
Gokyo	4.6	9	0	1	1	11	2.4	2.0
Namche	3.6	21	6	4	3	34	9.4	5.8
Phortse	5.8	25	4	2	1	32	5.5	4.3
Thame	5	6	2	0	0	8	1.6	1.2
Total	19	61	12	7	5	85	4.5	3.2

Namche valley had a higher mean density of sign/km of transect when compared to other valleys in 2005 and 2006, whereas Phortse exhibited the highest sign density in 2004. Gokyo, Namche and Phortse revealed more scrapes proportionately than any other sign type (cumulative data 2005-2006, Figure 7, $\chi 2=41.1$, *d.f.=9*, $P<0.01$). The sign percentage derived from transects and the incidental method showed a close match (Figure 8, chi-square not significant).

Sign abundance along one-time transects may vary seasonally (Figure 9) and yearly (Figure 10). The frequency of sign in August 2005 was lower than in October 2005 (Figure 9, $\chi 2=6.9$, *d.f.=1*, $P<0.01$). There were more signs in October 2005 than in October 2004 (Figure 10, $\chi 2=5.9$, *d.f.=1*, $P<0.05$).

Figure 7: Sign distribution across valleys (2005-2006)

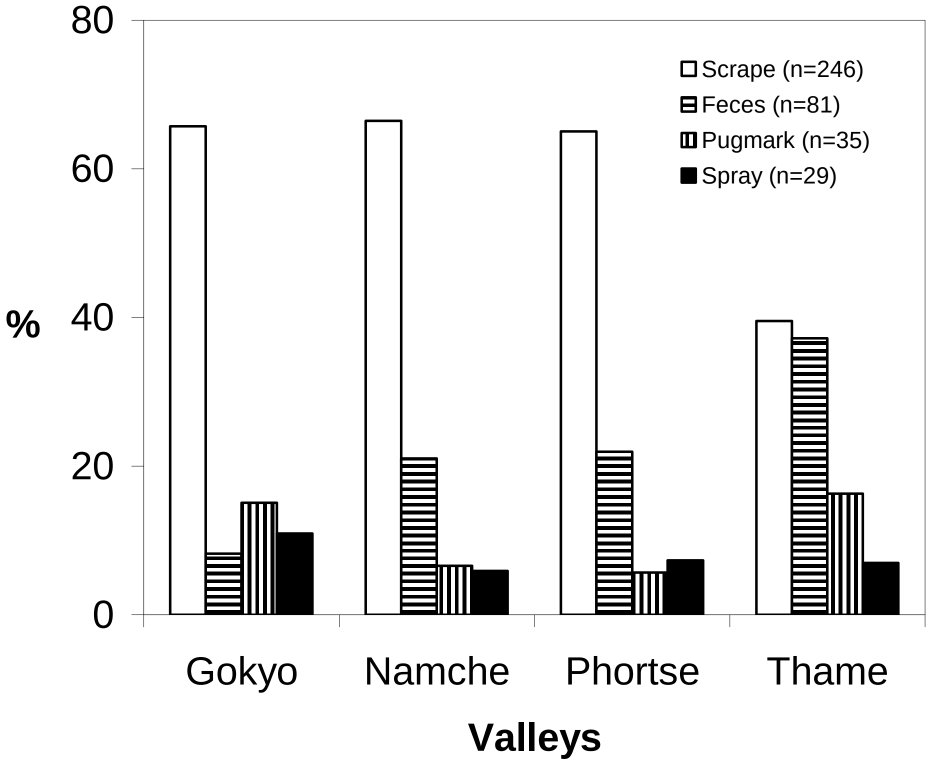


Figure 8: Snow leopard signs (transects vs. incidental method, 2005-2006)

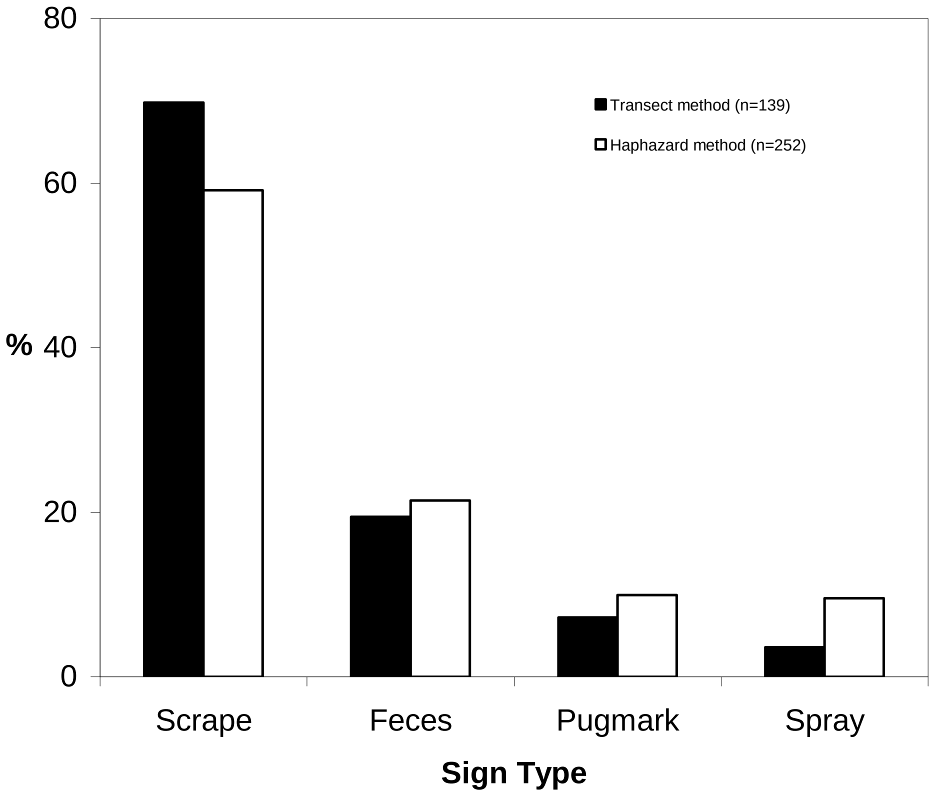


Figure 9: Seasonal variation in sign abundance across valleys in 2005

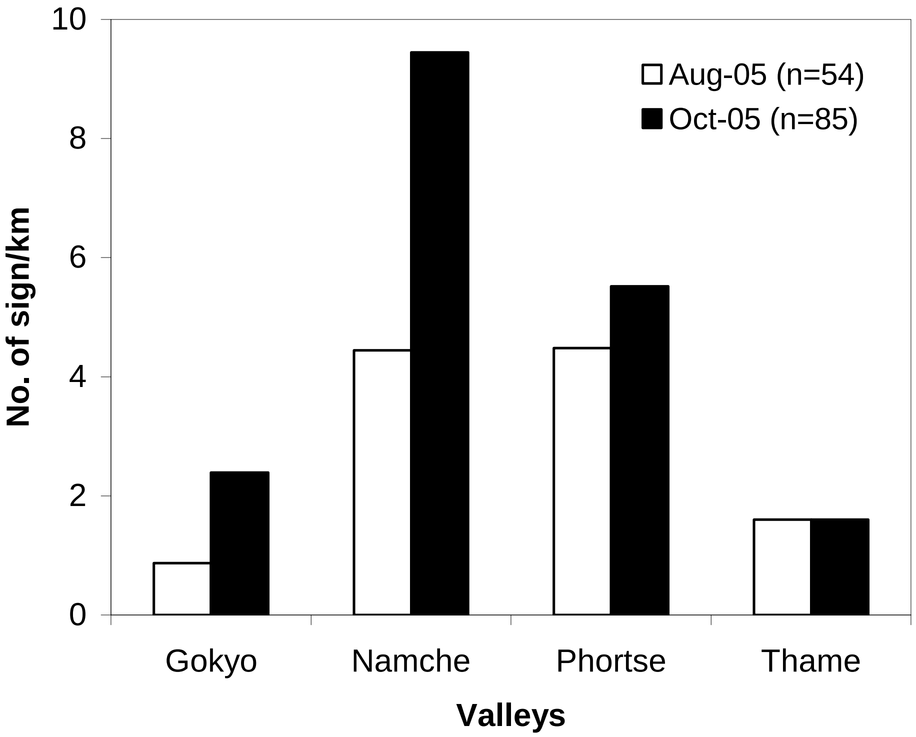
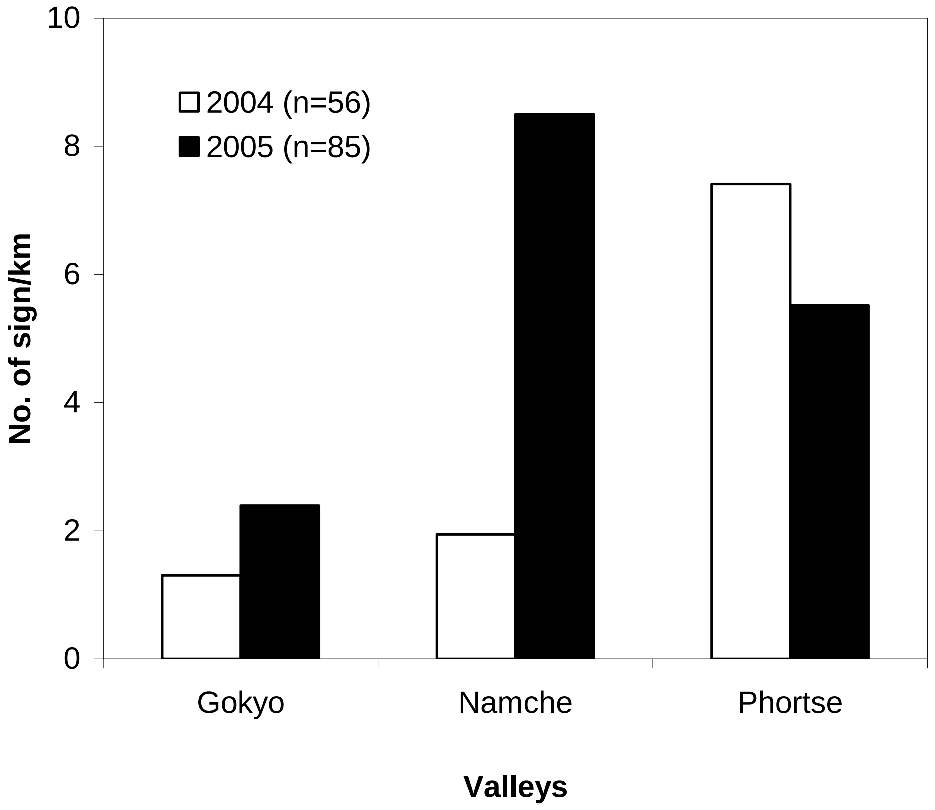


Figure 10: Yearly variation in snow leopard sign abundance across valleys



I compared altogether 330 sites, including 193 sign sites and 137 random sites, to compare use and availability. Four attributes were tested using Chi-square goodness-of-fit: elevation, slope, terrain ruggedness, and habitat type (vegetative cover). Use of each habitat variables differed significantly from availability (Table 5).

Table 5: Habitat characteristics of snow leopard sign sites and random sites along transects (2004-2006)

	Sign sites (n=193)		Random sites (n=137)		Chi2	Selectivity	P-value
	Freq	%	Freq	%			
Elevation (m) (χ2=8.07, df=2, p<0.01)							
3000-3500	4	2.1	9	5.4	2.0	0	
3501-4000	101	52.3	66	39.3	4.3	+	p<0.05
>4001	88	45.6	93	55.4	1.7	0	
	193	100	168	100	8.1		
Slope (deegre) (χ2=32.19, df=2, p<0.001)							
0-20	18	9.3	52	31.1	15.3	-	p<0.01
21-40	90	46.6	75	44.9	0.1	0	
>40	85	44.0	40	24.0	16.8	+	p<0.01
	193	100	167	100	32.2		
Ruggedness (χ2=68.04, df=2, p<0.001)							
Broken	85	44.0	99	61.1	4.8	-	p<0.05
Cliff	64	33.2	15	9.3	61.7	+	p<0.01
Rolling	44	22.8	48	29.6	1.6	0	
	193	100	162	100	68.0		
Habitat Type (χ2=78.08, df=1, p<0.001)							
(sparse) Forest	82	42.5	21	12.9	68.0	+	p<0.01
Scrubland	111	57.5	142	87.1	10.1	-	p<0.01
Total	193	100	163	100	78.1		

Marking activity indicated a selection for open forest habitats with elevations between 3,501 to 4,000 m in cliffy terrain. Snow leopards selectively marked areas with steep slopes (excess to 40^0) and avoided gentle slopes ($<20^0$).

Habitat use patterns of snow leopards and tahr closely matched (Figs. 6a-e). Snow leopard signs were located at a mean altitude of 3,914 m (*SD=323.4, n=422*) and in sites with the mean slope of 40.8^0 (*SD=15.9, n=407*).

I recorded ten different sets of pugmarks in Sagarmatha in 2005 (Table 6).

Table 6: Snow leopard pugmarks (mean length and width in cm) across valleys in Sagarmatha in 2005

Individuals	Length	SE	Width	SE	n	Valley
1	9.48	0.01	9.16	0.01	5	Gokyo
2	8.50	0.00	7.97	0.01	6	Gokyo
3	8.95	0.01	8.43	0.01	4	Namche
4	9.90	0.01	9.50	0.03	3	Namche
5	7.98	0.00	7.50	0.01	4	Namche
6	8.67	0.03	8.17	0.91	3	Phorste
7	7.03	0.01	6.27	0.01	3	Phorste
8	7.17	0.06	6.73	0.06	3	Phorste
9	8.32	0.01	7.65	0.01	6	Thame
10	7.97	0.03	7.10	0.02	3	Thame

3.4 DISCUSSION

The presence of snow leopards in all four major valleys, as determined in this study, varies from what was reported previously by Ahlborn and Jackson (1987) who recorded sign possibly made by (transient) cats from Tibet only in Gokyo in 1987. Apparently, snow leopards have expanded their range in Sagarmatha. In 2004, I located signs in 58% of 24 transects walked, with 2.5 sites/km and 4.2 all signs/km (2.5 scrape/km). In contrast, Ahlborn and Jackson (1987) reported signs in 13% of 31 transects laid out, with 0.7 sites/km and 2.6 all signs/km (0.5 scrapes/km). The subsequent findings in 2005 (Table 4) and in 2006 showed similar trends. Snow leopards have actually increased in abundance in Sagarmatha, as indicated by ample signs recorded from four valleys, with actual sightings of the cat in all valleys except Gokyo (three times in Namche, twice in Phortse, and once in Thame). Apparently, snow leopards now are resident in Sagarmatha.

Reported snow leopard densities based on sign surveys vary across snow leopard range countries, although the same method (SLIMS: Jackson and Hunter 1996) was followed. The sign density (4.5 all sign/km, 3.2 scrape/km) in Sagarmatha was higher than that reported from central Ladak, India (2.6 scrapes/km, with 1 cat/100 km^2: Fox et al. 1991) and northern Pakistan (2.4 all sign, with 1.2-2 cats/100 km^2: Hussain 2003). Mallon (1991) came up with much lower sign density in Ladak (0.8 scrape/km, with cat density <1-4 cats/100 km^2). McCarthy (2000) assessed the entire Mongolia and provided his estimate of snow leopard numbers in between 1-4 cats/100 km^2 based on 1.92-38.5 sign densities per km. The Langu valley of west Nepal, with snow leopard density of 8-10 cats/100 km^2, the densest population of the snow leopard recorded so far, had 36 all signs/km (11 scrapes per kilometer).

Following SLIMS, my sign density may yield 1-2 snow leopards per 100 km^2 in Sagarmatha (Jackson and Hunter 1996). However, judging from different sets of pugmarks (two different individuals actually sighted), I obtained evidence of four snow leopards using a minimum area of 60 km^2 in 2004, and at least 6 or possibly more different individuals (Table 6) in 86 km^2 in 2005 (two individuals sighted feeding from the same carcass). This suggests a higher abundance than the estimate based on sign density alone. This disparity may arise because all earlier surveys on snow leopards were done in dry and arid parts of the snow leopard range. Sagarmatha, in contrast, is relatively more mesic and vegetated. Cats may rake a tuft of grass that may not be very obvious to human eyes. Monsoons may simply shorten age of a sign or cause signs (e.g. feces) to disappear completely. All these confounding factors may have led to underestimated sign counts in Sagarmatha.

Sign density on transects may be a function of more than cat density. Snow leopards tend to move, bed and mark along linear geographical features such as crests, major ridgelines, at the base of cliffs and in gullies (Jackson and Ahlborn 1984, Mallon 1984, 1991, Fox et al. 1991, Fox 1994, Jackson 1996, McCarthy et al. 2005). Monitoring for signs along these features is therefore the best possible way at present of estimating snow leopard population trends in an area (Jackson and Hunter 1996). Indeed the number of scrapes, feces and other sign in an area gives an indication of the cat's presence and distribution, but such data along “one-time” transect may contain biases. Different use of terrain must be accounted for when using scrape (and other sign) to estimate abundance (Schaller 1998). The abundance of sign in an area is also influenced by differential sign longevity and how it is influenced by seasonal changes in livestock disturbance, weather, and different topography (Fox et al.

1991). The relation between territorial marks and density is not a linear one. At very low densities, animals may mark very little - if at all; at high densities they may do it very much, more than expected. No mark does not necessarily mean no individual is present. Clearly, there are difficulties in comparing sign densities to draw inferences, but if limitations are recognized and addressed, sign density as a predictor of leopard density may provide the best available and easily applied method to assess relative snow leopard densities (Jackson and Hunter 1996, McCarthy 2000).

Upper portions of Gokyo valley provide a poor habitat for snow leopards, whereas much rugged lower Gokyo offer quality habitat. I inquired with several local herders about the status of cats in upper Gokyo. "*Sarken mindu*" (no snow leopard), replied a local herder. That I recorded only one scrape at the elevation of 5,080 m, the highest record of snow leopard sign for the Everest, indicates that snow leopards are sparse in upper Gokyo. With only one mixed herd of 11 tahr, snow leopards may have little incentive to make regular excursions up to this highland. In Gokyo, at least two individuals were active from 13-19 September 2005. The smaller one walked twice along my transects. Their home range may cover adjacent portions of Phortse. In October 2004, for example, I tracked a trail of fresh scrapes, along *ca.* 15 km of the main trail that connects Gokyo and Phortse. Two snow leopards, perhaps a mother (with characteristically distinct lobes in its hind pad) and a cub (with a smaller set of pugmarks), entered Gokyo from Konar (Phortse) crossing Khumjung Chhorten (4,250 m). Snow leopards heavily marked this narrow very rugged corridor which divides Gokyo and Phortse valleys. Two additional travel routes for snow leopard exist in between Gokyo and Phortse.

Most of Thame, in particular the upper region on the way to Tibet, consists of broad valleys flanked with hills much less suited for snow leopards, although it may have been the very travel route for the first snow leopards entering Sagarmatha from Tibet in the 1980s. Most of Thame does not support snow leopards. However, the lower Thame offers one of the best cliffy (thinly forested) slopes for cats to hunt tahr (as excerpt from my field notes indicate):

> *On 8 June 2006 (5:45 am), a lone tahr female, with her four-day old kid, continuously blew alarming whistles dozens of times. The female has been resting in this ledge since 4 June, after it had given birth to a kid, the first kid for the year 2006. My sixth sense was alert: something was wrong! In such steep terrain of Thame, my first reaction was perhaps lammergeyer, or hill fox, both known to prey on tahr kids, was nearby. My careful scanning of the nearby slopes via binoculars, however, revealed an adult snow leopard, climbing up! In three field seasons of snow leopard survey, following the vigilance behavior of the prey led us for the sixth time to its predator, the snow leopard. I tracked the cat for almost three hours (6:15- 9:20 am) with the aid of my telescope (it climbed almost four hundred meters up the sheer cliff, four times it fell off the slope). I learnt one thing - snow leopard can stalk tahr in cliffs (this may explain why tahr were significantly more vigilant in cliffs in 2005!).*

I traveled all the way to Lung (5,090 m) on the way to the Tibetan plateau (north-west of Thame) and recorded no snow leopard sign, but local herders and Tibetan nomads with caravans of yaks at Khusum (4,500 m) reported that they sometimes lose their stocks to snow leopards. Cats may roam up to Marulung (4,210 m) and its surrounding hills (>4,500 m) perhaps to hunt baby yaks (tahr are uncommon here) and may cross Renjo-La pass (5,340 m) leading to Gokyo. That I encountered only two scrapes despite my intensive search for five full days indicates that snow leopards are indeed rare visitors in this part of Thame.

In Namche, I found evidence of snow leopards throughout my survey area, and so was the case with Phortse. My spoor hunt in Namche revealed three different snow leopards in 15 km^2 (Table 6). Do the same individuals travel to adjoining Thame and Phortse? This is difficult to answer, but they may do so by judging the size of their home range, i.e. 11-37 km^2 in west Nepal (Jackson 1996) or much larger (four times) in areas with sparse prey in Mongolia (McCarthy et al. 2005).

Beyond Pangboche (north east of Namche) on the way to the Everest base camp, local herdsmen claimed that cats are rare in Pheriche and Chukhung. This large chunk of arid land of the Everest massif is farthest from the source if we consider Nagpa-La the travel route of the first snow leopards to Sagarmatha and Tibet as the source of snow leopards. Cats may wander up to Pheriche and Dingboche (both above 4,300 m) in summer (I located two scrapes in July 10, 2006). Areas further beyond, e.g. Lobuche (5,018 m), Gorak Shep (5,170 m) and the Everest base camp (5,364 m), with no resident tahr, are less likely to support snow leopards. At least three different cats were using my intensive search area (18 km^2) in Phortse. Perhaps these same individuals also traveled to Gokyo. Among three, one was adult and two sub-adults. One of the sub-adults had a distorted middle toe! I followed the other sub-adult on 22 September 2005:

> *On 22 September 2005 (10 am), I walked snow leopard transect number three (Phortse), recording 9 signs at 7 sites, and took vigilance data on a group of six adult males. At 12 noon, thick mist covered surrounding hills making tahr invisible. I ambled to the nearby ridgeline where I was fortunate to collect a huge pile of (fresh) scats. This snow leopard was apparently well fed! Had it made a recent kill? But, I saw no Himalayan griffons hovering around anywhere nearby. I waited on this ridge for about two hours till 6 pm in case snow leopard would make its majestic appearance. As I headed to my camp, I heard distant sharp whistles made by an obviously alarmed tahr somewhere near my transect one. The following day at 5 am, I hurried to the site only to discover scrapes and a set of several pugmarks of a snow leopard and numerous hoof-marks hastily made by escaping tahr. The group of six males had split into two, >200 m apart from one another. I tracked this snow leopard, which obviously scared these tahr, for 2.3 km and counted 13 scrapes. It had raked one scrape per 174 m linear distance traveled. I discovered its pugmarks in two sites and collected fresh scats. The cat scented an overhanging rock before disappearing into nearby cliff leading to Imaja (river).*

Snow leopards make scrapes at conspicuous locations such as the base of cliffs and ridgelines (Schaller 1977, Jackson and Ahlborn 1984, Mallon 1991, Fox et al. 1991). Most areas of Thame (and upper Gokyo) are flanked by hills with broad ridges where snow leopards rarely patrol in search of tahr but rather follow regular human or livestock trails. The cat's travel routes were less well defined in these massifs, making it difficult to locate signs along ridges. Relatively much rugged Namche and Phortse revealed higher abundance of scrapes (Figure 7). Although the rank order of sign frequency is the same regardless of method (Figure 8), a more even distribution of signs among types occurs under the incidental method than the transect method. Although this suggests the utility of the transect method in locating scrapes (the first radio-telemetry study on snow leopard reported that scrapes predicted 87% of snow leopard use of an area: Ahlborn and Jackson 1988), other sign type (e.g. feces), however, may be under-represented in the transect method.

Phortse exhibited the most abundant snow leopards signs in 2004 among three valleys sampled (Gokyo, Namche and Phortse). The 2005 survey, however, indicated Namche with the greatest signs (Table 4). This disparity may be observer-biased, or other factors such as livestock movement may have been involved. In 2004, there was an excessive movement of yaks (*ca*. 1000) in Namche that came from Tibet with Tibetan traders. In 2005, no trading (by Tibetan traders) was allowed in Namche, which minimized the subsequent impact of yaks.

Sign abundance along one-time transects may vary seasonally (Figure 5). For example, the frequency of sign in August 2005 was lower than in October 2005 because monsoon rain quickly destroys most sign during July and August in the Himalaya. Since the production of scrapes by snow leopards is apparently greatest during the breeding seasons of January and February (Jackson 1996), the timing of comparative surveys is important, and surveys conducted soon after breeding (April-May) on the south side of the Himalaya could be expected to have a seasonal high sign frequency (Fox et al. 1991). However, surveys conducted too early in the spring may under-estimate density because the snow can hide sign

(Ahlborn and Jackson 1988). The sign transect can, however, provide reasonable assessments of change given sufficient sampling effort when repeated same-site/season monitoring (Figure 10). Incorporation of such simple monitoring as part of protected area management in the Himalaya can be instrumental in research on snow leopards and their prey.

Snow leopard in Sagarmatha selected cliffs, steep slopes excess to $>40^0$ and open forest (Table 5). Cats prefer broken terrain with cliffs and habitat edges (Schaller 1977, Ahlborn and Jackson 1988, Chundawat 1990, Fox et al. 1991, Jackson 1996, McCarthy et al. 2005). They may also traverse relatively gentle terrain (Schaller et al. 1988), village trails and agricultural fields if vegetation patches and rock outcrops offer cover and especially if cliffs grade into these landforms. The radio-tagged snow leopard in Langu valley, west Nepal significantly over-utilized cliffs (Jackson 1996). So did the radio-collared snow leopards in Mongolia (McCarthy 2000) and in Ladak, India (Chundawat 1990). Snow leopard in India and west Nepal over-used steep slopes more than 40^0 (Chundawat 1990 Jackson 1996). Cats in Mongolia preferred even steeper slopes ($>60^0$) (McCarthy 2000). They were found in lower mean altitude (2,501-3,500 m) than those in Nepal (3,501-4,000 m) (Jackson 1996, this study). A predator's whereabouts is governed by prey distribution (Fuller and Sievert 2001). Habitat use patterns of snow leopard exhibited similar trends to those of tahr, snow leopards' main prey in Sagarmatha (Figures 11 and 12a-d). Both snow leopards and tahr used areas proximal to cliffs (<50 m) more than expected. Cliffs may serve as escape cover for tahr where they may retreat in times of danger (Schaller 1973, 1977). As expected, the habitat exploitation pattern of snow leopards in terms of elevation, slope, vegetation habitat, and ruggedness closely matched with that of tahr.

Figure 11 : Distance to nearest cliff from snow leopard sign sites and tahr groups

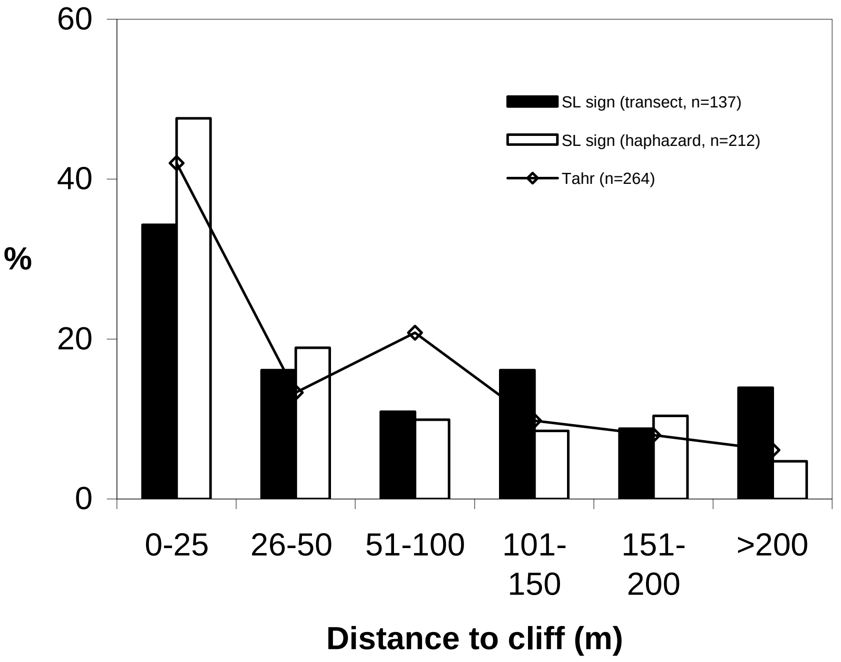
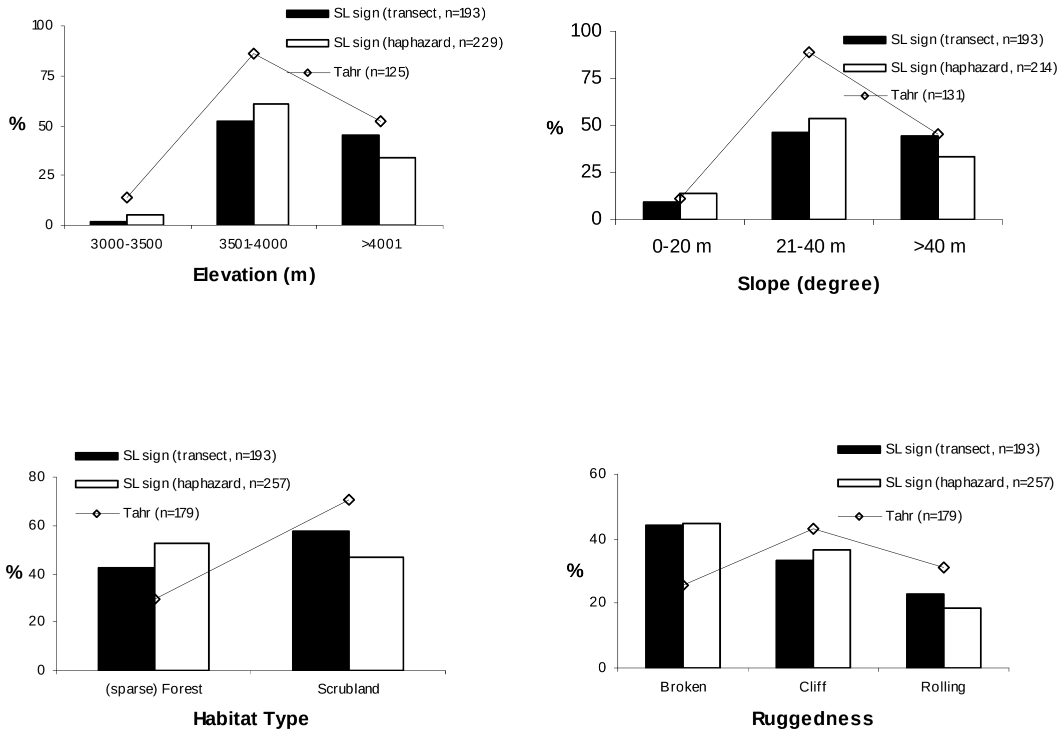


Figure 12 a-d: Snow leopard and tahr use of different habitat features: Elevation, Slope, Habitat (vegetation) Type and Ruggedness.



A snow leopard would need 1.5 kg per day or 548 kg per year (Schaller 1977). Inedible parts such as large bones and stomach contents average about one-third of the prey's total weight (Jackson & Ahlborn 1984), making it necessary for a snow leopard to kill at least 822 kg a year to survive. Based on this, my minimum count of 277 tahr (16,760 kg- the average weight of females as 60.5 kg: S. Lovari pers. comm.), along with the current abundance of other prey (e.g. musk deer, game birds and livestock), would provide sufficient food for snow leopards to sustain themselves and build up their population in Sagarmatha at least for several years to come.

References

Ahlborn, G. and Jackson, R.M. 1987. A survey of Sagarmatha National Park for the endangered snow leopard. Department of National parks and Wildlife Conservation, and King Mahendra Trust for Nature Conservation, Nepal. Unpub. Report, 18 pp.

Ahlborn, G. and Jackson, R.M. 1988. Marking in free-ranging snow leopards in west Nepal: a preliminary assessment. In: *Proceedings 5th International Snow Leopard Symposium*, ed. H. Freeman, pp. 25-49. International Snow Leopard Trust, Seattle and wildlife Institute of India, Dehradun, India.

Brower, B. 1991. Sherpa of Khumbu: People, livestock, and landscape. Oxford University Press.

Chundawat, R.S. 1990. Habitat selection by a snow leopard in Hemis National Park, India. *Int. Ped. Book of Snow leopards* 6: 85-92.

Fox, J.L. 1994. Snow leopard conservation in the wild - a comprehensive perspective on a low density and highly fragmented population. In: *Proceedings of the Seventh International Snow Leopard Symposium,* eds. J.L. Fox and D. Jizeng, pp. 3-15. International Snow Leopard Trust, Seattle, USA.

Fox, J.L., Sinah, S.P., Chundawat, R.S. and Das, P.K. 1991. Status of the snow leopard in northern India. *Biol. Conserv*. 55: 283-298.

Fuller, T.K. and Sievert, P.R. 2001. Carnivore demography and the consequences of changes in prey availability. In: *Carnivore Conservation*, eds. J.L. Gittleman, S.M. Funk, D. Macdonald and R.K. Wayne, pp 163-178. Cambridge Univ. Press.

Green, M.J.B. 1993. *Nature reserves of the Himalaya and the mountains of Central Asia*. IUCN, Cambridge and Gland.

Grigione, M.M., Burman, P., Bleich, V.C. and Pierce, B.M. 1999. Identifying individual mountain lions *Felis concolor* by their tracks: refinement of an innovative technique. *Biol. Conserv*. 88: 25-32.

Hussain, S. 2003. The status of the snow leopard in Pakistan and its conflict with local farmers. *Oryx* 37: 26-33.

Jackson, R. and Ahlborn, G. 1984. A preliminary habitat suitability model for the snow leopard, *Panthera uncia*, in West Nepal. *Int. Ped. Book of Snow leopards* 4: 43-52.

Jackson, R. and Hunter, D.O. 1996. *Snow Leopard Survey and Conservation Handbook.* International Snow Leopard Trust, Seattle, USA.

Jackson, R. 1996. *Home range, movements and habitat use of snow leopard in Nepal,* PhD Thesis. Univ. London, London.

Jackson, R. and Ahlborn, G. 1991. The Role of Protected Areas in Nepal in Maintaining Viable Populations of Snow Leopards. *Int. Pedigree Book of Snow Leopards* 6: 51-69.

Jackson, R., Zhongyi, W., Xuedong, Y. and Yun, C. 1994. Snow leopards in the Qomolangma Nature Preserve of the Tibet Autonomous Region. In: *Proc. 7th Int. Snow Leopard Symp*, eds. J.L. Fox and D. Jizeng, pp 85-95. International Snow Leopard Trust, Seattle and Northwest Plateau Institute of Biology, China.

Lovari, S., Ale S. B. And Boesi, R. *in press*. Notes on the large mammal community of Sagarmatha National Park (Nepal) In: Proceedings of International Karakorum Conference. Islamabad 2005.

Mallon, D. 1984. The snow leopard in Ladakh. *Int. Ped. Book of Snow leopards* 4: 23-37.

Mallon, D. 1991. Status and conservation of large mammals in Ladakh. *Biol. Conserv.* 56: 101-119.

McCarthy, T.M. 2000. Ecology and conservation of snow leopards, Gobi brown bears, and wild Bacterian camels in Mongolia, PhD Thesis, The University of Massachusetts, USA.

McCarthy, T.M., Fuller T.K. and Munkhtsog, B. 2005. Movements and activities of snow leopards in Southwestern Mongolia. *Biol. Conserv*. 124: 527-537.

Schaller, G. B. 1977. *Mountain Monarchs: Wild Sheep and Goats of the Himalaya.* The University of Chicago Press: Chicago.

Schaller, G.B. 1998. *Wildlife of the Tibetan Steppe.* The University of Chicago Press: Chicago.

Schaller, G.B., Junrang, R. and Mingjiang, Q. 1988. Status of the snow leopard in Qinghai and Gansu provinces, China. *Biol. Conserv.* 45: 179-194.

Sherpa, L.N. 1987. A proposal for forest research and management in Sagarmatha (Mt. Everest) National Park, Nepal. Working Paper No. 8. East-West Center, Hawaii.

Sherpa, M.N. 1985. *Conservation for survival: a conservation strategy for resource self-sufficiency in the Khumbu region of Nepal,* M.Sc. Thesis. University of Manitoba, Canada.

Smallwood, K.S. and Fitzhugh, E.L. 1993. A rigorous technique for identifying individual mountain lions Felis concolor by their tracks. *Biol. Conserv.* 65:51-59.

Stander, P.E, Ghau, D. Tsdisaba et al. 1997. Tracking and the interpretation of spoor: a scientifically sound method in ecology. *J. Zool.(Lond.)* 242: 329-341.

Wilson, G.J. and Delahay, R.J. 2001. A review of methods used to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research* 28: 151-164.

CHAPTER FOUR

4. DISCOVERING ELUSIVE SNOW LEOPARDS BY THE FEAR OF THEIR PREY

4.1 INTRODUCTION AND OBJECTIVES

Rare, elusive predators offer few sightings. This hampers research because of small sample sizes and lack of opportunities for experimentation. Consequently, field studies of large carnivores often reside outside of main-stream ecology, and our understanding of their role in ecosystems remains unclear and contentious. Unlike predators, prey is more abundant and its behavior can be more readily observed. The foraging theory assumes that prey should adopt adaptive foraging strategies that reduce or eliminate predation risk (Lima and Dill 1990, Abrams 2000). Prey responds to the presence of a predator (Elgar 989) and these fear responses have population and community level consequences (Sinclair and Arcese 1995, Schmitz et al. 1997, Brown et al. 1999). Such adaptive behaviors should be subject to strong selection (Stephens and Krebs 1986, Abrams 2000).

Predator reintroductions or re-colonization provide “natural experiments” into how prey behaves in the presence or absence of predators (Berger et al. 2001). Behavioral responses, such as vigilance behavior, allow us to sidestep the difficulty of direct field studies of large predators by studying them indirectly through their prey. However, no field studies have yet used prey behavior to assess the status of its predator on large mammal communities. Here, I use the foraging and vigilance behavior of Himalayan tahr *Hemitragus* *jemlahicus* (hereafter tahr) to infer indirectly the status and whereabouts of the snow leopard *Uncia uncia* in the Everest region of Nepal.

Snow leopards disappeared from the Everest region in the 1960s. Tourism has flourished since the first ascent of Mt. Everest in 1953. This has brought both prosperity and adverse ecological impacts to the region. In 1976 the Everest region (area of 1,148 km^2) was designated as the Sagarmatha (Mt. Everest) National Park (hereafter Sagarmatha) to better balance the opportunities from tourism with the needs for conservation. By the late 1980s, anecdotal reports noted the presence of transient snow leopards visiting from adjacent Tibet, China.

In this study, I ask three questions. Have snow leopards permanently returned to and re-inhabited Sagarmatha? As a novel predator, are they affecting the behavior and habitat use of tahr? Can the vigilance behavior of tahr facilitate monitoring the presence and whereabouts of snow leopards? To answer these questions I combined old-fashioned, mud-and-boots field biology (searching for spoor and sign- Schaller 1977, Jackson and Hunter 1996), with techniques and concepts from foraging theory (Stephens and Krebs 1986). Assuming that food resources (Jarman 1974, Carbone and Gittleman 2002) and predator pressures (Hunter and Skinner 1998) govern animal distributions, foraging theory predicts that 1) terrains and habitats exhibiting heightened tahr vigilance should reveal higher abundance of snow leopards as indicated by their sign, and 2) valleys with the most alert tahr should have the most snow leopard signs.

4.2 METHODS

4.2.1 Study area

The Sagarmatha National Park (86^0 30' - 86^0 99' E, 27^0 46' - 27^0 6' N) lies in Solu-Khumbu district of the northeastern region of Nepal. It encompasses the upper catchments of the Dudhkosi River system (Figure 1). My survey area consists of four survey blocks 15-33 km^2 in size, a total of c. 86 km^2. These survey blocks represent the four main valleys of Sagarmatha: Namche (15 km^2), Phortse (18 km^2), Gokyo (33 km^2) and Thame (20 km^2), with elevations of 3,000 to 5,000 m. In my study area, snow leopards and tahr approximate a 1 predator species-1 prey species system. The area holds most of the tahr in Sagarmatha.

4.2.2 Observations on tahr behaviours

In the autumn (August to October) of 2004 and 2005, I followed tahr on foot, closely observing their anti-predator vigilance behavior. These observations tested for the association of vigilance with risky valleys, terrain and vegetation types; and I used them to increase the likelihood of actually spotting snow leopards. Repeated yearly sightings would confirm the snow leopard's permanent return. To infer the land use patterns and the abundance of snow leopards, I quantified foraging and vigilance behavior of tahr in different terrains (cliff, broken and rolling) and vegetation habitats (scrubland versus open conifer forest) across all four valleys.

I used focal animal sampling (Martin and Bateson 1986) to collect information on tahr foraging behavior. I watched each individual for 20 minutes and recorded its activities in the following four categories: foraging (grazing or browsing), scanning (alert stance with raised ears), moving (walking, trotting and running), and other (grooming, aggression etc.). I then switched to another suitable animal for another bout of observations. Observation periods were initiated only when animals were feeding. The tahr in Sagarmatha are continually exposed to visitors and mostly ignore them. Nonetheless, to eliminate any visitor effect, animals were allowed to settle down for a minimum 5 minutes before beginning observations (see Hunter and Skinner 1998). I recorded the behavior from 7 am to 5 pm whenever I saw tahr. I sampled 286 different individuals, each individual observation lasting for 20 minutes (i.e. a total of ca. 95 h of observation). Measures of scanning were expressed as the proportion of time vigilant per observation period.

4.2.3 Snow leopard sign survey

I employed the techniques of the Snow Leopard Information Management System (Jackson and Hunter 1996), a standardized approach widely used in snow leopard research, to locate snow leopard sign and characterize the sign site. I looked for snow leopard signs in the autumn of 2004 and 2005 and in the summer of 2006. I used two independent methods to assess snow leopard: transect method in which I recorded snow leopard sign along pre-selected transects, predictable travel lanes used by snow leopards (Jackson and Hunter 1996), and a more wide ranging incidental method in which I opportunistically searched for snow leopard sign while locating tahr groups.

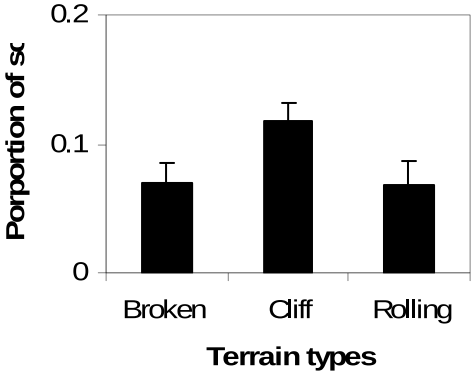
Sign transects were laid out along landforms such as ridgelines and bases of cliffs where cats are most likely deposit sign (Jackson and Hunter 1996). For each sign (scrape, scats, pug-marks or urine/scent-spray), I recorded the date, global positioning system location, terrain and habitat type within a radius of 20 m. Prior to walking each transect, I randomly selected 6-8 sites per 1,000 m of transect to characterize the frequency of each terrain and habitat type. This random frequency could then be compared with the frequency of snow leopard sign sites using a chi-square test (McCarthy 2000).

I used standard ANOVA-F (GLM) to test for the effect of habitat, terrain and valley on tahr vigilance. Differences in sign frequency among habitats, terrain types and valleys were determined using chi-square analysis to test the null hypothesis of no difference.

4.3 RESULTS

Tahr exhibited the most heightened vigilance in cliffs ($F_{(2,283)} = 3.56, P=0.03$; Figure 13a). They were more alert in open forests than in scrubland ($F_{(1,286)} = 3.64, P=0.05$). Vigilance behavior corresponded exactly with the distribution of snow leopard sign within valleys. Snow leopards used cliffs ($\chi^2=16.3$, *d.f.=2*, $P<<0.001$; Figure 13b) and open forests ($\chi^2=163$, *d.f.=1*, $P<<0.001$) more than expected by chance. Based on their vigilance behavior, the tahr perceived a higher predation risk in areas with cliffs and in open forests. As predicted (prediction 1), snow leopards biased their activity towards cliffs and open forests. They typically left their sign in open forest. Use of terrain ruggedness and habitat type differed significantly from availability (see also Table 5, for cumulative data 2004-2006, CHAPTER 2). Marking activity of snow leopards in 2004, 2005 and 2006 indicated a selection for cliff and open forest.

a)



b)

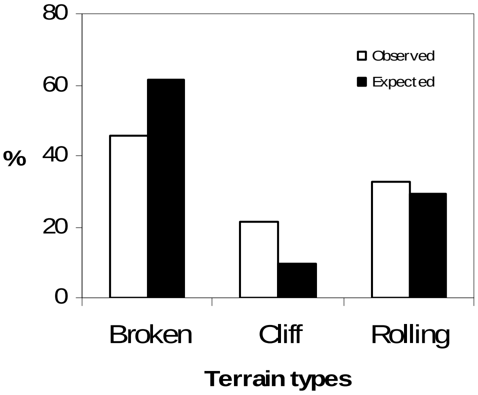
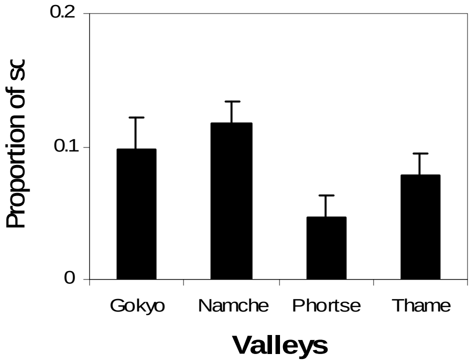


Figure 13. a) Tahr were most vigilant in cliffs (n=286). b) snow leopards preferred cliffs (n=85).

Among the valleys studied, the tahr in Namche were the most alert ($F_{(3,282)} = 2.84, P=0.03$; Figure 14a), and as predicted (prediction 2), Namche provided the highest number of snow leopard signs per survey day ($\chi^2 = 19.5, d.f.=3, P<<0.001$, adjusted for the overall survey days, Figure 14b, also refer to Table 4 in CHAPTER 4).

a)



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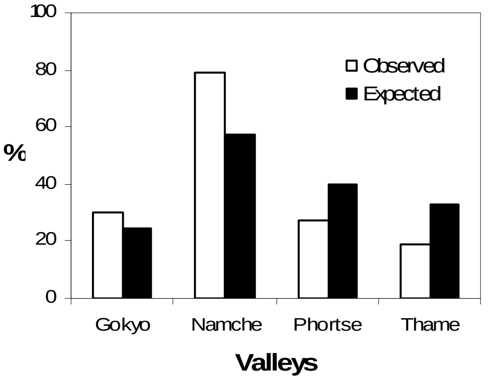


Figure 14. a) Namche had the most alert tahr (n=286). b) Namche revealed the most snow leopard signs per search day (n=155).

4.4 DISCUSSION

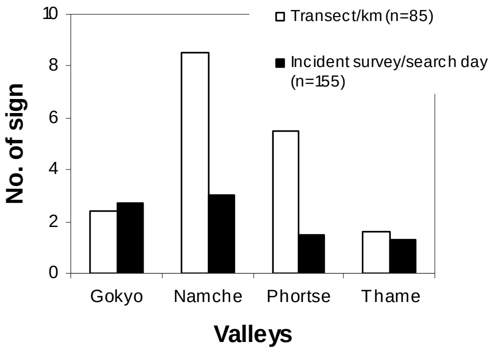
Snow leopards have returned to Sagarmatha. I encountered a minimum of six different adult snow leopards, based on sizes of their individual pugmarks, in *ca*. 86 km^2 of my study area. My focus on the tahr through their whereabouts and vigilance behaviors resulted in an unusually high number of fortuitous sightings. I spotted snow leopards three times in 2004, twice in 2005 and once in 2006, including two adult snow leopards feeding from the same yak carcass on 14 October 2005. I was able to photograph five different individuals, showing clear display of their stripe patterns. The relatively large number of sightings over such a short period of time resulted from my blending of conventional wildlife techniques (e.g., spoor hunting of predator), with new techniques (e.g., closely tracking vigilant prey).

Tahr vigilance behavior accurately identified variation in snow leopard activity among valleys, among terrain types, and between vegetation types. Tahr behavior accurately predicted snow leopards' whereabouts and relative abundance.

Both incidental method and transect method accurately predicted the risk perceived by tahr among terrain types and between vegetation habitats within valleys. Snow leopards in Sagarmatha preferred cliff and open forest (edge habitat). Radio-tagged snow leopards in Dolpo, west Nepal (Jackson 1996), Ladak, India (Chundawat 1990), and in Mongolia (McCarthy et al. 2005) prefer ridgelines interspersed with cliffs, and edge habitats. Within valley, both survey methods provided a good indicator of the presence of snow leopards and their habitat and terrain preferences.

Across valleys, the incidental method yielded abundances and distributions of snow leopard signs which corresponded closely with the vigilance levels of tahr occupying the same area. While the vigilance of tahr across valleys only slightly corresponded with the distribution of transect signs, the pattern is similar but less clear (Figure 15a). Given the rarity of signs and low density of snow leopards, transects are generally arranged in landforms (e.g., ridgelines, bases of cliffs) where snow leopards are most likely to travel (Jackson and Hunter 1996). Although the presence and distribution of snow leopard signs in an area may equate with the presence and distribution of snow leopards, the selection of transect locations may bias the occurrence of their sign. Snow leopard studies in Ladakh, India (Mallon 1991, Fox et al. 1991) and in Qinghai, China (Schaller et al. 1988) concluded that using fixed transects along routes frequented by snow leopards biases perceptions of snow leopard abundance and whereabouts. For example, in Qinghai (China), cats marked the bases of hills flanking broad valleys in certain survey blocks, whereas, in contrast, the cat's travel routes were less well defined in others, making it difficult to locate spoors along transects (Schaller et al. 1988). The transects, however, provide an effective means for comparing the abundance and the distribution of signs from one year to another in the same survey area (Fox et al 1991, Mallon et al. 1991, Jackson and Hunter 1996, Figure 15b). I conclude that the incidental collection of snow leopard signs that I encountered while seeking tahr represents more accurately the risk perceived by tahr.

a)



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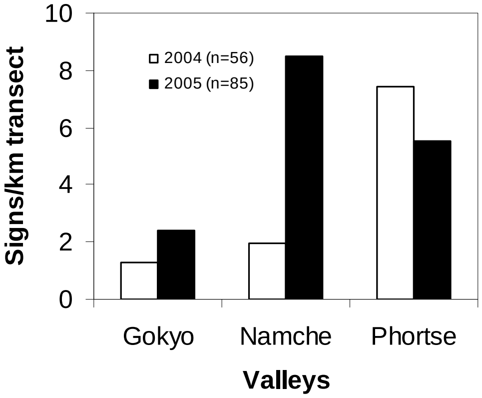


Figure 15. a) Both snow leopard survey methods (2005) indicated more signs in Namche than in any other valley. b) Temporal (yearly) variation in snow leopard signs along transects.

Although a recent event, the return of snow leopards to Sagarmatha is already reflected in the tahr's degree of alertness towards predators. A wealth of empirical evidence suggests that predation risk is a primary reason for alertness in animals (Elgar 1989). Within a single generation, the prey may be able to behaviorally adjust to big changes in the types and abundances of predators (Berger et al. 2001). Such adaptive decisions of prey reveal properties of the population and community (Sinclair and Arcese 1995, Schmitz et al. 1997, Brown et al. 1999).

The return of snow leopards and the associated fear responses of the tahr in Sagarmatha provide opportunities for academicians and wildlife managers, similar to what occurred after the return of wolves *Canis lupus* to Yellowstone (Ripple and Beschta 2004). The reintroduction of wolves caused rapid behavioral responses by elk *Cervus elaphus* (Laundré et al. 2001) and moose *Alces alces* (Berger et al. 2001) to the novel risk. Such predation risk altered habitat selection by elk (Creel et al. 2005). Prey can be expected to bias feeding activity towards safer habitats, and while in risky habitats, they should increase their vigilance levels in response to predation risk (Lima and Dill 1990; Brown et al. 1999). By constraining habitat selection and adaptive shifts in foraging behavior, predators may have greater effects on prey dynamics than would be predicted on the basis of direct predation alone (Brown et al. 1999). In Yellowstone, behavioral responses by elk, provoked by wolves, cause cascading effects on plants (Laundré et al. 2001, Ripple and Beschta 2004, Creel et al. 2005). Interestingly, such behavioral effects have been shown as large as (Preisser et al. 2005) or even larger than density effects (Schmitz et al. 1997). Ungulates likely rely heavily on vigilance to avoid being killed (Elgar 1989, Hunter and Skinner 1998). My work on the snow leopard and tahr represents a direct application of these principles to communities of large mammals, and it should be possible to extend these techniques to systems with higher diversities of prey and predators.

Because snow leopards are declining throughout their range (Fox 1994), my findings have conservation relevance that goes well beyond the local level. Very few protected areas in Asia are large enough to contain viable populations of snow leopards and other large predators. Sagarmatha National Park together with other two parks in Nepal and Qomolongma Nature Preserve in Tibet form a large trans-frontier landscape conservation area (*ca.* 40,000 km^2) which may ensure their long-term survival (Singh and Jackson 1999). As long recommended by island bio-geographers (Wilcove and May 1986), conservation strategies today rely on landscapes in and outside the national boundary encompassing larger spaces for the big predators to hunt and disperse their genes to counterbalance edge effect. Recently, given that top predators are heralded as both the target and the means to conserve biodiversity at landscape level (Ray et al. 2005) and that re-colonization is a fundamental goal of conservation biology either via reintroduction or returning of predators with effective conservation (Gittleman and Gompper 2001), my work may serve as a model for areas with limited resources. Here I have shown that a predator as rare and as elusive as the snow leopard can be sighted and studied indirectly using a combination of appropriate wildlife techniques, an approach which not only generates scientific information but also helps promote wildlife-based ecotourism to generate widely needed resources for conservation.

References

Abrams, P.A. 2000. The evolution of predator-prey systems: theory and evidence. *Ann. Rev. Ecol. Syst.* 31: 79-105.

Berger, J., Swenson, J.E. and Persson, I.L. 2001. Re-colonizing carnivores and naïve prey: Conservation lesson from Pleistocene extinctions. *Science* 291: 1036-1039.

Brown, J.S., Laundre, J.W. and Gurung M. 1999. The ecology of fear: Optimal foraging, game theory and trophic interactions. *J. Mammal*. 80: 385-399.

Carbone, C. and Gittleman, J.L. 2002. A Common Rule for the Scaling of Carnivore Density. *Science* 295: 2273-2276.

Chundawat, R.S. 1990. Habitat selection by a snow leopard in Hemis National Park, India. *Int. Ped. Book of Snow leopards* 6: 85-92.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K., and Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86: 3387-3397.

Elgar, M.A. 1989. Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc*. 64: 13-33.

Fox, J.L. 1994. Snow leopard conservation in the wild: a comprehensive perspective on a low density and highly fragmented population. In *Proceedings of the Seventh International Snow Leopard Symposium*, eds. J.L. Fox and D. Jizeng, pp. 3-15. International Snow Leopard Trust, USA.

Fox, J.L., Sinha, S.P., Chundawat, R.S., and Das, P.K. 1991. Status of the snow leopard in northern India. *Biol. Conserv*. 55: 283-298.

Gittleman J.L. and Gompper, M.E. 2001. The Risk of Extinction-What You Don't Know Will Hurt You. *Science* 291: 997-999.

Hunter, L.T.B., and Skinner, J.D. 1998. Vigilance behaviour in African ungulates: The role of predation pressure. *Behaviour* 135: 195-211.

Jackson, R. and Hunter, D.O. 1996. *Snow Leopard Survey and Conservation Handbook*. International Snow Leopard Trust, Seattle, USA.

Jackson, R. 1996. *Home range, movements and habitat use of snow leopard in Nepal*, PhD Thesis. Univ. London.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-267.

Laundré, J.W., Hernández, L. and Altendorf, K.B. 2001. Wolves, elk, and bison: Re-establishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Can. J. Zool*. 79: 1401-1409.

Lima, S.L. and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool*. 68: 619-640.

Mallon, D.P. 1991. Status and conservation of large mammals in Ladakh. *Biol. Conserv.* 56: 101-119.

Martin, P. and Bateson, P. 1986. *Measuring Behaviour: An Introductory Guide*. Cambridge Univ. Press.

McCarthy, T.M. 2000. *Ecology and conservation of snow leopards, Gobi brown bears, and wild Bacterian camels in Mongolia*, Ph D Thesis. The university of Massachusetts, USA.

McCarthy, T.M., Fuller T.K. and Munkhtsog, B. 2005. Movements and activities of snow leopards in Southwestern Mongolia. *Biol. Conserv.* 124: 27-537.

Ray, J., Redford, K., Steneck, R. and Berger, J. 2005. Large carnivores and the conservation of biodiversity. Island Press: Washington.

Ripple, W.J. and Beschta, R.L. 2004. and the ecology of fear: Can predation risk structure ecosystems? *BioScience* 54: 755-766.

Schaller, G.B. 1977. *Mountain Monarchs: Wild Sheep and Goats of the Himalaya.* The University of Chicago Press: Chicago.

Schaller, G.B., Junrang, R. and Mingjiang, Q. 1988. Status of the snow leopard in Qinghai and Gansu provinces, China. *Biol. Conserv*. 45: 179-194.

Schmitz, O. J., Beckerman, A. P. and O'Brien, K. M. 1997. Behaviourally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78: 1388-1399.

Sinclair, A.R.E. and Arcese, P. 1995. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology* 76: 882-891.

Singh, J.J. and Jackson, R. 1999. Transfrontier Conservation Areas: creating opportunities for conservation, peace and the snow leopard in Central Asia. *International Journal of Wilderness* 5: 7-12.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging theory*. Princeton University Press.

Wilcove, D.S. and May, R.M. 1986. National park boundaries and ecological realities. *Nature* 324: 206-207.

CHAPTER FIVE

5. HABITAT SELECTION UNDER PREDATION RISK

5.1 INTRODUCTION AND OBJECTIVES

Organisms make decisions that tend to maximize fitness, i.e. per capita population growth rate (MacArthur and Pianka 1966, Mitchell and Valone 1990). One of the mechanisms to achieve this is to select the best habitats, within spatially heterogeneous landscape, that guarantee the greatest fitness. This is the cornerstone idea of density-dependent habitat selection theory (Rosenzweig 1981, 1991). To explain patterns of animal distribution in heterogeneous landscape, Fretwell and Lucas (1970) proposed the simplest form of the density-dependent habitat selection (DDHS), i.e. the ideal free distribution (IFD)- an equilibrium distribution of individuals such that their fitness is equivalent across habitats. While the theoretical implications of habitat selection theory may be clear, observing these patterns in natural populations remains elusive. One established approach to detect these patterns in nature is through isodar analysis- an isodar is a plot of the density of a species in one habitat versus its corresponding density in a second habitat such that an individual's expected fitness in the two adjacent habitats is the same (Morris 1987, 1988, 1994, 2003, 2005).

The IFD model demonstrates that animals compete for resources on the basis of resource sharing, but animals also compete for resources on the basis of resource defense (e.g. because of territorial behavior). The later situation gives rise to yet another form of

DDHS, the ideal despotic distribution (Fretwell 1972). Furthermore, competition may not be involved in the process of resource acquisition - animals simply occupy resources on a “first come, first serve” basis. This is the concept of the ideal preemptive distribution (Pulliam and Danielson 1991). Here, I will deal with isodars, only under the IFD model.

The idea behind the isodar model is that isodars can be estimated from census data on population density. The number of individuals (or the allocation of time), in the various available adjacent habitats, may reflect relative habitat quality. A plot of population density in one habitat against population density in another habitat, therefore, should tell us something about the relationship between fitness and density in each habitat given that individuals are distributed according to the IFD. In isodar analysis, one treats the population density in the habitat having the lowest density as the independent variable and population density in the high-density habitat as the dependent variable and fits a linear regression model to the data. The intercept of an isodar indicates the quantitative differences in resource availability of two habitats (e.g. density), and its slope the qualitative habitat differences (e.g. rate of resource acquisition, structure of habitat) (Morris 1987, 1988). Significant regressions imply density-dependent habitat selection whereas non-significant regressions density-independent habitat selection.

Isodars, however, yield only the net pattern of density between habitats, and therefore may be effective at detecting density-dependent habitat selection but are rather a poor tool to explain causal processes (Jonzen et al. 2004). To date, isodars have been modeled for systems with no predators (but see the recent effort of Morris 2005 in this direction). Because most systems support predators, animals likely consider predation risk in the use and evaluation of habitats (Brown 1988, 1992, 1998, McNamara and Houston 1990, Lima and Dill 1990). Does adding a predation component into isodar models help explain the underlying mechanisms of habitat selection? Predators not only remove individual victims but also change the behavior of potential victims, thereby influencing their habitat selection (Brown 1988, 1998, Lima and Dill 1990, Abramsky et al. 1997, Brown et al. 1999). Because the qualitative habitat differences represented by the isodar slope include differences in resource use, it follows that predation risk may be represented by the isodar slope. Does the isodar slope consistently reflect predation risk?

The habitat matching rule predicts that when an individual's fitness is proportional to its fraction of the total resources, the number of foragers should match habitat differences in resource availability (Sutherland 1983, Pulliam and Caraco 1984). In nature, however, one often observes more individuals in a habitat (especially poor ones) than expected from its resource quality (Van Horne 1983, Pulliam and Danielson 1991, Kennedy and Gray 1993, Tregenza 1995) and foragers frequently under-match their consumption of resources by consuming proportionately more resources from poor patches than they do from rich ones (Kennedy and Gray 1993, Tregenza 1995). Differential predation risk among habitats may explain such mismatches between resource availability and animal distribution (Brown 1988, 1992, 1998, McNamara and Houston 1990, Lima and Dill 1990, Morris 2005). Predation risk and associated ecology of fear are so pervasive in nature (Brown 1988, 1992, Brown et al. 1999, Ripple and Beschta 2004) that it becomes tempting to know the shape of isodars under predation risk. Is the pattern of distribution revealed by isodar with predation component more realistic than the original model without it? Is the isodar under predation risk linear or non-linear? Do isodars under predation risk complicate their application to empirical ecology or do they provide additional predictive power and insights?

Here I model isodars under predation risk. I 1) compare and contrast the slope, intercept and shape (linear vs. non-linear) of isodars with and without a predation component, and 2) discuss the overall isodar approach and its utility from conservation perspectives. To do this I extend standard models of population growth and habitat selection to include the effects of predation risk.

5.2 MODELLING ISODARS

5.2.1 Isodar with no predation risk

The Verhulst-Pearl logistic equation (see Morris 1987) provides a simple model of population growth of a single species in a landscape with two different and (for convenience) equal sized habitats (habitats 1 and habitat 2 respectively). For habitat 1 let:

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1\left(\frac{K_1 - N_1}{K_1}\right) \quad (1),$$

and for habitat 2 let:

$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2\left(\frac{K_2 - N_2}{K_2}\right) \quad (2)$$

where for habitat *i*, N_i is the population density, r_i is the intrinsic growth rate, and K_i is carrying capacity (habitat productivity or food) at which the realized rate of increase is zero.

If the animals always maintain the IFD, then fitness (per capita population growth rate) should always be equal in the two habitats:

$$\frac{1}{N_1}\frac{dN_1}{dt}=\frac{1}{N_2}\frac{dN_2}{dt} \tag{3}$$

We can obtain the isodar (equation 4) from substituting terms from equation (1) and (2) into equation (3) (Morris 1988, 2003 a and 2003 b).

$$N_2=K_2\left(\frac{r_2-r_1}{r_2}\right)+\left(\frac{r_1K_2}{r_2K_1}\right)N_1 \tag{4}$$

The isodar (equation 4) shows the distribution of individuals among habitats that equalizes fitness when there is no predation risk.

I will construct an isodar between two habitats varying in food availability and predation risk. I will consider, in turn, a predator with a Type I functional response (model I) and then a predator with a Type II functional response (model II).

5.2.2 Isodar under predation risk

Model I: When predation risk (Type I functional response) is added into equations (1) and (2), we have for habitat 1:

$$\frac{1}{N_1}\frac{dN_1}{dt}=r_1\left(\frac{K_1-N_1}{K_1}\right)-a_1 \qquad (5),$$

and for habitat 2:

$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2\left(\frac{K_2 - N_2}{K_2}\right) - a_2 \qquad (6)$$

where a_i gives the density-independent risk of being preyed upon while in habitat *i*. In this formulation, the term "a_i" is being used as a surrogate for both the number of predators and their encounter probability on the foragers.

Setting equations (5) and (6) equal, we obtain a *linear* isodar:

$$N_2 = \frac{K_2}{r_2}\left(r_2 - a_2 - r_1 + a_1\right) + \frac{r_1 K_2}{r_2 K_1} N_1 \qquad (7)$$

Equation (7) shows how all three variables (productivity, intrinsic growth rate and predation risk) affect the intercept of the isodar. In contrast, the slope of isodar is independent of predation risk (Appendix I). Altering predation risk has no effect on the slope but only on the intercept of isodar (Figure 16).

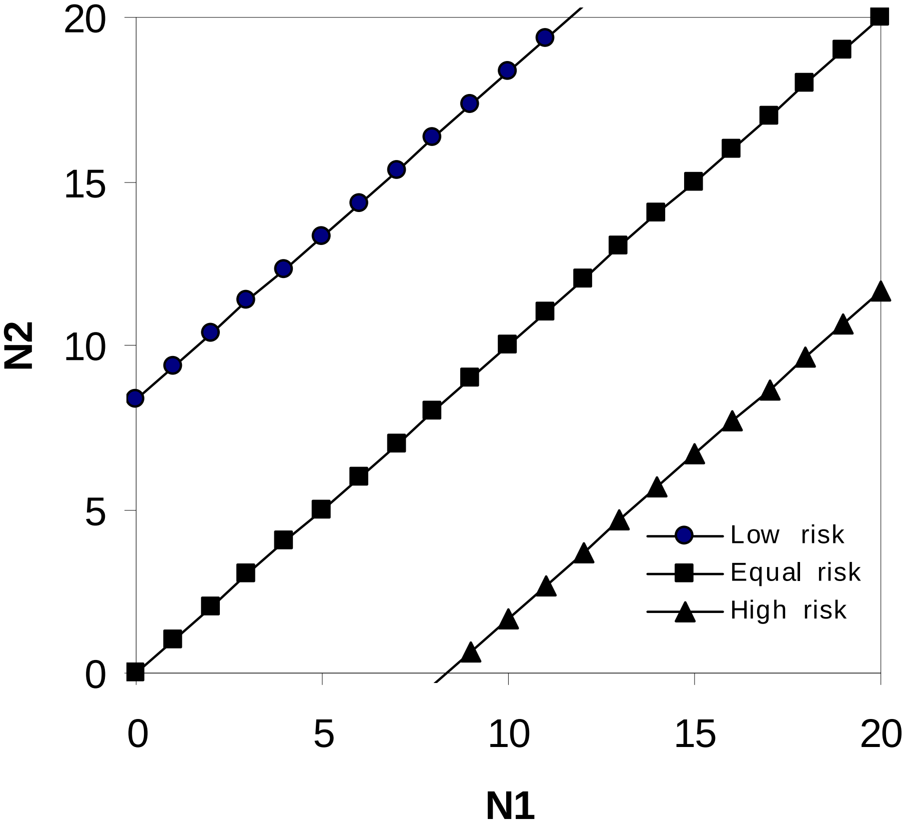


Figure 16: Isodars under varying predation risk for two habitats (habitat 1 and habitat 2), with equal productivity (K_1=K_2=5). The intercepts of isodar change with predation risk but slopes remain unaffected. For illustration purposes, in habitat 2 with respect to habitat 1, the following values precipitate "low risk" (a_1=0.1, a_2=0.05), "equal risk" (a_1=a_2=0.1), and "high risk" (a_1=0.1, a_2=0.15). For all situations, r_1=r_2=0.03.

Model II: The logistic equations (1) and (2), modified to include a Type II functional response, can be written as:

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1\left(\frac{K_1 - N_1}{K_1}\right) - \left(\frac{a_1 P}{1 + a_1 h_1 N_1}\right) \qquad (8),$$

and:

$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2\left(\frac{K_2 - N_2}{K_2}\right) - \left(\frac{a_2 P}{1 + a_2 h_2 N_2}\right) \qquad (9)$$

for habitats 1 and 2; where h_i represents the handling time of the predators on each prey captured in habitat *i*. Implicitly, I have scaled the number of predators to be "1" (i.e. *P*=1). The, setting equations (8) and (9) equal, we obtain a *non-linear i*sodar that is quadratic of the form,

$$(A)N_2^2 + (B)N_2 + C = 0 \qquad (10)$$

where:

$$\text{A}=\left[a_2 h_2 k_1 r_2 + (a_1 a_2 h_1 h_2 k_1 r_2)N_1\right]$$

$$\text{B}=\Big[\left(a_2 h_2 k_1 k_2 r_1\right) - \left(a_2 h_2 k_2 r_1 N_1\right) + \left(a_1 a_2 h_1 h_2 k_1 k_2 r_1 N_1\right) - \left(a_1 a_2 h_1 h_2 k_2 r_1 N_1^2\right)$$

$$-\left(a_1 a_2 k_1 k_2 h_2\right) + \left(k_1 r_2\right) - \left(a_2 h_2 k_1 k_2 r_2\right) + \left(a_1 h_1 k_1 r_2 N_1\right) - (a_1 a_2 h_1 h_2 k_1 k_2 r_2 N_1)\Big]$$

$$C=\left(k_1k_2r_1\right)-\left(k_2r_1N_1\right)+\left(a_1h_1k_1k_2r_1N_1\right)-\left(a_1h_1k_2r_1N_1^2\right)-\left(a_1k_1k_2\right)$$

$$-\left(k_1k_2r_2\right)+\left(a_2k_1k_2\right)-\left(a_1k_1k_2h_1r_2N_1\right)+\left(a_1a_2k_1k_2h_1N_1\right)$$

In equation (10), “*A*” and “*B*” represent the slope and “*C*” the intercept of isodar. The value of “*A*” determines the shape of the isodar at high N, whereas the value of “*B*” determines it at low *N*. Under high predation risk, the alternative habitat (or habitat 1 with low food) is favored (Figures 17). In Figure 17, “High food” in habitat 2, relative to habitat 1, means “$K_2>K_1$”; “High risk” in habitat 2, relative to habitat 1, means “$a_2>a_1$” and “$h_2<h_1$”, and vice versa for “low risk” scenarios, respectively.

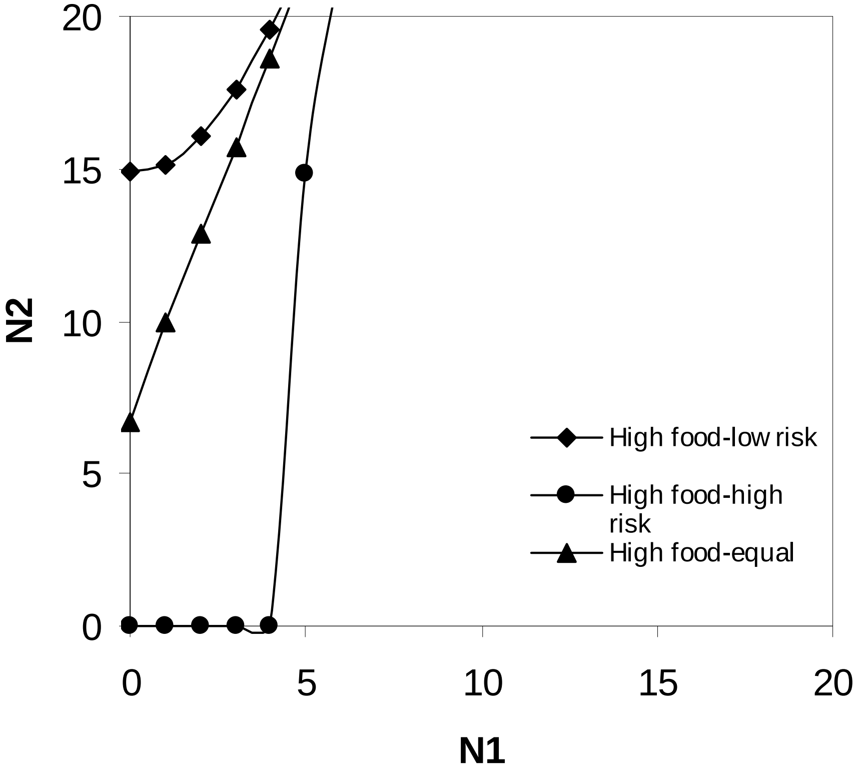


Figure 17: Effect of different levels of predation risk on isodar slope and intercept. "High food-low risk" (a_1=0.1, a_2=0.05, h_1=1, h_2=5), "high food-high risk" (a_1=0.1, a_2=0.5, h_1=5, h_2=1), and "high food-equal risk" (a_1=a_2=0.1, h_1=h_2=1). For all cases, K_1=1, K_2=5, and r_1=r_2=0.03.

Low food abundance also drives animals to choose the alternative habitat (Figure 18). At high population, the safety in numbers component of the Type II functional response comes into play. Clearly, under predation risk, both the intercept and slope of the isodar change.

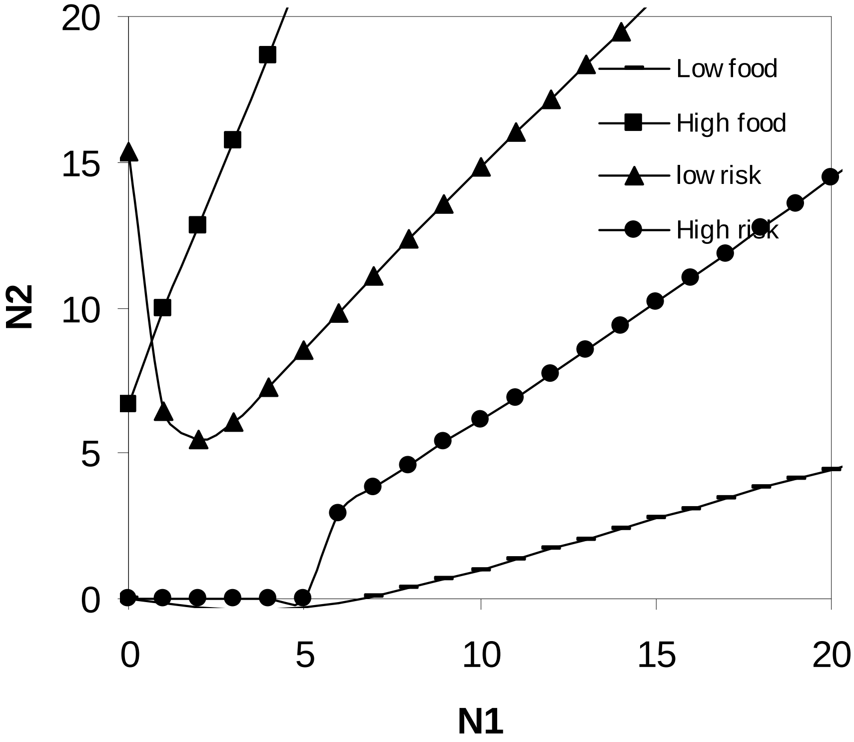


Figure 18: Effect of food abundance and predation risk. In habitat 2, relative to habitat 1, "Low food" (K_1=5, K_2=1, a_1=a_2=0.1, h_1=h_2=1), "high food" (K_1=1, K_2=5, a_1=a_2=0.1, h_1=h_2=1), "low risk" (a_1=0.5, a_2=0.1, h_1=1, h_2=5, K_2=K_1=1), and "high risk" (a_1=0.1, a_2=0.5, h_1=5, h_2=1, K_2=K_1=1). For all cases, r_1=r_2=0.03.

5.3 DISCUSSION

The basic quest of ecologists is to analyze the interactions that determine the distribution and abundance of organisms (Elton 1933, Krebs 2006). Spatial heterogeneity in habitat is a fundamental variable that determine the distribution and abundance of animals (Elton 1949, Andrewartha and Birch 1954). How should individuals choose which habitat to live in? In searching for mechanisms of habitat selection, early ecologists found that birds use optimal habitats at first and there after sub-optimal habitats as their population grows. By the 1950s, ecologists wrote about the generality of the principle that intra-specific competition causes animals to use varieties of habitats (Sva¨rdsson 1949, Morisita 1950, reviewed in Ronsenzweig 1991). With the development of foraging theory (MacArthur and Pianka 1966) and island biogeography theory (MacArthur and Wilson 1967) in the late 1960s, ecologists began to use concepts of evolutionary theory to understand population level phenomenon, ingredients that would soon be built into the coherent theory of habitat selection in the subsequent decades.

Fretwell and Lucas (1970) proposed the IFD concept to explain density-dependent habitat selection in a single species. The IFD model was simple and intuitive. Animals should live in the habitat that will produce the most descendants to maximize their fitness. But if all individuals make the same choice, the habitat will become crowded, and fitness will decline. It follows, hence, that animals maximizing fitness through habitat selection will disperse among habitats until no individual can improve its fitness by moving elsewhere. IFD, an equilibrium state of distribution, assumes that an individual can estimate accurately the fitness that can be attained in different habitats, and is free to move and occupy the ideal place that maximizes fitness. Parker (1970) also independently proposed a similar concept predicting the “equilibrium position”, in dung flies. While many organisms from different taxa deviate from IFD predictions (Kennedy and Gray 1993, Shochat et al. 2002), supporting evidence is mounting across many species, both at small scales where foragers choose between patches differing in food supply (Tregenza 1995, for a review) and recently at much larger scales where populations are regulated (for pike in northern English Lake, Windermere: Morris 2006).

The theoretical foundation for habitat selection has been nicely laid out (Rosenzweig 1981, 1991), but how do we reveal it in nature? The theory of DDHS suggests that habitat quality (expressed as the fitness or per capita population growth rate) should generally decline with increasing population density. To reveal the DDHS, one needs to measure the fitness across habitats which may take a long time. For some organisms, measuring reproductive success may not be even possible. Currently two approaches exist as field test of the DDHS, 1) the resource/habitat-matching rule and 2) the isodar analysis. The first approach, the habitat-matching rule (Parker 1978, Pulliam and Caraco 1984), is based on habitat or patch quality in terms of resource distribution across habitats/patches. In general, this approach demonstrated that when an individual’s fitness is proportional to its fraction of the total resources, that the number of foragers should match habitat differences in resource availability (Sutherland 1983, Pulliam and Caraco 1984). In small scales (e.g. patch scales or experimental settings) the habitat matching rule may work because the assumption of continuous resource input is likely to be valid, but at larger habitat or landscape scales the assumption may be unrealistic.

Morris (1987, 1988) suggested the isodar approach for larger, coarser habitat or landscape levels. Empirical studies have shown that isodar analysis is fruitful for a range of animal species, particularly small mammals (Rodriguez 1995, Knight and Morris 1996, Abramsky et al. 1997, Ramp and Coulson 2002, Morris 2006). Isodars not only demonstrate descriptive habitat selection patterns, but if habitats demonstrate regular seasonal variation, it is possible to expect predictable seasonal differences in isodar slope and/or intercept (Morris 1990, Ramp and Coulson 2002 for Kangaroo, and Shenbrot 2004 for sand rat). Although mounting evidence supports the isodars analysis, it has its limitation particularly in systems with inherent habitat stochasticity.

Plotting pairwise densities in adjacent habitats show us why individuals are distributed the way they are. The isodar analysis assumes that the exchange of individuals along two adjacent habitats occurs due to density-dependent movement and not because of Brownian motion. This assumption of density-dependence again relies on the assumption that animals follow the IFD, limiting isodar applicability in depicting patterns of distributions in nature. One reason for this limited scope may be that the original isodar model does not incorporate predation, one of the most significant factors that influence distribution of animals across habitats. The role of predation is pervasive, influencing distribution via varieties of mechanisms. For instance, when patches are subject to predation risk, dilution of risk favors more extreme distributions, and may lead to more than one stable distribution (Moody et al. 1996). Isodars should be effective at detecting density-dependent habitat selection, but are rather a poor technique to explain causal processes (Jonzen et al. 2004). Jonzen et al. (2004), deriving a stochastic equivalent of the IFD, suggested that isodar analysis should be used as an exploratory rather than a confirmatory tool to generate hypotheses about the underlying processes.

The most appealing aspect of the isodar analysis is that the isodar intercept and slope indicate the differences in habitats in terms of their quantity and quality, respectively. This claim may not be general in applicability. Differentiating habitat difference into quantitative and qualitative (Morris 1987, 1988, 1994, 2003) may imply that predation risk is a component of habitat quality. This means only the slopes of isodars varying in predation risk should reflect predation risk. My results, however, show that both intercepts and slopes of isodars may represent difference in predation intensity between adjacent habitats. Habitat differences on the basis of quantity and quality, as represented by corresponding isodar intercepts and slopes (Morris 1987, 1988), may need further work. Isodars among habitats varying in predation risk is non-linear in our model II, but linear in model I. The non-linearities are inherent characteristics of density-dependent interactions in ecological systems (May 1999). Non linear isodars under predation may depict nature more realistically and may be relevant to conservation.

5.3.1 Conservation relevance of the isodar analysis

Habitat degradation, introduction of alien species, and over-harvesting are the three main causes of threats to species loss (Pimm and Lawton 1998, Rosenzweig 2003). No species are immune to these threats, but they are particularly vulnerable to habitat change or degradation, causing their populations to decline and eventually disappear. Introduced predators or over-harvesting in a system are relatively easy to diagnose, but diagnosis of habitat degradation, an often slow transformation from optimal to suboptimal to unsuitable conditions for a species' survival and reproduction, is harder to detect and is may be a more serious conservation concern (Caughley and Gunn 1996). In preserving and monitoring biodiversity, the standard practice has been to manage habitat (keeping tracks of resource abundance) and constituent species therein. Such traditional monitoring programs may not be adequate to detect the consequences of habitat degradation. Doak's (1995) model on grizzlies showed that when degradation is slow (e.g. 1%), it may take more than a decade for its detection, when population in target would have already declined (Norris 2004). We need leading indicators that reflect the current status of the environment that can anticipate probable changes in population sizes ahead of time.

How do we detect habitats that are deteriorating to the disadvantage of population occupying it? The deteriorating habitat quality is harbinger to population decline. Population decline, i.e. a negative, deterministic trend in population size over time, is a pattern. The process behind this pattern is the way the strategies of individuals in the population are affected by and respond to environmental change caused by man. Drawing isodars under predation risk, among adjoining habitats, may indicate habitat quality as perceived by individuals distributed among them. Isodar theory has been fruitful for detecting ecological traps (Shochat et al. 2005), an important and potentially widespread conservation concern (Kristan 2003). Norris (2004) suggests that evolutionary theory may provide the theoretical framework for the declining species paradigm comparable with the stochastic models underpinning the small population size paradigm (Caughley 1994). Specifically the DDHS in conjunction with foraging theory may provide such theoretical framework which may be useful to guide management, a concern increasingly being highlighted (Ashley et al. 2003, Norris 2004, Sutherland 2006).

By combining measures of optimal (feeding vs. vigilance) behavior and habitat use, leading indicators of population and habitat status may be revealed for monitoring purposes. Such model estimates habitat quality at least for large ungulates across available habitats. In conjunction with vigilance, the actual habitat use (proportion of time allocated for feeding) reveals the current role that a habitat plays in the well being of the species. Consider all combinations of vigilance and actual feeding activity that may occur within a habitat type. A habitat with a low vigilance and a low level of actual feeding activity indicates a habitat low in productivity or food availability, but which is safe and may act as a refuge. A habitat with a high vigilance and a high level of feeding activity indicates high productivity and high predatory risk. These first two habitats together can provide a high quality environment for the animal. As a third possibility, a habitat may have a high vigilance and a low level of actual feeding activity. Such a habitat is unsuitable. Finally, a habitat may have a low vigilance and a high level of activity therein. This last scenario represents a highly suitable core habitat. The identification of habitats according to the fitness animals perceive is the first conservation priority to quantify the likelihood of a population declining in the future in the face of specific changes in the environment.

Because most predators follow Type II functional response, isodar analysis with Type II functional response (rather than Type I functional response) depicts nature more realistically. Non-linear isodar is close to what we may get in nature. In other words, isodars under predation risk may provide additional predictive power and insights to empirical ecology, but this needs further probing into the theoretical realm of ecology.

References

Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1997. Gerbils under threat of owl predation isoclines and isodars. *Oikos* 78: 81-90.

Andrewartha, H.G. and Birch, L.C. 1954. *The distribution and abundance of animals.* The University of Chicago Press: Chicago.

Ashley, M.V., Willson, M.F., Pergams, O.R.W., O'Dowd D.J., Gende, S.M. and Brown, J.S. 2003. Evolutionarily enlightened management. *Biol. Conserv.* 111: 115-123.

Brown, J.S. 1992. Patch use under predation risk: I. Models and predictions. *Annales Zoologici Fennici* 29: 301-309

Brown, J.S. 1998. Game theory and habitat selection. In: Game Theory and Animal Behavior, eds. L.A. Dugatkin and H.K. Reeves, pp. 188-220. Oxford University Press: Oxford.

Brown, J.S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. *Evol. Ecol. Res.* 1: 49-71.

Brown J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol*. 22: 37-47.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63: 215-244.

Caughley, G. and Gunn, A. 1996. *Conservation biology in theory and practice*. Blackwell Science: Cambridge.

Doak, D.F. 1995. Source-sink models and the problem of habitat degradation: General models and applications to the Yellowstone Grizzly. *Cons. Biol.* 9: 1370-1379.

Elton, C. 1933. *The ecology of animals*. London, U.K.

Elton, C. 1949. Population interspersion: an essay on animal community patterns. *J. Ecol.* 37: 1-23.

Fretwell, S.D. and Lucas, H.L. Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19: 16-36.

Fretwell, S.D. 1972. *Populations in a seasonal environment*. Princeton University Press: Princeton.

Kennedy, M. and Gray, R.D. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments in the ideal free distribution. *Oikos* 68: 158-166.

Knight, T.W. and Morris, D.W. 1996. How many habitats do landscapes contain. *Ecology* 77: 1756-1764.

Krebs, C.J. 2006. Ecology after 100 years: Progress and pseudo-progress. *NZ J. Ecol.* 30: 3-11.

Kristan, W.B. 2003. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos* 103: 457-468.

Laundré, J. W., Hernández, L. & Altendorf, K. B. 2001. Wolves, elk, and bison: Re-establishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Can. J. Zool.* 79: 1401-1409.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool*. 68: 619-640.

MacArthur, R.H and Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press: Princeton.

MacArthur, R.H. and Pianka, E.R. 1966. On optimal use of a patchy environment. *Am.Nat*. 100: 603-609.

May, R. 1999. Unanswered questions in ecology. *Phil. Trans. R. Soc. Lond. B* 354: 1951-1959.

McNamara, J.M. and Houston, A.I. 1990. State-dependent ideal free distributions. *Evol. Ecol*. 4: 298-311.

Mitchell, W.A. and Valone, T.J. 1990. The optimization research program: studying adaptations by their function. *Quar. Rev. Biol*. 65: 43-52.

Moody, A. L., Houston, A. I. and McNamara, J. M. 1996. Ideal free distributions under predation risk. *Behav. Ecol. Sociobiol.* 38: 131-143.

Morisita, M. 1950. Dispersal and population density of a water strider, Gerris lacustris L. *Contributions to Physiology and Ecology, Kyoto University* 65: 1-149. [In Japanese].

Morris D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. *Evol. Ecol*. 6: 412-32.

Morris, D.W. 1987. Spatial scale and the cost of density-dependent habitat selection. *Evol. Ecol.* 1: 379-388.

Morris, D.W. 1988. Habitat-dependent population regulation and community structure. *Evol. Ecol.* 2: 80-94.

Morris, D.W. 1994. Habitat matching- alternatives and implications to populations and communities. *Evol. Ecol.* 8: 387-406.

Morris, D.W. 2003a. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136: 1-13.

Morris, D.W. 2003b. How can we apply theories of habitat selection to wildlife conservation and management? *Wildlife Research* 10: 303-319.

Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *J. Appl. Ecol.* 2004 41: 4130-426.

Parker, G.A. 1978. Searching for mates. In: Behavioural ecology: an evolutionary approach, eds. J.R. Krebs and N.B. Davies, pp. 214-244. Blackwell Scientific Publications: Oxford.

Parker, G. 1970. The reproductive behaviour and the nature of sexual selection in Scatophaga stercoraria L. (Diptera: Scatophagidae). II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *J. Anim. Ecol.* 39: 205-228.

Pimm, S.L. and Lawton J.H. 1998. Planning for biodiversity. *Science* 279: 2068-2069.

Pulliam, H. R. and Caraco, T. 1984. Living in groups: is there an optimal group size? In: Behavioural ecology: an evolutionary approach, eds. J.R. Krebs and N.B. Davies, pp. 122-147. Blackwell Scientific Publications: Oxford.

Pulliam, H.R. and Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat*. 137: s50–s66.

Ramp, D. and Coulson, G. 2002. Density dependence in foraging habitat preference of eastern grey kangaroos. *Oikos* 98: 393-2002.

Ripple, W.J. and Beschta, R.L. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience* 54: 755-766.

Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology* 62: 327-335.

Rosenzweig, M.L. 2003. *Win Win Ecology: how the earth's species can survive in the midst of human enterprise.* Oxford University Press: New York.

Shenbrot, G. 204. Habitat selection in a seasonally variable environment: test of the isodar theory with the fat sand rat, *Psammomys obesus*, in the Negev Desert, Israel. *Oikos* 106: 359-365.

Shochat, E., Abramsky, Z., Pinshow, B., and Whitehouse, M.E.A. 2002. Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? *Evol. Ecol.* 16: 469-488.

Shochat, E., Patten, M.E., Morris, D.W., Reinking, D.L., Wolfe, D.H. and Sherrod, S.K. 2005. Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos* 111: 159-169.

Sutherland, W.J. 2006. Predicting the ecological consequences of environmental change: a review of the methods. *J. Appl. Ecol.* 43: 599-616.

Sutherland, W.J. 1983. Aggregation and the ideal free distribution. *J. Anim. Ecol.* 52: 821-828.

Sva¨rdsson, G. 1949. Competition and habitat selection in birds. *Oikos* 1: 157-174.

Tregenza, T. 1995. Building on the ideal free distribution. *Adv. Ecol. Res.* 26: 253-307.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildlife Manage*. 47: 893-901.

Williams, B.K. and Nichols, J.D. 1984. Optimal timing in biological processes. *Am. Nat.* 123: 1-19.

CHAPTER SIX

6. WHY THE GROUP SIZE EFFECT ON VIGILANCE SHOULD BE CONTINGENT

6.1 INTRODUCTION

Animals often take time from feeding to raise their heads to scan the surrounding. This behavior is called anti-predator vigilance when it serves to detect approaching predators (Roberts 1996, Bednekoff and Lima 1998). In addition to its own vigilance, a foraging animal may gain additional protection from predators through group membership (William 1966, Hamilton 1971). Vigilance and group size should be tightly linked. With this well-established view, a major quest in the study of vigilance includes documenting the scanning behavior of individuals in the context of group size. Many studies have documented a negative relationship between group size and the rates of scanning by individuals (Elgar 1989, Lima and Dill 1990, Quenette 1990, Roberts 1996). However, some studies have found either no effect or the opposite effect of group size on vigilance (Elgar 1989, Lima 1995, Treves 2000, Beauchamp 2003). Here I develop a game theory model of group-size and vigilance that includes the documented ways by which group membership can influence predation risk and the value of vigilance. I can then evaluate some of the discrepancies in prior theoretical and empirical studies.

Pulliam (1973) modeled a scenario in which the independent scans of group members benefited both the scanning individual and the other group members. The combined vigilance of the group should permit earlier predator detection than that of solitary individuals. This "many eyes" effect is intuitive and straightforward. As group size increases, progressively more eyes scan the environment for predators (Powell 1974, Kenward 1978, Lima 1995, Bednekoff and Lima 1998a). While the many eyes effect (which is also referred to as group vigilance, detection effect, or collective detection) has received the most attention, grouping may confer additional benefits such as the dilution effect. Safety in numbers under the risk-dilution concept (or dilution effect) occurs because if predators attack a single prey per group, the presence of companions in a group dilutes individual risk (Bertram 1978, Foster and Treherne 1981). If vigilance increases with predation risk, then with the dilution effect individual vigilance should decline with group size (Bertram 1978, Pulliam et al. 1982, Dehn 1990, Packer and Abrams 1990, McNamara and Houston 1992).

A strict distinction between detection and dilution, however, disappears when information about attacks is imperfectly shared (Bednekoff and Lima 1998a). Pulliam's (1973) model does not include the dilution effect but subsequent models (e.g. Pulliam et al. 1982, Parker and Hammerstein 1985, Dehn 1990, Bednekoff and Lima 1998b, Beachamp 2003) do. Both detection and dilution effects explain more of the variance in the group size–vigilance relationship of foraging elk *Cervus elaphus* than does a solely detection-based model (Dehn 1990).

In addition to the many eyes effect and the dilution effect, the degree to which group size attracts predators also should influence the relationship between group size and vigilance. This attraction effect incorporates the notion that aggregations may attract predators (Howe 1979, Parrish and Edelstein-Keshet 1999, Hebblewhite and Pletscher 2002). These three effects are not mutually exclusive and all may be operating simultaneously to influence predation risk, the optimal level of vigilance and optimal group size. Furthermore, under all of these effects the optimal level of vigilance for the individual will depend in part on the vigilance levels of others. Within a group, vigilance becomes a game, and the evolutionarily stable strategy (hereafter ESS) of these vigilance games may determine the individual's optimal level of vigilance.

No models have incorporated all three effects: many eyes, dilution and attraction. My goal is to extend the vigilance model of Brown (1999) into a group size-vigilance game that simultaneously includes the many eyes, dilution and attraction effects. I then investigate how the relationship between group size and ESS levels of vigilance change as a consequence of these effects and interactions among the effects. In my model, variation in predation risk drives the effects of group size on ESS levels of vigilance, as individuals balance the tradeoffs between the fitness gains from feeding with the risk of death. The model re-enforces how vigilance within a group context is a game. The optimal vigilance of a forager depends on that of its group mates. As a game of private costs and public benefits, the relationship between individual vigilance and group size is not straight-forward. The vigilance-group size effect is highly contingent on the contributions of the many eyes, dilution, and attraction effects, but in predictable ways.

6.2 MODELLING OPTIMAL VIGILANCE IN AGGREGATION

Feeding animals may 1) vary the amount of time they devote among habitats that vary in predation risk and feeding rates and 2) use vigilance to trade-off food and safety while in a habitat. Assuming an organism's fitness (i.e. per capita population growth rate) is the product of its survivor's fitness, F, and the probability of surviving to predation, p, i.e. $G=pF$, then Brown's (1999) model predicts the effect of vigilance on predation risk and feeding rate. According to Brown's (1999) model (represented here by equation 1, below), the optimal amount of vigilance, u^*, increases with the predator-encounter rate, m, the survivor's fitness, F, and the predator's lethality, $1/k$ (a predator is most lethal when k=1). Vigilance decreases with the feeding rate, f, and the marginal value of energy, $\partial F/\partial e$. In this formulation, vigilance reduces feeding rate according to $f_{actual}=(1-u)f_{max}$ where $f_{\max}$ gives the forager's feeding rate in the absence of vigilance. Vigilance increases and then decreases with the effectiveness of vigilance, b.

$$u^* = \sqrt{\frac{mF}{bf_{\max}\partial F/\partial e}} - \frac{k}{b} \tag{1}$$

In this model, predation risk, μ, has four components, i.e. $\mu = \frac{m}{k+bu}$, where u is the vigilance of a focal individual. Equation (1) reflects what an optimal forager should do when foraging under predation risk. It tells us nothing about how vigilant an individual should be when it is in a group. In other words, Brown's (1999) model does not incorporate a group size effect. I extend the vigilance model of Brown (1999) into a group size-vigilance game. The vigilance game model may be appropriate for gregarious animals (e.g. ungulate herds). I build my model in two steps.

First, I modify predation risk of Brown's (1999) original model by incorporating into it all three components of group size effect (many eyes, dilution and attraction) such that it reflects a more realistic scenario in gregarious life. The resultant equation (2) for predation risk now has all three components of group size effect as well as Brown's (1999) original parameters.

$$\mu = \frac{\frac{mN^{\alpha}}{N}}{k + (N-1)\beta\bar{u} + bu} \tag{2}$$

In equation (2) N is the number of individuals in a group such that $1/N$ represents the dilution effect and the exponential term, α, in N^{α} the attraction effect. The dilution effect and the attraction effect interact with each other. When $\alpha=0$, there is only the dilution effect but no attraction effect. The condition $\alpha=1$ precipitates a canceling of two effects, i.e. the attraction effect exactly cancels the dilution effect. There is no net effect of group size. The situation $\alpha > 1$ causes the attraction effect to dominate the dilution effect. When $\alpha < 1$, exactly the opposite effect occurs, i.e. the dilution effect is more than the attraction effect. Increasing N will increase the risk of predation. The term β reflects the many eyes effect such that $\beta=0$ (no many eyes effect), $\beta < b$ (better check yourself- individuals do not trust friends for vigilance), $\beta > b$ (individuals trust friends), and $\beta=b$ (when individuals value their own vigilance as much as that of their group mates). The term $\bar{u}$ is the vigilance of everybody else in the group except the focal individual whose vigilance is u. Vigilance behavior or attention to predators permits prey to reduce predation risk while engaged in a particular feeding behavior, allowing an organism to balance food and safety while engaged in particular fitness enhancing activities (Lima and Dill 1990). Measures of vigilance may have units of scans per unit time, or percent of time spent scanning.

Second, I incorporate equation (2) into a fitness generating function or *G*- function (Brown 1998, 1999), to obtain the level of individual vigilance within a group. A forager maximizes fitness, *pF*, by adopting an optimal vigilance level, $u*$ (equation 3):

$$u* = \sqrt{\frac{FmN^{\alpha}}{bf_{\max} N(\partial F / \partial e)}} - \frac{k + (N-1)\boldsymbol{\beta}\bar{u}}{b} \qquad (3)$$

Equation (3) identifies an element of a game: an individual's vigilance, $u*$, depends on the average vigilance level of others ($\bar{u}$) in groups. Within a group, vigilance becomes a game, and the ESS of these vigilance games may represent the optimal levels of vigilance. Note that when N=1, equation (3) collapses to Brown's equation (1). It's tempting to know what the ESS should be in this vigilance- group size game. The ESS value ($\boldsymbol{u*}$) of $u*$ can be obtained from equation (3) under the condition of $u*=\bar{u}$, as expressed by equation (4):

$$\boldsymbol{u*} = \frac{\sqrt{\dfrac{bmFN^{\alpha}}{f_{\max} N(\partial F / \partial e)}}}{b + K + (N-1)\boldsymbol{\beta}} \qquad (4)$$

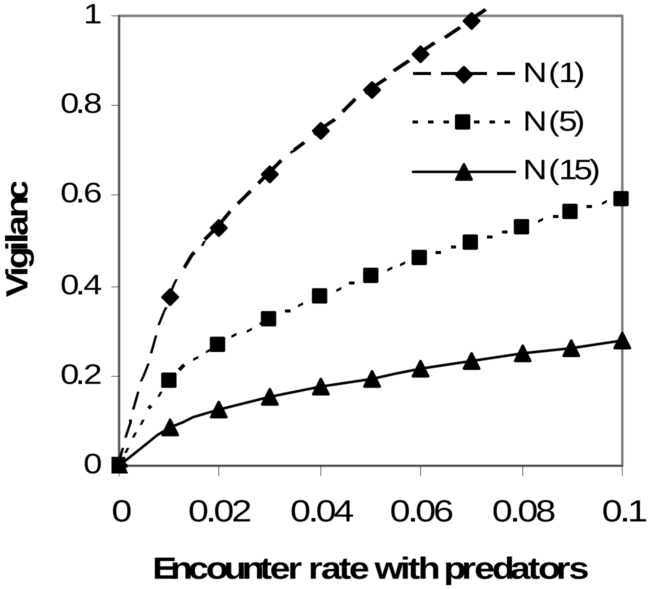
6.3 HOW DOES GROUP SIZE-VIGILANCE GAME MODEL COMPARE WITH THE BROWN'S (1999) VIGILANCE MODEL?

In Brown's (1999) vigilance model, the optimal amount of vigilance increases with the predator-encounter rate, the forager's survivor's fitness, the predator lethality, and decreases with the marginal value of energy. It increases and then decreases with the effectiveness of vigilance (equation 1). My game model on group size-vigilance shows the same patterns (see Table 7, Figure 19a-e). Increasing group size causes the group size-vigilance slopes to become shallower (Figure 19a-e, Appendix II).

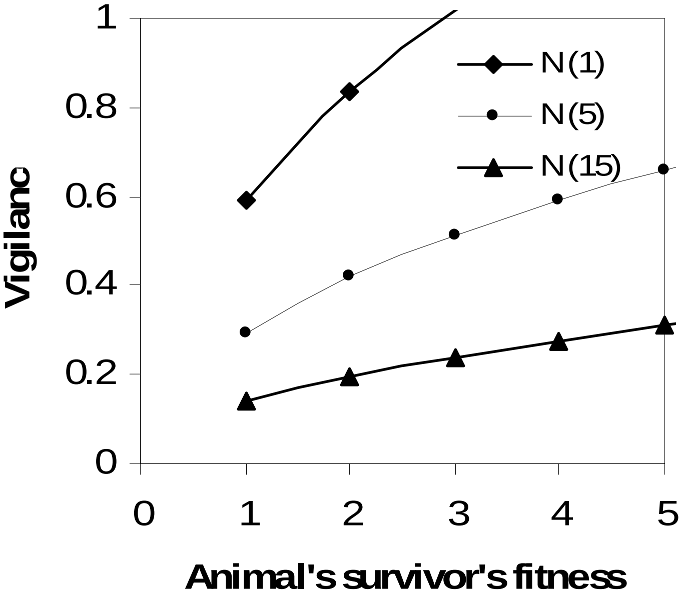
Table 7: Predictions for the effects on vigilance level from increasing 1) Encounter rate with predator, 2) Encounter rate with predator, 3) Predator lethality, 4) Marginal value of energy, and 5) Effectiveness of vigilance, as group size increases.

Variables	Vigilance rate
Encounter rate with predator	↑
Survivor's fitness	↑
Predator lethality	↑
Marginal value of energy	↓
Effectiveness of vigilance	at low b↑, at high b ↓

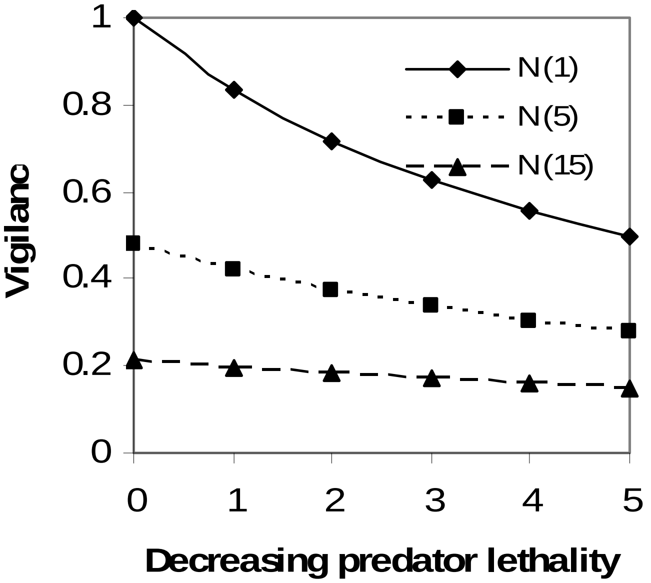
a)


Vigilanc
1
0.8
0.6
0.4
0.2
0
0
0.02
0.04
0.06
0.08
0.1
Encounter rate with predators
N(1)
N(5)
N(15)

b)

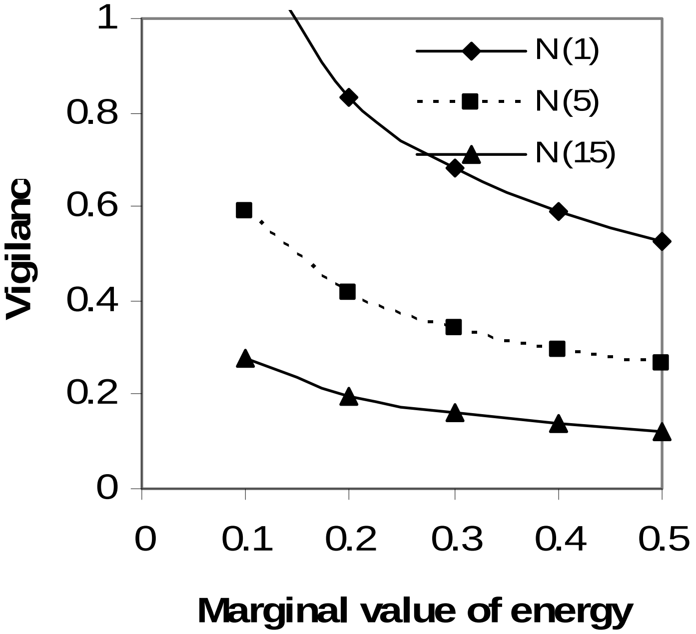

Vigilanc
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
Animal's survivor's fitness
N(1)
N(5)
N(15)

c)



1
0.8
0.6
0.4
0.2
0
Vigilanc
N(1)
N(5)
N(15)
0
1
2
3
4
5
Decreasing predator lethality

d)



1
0.8
0.6
0.4
0.2
0
Vigilanc
N(1)
N(5)
N(15)
0
0.1
0.2
0.3
0.4
0.5
Marginal value of energy

e)

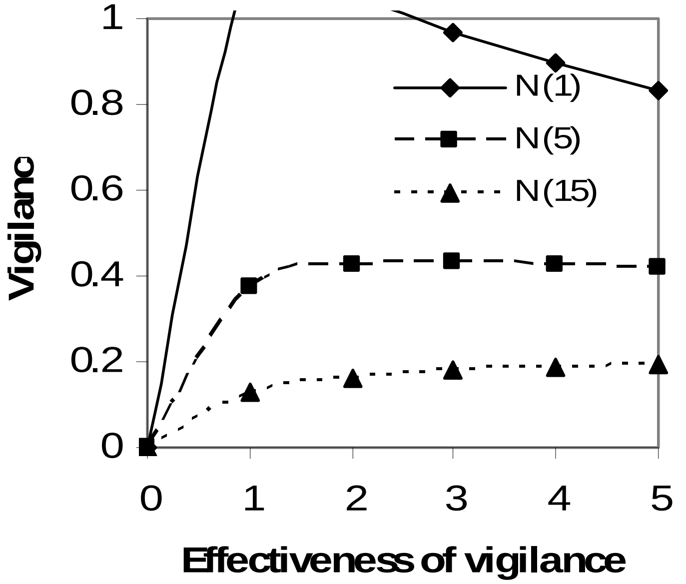


Figure 19a-e: The effects of a) the encounter rate with predators, b) the animal's survivor's fitness, c) predator lethality, d) the marginal value of energy, and e) the effectiveness of vigilance, on the optimal level of vigilance across group sizes. The line shift to lower levels of vigilance as group size increases, and the relationship between vigilance and the model parameter weakens with increasing group size. For illustration: *m*=0.05, $\partial F / \partial e = 0.2$, ***k*=1, *f*=0.1, *b*=5, *F*=2, *β*=0.5, and *α*=0.5.**

6.4 GROUP SIZE EFFECT AND ESS LEVELS OF VIGILANCE

Group size influences ESS levels of vigilance as a consequence of the many eyes, dilution, and attraction effects. Equation (5), the derivative of equation (4), indicates that the overall group size effect (*N*) on the ESS levels of vigilance are contingent upon parameters in the numerator.

$$\frac{\partial \boldsymbol{u}^*}{\partial N} = \frac{\left(\frac{1}{2}\left(b+K+(N-1)\beta\right)\right)\left(\sqrt{\frac{f_{\max} N(\partial F/\partial e)}{bFmN^{\alpha}}}\right) - \left(\sqrt{\frac{bFmN^{\alpha}}{f_{\max} N(\partial F/\partial e)}}\right)\beta}{\left(b+K+(N-1)\beta\right)^{2}} \tag{5}$$

The ESS levels of vigilance increase with the attraction effect, but decrease with the many-eyes effect, and the dilution effect (Figure 20, Appendix III). Vigilance may decline with group size owing to the combined effect of all three effects (Figure 20), but this depends on the strength of attraction effect (Figure 21). For example, with a high attraction effect, individual vigilance does not decline with group size but rather increases with it. With a moderate attraction effect, vigilance first increases and then decreases with group size. With a low attraction effect, it declines with group size (Figure 21). Simulations on pair-wise effects show that all two pair-wise combinations result in the inverse relationship between the group size and vigilance when the attraction effect is low. When the attraction effect is high, there is no group size effect on vigilance. The attraction effect makes the group size-vigilance curve shallower. Vigilance does not decline under the attraction effect as group size increases (Figure 22).

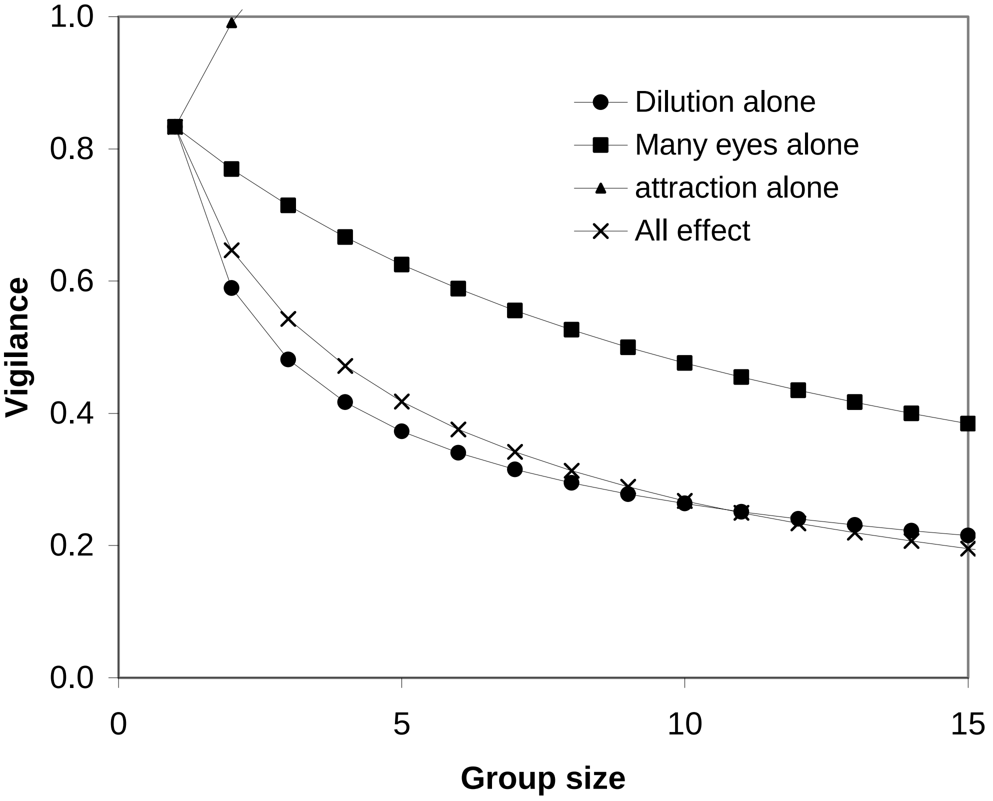


Figure 20. Only under the attraction effect does vigilance increase with group size. Given the parameters of this example, vigilance declines with group size when all effects are combined. The following values of *α* and *β* were used: dilution effect (*β*=*α*=0), many-eyes effect (*β*=0.5, *α*=1), attraction (*β*=0, *α*=1.5), and all effects combined (*β*=*α*=0.5). Other parameters as in Figure 19.

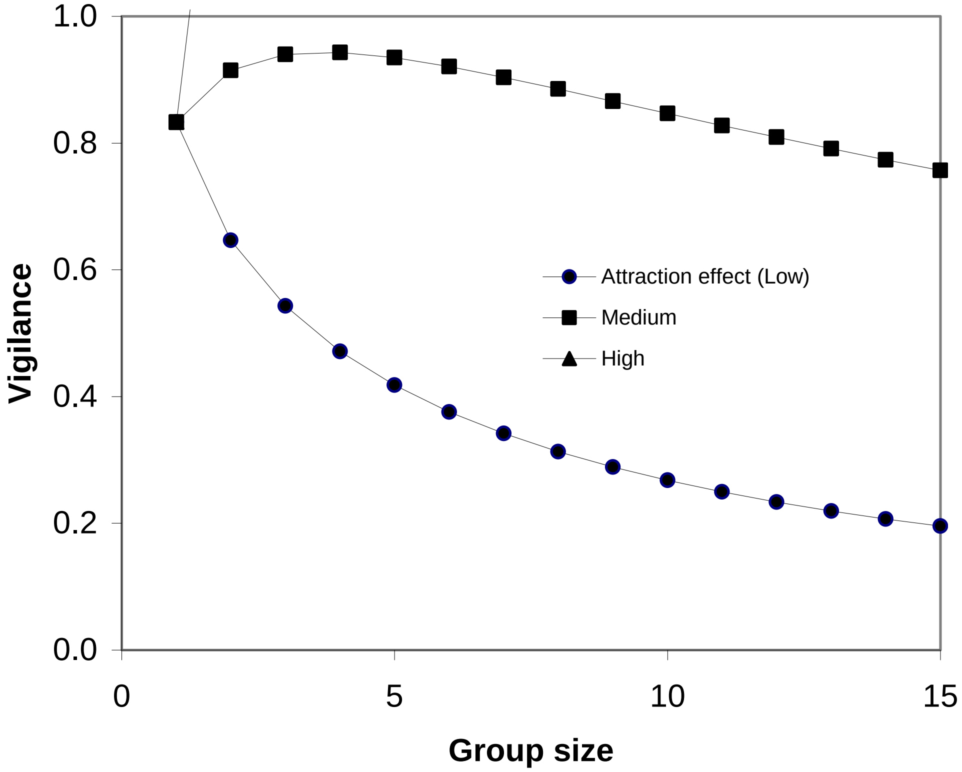


Figure 21. The effect of increasing the attraction effect on the relationship between vigilance and group size. Each successive line represents a higher attraction effect. At a very high attraction effect, the ESS level of vigilance jumps to 1 with just a small increase in group size. For the three lines: High α=3, Medium α=1.5 and Low α =0.5. Other parameters as in Figure 19.

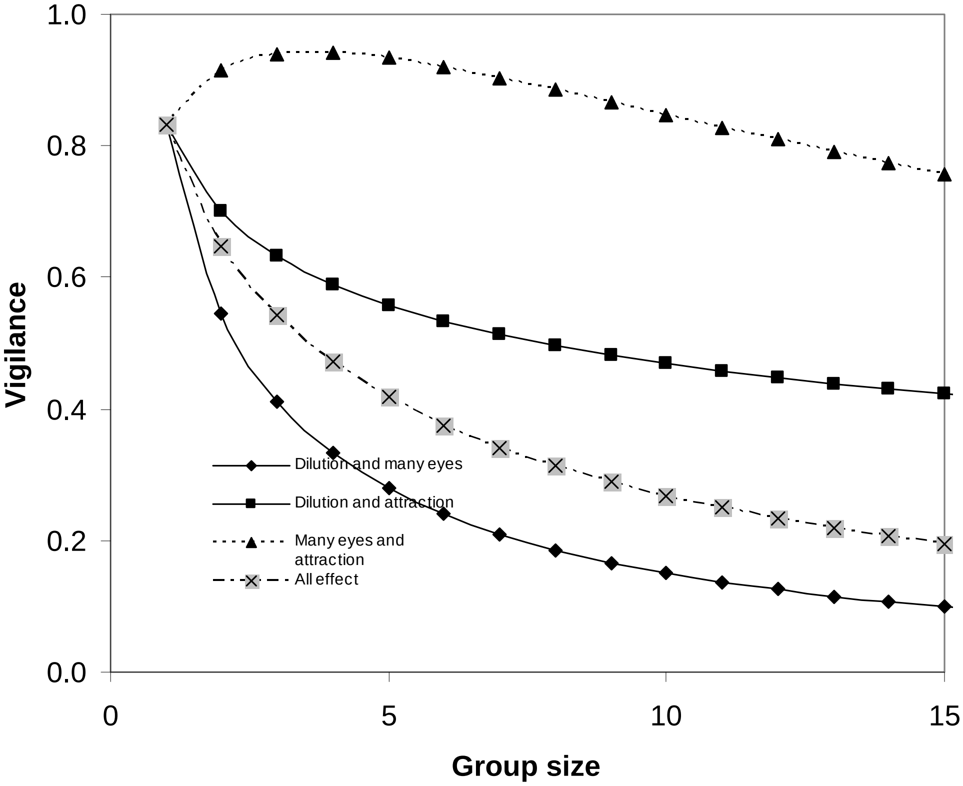


Figure 22. The effect of combinations of effects on the relationship between the ESS level of vigilance and group size: The attraction effect (the value of α) determines the shape of group size-vigilance curve. When the attraction effect is low, there is an inverse relationship between group size and vigilance. For illustration purposes, the following values of α and β were used for different combinations: dilution-many-eyes (α=0, β=0.5), dilution-attraction (α=β=0), attraction-many-eyes (α=1.5, β=0.5), and for all effects (α=β=0.5). Other parameters as in Figure 19.

Vigilance is higher in “Self-trust” scenario ($\beta < b$) than either in “Trusting friends” ($\beta > b$) or “Equal-trust” scenarios. When the value of β is larger than b (trusting one’s friends in the group) or equal to b (when individuals consider their vigilance as valuable as that of their friends), the resulting decline in vigilance with group size is very steep. Individuals prefer the vigilance of others rather than their own with the increase of group size (Figure 23).

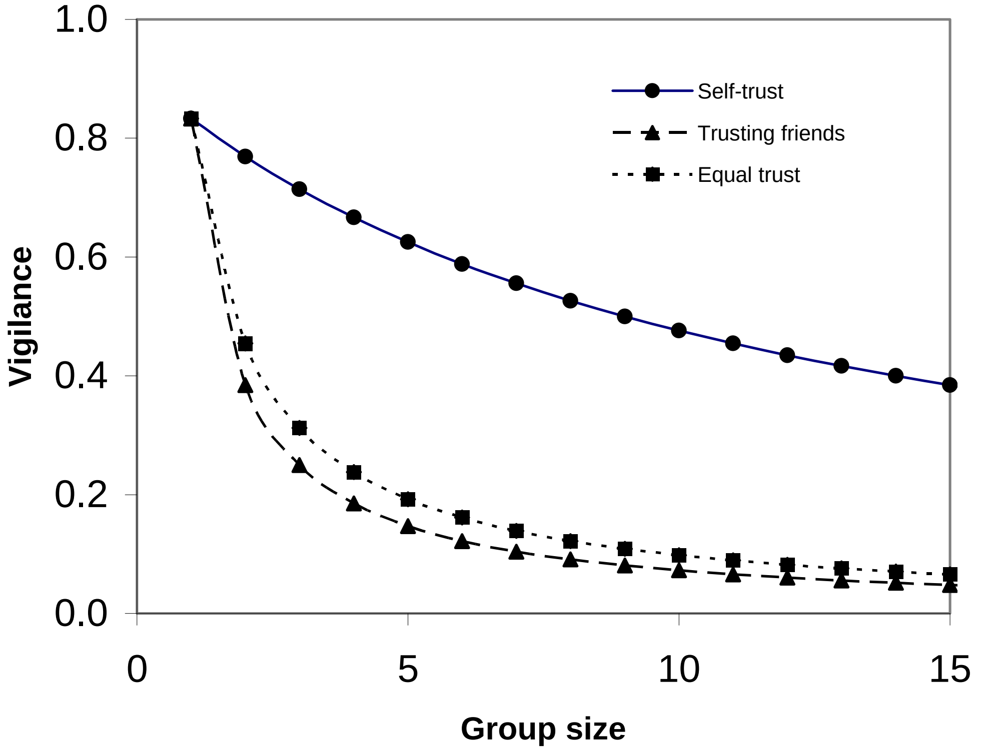


Figure 23. Individuals are less vigilant, under the vigilance of others, as group size increases. For illustration purposes, the following values of *α*, *β* and *b* were used: Self-trust (*α*=1, *β*=0.5, *b*=5), Trusting friend (*α*=1, *β*=10, *b*=5) and Equal-trust (individuals valuing the vigilance of their group-mates as that of their own) (*α*=1, *β*= *b* =5). Other parameters as in Figure 19.

6.5 DISCUSSION

In nature, all components of the group size effect (i.e. dilution, detection and attraction) likely intertwine with each other. This makes the relationship between the ESS level of vigilance and group size highly contingent.

Factors such as competition and scrounging may be important that potentially influence vigilance in a group context (Beauchamp 2003), but the fitness costs of predation (i.e. death) may exceed starvation costs and social benefits at long time scales if the predation risk is relatively high (Abrams 1993). Predation is a prime mover of social evolution (Wilson 1975). Our understanding of predation as leading to sociality derives mainly from studies of aggregation in prey and individual vigilance. The first models to explain the evolution of animal aggregation were “selfish herd” models that showed how individuals decrease their danger by putting other individuals between themselves and other predators (Hamilton 1971). The selfish herd models, however, were not adequate to explain why individuals at the edge of a group would not depart, thereby disintegrating groups. Pulliam (1973) proposed a model showing that animals benefit by grouping, assuming that detection of predators by any group member results in equal safety for all members (many eyes effect). The direct relationship between vigilance and aggregation was attractive because animals in groups may rely on associates for early warning of danger. This group vigilance hypothesis (Robert 1996) has been widely interpreted as predicting an inverse relationship between group size and vigilance. That is to say, individuals can decrease their personal commitment to vigilance without increasing their risk of failing to detect an attack.

Because the many eyes models were not adequate to explain group size effect, in the subsequent years after the publication of Pulliam's (1973) work, scholars began to evaluate yet another intuitive idea that the presence of companions in a group dilutes individual risk (Bertram 1978, Foster and Treherne 1981). If vigilance increases with predation risk, then with the dilution effect individual vigilance should decline with group size. Lazarus (1979) commented that part of the group size effect may be due to a reduced risk of capture in larger groups. This is the 'dilution' effect. That is, for any one predator attack, the larger the group of prey animals, the smaller is the chance that any particular individual will be the victim. A solid evidence that dilution effect operates in nature came from the insect world (Foster and Treherne 1981). In the mean time, assumptions of the many eyes models that 1) collective detection of predators by group members and 2) behavior monitoring of group mates did not come through the test under controlled conditions (Lima 1995, Roberts 1996). The central idea in these models that all group members are at equal risk (as a consequence of perfect collective detection) may not be realistic biologically. Individuals who first detect the predators should be less at risk than those who learn about it secondarily (McNamara and Houston 1992, Bednekoff and Lima 1998b). Field studies on predators show that large predators target less vigilant prey (Schaller 1972, FitzGibbon 1989).

Pulliam's (1973) model does not include the dilution effect, but subsequent models (e.g. Pulliam et al. 1982, Parker and Hammerstein 1985, Dehn 1990 Beauchamp 2003) do. A model incorporating both detection and dilution effects explains more of the variance in the group size–vigilance relationship of foraging elk *Cervus elaphus* than does a solely detection-based model, and therefore, provides some evidence of the importance of both effects (Dehn

1990). Dehn (1990) concluded that both group vigilance and dilution effects were important, with group vigilance particularly important at small group sizes and the dilution effect at higher group sizes. Bednekoff and Lima (1998b) suggest that dilution and detection effects are likely to be intertwined because collective detection is imperfect. Bednekoff and Lima's (1998b) work on *Accipitor* hawk attacks on small birds showed that interactions between risk dilution and collective detection depend on predator targeting behavior: less vigilant prey are at high risk.

Field studies on vigilance and group size reveal contrasting results and discrepancies. Although many studies have documented a negative relationship between group size and rates of scanning by individuals (Lagory 1986, Elgar 1989, Lima and Dill 1990, Quenette 1990, Roberts 1996, Hunter and Skinner 1998), empiricists suggest that evidence for such cooperation is not convincing, particularly in birds and mammals and that most correlations were weak with high amounts of unexplained variation (Elgar 1989). In Yellowstone National Park, USA, one of the most thoroughly studied systems in the world, ungulates, e.g. elk *Cervus elaphus* and bison *Bison bison* failed to show group size effect (Laundré et al. 2001). Lima (1995) found no support for the two essential elements of the group size effect: collective detection and behavioral monitoring. Re-evaluations of the group-size effect have, therefore, been suggested (Lima 1995, Treves 2000, Beauchamp 2003).

Such results militate against models that use a single component of group size effect in isolation. For the realistic representation of nature, vigilance models should combine all possible group size effects. My model with all three effects (many eyes, dilution and attraction) may explain some of the discrepancies in both theoretical and empirical studies.

This model indicates that the relationship of vigilance and group size as a consequence of the combined effect of both dilution and detection produces a stronger effect than that predicted by the detection effect or dilution effect alone (*cf.* Beauchamp 2003). What will be the relationship when we incorporate a parameter which denotes the idea that gregarious behavior often facilitates rather than hinders predation?

My model clearly shows that group size effect on vigilance behavior is contingent upon the strength of interacting effects particularly the attraction effect. Incorporating attraction effect makes my model more realistic. Hebblewhite and Pletscher (2002) found that wolves *Canis lupus* encountered larger elk *Cervus elaphus* groups than expected based on availability, and killed more elk from larger groups than expected based on numbers of encounters, in Banff National Park (BNP), Alberta. Elk appeared to adopt two different strategies to minimize predation risk: living in small herds that were rarely encountered by wolves or living in large herds that reduced their predation risk through dilution (Hebblewhite and Pletscher 2002). Attack success of lions *Panthera leo* was higher on the largest and smallest groups of zebra *Equus burchelli*, wildebeest *Connochaetes taurinus*, and gazelles *Gazella* spp. (Schaller 1972; Van Orsdol 1984). African wild dogs *Lycaon pictus* attacked and success rate was higher on gazelle groups of >200 than on groups of 1 (Fanshawe and Fitzgibbon 1993). Crisler (1956), a long way back, suggested that wolf attack success increased with the group size of migratory caribou *Rangifer tarandus*. That large aggregations attract predators is the fact not only of predator-prey system (Parrish and Edelstein-Keshet 1999) but also of plant-animal interactions. Howe (1979) suggested that clump of fruiting trees attract frugivores which, in turn, attract their predators, the idea that predators, like other animals, are likely to seek out abundant sources of food. Larger groups may be more likely to be detected and attacked by a predator (Turner and Pitcher 1986, Cresswell 1994), but this increase is unlikely to keep pace with an increase in group size (Roberts 1996). Both attraction effect and dilution may act together. The combined effects have been referred to as an encounter-dilution effect (Mooring and Hart 1992). These studies suggest that attraction effect is an important variable influencing the relationship between vigilance and group size effect.

An aggregation may form initially by random encounter and grow by density-dependent interactions (Parrish and Edelstein-Keshet 1999). Group size is then determined by the balance of payoffs to individual members, where size of the group affects its performance. At large sizes, individuals face low risk when they enjoy collective detection and benefit from their associates through the dilution effect. They may cooperate to deter or confuse predators. They, however, face more risk when, as a group, they are more conspicuous (the group-level predation risk) and when members interfere with each other's vigilance and movements. Within the midrange is the equilibrium or critical group size at which the average vigilance of everybody else (except the focal individual), $\bar{u}$, is equal to the optimal vigilance of the focal individual, u^*. At this point, the vigilance strategy of the individual is at the ESS, i.e. $\boldsymbol{u^*}$ in my model**.** The ESS is itself contingent, dependent upon the targeting strategy of the predator and the strength of dilution, attraction and many eyes effects owing to group size.

References

Abrams, P.A. 1993. Optimal traits when there are several costs: the interaction of mortality and energy costs in determining foraging behaviour. *Behav. Ecol.* 4: 246-253.

Beauchamp, G. 2003. Group-size effects on vigilance: a search for mechanisms. *Behavioural Processes* 63: 111-121.

Bednekoff, P.A. and Lima S.L. 1998. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proc. R. Soc. London B*. 265: 2021-2026.

Bednekoff, P.A. and Lima, S.L. 1998a. Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol. Evol.* 13: 284-287.

Bednekoff, P. A. and Lima, S. L. 1998b. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proc. R. Soc. London B.* 265: 2021-2026.

Bertram, B.C.R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology: An Evolutionary Approach*, eds. J. R. Krebs and N. B. Davies, pp. 64-96. Blackwell Scientific Publications.

Brown, J.S. 1998. Game theory and habitat selection. In: *Game Theory and Animal Behavior*, eds. L.A. Dugatkin and H.K. Reeves, pp. 188-220. Oxford University Press.

Brown, J.S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. *Evol. Ecol. Res.*1:49-71.

Cresswell, W. 1994. Flocking is an effective anti-predator strategy in redshanks, Tringa totanus. *Anim. Behav.* 47: 433-442.

Crisler, L. 1956. Observations of wolves hunting caribou. *J. Mammal.* 37: 337-346.

Dehn, M.M. 1990. Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* 26: 337-342.

Elgar, M.A. 1989. Predator vigilance and group size in mammals and birds. *Biol. Rev.* 64: 13-33.

Fanshawe, J.H. and Fitzgibbon, C.D. 1993. Factors influencing the hunting success of an African wild dog pack. *Anim. Behav.* 45: 479-490.

Fitzgibbon, C.D. 1989. Why do hunting cheetahs prefer male gazelles? *Anim. Behav.* 40: 837-845.

Foster, W.A. and Treherne, J.E. 1981. Evidence for the dilution effect and the selfish herd from fish predation on a marine insect. *Nature* 293: 466-467.

Hamilton, W.D. 1971. Geometry for the selfish herd. *J. Theor. Biol*. 31: 295-311.

Hebblewhite, M. and Pletscher, D.H. 2002. Effects of elk group size on predation by wolves. *Can. J. Zool.* 80: 800-809.

Howe, H.F. 1979. Fear and Frugivory. *Am. Nat.* 114: 925-931.

Hunter, T.B. and Skinner, J.D. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135: 195-211.

Kenward, R.E. 1978. Hawks and doves: attack success and selection in goshawk flights at wood-pigeons. *J. Anim. Ecol*. 47: 449-460.

Lagory, K.E. 1986. Habitat, group size, and the behaviour of whitetailed deer. *Behaviour* 98: 168-179.

Laundré, J.W., Hernández, L. and Altendorf, K.B. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Can. J. Zool.* 79: 1401-1409.

Lazarus, J. 1979. The early warning function of flocking in birds: an experimental study with captive quelea. *Anim. Behav.* 27: 855-865.

Lima, S.L. 1995. Back to the basics of anti-predatory vigilance: the group size effect. *Anim. Behav.* 49: 11-20.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619–640.

McNamara, J.M. and Houston, A.I. 1992. Evolutionarily stable levels of vigilance as a function of group size. *Anim. Behav.* 43: 641-658.

Mooring, M. S. and Hart, B. L. 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123: 173-191.

Packer, C. and Abrams, P. 1990. Should co-operative groups be more vigilant than selfish groups? *J. Theor. Biol*. 142: 341-357.

Parker, G.A. and Hammerstein, P. 1985. Game theory and animal behaviour. In: *Evolution: Essays in Honour of John Maynard Smith*, eds. P.J. Greenwood, P.H. Harvey and M. Slatkin, pp. 73-94. Cambridge University Press: New York.

Parrish, J.K. and Edelstein-Keshet, L. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* 284: 99-101.

Powell, G.V.N. 1974. Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. *Anim. Behav.* 22: 501-505.

Pulliam, H.R. 1973. On the advantages of flocking. *J. Theor. Biol.* 38: 419-422.

Pulliam, H.R., Pyke, G.H. and Caraco, T. 1982. The scanning behavior of juncos: a game-theoretical approach. *J. Theor. Biol.* 95: 89-103.

Quenette, P.Y. 1990. Functions of vigilance in mammals: a review. *Acta Oecol.* 11: 801-818.

Roberts, G. 1996. Why individual vigilance declines as group size increases*. Anim. Behav.* 51: 1077-1086.

Schaller, G.B. 1972. *The Serengeti lion.* University of Chicago Press.

Treves, A. 2000. Theory and method in studies of vigilance and aggregation. *Anim. Behav.* 60: 711-722.

Turner, G.F. and Pitcher, T. J. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *Am. Nat.* 128: 228-240.

Van Orsdol, K.G. 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *Afr. J. Ecol.* 22: 79-99.

Williams, G.C. 1966. *Adaptation and Natural* Selection. Princeton University Press.

Wilson, E.O. 1975. *Sociobiology: The new synthesis.* Harvard University Press.

CHAPTER SEVEN

7. RECONSTRUCTING THE REALM OF THE BIGGIES!

Abstract

The suggestion in the early 20th century that top predators were a necessary component of ecosystems because they hold herbivore populations in check and promote biodiversity was at first accepted and then largely rejected. With the advent of Evolutionary Ecology and a more full appreciation of direct and indirect effects of top predators, this role of top predators is again gaining acceptance. The previous views were predicated upon lethal effects of predators but largely overlooked their non-lethal effects. I suggest that conceptual advances coupled with an increased use of experiments have convincingly demonstrated that prey experience costs that transcend the obvious cost of death. Prey species use adaptive behaviors to avoid predators, and these behaviors are not cost-free. With predation risk, prey species greatly restrict their use of available habitats and consumption of available food resources. Effects of top predators consequently cascade down to the trophic levels below them. Top predators, the biggies, are thus both the targets of and the means for conservation at the landscape scale.

Amid concern over the increasing impact of humans on earth's biota, ecologists have increasingly sought clues to the maintenance of biodiversity. A growing number of studies point to the powerful role played by top predators. The loss of predators, particularly top predators, leads to biodiversity loss (Terborgh et al. 2001, Estes et al. 2001), thus jeopardizing ecosystem integration. Top predators, the biggies, are thus heralded as both the target of and the means to conserve biodiversity at the landscape scale (Ray et al. 2005). Such efforts are epitomized by slogans like, ‘Save the tiger’, ‘Save the white shark’, ‘Save the grizzly’, or other large carnivore-orientated campaigns (Seidensticker 1997) and are reflected in ecologists’ present endeavors to scientifically justify the connection between predators and biodiversity (Soulé and Terborgh 1999, Estes et al. 2001). Various claims are made that charismatic species such as large carnivores can act as important flagships, umbrellas or indicators (Simberloff 1998) for the conservation of the rest of the biodiversity, and even that some are vital keystone species for ecosystem function (Noss et al. 1996). The mounting evidence of a tight association between apex predators and high biodiversity justifies targeting top-predator species for their conservation utility on ecological grounds (Ray et al. 2005, Sergio et al. 2005).

Here I examine the recent arguments concerning the role of apex predators on ecosystem structure and function from an historical perspective. I will show that Ecologists are reinventing the wheel! I consider the reasons why, and I end with a reminder that old science can be good science, and knowledge of the historical development of a field can be a potent component of a scientist’s intellectual arsenal. Oksanen made a similar argument 15 years ago.

Over half a century ago, Aldo Leopold suggested that predation was a necessary component of all ecosystems and that their loss could lead to grave ecological consequences. He argued that the loss of predators set the stage for an irruption of the Kaibab (mule) deer population followed by a degradation of habitat and an eventual reduction in carrying capacity (Leopold 1943). This study, once considered a classic, was widely reported in the ecology textbooks of the 1960s as an example of an ungulate population eruption in the absence of their predators. In a powerfully constructed article, Caughley in the early 1970s criticized Leopold's interpretations and forwarded alternative hypotheses for the deer irruptions, such as interrelationship of livestock grazing and fire control. New analyses of aspen tree rings from the Kaibab are, however, consistent with Leopold's hypothesis of extreme deer herbivory following predator removal, as well as the importance of predation in controlling deer populations on the Kaibab (Ripple and Beschta 2005, for a review). Using modern analyses, today ecologists are finding Leopold's interpretations to be right on the mark, several decades after their publication. In fact, Leopold may have been more correct than he could know. Given modern paradigms, one can envision situations in which, in the absence of predators, an herbivore species depletes its food reserves simply by experiencing no fear. In the absence of fear, herbivores can increase both their use of available habitats and food resources.

Naturally, one wonders why was there such a delay reinventing the wheel. Perhaps Caughley's devastating re-analysis of the Kaibab deer story made ecologists "gun shy" over the potential of top-down community effects. Alternatively, perhaps due to small sample sizes, large ranges, and the logistical challenges of performing manipulative experiments with top predators, our understanding of the role of large carnivores in ecosystem function has remained unclear and contentious (Soulé and Terborgh 1999). Or, as suggested recently by Knight et al. (2006), ripple effects of predators on lower trophic levels, particularly the producer, depend on relative consumption of mutualists versus antagonists of producers. Trophic cascades are not likely observed when predators consume producer mutualists, which may obscure their ecosystem-wide effects.

Science emerged from the Second World War with a new paradigm, systems analysis (Bode 1945). Under this view, complex systems are conceptualized as interconnected components with feedback loops that stabilize the system at an equilibrium. This paradigm established the notion that living and non-living parts interact via fluxes of matter and energy. Further, apex predators, as end points of those fluxes, are of minor consequence to ecosystem function (Estes et al. 2001). Ecosystems are regulated by forces acting from lower to higher trophic levels. With these views dominant, it is perhaps unsurprising that top-down control by predators was not considered an essential process in shaping communities.

As argued earlier by others (Cody and Diamond 1975, see also American Naturalist, volume 122, number 5, 1983), competition was long held to be the principal factor structuring natural communities. Emphasis on competition may be traced to Darwin, who asserted that the struggle for existence should be most keen among species the most similar (Darwin 1859). Gause's laboratory experiments in the early 1930s, the first controlled tests of species interactions, bolstered that competition could decide the outcome of the struggle (Gause 1934). By the mid-20th century, competition was widely viewed as the principle organizing force in communities, and the niche was the fundamental unit of that organization (MacArthur 1972). Given that the Lotka-Volterra predator-prey model was neutrally stable and that Gause's predator-prey system usually went to extinction, the ecological realm fortified by the process of competition seemed impenetrable. The period from the 1960's through the early 1970s was indeed the heyday of competition.

The questioning of the ubiquity of competition as the dominant factor structuring natural communities, coupled with increasing use of field experiments in the 1970s and 1980s led to a growing consensus regarding the importance of predation relative to competition (Sih et al. 1985). This was a much delayed response following the first incontrovertible evidence of the keystone role of predators in regulating the diversity of the prey community (Paine 1966). This is surprising when considering that the keystone concept fit nicely with the notion of cascading effects of predators in a food chain (Hairston et al. 1960). Paine's manipulations of seastar densities provided a central body of evidence in the formative period of the predation paradigm (sensu Kuhn 1966) that was characterized by innovative field experiments and hypothesis testing in the context of historical arguments of competition theory (Robles and Desharnais 2002). Evidence from field studies was also encouraging: A principal result of the first scientific effort to understand tiger ecology (Schaller 1967) posited the tiger as the main factor limiting the growth of the populations of its prey.

I suggest that the full significance of predation on communities was not possible until all the costs of predation were more fully appreciated. Predation, even on large prey, can often be of large magnitude. The percent mortality among large herbivores – such as buffalo, springbok, and wildebeest – by predators in natural ecosystems in Africa ranges from 59 to 96% (Prins and Iason 1989). No surprise that predation affects prey population directly via mortality (Crawley 1992): Predators consume prey, thus affecting their density. But prey try to avoid being eaten, often at considerable costs (though obviously not as great a cost as death). The former is the domain of population ecology and the latter is that of evolutionary ecology. Classic population ecological studies and models of community dynamics incorporate only how changes in predator densities affect community dynamics by directly killing their prey (e.g. Hairston et al. 1960, Rosenzweig 1973, Oksanen et al. 1981). Evolutionary ecology teaches us that prey adopt adaptive behavioral strategies that reduce or eliminate their probability of death by predation (Mangel and Clark 1988, Lima and Dill 1990, Lima 1998, Brown et al. 1999) – and that these strategies come with significant costs to the prey species using them.

Traits that allow prey to avoid predation and thus strongly affect fitness will be under strong selection (Abrams 2000). Today, many evolutionary biologists believe that predation has played a major role in determining patterns in the history of life on this planet. The mere presence of predators in a community can force prey to make behavioral choices between vital activities such as feeding and avoiding contact with predators. The effects that ripple through the food web via evasive behaviour of herbivores are known as higher order (Werner 1992) or behavioral or trait-mediated indirect interactions (Abrams 1995, Werner & Peacor 2003, Schmitz et al. 2004). This recent avenue of research has brought new insights into how predation risk, in addition to actual predation, affects population, communities and entire ecosystems (Sinclair et al. 1995, Berger et al. 2001, Brown and Kotler 2004). Today ecologists recognize the significance of higher order interactions. The 91st Annual Meeting of the Ecological Society of America (2006) held in Memphis, TN (USA) devoted an entire oral session (out of 18) on implications of trait-mediated effects (http://www.esa.org/memphis/sessionSchedule2.php). Interestingly, trait effects have been shown as large as (Preisser et al. 2005) or even larger (Schmitz et al. 1997) than density effects. When faced with predation risk, prey select relatively safe habitats which are often poor in resources (Bergerud et al. 1983, Creel et al. 2005) and they increase vigilance in risky habitats (Elgar 1989). By constraining habitat selection and adaptive shifts in foraging behaviour, predators may have greater effects on prey dynamics than would be predicted on the basis of direct predation alone. Apparently, a predators' mere presence may bring changes in prey's behaviour, i.e. foraging mode, habitat use patterns, mating system and life history traits that determine prey's niche. Subsequently, by the early 1990s assumption that niches are primarily determined by competition was no longer held, but instead it was suggested that both competition (resource related) and anti-predator needs affect niche characters (Sih et al. 1985).

With the onset of the current millennium, ecologists have amassed a plethora of evidence demonstrating that predators can have tremendous influences on the structure of and the dynamics of ecological populations and communities. Apparently, predators do so 1) by limiting or even regulating their prey, 2) by their keystone effect (wherever keystone predators are present) and the subsequent cascading impacts down the food chain and 3) via higher order interactions. Such insight was made possible by looking at predation with broader perspectives in light of the conceptual framework and present techniques of community ecology and evolutionary ecology. From my current perspectives, Leopold was correct in his predictions about the consequences of predation on communities and ecosystems.

Although I directed my comments toward top predators, the biggies, I suspect that the same points hold for many other predators, independent of body size (Terborgh 1988). Insectivorous birds control herbivorous insects and can significantly affect plant fitness (Marquis and Whelan 1994, Mols 2002), effects that could affect forest composition and structure (Whelan and Marquis 1996). The composition of tallgrass prairies of North America can be profoundly affected by vole herbivores (Howe and Brown 1999), but this effect is likely strongly modulated by lethal and non-lethal effects of their predators. With predators, voles restrict their habitat use and reduce damage to favored food plants (Desy and Batzli 1989). The mere presence of spiders affects habitat use and foraging activity of grasshoppers (Schmitz et al. 1997). Effects of these smaller predators, too, clearly transcend consumption of prey. Now, where should we go? First, not only density effects, but also trait effects, must be integrated into empirical and theoretical studies (Luttbeg and Kerby 2005). Second, the role of predators must be incorporated into the doctrine and practice of conservation (Soulé and Terborgh 1999, Ray et al. 2005). Third, Conservation Biologists must develop monitoring programs capable of detecting trends in predator populations and their effects on biodiversity.

References

Abrams, P.A. 2000. The evolution of predator-prey interactions: Theory and Evidence. *Annu. Rev. Ecol. Syst.* 31: 79-105.

Abrams, P.A. 1995. Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *Am. Nat.* 146: 112–134.

Brown, J.S. and Kotler, B.P. 2004. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7: 999-1014.

Brown, J.S., Laundre, J.W. and Gurung M. 1999. The ecology of fear: Optimal foraging, game theory and trophic interactions. *J. Mammal.* 80: 385-399.

Berger, J., Swenson, J. E. and Persson, I. L. 2001 Re-colonizing carnivores and naïve prey: Conservation lesson from Pleistocene extinctions. *Science* 291: 1036-1039.

Bergerud, A.T., Butler, H.E. and Miller, D.R. 1983. Antipredator tactics of calving caribou: dispersion in mountains. *Can. J. Zool.* 62: 1566-1575.

Bode, H. W. 1945. *Network analysis and feedback amplifier design.* Princeton, New Jersey.

Caughley, G. 1970. Liberation, dispersal and distribution of Himalayan tahr in New Zealand. *N. Z. J. Sci*. 13: 220-239.

Cody, M.L. and Diamond, J.M. 1975. *Ecology and evolution of communities.* Cambridge, Mass, Beldnap.

Crawley, M.J. 1992. *Natural Enemies*. Blackwell, Oxford.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K. and Creel M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86: 3387-3397.

Darwin, C. 1959. *On the Origin of Species by Means of Natural Selection, or, the Preservation of Favoured Races in the Struggle for Life*. London, J. Murray.

Desy, E.A. and Batzli, G.O. 1989. Effects of food availability and predation on vole demography: a field experiment. *Ecology* 70: 411-421.

Elgar, M.A. 1989. Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* 64: 13–33.

Estes, J.A., Crooks, K. and Holt R. 2001. Predators, ecological role of. In: *The Encyclopedia of Biodiversity*, ed. S. Levin, pp. 857-878. Academic Press.

Gause, G. F. 1934. *The struggle for existence.* Baltimore, Williams and Wilkins.

Hairston, N.G., Smith, F.E. and Slobodkin, L.B. 1960. Community structure, population control, and competition. *Am. Nat*. 94: 421-425.

Howe, H.F. and Brown, J.S. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80: 1776-1781.

Knight, T. M., Chase, J. M., Hillebrand, H., Holt, R. D. 2006. Predation on mutualists can reduce the strength of trophic cascades. *Ecol. Lett.* 9: 1173-1178.

Kuhn, T. S. 1962. *The structure of scientific revolution*. University of Chicago Press.

Leopold, A. 1943. Deer irruptions. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 35: 351-366.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619-640.

Lima, S.L. 1998. Nonlethal effects in the ecology of predator-prey interactions. What are the ecological effects of anti-predator decision-making? *Bioscience* 48: 25-34.

Luttbeg, B. and Kerby, J.L. 2005. Are scared prey as good as dead? *Trends Ecol. Evol.* 20: 416-418.

MacArthur, R.H. 1972. *Geographical Ecology*. New York, Harper and Row.

Marquis, R.J. and Whelan, C.J. 1994. Insectivorous birds increase growth of white oak by consuming its herbivores. *Ecology* 75: 2007-2014.

Mangel, M. and Clark, C.W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton University Press.

Mols, C.M.M. and Visser, M.E. 2004. Great tits can reduce caterpillar damage in apple orchards. *J. Appl. Ecol.* 39: 888-899.

Noss, R.F., Quigley H.B., Hornocker M.G., Merrill T. and Paquet P.C. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Cons. Biol.* 10: 949-963.

Oksanen, L. 1991. A century of community ecology: how much progress? *Trends Ecol. Evol.* 6: 294-296.

Oksanen, L., Fretwell, S.D., Arruda, J. and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118: 240-262.

Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65-75.

Preisser, E.L., Bolnick, D.I., Benard, M.F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86: 501-509.

Prins, H. H. T. and Iason, G. R. 1989. Dangerous lions and non challant buffalo. *Behaviour* 108: 262-296.

Ray, J., Redford, K., Steneck, R. and Berger, J. 2005. *Large carnivores and the conservation of biodiversity*. Island Press.

Ripple, W. and Beschta, R.L. 2005. Linking Wolves and Plants: Aldo Leopold on Trophic Cascades. *Bioscience* 55: 613-621.

Robles, C and Desharnais, R. 2002. History and current development of a paradigm of predation in rocky intertidal communities. *Ecology* 83: 1521-1536.

Rosenzweig, M.L. 1973. Exploitation in three trophic levels. *Am. Nat*. 107: 275–294.

Schaller, G. B. 1967. *The deer and the tiger.* University of Chicago Press.

Schmitz, O.J., Beckerman, A.P. and O'Brien, K.M. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78: 1388-1399.

Schmitz, O. J., Krivan V. and Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* 7: 153-163.

Seidensticker, J. 1997. Saving the tiger. *Wildlife Society Bulletin* 25: 6-17.

Sergio, F. Newton, I. and Marchesi L. 2005. Top predators and biodiversity. *Nature* 436: 192.

Sih, A., Crowley, P., McPeek, M., Petranka, J., and Strohmeier, K. 1985. Predation, competition, and prey communities: A Review of Field Experiments. *Ann. Rev. Ecol. Syst.* 16: 269-311.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era. *Biol. Conserv.* 83: 247-257.

Sinclair, A. R. E. and Arcese, P. 1995. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology* 76: 882-891.

Soulé, M. E. and Terborgh J. 1999. *Continental Conservation-Scientific foundations of regional reserve networks.* Island Press.

Terborgh, J. 1988. The big things that run the world - a sequel to E.O. Wilson. *Cons. Biol.* 2: 402-403.

Terborgh, J., Lopez, L., Nunez, P., et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294: 1923-1925.

Werner, E.E. 1992. Individual behavior and higher-order species interactions. *Am. Nat.* 140: S5-32.

Werner, E.E. and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84: 1083-1100.

Whelan, C.J. and Marquis, R.J. 1996. Indirect effects of insectivorous birds on forest trees-conservation and management implications. In: *Songs from the Deep Woods*, eds. W.B. King and S. Drennen, pp. 10-12. National Audubon Society, NY.

CHAPTER EIGHT

8. WHAT DO ECOLOGICAL PARADIGMS CONTRIBUTE TO CONSERVATION?

Abstract

As a science, ecology ideally contributes to the conservation of natural systems by unraveling the complexity of nature, thereby allowing management of natural or exploited systems on a rational basis rather than intuition or guesswork. Unfortunately, ecology as rigorous science often does not help those who actually manage natural systems. One possibility is that heuristic theories of a young science may be too flawed to provide rational guidance. Logistic growth predicts a carrying capacity, and application of Lotka-Volterra predation equations is eminently logical, but fisheries managed with theory based on the Lotka-Volterra paradigm continue to collapse, while local government management of small game continues to succeed. A different reason is that predictions may not be relevant to particular species of interest, which may be identified for aesthetic, emotional, or economic reasons rather than their appropriateness for a particular paradigm. Island biogeography predicts species loss as a function of habitat area and has become a pillar of modern conservation biology, but is silent on which species might be lost. A third reason that theory fails to help practice is that the theory itself may not have much to do with nature. A theory of metapopulations is plausible, appealing, and conceptually relevant to conservation challenges, but metapopulations might not be common in nature. A fourth reason is that theory may be sound, but empirical parameterization is infeasible. Spotted owl

metapopulations do exist, but who is to provide the patch-specific demographic estimates to make the theory operational? No one has provided required data with sufficient precision to quell criticism.

Despite weaknesses in the architecture of a science, science has helped manage nature. As important as examining flawed blueprints of scientific paradigms is the observation that management of nature is much stronger for the effort than it otherwise could be. The challenge then is to determine why ecology fails to match needs of managers sometimes and helps at other times. It is also worth examining the customers and marketers of ecology. Managers may expect too much of paradigmatic blueprints, while ecologists believe them too much. The problems may be exacerbated because ecologists who create theory often are ignorant of what park managers, conservation planners, and forest rangers need at local scales. Those who create and implement biodiversity conservation plans need simple, pragmatic management and monitoring guidelines based on science to do their jobs. Is this possible? What is possible?

8.1 INTRODUCTION

A paradigm in ecology is a set of concepts, standards, or ideas that guide the advancement of scientific knowledge at any of a variety of spatial and temporal scales (Graham and Dayton 2002, see Kuhn 1970). Such conceptual frameworks as the niche, species interactions of competition and predator-prey relationships, foraging theory, island biogeography, and meta-population dynamics are paradigmatic in the sense that they are socially constrained ideas about how organisms interact with nature, major aspects of which are socially constrained standards for determining the questions worth asking and the answers worth accepting. The hope is that paradigm refinement and extension allow theoretical and practical ecologists to construct and apply predictive models that both explain and guide the management of nature. Paradigm refinement in an effective science makes theory operational. In ecology, operational theory should guide management recommendations for conservation, restoration, and resource management.

The stakes in finding a rational basis for management of nature are high. No part of the earth is immune from human impacts, humans directly use many living natural resources, and species presently face extinction at unprecedented rates (Smith et al. 1993, Pimm et al. 1995, Pimm and Lawton 1998, Rosenzweig 2003), despite investment of billions of dollars worldwide to stem biodiversity loss (see Agrawal and Gibson 1999, James et al. 2001, Ferraro and Kiss 2002). To the degree that species or ecological systems provide food or materials needed by people, the stakes have financial value that can be estimated, whether it is a $230 million commercial salmon fishery in Alaska or a $2 million annual economic value of deer hunting in a single New Brunswick forest (MacGregor 1998). Summed over relevant industries, the calculable costs of failing to manage nature are immense. Far broader impacts, falling loosely under the rubric “ecosystem services,” might occur with poor management with costs that are far more difficult to calculate even when the variables are known, which they may not be for some years. A risk is that costs of failure including such unknowns dwarf “immense” and unexpected anomalies in the shape of the (log) species number versus (log) area relationship for some communities (e.g. Plotkin et al. 2000).

One would think that investment of large sums of money in accordance with the best available science would stem the loss of the most obvious species of public concern, but the hope is often misplaced. Humans depend on commercial fisheries for food, yet one after another has collapsed, and some, like the Pacific salmon industry, that have survived under exploitation has done so for unknown reasons (e.g. Ludwig et al. 1993). Attempts to ensure a legacy of nature as we know it fare no better. In recent decades, for example, a focus on taxa shows that 173 species of mammals have lost > 50% their historic range areas (Ceballos and Ehrlich 2002), destruction, fragmentation, and disruption of entire ecosystems races forward (Laurance and Peres 2006), raising the prospect that many species will be lost before they are even identified, much less known. Despite unprecedented financial investment by governments and the private sector (Shellenberger and Nordhaus 2005), conservation appears to be failing.

Could faithful application of basic principles of ecology stem this loss? Or are the principles failing because they cannot be applied competently? An easy but insufficient answer is that the principles are adequate, but their application is flawed because of social or political concerns. In fisheries, for instance, it is quite clear that management is largely of people, bringing to bear such variables as seasons, intensity of individual efforts, differences in equipment, and manipulation of political processes (Ludwig et al. 1993). I argue that social control reaches a deeper level in the structure of science itself. Ecological paradigms themselves evolve and are applied in ways that limit their utility. If this is true, what should resource managers expect of ecology as a science? How can academics change ecology as a science to make it more operational? These are not questions that can be answered in a short opinion piece. I examine how some central ecological ideas fail or succeed in conservation, and explore ways in which the social component of the ecological paradigm evolution can do a better job.

8.2 WHERE PARADIGMS SUCCEED AND FAIL

8.2.1 Sustainable yield

A central paradigm in the management of exploitable resources is sustainable yield (Hilborn et al. 1995). The central assumption is that wild populations produce ”excess” individuals, which then can be ”harvested” without diminishing the capacity of the population to maintain a more or less steady state, much like a maize crop can be harvested without diminishing prospects for the future as long as sufficient seed is protected for future use. The ecological basis for this idea is logistic thinking (e.g. Gause 1934). Populations reach a carrying capacity (*K*), representing a number of individuals that fully uses the available resources, above which population growth slows and starvation or disease take their toll. If a population has age structure, like a fish, grouse, or pine tree, births exceed deaths (the difference being the intrinsic rate of increase, *r*) and offspring cohorts overshoot carrying capacity. These are the ”excess” individuals to be ”harvested.” What managers must do is maintain populations at levels at or below *K* where they produce abundant excess individuals, without depressing the population so much that production of harvestable ”excess” is not economically useful, and without depressing populations so much that they cannot recover. An issue is whether harvest is set at some level below maximum sustainable yield as indicated by a specific projection of excess, or some sustainable level below that maximum which adds resilience to use (e.g. Peterson 2005). Managers must avoid exploitation so severe as to “eat the seed corn” or precipitate accidents that have the same effect.

The virtually universal concept of sustainable yield has mixed results. Its success is evident in management of game animals in North America, where provincial and state governments in Canada and the United States successfully regulate small and large game populations and sport fisheries. Basic demographic estimators set limits for “harvest” of animals as diverse as bobwhite quail (Guthery et al. 2004) and black bear (Diefenbach et al. 2004). For heavily hunted species, manipulation of the breeding system and effective breeding population (N_e), such as occurs in male-only hunts for deer (e.g. Giles and Findlay 2004), or of hunting season effects of demography in turkeys (e.g. Norman et al. 2004), allow sustainable harvest indefinitely. Targeted protection and active management can even bring some game species, like the Masked Quail in the southwestern United States, back from the brink of extinction (Hernandez et al. 2006). On a much larger scale, wild turkeys, diminished to 30,000 birds across the entire United States by 1900, now approach 7 million birds, with active hunting seasons throughout the country (see Dickson 1992). Not only have sport game animals in North American avoided extinction under management for sustainable ”harvest,” most have prospered.

Commercial fisheries are managed on the same general assumption of a sustainable “harvest,” but with much less success (Ludwig et al. 1993). The decline in coastal fisheries began during the colonial period in North America, with the largest size classes of many species disappearing by the time biologists began keeping track in the mid 20th Century, just as industrial fisheries took hold (Jackson et al. 2001). The absence of management may have contributed to drastic declines of many coastal fisheries, as did confounding pollution and other forms of habitat destruction.

On a global scale, however, fisheries have benefited from sophisticated management plans, international treaties, and close scrutiny in the last half of the last century to the present, yet still fail (Pauly et al. 2005). A careful evaluation shows that 24% of 1519 fish stocks across numerous species collapsed between 1950 and the year 2000 (Mullon et al. 2005). Of these 33% of the stocks showed a steady regular decline (smooth collapse), 45% fell after ups and downs (erratic collapse), and 21% appeared to be healthy, and then disappeared abruptly (plateau collapse). Smooth collapses suggest steady overexploitation, sometimes confounded by increasing environmental stress from pollution. Erratic collapses might be expected in species that fluctuate greatly in numbers from the dynamics of age structure or because they are driven by external events, such as El Nino changes in water temperature that affect food resources. Harvest levels based on steady-state assumptions are bound to fail if substantial pressure is applied to populations that for one reason or another are in decline or free-fall at the time. Plateau collapses, to which sardines and herrings seem most vulnerable, occur when cryptic increases in harvest efficiency occur, such as increased capture efficiencies or navigation improvements that allow concentrations of fish to be found more easily than before (i.e. regulatory definitions of effort intensity become obsolete), and when reduced populations show “depensatory” inability to recover, amounting to negative Allee effects (e.g. members of small populations have a poorer chance of finding food, finding mates, or avoiding predation than those in large populations). A result of sequential depletion of traditional fishing stocks is sequential exploitation of previously ignored species at lower depths, what Morato and colleagues (2006) term “fishing down the deep.”

It is fair to ask why the same principles applied to sport game succeed, but fail when applied to commercial fisheries. Capital-intensive industrialized fishing fleets are politically and logistically difficult to modulate (Ludwig et al 1993). Lotka-Volterra theory might work in fisheries if instant feedback of demographic trends allowed effective regulation of the intensity of effort. It does not occur. Constant pressure on inherently stable populations often results in slow decline to collapse, and constant pressure (or the amplitude of fishing intensity much less than the amplitude of population fluctuation) on erratic populations leads to erratic collapse. Constant improvement in technique, magnified across a large scale of effort in an industrialized fishing industry, contributes to all three patterns of collapse.

Can anything be learned from successful game management? A key difference seems to be that sport hunting in North America is a far less intense risk to game populations than commercial fishing is to fish stocks. Strictly enforced hunting seasons, bag limits, regulations constraining equipment (e.g. cartridge limits for shotguns, bans on fully automatic rifles), and the fact that most sport hunters do not hunt from necessity ensure that a human predator is as inherently inefficient as industrial fishing fleets are inherently efficient. Moreover, hunting seasons only occupy a few days or weeks of the year, leaving a refuge in time, while many hunted birds or mammals also have refuges in space (parks, proximity to human habitation, inaccessible habitats). Even the protozoa that introduced us to logistic thinking survive intense predation in a vial if they have refuges (Gause 1934). Enforced regulations that ensure inefficiency distinguish sport hunting from commercial fishing or subsistence hunting, where there is a premium on increasing efficiency. In this sense Roughgarden and Smith (1996), in suggesting that harvest targets simply be lowered to leave more leeway for fluctuations, and therefore more likelihood that “seed stocks” will be preserved, seeks to make multibillion dollar commercial industry more like sport hunting.

8.2.2. Island biogeography

One of the most influential ecological paradigms in conservation is the theory of island biogeography (MacArthur and Wilson 1967, Simberloff 1988). The theory predicts that the log of species number increases with the log of habitat area due to an equilibrium of immigration and extinction in each habitat island separated from other habitat islands by unforgiving matrix. A corollary is that species number declines as large habitat areas are carved up into small ones. The theory is used as a heuristic for predicting the number of species that might be expected in a given habitat unit, for planning refuge areas, and for the number of species likely to be lost if a large patch is fragmented into small patches.

The theory of island biogeography has contributed to important insights about the efficacy of refuge design (reviewed by Doak and Mills 1994). Large refuges hold important species that small ones do not, heterogeneous refuges hold more than homogeneous ones, communities on islands surrounded by truly unforgiving habitat (e.g. land surrounded by water) have different dynamics than communities on habitat islands surrounded by more amenable matrices of vegetated land, and the slopes of species area relationships reflect taxon vagility. The theory has also catalyzed debate about conservation values. For instance, numerous small refuges hold as many or more species than a single large refuge of the same aggregate area (Simberloff and Abele 1976, 1982), but the identity of species differs (Taylor 1991). Large patches hold habitat specialists that small patches do not (e.g. Wilcox and Murphy 1985, Hansson 1991). For instance in tropical forests, 80% of tree species in continuous forest are late-successional and often quite rare, and 20% are pioneer or early successional species that are often quite common in disturbed areas (Finegan 1996). A constellation of small fragments might successfully encourage a fair number of the 20 % secondary forest species, but under-represent the majority 80%. In general, the theory of island biogeography has been a useful heuristic concept; in particular, it forces ecologists to decide which species are more equal than others.

Limitations of this theory for managers are due to weak predictability and sometimes misapplication (see Doak and Mills 1994). The total number of species likely to persist in island habitats of different size often has broad confidence intervals (Connor and McCoy 1979, Boecklen and Gotelli 1984), and unexpected anomalies in the shape of the (log) species number versus (log) area relationship for some communities add to statistical imprecision (e.g. Plotkin et al. 2000). More fundamental, the theory itself predicts vulnerability to extinction solely from increasing proportion of species with very small population sizes as island size decreases (MacArthur 1972). It is silent on which species are vulnerable for reasons other than small population size. For that, one must know more about species involved, such as the existence of obligate mutualisms that link fates of species (e.g. Cordeiro and Howe 2003; see “nested subsets” by Patterson 1987), developmental stability of morphological characters (Lens et al. 2002), or if some small populations are simply much better adapted to a site than others. In the first case, chance loss of avian dispersal agents reduced dispersal and establishment of seedlings of an endemic tree (*Leptonychia usambarensis*) in Tanzania. In the second case, species mobility and developmental stability (low fluctuating asymmetry) of morphological characters were positively associated with persistence of bird species in forest fragments in Kenya. Whereas the general theory is operational in a limited sense of predicting total species richness, studies of a few focal species can make these issues operational on a much more specific level. Implementing Lens' perspective, for instance, bird species with low mobility and high fluctuating asymmetry would need larger reserves than those with higher mobility and greater developmental stability.

Application of the theory of island biogeography to the worldwide phenomenon of habitat fragmentation is both important and problematic (e.g. Harrison and Bruna 1999). Not all matrices are created equal from the perspective of particular taxa (e.g. MacArthur 1972, Vandermeer and Carvajal 2001, Martinez-Garza and Howe 2003). Water is a more alien matrix than agricultural land, and water is more alien for arboreal or terrestrial mammals than for bats. Forest fragments separated by matrices of vegetated land will be islands for some species, but to a lesser degree or not at all for others. Kramer and colleagues (2007) point out that predictions of genetic inbreeding in small stands of forest trees in landscapes of fragmented forests often fail to find genetic anomalies because long-distance pollination or seed dispersal links many remnants. The assumption that the fragment edge stops pollen and seed dispersal is justified in some cases, not at all in others. Also controversial is whether habitat corridors linking remnant sites help maintain the flow of species among remnants that would otherwise be threatened by local extinction, or due to high edge to area ratios encourage invasion by common early successional species and alien invasives. Answers are unlikely without specific knowledge of the species involved.

8.2.3 Metapopulations

Metapopulations are populations of populations (Levins 1969). Much as individuals of populations are born, grow, die, and are replaced by new individuals, populations of a metapopulation establish, grow, die, and sooner or later re-establish in the same place or colonize new sites. Sub-populations of a species, separated from others by unsuitable habitat, come and go. If more populations decline and disappear than grow and establish, a species declines. If more populations grow than decline, a species increases in abundance. If more establish in new sites than are lost, the species spreads.

The theory has obvious relevance to conservation and restoration of species, as well as to habitat fragmentation (Hanski 1991). If metapopulations exist in nature and behave as models predict, this conceptual framework might integrate population and island biogeographic perspectives in a paradigm that has much to offer conservation and ecological restoration of populations. If a species is widely scattered in low densities, population viability analysis is inappropriate, and there is a large temptation to assume migrant interchange among small groups of individuals. If most species behave as metapopulations, communities of metapopulations, ”metacommunities,” may be modeled accordingly.

Despite its plausibility, the concept of metapopulations has not proven as operational as hoped (Doak and Mills 1994). First, not all sub-populations are created equal; larger populations or clusters of populations shed migrants as ”sources,” while others are small or in marginal habitats and absorb migrants as ”sinks” (see a general review in Vandermeer and Goldberg 2003, pp. 167 ff). Obvious inequality of parameters in different subpopulations require that modeling persistence of a species relies of site-specific rates of immigration, reproduction, growth, and death. In the western United States the spotted owl *Strix occidentalis* is a threatened bird of old growth conifer forests, now distributed in forest patches left by clear-cut logging (see Noon and McKelvey 1996). To simulate persistence of this species in a region, forest by forest estimates of habitat suitability, extinction, migration, and further dispersal must be modeled. Because such data are extraordinarily laborious to obtain estimates must be used. The model simulations can only be as accurate as the estimated parameter values. One level of analysis is possible for charismatic species, like the spotted owl. Most species receive no such attention.

Second, it is not clear that metapopulations are common (Taylor 1991, Doak and Mills 1994). For instance, molecular markers do not indicate much or any dispersal of spotted owls among forest patches, suggesting that the species, despite widely scattered groups of individuals and wings that imply the possibility of dispersal, does not behave as a collection of metapopulations (Gutierrez and Harrison 1996). Perhaps the owls disperse among forest habitats, but not across open ground. Indeed, patchy populations of many species may exist with some immigration, but no rhythms of turnover as required of the theory. Or, large “core” populations feed migrants to small “satellite” populations. Harrison (1991) argues that the butterfly *Euphydrias editha bayensis* has a large, essentially immortal core population, and many small satellites that superficially but erroneously appear to be metapopulation units. The core is not vulnerable to extinction, and the satellite dynamics are determined by patterns of dispersal from the core. This is more like MacArthur and Wilson's (1967) colonization from a source than metapopulation colonization and extinction dynamics. Similarly, in California the total spotted owl prognosis apparently reflects the growth or contraction of owl numbers a large area in the San Bernadino Mountains, with little influence of more marginal groups (Gutierrez and Harrison 1996). It is quite possible that many widely scattered populations do not operate as metapopulations. Perhaps a population viability analysis, but over much wider areas than previously attempted, will estimate persistence. Perhaps there is yet no family of models that will do the job well.

Some species do behave as metapopulations. The Florida scrub jay *Aphelocoma coerulescens* is an excellent case in point (Stith et al. 1996). Subpopulations range in size from many less than 10 to one of 1,500 individuals, so this is far from the classic Levins (1969) model. But exhaustive study shows that dispersal is consistent, populations disappear and re-colonize, and re-colonization is more likely close to than far from occupied patches of suitable habitat. In general the special conditions exist for metapopulation analysis. If one is interested in scrub jay management, the metapopulation paradigm provides important tools. Do all species in scrub jay habitat operate as metapopulations? No one knows, but it seems unlikely.

8.3 UNREALISTIC EXPECTATIONS

The examples discussed here represent a range of applications of ecological theory to ecological management. Each paradigm offers something important to resource managers, and each falls short of expectations. In the case of sustainable yield, precise predictions of

”excess” harvest of animals or plants often attempt to maximize harvest without depleting a theoretically self-regenerating resource. Under such management, commercial fisheries consistently collapse, while wildlife managed for sport, often below maximum projected yield, do not. The theory of island biogeography allows prediction of species diversity in preserved or restored habitats of different size, without offering guidance as to which species will be preserved, restored, or lost. Derivatives of that theory, subsumed under it in the case of forest fragmentation and treated as distinct in metapopulation dynamics, offer insights, and hopefully actionable predictions, into behavior of some species populations, and particular dynamics of elements of communities. Metapopulation theory offers elegant and coherent theory about how spatially distributed populations behave, but it has been a struggle to even show that metapopulations exist. What common threads can be discerned for these, and perhaps many other possible examples, of success and failure of ecological theory in practice? Are managers, and often ecologists themselves, asking too much of their theory?

8.3.1 Properties of ecological systems that matter

Numbers

Ecology offers a variety of conceptual frameworks that appear to explain the interactions of species with each other and the physical environment, and which sometimes allow clear predictions to those who manage nature. The clearest predictions are based on common ecological knowledge, and elicit little controversy. One does not find aquatic food webs without water, or high plant productivity on poor, dry soils. Difficulties appear when firm predictions are needed for species populations, for species populations embedded in dynamic communities in time and space, and for entire communities made up of species populations.

A basic difficulty with ecology is rooted in what, for lack of a better term, might be seen as statistical mechanics. The behavior of a single particle is less predictable than the average of several, and much less predictable than the average of trillions of atoms. In Newtonian mechanics, a falling iron canonball with a mass of 10 kg, containing trillions of iron atoms, is more predictable than the behavior of an iron atom, or 20 iron atoms. One effect is something like the average of trillions of units, atoms, instead of the uncertainty facing the descent of one atom, or 20 in a group (see Heisenberg 1922). Another effect is that the accumulated mass of the large body overcomes effects that might easily change the behavior of small particles, ranging from interactions with other ions or atoms encountered or air currents that can easily change the course of small particles but not large ones. Our civilization based on mechanical engineering, architecture, and related fields would be in dire straights if the properties of systems used in creating dams, bridges, automobiles, and rockets were deduced from the behavior of a single atoms or molecules, or even 20 independent or clumped atoms or molecules, rather than the accumulated or average effects of thousands, millions, billions, or trillions of such units. A single iron ball of 10 kg is more predictable than an iron atom, and 20 such balls are more predictable than 20 atoms. Yet many ecological principles are derived from studies of very few systems, and small samples of those.

Some of this is inherent in ecological systems. In a given community, some species are common, most are uncommon or rare (Preston 1962). The generalization holds across communities and ecosystems, meaning many species are so rare that they cannot be studied in numbers, anywhere. The extreme may be in hyperdiverse rainforests of the western Amazon, where most of a thousand or so tree species in a given area occur in densities of less than one per hectare, and many in densities of less than on in 10 hectares (Pitman et al. 2003). A small minority of trees, what the authors call oligarchs, are common across vast stretches of terra firma forest; these are common enough to lend themselves to models or tests of sustainable yield, island biogeography, or metapopulation dynamics. But the vast majority or the trees in these communities do not. Because of their inherent rarity (Maina and Howe 2000), average effects, or responses to effects, probably cannot be measured or estimated. An example of the conundrum of inherent rarity is my study: effects of snow leopards on Himalayan tahr on Mount Everest. In any given locale, several individual leopards occur. The effects of these few individual cats on their prey may be idiosyncratic, but they represent the total universe of leopard and tahr interactions in a given valley.

Imprecision that is not due to inherent rarity is often augmented by methods roughly analogous to following a few atoms around. In tropical forests, most tree species are dispersed by animals. A key study of dispersal of one (*Virola nobilis*) in Panama used animal activity at 22 individual trees (Howe and Vande Kerckhove 1981, Howe et al. 1985). This standard has been matched for another *Virola* in Peru (Russo 2003), but apparently has not surpassed in other studies seed dispersal of thousands of plant genera for which vagaries of animal activity might be important. If physics depended on principles deduced from the behavior of samples 20 or so atoms, molecules, or other units, civilization might not have progressed far.

Contingencies

Small numbers have ramifications. Ecological communities of a thousand species have roughly 1000^{1000} possible pairwise interactions with each other, and for practical purposes a virtually infinite number of possible multi-way direct and indirect interactions with each other and abiotic factors. Most of these never occur; some conditions force more consistent outcomes of interaction, but the potential for an enormous influence of contingent effects is clear (Lawton 1999). The smaller the number of individuals of a species, or communities in which a particular abiotic, animal, plant, or anthropogenic effect occurs, the more likely chance or historical contingencies will produce idiosyncratic outcomes. Contingencies emphasized by Lawton include those due to the particular species that are common or rare and their direct and indirect interactions with others. Subsumed under such effects are attributes of each population within a species, including size, local diet choices, local demographies, local behavioral patterns forced by predators, prey, or competitors, and local dispersal properties, as well as local responses to external abiotic factors and regional species distributions. It is obviously true that ecological communities are far from random assemblages of organisms in any given set of abiotic constraints, but Lawton is correct in calling attention to the fundamental role of contingency in determining the distribution, abundance and behavior of species.

8.3.2 Lessons from sustainability, islands, and metapopulations

Sustainability and contingencies

Success and failure in the best understood and most economically important examples discussed here, sustainable use of living resources, appears to hinge on the importance of and managing contingencies (see Lawton 1999). Statistical issues are less important; the definitive story about decline of fish stocks worldwide (Mullon et al. 2005) concerns > 1,500 managed units. Although they are not entirely independent, as many are of one species (e.g. salmon) or another (e.g. cod), conclusions concerning the general patterns of and reasons for sequential collapses of fisheries are not attributable to idiosyncrasies of a few units (stocks). Maintenance of sport fish and game populations of at least hundreds species around the world are some multiple of the commercial fisheries example. Successes of these efforts are not flukes.

Success or failure in the sustainable use of living resources amounts to success or failure in managing the other major characteristic of ecological systems discussed here, contingencies (see Mullon et al. 2005). In the case of maximum sustainable yield of commercial fish stocks, the theory assumes that human harvest is the prime driver of the system. In turn, this assumes a measurable level of harvest intensity that can be regulated. Repeatedly, increases in encounter rate and harvest efficiency skirt regulatory measures, allowing increasing intensity that leads to collapse. Other ecological contingencies that introduce other drivers do not enter the models, such as disappearance of food supplies due to weather or other fisheries, unanticipated competition from release of other fish species, changes in water temperature from El Nino effects, pollution, and other factors. The end result is that simplistic models that do not accommodate a variety of drivers set the ”harvest” level too high; fishing intensities that might be sustainable if nothing else influenced the fish stocks become one of many forces driving population levels into negative numbers, while relentlessly increasing search and harvest efficiencies leave targeted populations no refuge.

Sport fishing and hunting harvests work by different rules. There is ample room for failure despite the fact that much less attention is paid to usual optimal foraging considerations. Travel, vehicles, firearms, fishing gear, and other costs typically far exceed the food value of whatever is taken, introducing potential for massive overshoots in harvest. However, refuges in space (parks, wildlife refuges, inaccessible areas) and time (excluded times of the year) and closer regulation in more confined areas (e.g. designated hunting regions of states or provinces) typically leave a larger portion of a population ”unharvested.” In effect, sport fish and game populations experience a potential for ”tragedy of the commons” overexploitation (Hardin 1960), but regulation and refuges in space and time and harvest levels that admit room for effects of other contingencies allow recovery from one year to another. Where fish and wildlife agencies exist to regulate their charges, they set harvest levels that can sustain contingencies other than hunters or fishermen.

In short, failure in implementing maximum sustainable yield fails for errors of estimation and implementation as much as failure of theory itself, except in the sense that theory assuming sole effects of human use is incomplete theory. In commercial fisheries, management for maximum sustainable yield leaves too little room for errors in estimation of populations or harvest intensity, or for other ecological contingencies that might drive stocks below recovery points. Sport fisheries and game populations are regulated more tightly and populations are given more room to accommodate environmental contingencies other than anthropogenic use. This amounts to "building resilience" into policy (Peterson 2005). Roughgarden and Frasier (1998) advocate lower take in commercial fisheries, in effect giving commercial fish stocks more room to accommodate error and ecological contingency, which from a manager's perspective may indicate understood or stochastic effects on target populations. Designation of refuges for commercial fish stocks would tend to make the process of making commercial fisheries resemble sport fisheries and hunting populations in inherent resilience.

Island effects

Sufficiency and insufficiency of the theory of island biogeography can be attributed to the structure of the theory itself. As a model for predicting overall community size, the theory works if habitat islands are in fact isolated from each other, and even where they exist in a milieu of terrestrial vegetation, the theory works for sedentary taxa. The theory does not work for managers who need to predict fates of particular taxa, unless enough is known of key ecological features (e.g. age structure, special needs in different habitats, sex ratio, dispersal properties, response to loss of mutualists) or other attributes (e.g. fluctuating asymmetry, self-compatibility, social structure) that affect persistence. Predictions for most taxa, even those for which such details are known, are further subject to vagaries of sampling error. If most communities are characterized by a preponderance of scarce or rare species (Preston 1962), and the proportion of such species increases with decreasing area (e.g. MacArthur 1972, Hubbell and Foster 1983), predictions for the majority of species in a community are subject to large sampling errors. Immigration and extinction may be measurable for the few species in a community that are common, but these are not the ones likely to be at risk of extinction in small habitat fragments unless other factors, like loss of a pollinator or dispersal agent or dramatic deterioration of habitat quality from increases in edge to are ratio, alter the conditions under which even common species may persist. For most species in a given community, even measurement of immigration and extinction, much less prediction of either, are challenges.

Metapopulations

Metapopulation and metacommunitiy paradigms suffer from credibility issues on a different level than sustainable yield and island biogeography paradigms, as well as inherent sample size issues. While there is little question that populations often produce excess individuals that can be removed without affecting persistence, and that balances of extinction and immigration exist, there is a serious question as to whether many or most natural populations act as metapopulations, and serious questions as to what can be predicted of local communities of metacommunities (Harrison and Bruna l999). Without extensive understanding of particulars of a population, or local community, little can be predicted except broad generalizations (e.g. small ecological restorations will accumulate vagile species, many weeds, that are adapted for wide dispersal and may behave as metapopulations, Maina and Howe 2000). Exhaustive local information can yield definitive insights of metapopulation structure for very well known species, such as the scrub jay (Stith et al. 1996), but give partial and unsatisfying results for others of even more interest, such as the spotted owl (Gutierrez and Harrison1996). Thus the role of theory becomes marginal as compared to local understanding of the needs and trends of local populations, what Caughley (1994) warned as ’one off’ evaluations of needs and solutions. Given that small populations do not lend themselves to quantitative measures of immigration, extinction, and therefore local turnover, as required by theory, the metapopulation paradigm is likely to remain a plausible but largely unconfirmed framework in conservation biology.

8.4 WHAT CAN MANAGERS EXPECT?

Use of ecological theory for management of nature needs to follow different rules than use of physical theory to build skyscrapers or rockets. Whereas an engineer has a firm concept of stresses in constructing a structure of steel girders or thrust required to carry a payload, an ecologist has nothing comparable in concepts of sustainable yield, island biogeography, or metapopulation dynamics. In such cases the theory can guide insight, but the insight must be tempered by local understanding of how well the organisms in question fit assumptions of relevant models. A manager must also realize that if a population might be managed for sustainable yield, or maintained in habitat fragments of different size, populations might often be so small that firm estimates and therefore predictions of persistence, extinction, or colonization are infeasible. If a Himalayan valley houses three snow leopards, a manager of the cats and their prey may benefit from understanding that the local population may disappear and be replaced by other individuals, or that the cats may simply trade individuals with other valleys. The capacity to actually estimate turnover on a quantitative basis is quite likely out of reach.

8.5 HOW DO THEY GET IT?

For reasons inherent in the field and the nature of nature, resource managers should avoid the pretense of predicting precise population changes as a function of harvest, isolation, or metapopulation turnover. The concept of building resilience into policy to accommodate contingency, error, and chance, is an operational approach to using theory for guidance rather than certainty. So, for instance, a general prediction that abundance of edible fish will change the fortunes of whatever game animals are common that indigenous people deplete in the Amazon may be warranted (Brashares et al. 2004), but a pretense of predicting what each game or fish population will be given exploitation of it by indigenous people is not. Regarding reserve size, a prediction of persistence of animals and plants as a function of size of habitat patches may work well in uninhabited areas, but can be overshadowed by proximity of human settlements in many places (Brashares et al. 2001). Both examples are affected by contingencies that are not present in armchair models.

References

Agrawal, A., Gibson, C. C. 1999. Enhancement and disenhancement: The role of community in natural resources conservation. *World Development* 27: 629-649.

Boecklen, W.J. and Gotelli, N. 1984. Island biogeographic theory and conservation practice: species-area or specious-area relationships? *Biol. Conserv*. 29:63-80.

Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P. B., Sinclair, A.R.E. and Balmford, A. 2004. Bushmeat hunting, wildlife declines and fish supply in West Africa. *Science* 306: 1180-1183.

Brashares, J.S., Arcese, P. and Sam, M.K. 2001. Human demography and reserve size predict wildlife extinction in West Africa. *Proc. Roy. Soc. Lond. : B* 268: 2473-2478.

Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* 63: 215-244.

Ceballos, G. and Ehrlich, P. R. 2002. Mammal population losses and the extinction crisis. *Science* 296: 904-907.

Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. *Am. Nat*. 113: 791-833.

Cordeiro, N. and Howe, H.F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *PNAS* 100:14052-14054.

Dickson, J.G. 1992. *The Wild Turkey: Biology and Management.* Stackpole Press, Mechanicsburg, Pennsylvania.

Diefenbach, D.R., Laake, J.L. and Alt, G.L. 2004. Spatio-temporal and demographic variation in the harvest of black bears: implications for population estimation. *J. Wildl. Manage.* 68: 947-959.

Doak, D. F. and Mills, S. 1994. Useful Role for Theory in Conservation. *Ecology* 75: 615-626.

Ferraro, P.J. and Kiss, A. 2002. Direct payment to conservation. *Science* 298: 1718-1719.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forest: the first 100 years of succession. *Trends Ecol. Evol.* 11: 119-124.

Gause, G.F. 1934. *The struggle for existence*. Baltimore: Williams and Wilkins.

Giles, B.G. and Findlay, G.S. 2004. Effectiveness of a selective harvest system in regulating deer populations in Ontario. *J. Wildl. Manage.* 68: 266-277.

Graham, M.H. and Dayton, P.K. 2002. On the evolution of ecological ideas: paradigms and scientific progress. *Ecology* 83: 1481-1489.

Guthery, F.S., Crews, A.K., Lusk, J.J., Chapman, R.N. and Sams, M. 2004. Effects of bag limits on bobwhite hunters and harvest. *J. Wildl. Manage.* 68: 1095-1103.

Gutierrez, R. J., Harrison, S. 1996. Applying metapopulation theory to spotted owl management: a history and critique. In: *Metapopulations in wildlife conservation, e*d. D.R. McCullough, pp. 167-186. Island Press, Washington, D.C.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biol. J. Linn. Soc.* 42: 17-38.

Hardin, G. 1960. The competitive exclusion principle. *Science* 131: 1292-1297.

Harrison, S. 1991. Local extinction in a metepopulation context: an empirical evaluation. *Biol. J. Linn. Soc*. 42:73-88.

Harrison, S. and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225-232.

Heisenberg, W. (1922) *Archive of the Deutsches Museum*, Munich.

Hernandez, F., Kuvlesky, W.P. Jr., De Young, R.W., Brennan, L.A. and Gall, S. A. 2006. Recovery of rare species: case study of the masked bobwhite. *J. Wildl. Manage. 70*: 617-631.

Hilborn, R., Walters, C.J. and Ludwig, D. 1995. Sustainable exploitation of renewable resources. *Ann. Rev. Ecol. Syst*. 26:45-67.

Howe, H.F., E. Schupp, E. and Westley, L. 1985. Early consequences of seed dispersal in a neotropical tree (Virola surinamensis). *Ecology* 66:781-791.

Howe, H.F. and Vande Kerckhove, G. A. 1981. Removal of nutmeg (Virola surinamensis) crops by birds. *Ecology* 62: 1093-1106.

Hubbell, S. P. and Foster R. B.1983. Diversity of canopy trees in a neotropical forest and implications for the conservation of tropical trees. In: *Tropical rain forest: ecology and management*, eds. S. J. Sutton, T. C. Whitmore and A. C. Chadwick, pp. 25-41. British Ecological Society special publication 2. Blackwell: Oxford.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P, Kidwell, S., Lange, C. B., Lenihan, H. S, Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., Warner, R. R. 2001. Historical overfishing and the regional collapse of coastal ecosystems. *Science* 293: 629-638.

James, A., Gaston, K. J. and Balmford, A. 2001. Can we afford to conserve biodiversity? *BioScience* 51: 43–52.

Kramer, A. T., Ison, J., Ashley, M., and Howe, H. F. 2007. The paradox of forest fragmentation genetics. *Trends Ecol. Evol.* Submitted.

Kuhn, T.S. 1970. *The structure of scientific revolutions.* Second Edition. University of Chicago Press.

Laurance, W.F. and Peres, C. A. (Eds.) 2006. *Emerging Threats to Tropical Forests*. University of Chicago Press: Chicago.

Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84: 177-192.

Lens, L., Van Dongen, S., Norris, K., Githiru, M. and Matthysen, E. 2002. Avian persistence in fragmented rainforest. *Science* 298: 1236-1238.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of Entomological Society of America* 15: 237-140.

Ludwig, D., Hilborn, R. and Walters, C. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260: 17-36.

MacArthur, R.H. 1972. *Geographical ecology*. Princeton University Press: Princeton.

MacArthur, R.H and Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press: Princeton.

Maina, G. and Howe, H.F. 2000. Inherent rarity in community restoration. Conservation Biology 14: 1335-1340.

Martinez-Garza, C. And Howe, H. F. 2003. Restoring tropical diversity: beating the time tax on species loss. *J. Appl. Ecol.* 40: 423-429.

MacGregor, H. 1998. *The economic value of deer hunting and its distribution in the Fundy Model Forest – 1994,* Thesis. University of New Brunswick, Canada.

Morato, T., Watson, R., Pitcher, T. J. and Pauly, D. 2006. Fishing down the deep. *Fish and Fisheries* 7: 24-34.

Mullon, C., Freon, P. and Cury, P. 2005. The dynamics of collapse in world fisheries. *Fish and Fisheries*, 6: 111-120.

Noon, B.R. and McKelvey, K.S. 1996. A common framework for conservation planning: linking individual and metapopulation models. In: *Metapopulations in wildlife conservation,* ed. D.R. McCullough, pp. 139-166. Island Press: Washington D.C.

Norman, G.W., Conner, M.M., Pack, J. C. and White, G.C. 2004. Effects of fall hunting on survival of male wild turkeys in Virginia and West Virginia. *J. Wildl. Manage.* 68: 393-404.

Patterson, B.D. 1987. The principle of nested subsets and its implications for biological conservation. *Cons. Biol.* 1:323-333.

Pauly, D., Watson, R. and Alder, J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Phil. Trans. Roy. Soc.* 360: 5-12.

Peterson, G.D. 2005. Ecological management: control, uncertainty, and understanding. In: *Ecological paradigms lost*, eds. K. Cuddington and B. Beisner, pp. 371-396. Elsevier Academic Press: London.

Pimm, S.L. and Lawton J.H. 1998. Planning for biodiversity. *Science* 279: 2068-2069.

Pimm, S.L. Russell, G.J., Gittleman, J.L. and Brooks, T.M. 1995. The future of biodiversity. *Science* 269: 347-350.

Pitman N.C.A. Terborgh, J.W., Silman, M.R., et al. 2002. A comparison of tree species diversity in two upper Amazonian forests. *Ecology* 83: 3210-3224.

Plotkin, J. B., Potts, M. D., Yu, D. W., Bunyavejchewin, S., Condit, R., Foster, R., Hubbell, S., La Frankie, J., Manokarani, N., Seng, L. H., Sukumar, R., Nowak, M. A., Ashton, P. S. 2000. Predicting species diversity in tropical forests. *PNAS* 97: 10850-10854.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43: 185-215.

Rosenzweig, M.L. 2003. *Win Win Ecology: how the earth's species can survive in the midst of human enterprise.* Oxford University Press.

Roughgarden, J. and Smith, F. 1998. Why fisheries collapse and what to do about it. *PNAS* 93: 5078-5083.

Ruggiero, L.F., Hayward, G.D. and Squires, J.R. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. *Cons. Biol.* 8: 364-372.

Russo, S.E. 2003. Responses of dispersal agents to tree and fruit traits in Virola calophylla (Myristicaceae): implications for selection. *Oecologia* 136: 80-87.

Shellenberger, M. and Nordhaus, T. 2005. Death of environmentalism: Global warming politics in a post-environmental world. *Grist Magazine, 13 January 2005. http://www.grist.org/news/maindish/2005/01/13/doe-reprint/index.html.* Accessed 15 October 2006.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Ann. Rev. Ecol. Syst.* 19: 473-511.

Simberloff, D.S. And Abele, L. G. 1976. Island biogeographic theory and conservation practice. *Science* 191: 285–286.

Simberloff, D. and Abele, L. G. 1982. Refuge design and island biogeographic theory: effects of fragmentation. *Am. Nat.* 120: 41-50.

Smith, F.D., May, R.M., Pellew, R., Johnson, T.H. and Walter, K.R. 1993. How much do we know about the current extinction rate? *Trends Ecol. Evol.* 16: 431.

Stith, B.M., Fitzpatrick, J.W., Woolfenden, G.E., Pranty, B. 1996. Classification and conservation of metpopulations: a case study of the Florida scrub jay. In: *Metapopulations in wildlife conservation*, ed. D.R. McCullough, pp. 187-216. Island Press: Washington, D.C.

Taylor, B. 1991. Investigating species incidence over habitat fragments – a look at error estimations. *Biol. J. Linn. Soc*. 42: 177-191.

Vandermeer, J. and Carvajal, R. 2001. Metapopulation dynamics and the quality of the matrix. *Am. Nat.* 158: 211-220.

Vandermeer, J. and Goldberg, D. 2003. *Population ecology: first principles.* Princeton University Press: Princeton.

Wilcox, B.A. and Murphy, D.D. 1985. Conservation strategy - effects of fragmentation on extinction. *Am. Nat.* 125: 879-887.

APPENDICES

Appendix I

Model I Isodars:

$$N_2 = \frac{K_2}{r_2}\left(r_2 - a_2 - r_1 + a_1\right) + \frac{r_1 K_2}{r_2 K_1} N_1$$

$$intercept = \frac{K_2}{r_2}\left(r_2 - a_2 - r_1 + a_1\right) \qquad slope = \frac{r_1 K_2}{r_2 K_1}$$

Model 1 Isodarivatives:

$$\frac{\delta intercept}{\delta a_1} = \frac{K_2}{r_2} \qquad \frac{\delta slope}{\delta a_1} = 0$$

$$\frac{\delta intercept}{\delta a_2} = -\frac{K_2}{r_2} \qquad \frac{\delta slope}{\delta a_2} = 0$$

$$\frac{\delta intercept}{\delta K_1} = 0 \qquad \frac{\delta slope}{\delta K_1} = -\frac{r_1 K_2}{r_2 K_1^2}$$

$$\frac{\delta intercept}{\delta K_2} = \frac{\left(r_2 - a_2 - r_1 + a_1\right)}{r_2} \qquad \frac{\delta slope}{\delta K_2} = \frac{r_1}{r_2 K_1}$$

$$\frac{\delta intercept}{\delta r_1} = -\frac{K_2}{r_2} \qquad \frac{\delta slope}{\delta r_1} = \frac{K_2}{r_2 K_1}$$

$$\frac{\delta intercept}{\delta r_2} = -\frac{K_2\left(r_2 - a_2 - r_1 + a_1\right)}{r_2^2} + \frac{K_2}{r_2} \qquad \frac{\delta slope}{\delta r_2} = -\frac{r_1 K_2}{r_2^2 K_1}$$

$$\frac{\delta intercept}{\delta r_2} = -\frac{K_2\left(r_2 - a_2 - r_1 + a_1\right)}{r_2^2} + \frac{K_2}{r_2} \qquad \frac{\delta slope}{\delta r_2} = -\frac{r_1 K_2}{r_2^2 K_1}$$

Appendix II

The derivatives of $\boldsymbol{u}^* = \dfrac{\sqrt{\dfrac{bFmN^{\alpha}}{f_{\max} N(\partial F/\partial e)}}}{b+K+(N-1)\beta}$ with respect to 1) predator-encounter rate, 2) forger's survivor's fitness, 3) predator lethality, 4) marginal value of energy, and 5) effectiveness of vigilance:

1) $$\frac{\partial \boldsymbol{u}^*}{\partial m} = \frac{\sqrt{\dfrac{f_{\max} N(\partial F/\partial e)}{bFmN^{\alpha}}}}{2\left(b+K+(N-1)\beta\right)} > 0$$

2) $$\frac{\partial \boldsymbol{u}^*}{\partial F} = \frac{\sqrt{\dfrac{f_{\max} N(\partial F/\partial e)}{bFmN^{\alpha}}}}{2\left(b+K+(N-1)\beta\right)} > 0$$

3) $$\frac{\partial \boldsymbol{u}^*}{\partial k} = -\frac{\sqrt{\dfrac{bFmN^{\alpha}}{f_{\max} N(\partial F/\partial e)}}}{\left(b+K+(N-1)\beta\right)^2} < 0$$

4) $$\frac{\partial \boldsymbol{u}^*}{\partial(\partial F/\partial e)} = \frac{\sqrt{\dfrac{f_{\max} N(\partial F/\partial e)}{bFmN^{\alpha}}}}{2\left(b+K+(N-1)\beta\right)} > 0$$

5) $$\frac{\partial \boldsymbol{u}^*}{\partial b} = \frac{\dfrac{1}{2}\left(b+K+(N-1)\beta\right)\left(\sqrt{\dfrac{f_{\max} N(\partial F/\partial e)}{bFmN^{\alpha}}}\right) - \sqrt{\dfrac{bFmN^{\alpha}}{f_{\max} N(\partial F/\partial e)}}}{\left(b+K+(N-1)\beta\right)^2}$$

Appendix III

The derivatives of $\boldsymbol{u}^* = \dfrac{\sqrt{\dfrac{bFmN^{\alpha}}{f_{\max} N(\partial F / \partial e)}}}{b + K + (N-1)\beta}$ with respect to 1) attraction effect (*α*), and 2) many eyes effect (*β*):

1) $$\frac{\partial \boldsymbol{u}^*}{\partial \alpha} = \frac{\left(b + K + (N-1)\beta\right)\left(\sqrt{\dfrac{f_{\max} N(\partial F / \partial e)}{bFmN^{\alpha}}}\right)}{2\left(b + K + (N-1)\beta\right)} > 0$$

2) $$\frac{\partial \boldsymbol{u}^*}{\partial \beta} = \frac{\dfrac{1}{2}\left(b + K + (N-1)\beta\right)\left(\sqrt{\dfrac{f_{\max} N(\partial F / \partial e)}{bFmN^{\alpha}}}\right) - \left(\sqrt{\dfrac{bFmN^{\alpha}}{f_{\max} N(\partial F / \partial e)}}\right)(N-1)}{\left(b + K + (N-1)\beta\right)^2} < 0$$

VITA

PERSONAL

Country of Citizenship: Nepal

Education
2002-2007: PhD Ecology and Evolution- University of Illinois at Chicago, USA.
1997-1999: MS Ecology- University of Tromso, Norway.
1989-1992: MSc Zoology- Tribhuvan University, Kathmandu, Nepal.
1984-1988: BSc Biology and Chemistry- Tribhuvan University, Kathmandu, Nepal.

EMPLOYMENT RECORDS

2001-2002. NATIONAL PROGRAM MANAGER

GEF-UNDP "Upper Mustang Biodiversity Conservation Project" (NEP/99/G35 GEF; NEP/99/021 TRAC), GEF medium grant project (US$ 2.215 million dollar). The maximum number of regular employees supervised: 36. For information, see the website, http://www.thegef.org/MonitoringandEvaluation/MEOngoingEvaluations/MEOLocalBenefits/Local_Benefits_Case_Study_Nepal_Biodiversity_.doc

1995-2000. OFFICER IN CHARGE

National (erstwhile King Mahendra) Trust for Nature Conservation - Annapurna Conservation Area Project (http://www.kmtnc.org.np/about-conservations.php). With annual budgetary expenditure of over US$ 1 million, I was responsible for the overall project from planning, executing to monitoring of all aspects of the project. The maximum number of regular employees supervised: 38.

1993-1994. CONSERVATION OFFICER

National (erstwhile King Mahendra) Trust for Nature Conservation - Annapurna Conservation Area Project. The maximum number of regular employees supervised: 20

1988-1990. COORDINATOR I

Wildllands Research and Education, San Francisco State University, USA. Nepal program. Coordinated under-grad level research projects for American college students.

1986-1987. COORDINATOR II

World College West, 101 South San Antonio Road, Petaluma, California 94952. Nepal Kathmandu office. Coordinated "home-stay" in rural Nepal for American college students to facilitate their research projects.

RESEARCH EXPERIENCE

- 2006/2007. Co-Investigator. "VANISHING TRACKS on the Roof of the World". Ev-K2-CNR (Italy) and World Wildlife Fund (WWF)-Nepal.
- 2004-2006. Researcher. Ecology and conservation of the snow leopard and the Himalayan tahr in Sagarmatha (Mt. Everest) National Park, Nepal. PhD thesis work, University of Illinois-Chicago. See the highlight in nature.com (http://www.nature.com/news/2006/060807/full/060807-12.html).
- 2004-Present. RESEARCH COLLABORATOR: Conservation of biodiversity: The large mammal community of Sagarmatha (Mt. Everest) National Park (Nepal). The joint venture of Ev-K2-CNR (Italy), RONAST and DNPWC (Nepal).
- 1999-2002. CO-PRINCIPAL INVESTIGATOR: Ecology of snow leopard and blue sheep in the trans-Himalayan regions of Nepal adjoining Tibet/China. The Snow Leopard of Nepal Project, Earthwatch Institute, Watertown, MA, USA.
- 1999-2000. WILDLIFE BIOLOGIST: Investigation on the status of large mammals in Modi watershed in the southern flank of the Annapurna Himalaya, Landruk Integrated Micro-hydro Project. GEO/Germany.
- 1997-1999. RESEARCHER: Rutting behavior of blue sheep in Manang valley, mid-west Nepal. Masters thesis work.
- 1993. BIOLOGIST: Assessment of crop damage by wildlife. Makalu Barun National Park and Conservation Area, east Nepal.
- 1992-1993. CO-INVESTIGATOR: Livestock Depredation Project/Biosystem Analysis/California (No R. D. 424/084/049 Disp. No. 698). A five-year USAID project that addressed livestock depredation, grazing and wildlife conservation in Nepal Himalayaimalaya .

TEACHING EXPERIENCE

- 2002 to 2006: TEACHING ASSISTANT, University of Illinois at Chicago-UIC, Chicago, USA.
- 2000-2002: VISITNG SCHOLAR, Institute of Forestry (IOF), Tribhuvan University, Pokhara.
- 1989: SCIENCE TEACHER, Prithiwi high school, Kathmandu.

CONSULTANT

- 2001 (Nepal). External Expert: I helped develop the first "curriculum on wildlife and natural resource management" for MASTERS OF SCIENCE in Forestry. Institute of Forestry. Pokhara, Nepal.
- 1997 (INDIA). Scientific Advisor: I participated on the "Land of the Snow Leopard" project (Ladakh, India) led by the Earthwatch and the International Snow Leopard Trust (Seattle, USA). This was to assess the status of snow leopards and their prey in Ladakh, India.
- 2007 (USA): Snow leopards and other wildlife in Bhimthang, a corridor habitat, in mid-west Nepal. Snow Leopard Conservancy/Felidae Conservation Fund, California, USA.

SELECTED PROFESSIONAL ACTIVITIES

- 2004/5. Discovery (Nepal). I recorded the return of the snow leopard in Sagarmatha (Mt. Everest) National Park, Nepal, for the first time in forty years (October 2004). Website news, CNN: http://www.cnn.com/2005/TECH/science/05/23/snowleopard/index.html.
- 2003. Contributor and Reviewer (USA). Snow Leopard Survival Strategy, Seattle, USA, pp 106.
- 2002. Speaker (USA). International Snow Leopard Symposium. Seattle. May 2002.
- 2002. Founder member. Snow Leopard Network (SLN), USA.
- 1991, Founder Member. Natural History Society of Nepal (NAHSON). Kathmndu, Nepal. Nepal's current leading scientific journal.
- 2001. Discovery (Nepal). As a 5-person biodiversity survey team member, I recorded two new species of large mammals for Nepal -Tibetan wild ass *Equus hemionus kiang* (Mustang/Chhujung, 4,650 m) and Tibetan gazelle *Procapra picticaudata* (Mustang/Chhujung, 4,650 m).
- 1998. Volunteer (USA). Volunteered to collect vigilance and foraging data on elk, pronghorn antelope and American bison for the Mountain Lion Project in Yellowstone National Park and Titan National Park, USA.
- 1997. Speaker (Italy). Blue sheep of Manang (Nepal). International Conference on the Mountain Ungulates. May 5-7, 1997. Aosta valley, ITALY.
- 1996. Task Force Member (Nepal). Prepared the Annapurna Conservation Area Management Plan. Nepal.
- 1996, Speaker (Pakistan). The International Snow Leopard Conservation Conference, Islamabad, PAKISTAN, November 1996.

PUBLICATIONS (peer-reviewed)

- Ale, S.B., Yonzon, P. and Thapa, K. 2007. Recovery of snow leopard Uncia uncia in Sagarmatha (Mount Everest) National Park, Nepal. Oryx 41: 89-92.
- Shah K. B, Ale S. B., Chapagain, N. R. Acharya, R. Thapa, K., Gurung, A. and K.C., H. 2002. New mammal records from upper Mstang, Nepal with the notes on mammalian fauna of the area. Journal of Natural History Society 21: 33-44.
- Lovari, S. and Ale, S.B. 2001. Are there multiple reproductive strategies in blue sheep? Behavioural Processes 53: 131-135.
- Ale, S.B. and Whelan, C.J. (under review). Reconstructing the realm of the biggies! Biodiversity and Conservation.
- Ale, S. B. Brown, J. S. (submitted). Discovering snow leopards through the fear of their prey. Ecological Applications.
- Ale, S. B. Brown, J. S. (under review). The Contingencies of Group Size and Vigilance. Evolutionary Ecology Research.
- Ale, S.B. and Howe, H. F. (under review). What do ecological paradigms offer to conservation? J. Anim. Ecol.

CONFERENCE PAPERS

- Lovari, S., Ale S. B. & Boesi, R. 2005. The large mammal community of Sagarmatha National Park, Nepal. Proceedings of International Karakorum Conference (Islamabad 2005).
- Ale, S. B. and Karky, B. K. 2002. Observation on conservation of snow leopards in Nepal. Proceedings of the 9th International Snow Leopard Symposium (ISLT, Seattle, 2002).
- Ale, S. B. 2000. Rangeland, animal husbandry and wildlife in Annapurna, Nepal: A case study from Manang valley. C Richard, K. Basnet, J. P. Shah and Y. Rout (eds.). Grassland ecology and management in Protected Areas of Nepal, pp 45-51.
- Jackson, R. M., G. Ahlborn. M. Gurung, and S. Ale. 1996. Reducing livestock depredation losses in the Nepalese Himalaya. R. M. Timm and A. C. Crabb (eds.). Proceedings of the 17th Vertebrate Pest Conference. University of California, Davis, pp 241-47.
- Ale, S. B. 1995. The Annapurna Conservation Area project: A case study of an integrated conservation and development project in Nepal. R. Jackson and A. Ahmad (eds.). Proceedings of the Eighth International Snow Leopard Symposium. Islamabad, Pakistan, pp 155-169.

SELECTED REPORTS

- Upper Mustang Biodiversity Conservation Project. Project status brief, a booklet, GEF-UNDP, pp 30. 2001.
- Species diversity of Modikhola watershed. A comprehensive analysis, GEO Schultzt Den Regenwald e.V Vereiinsregister VR 12380 Beim Amtsgericht, Hamburg Germany. 2000.
- A conservation biology perspective on protected areas in Nepal: A case from Annapurna Conservation Area. King Mahendra Trust for Nature Conservation, Nepal, pp 11. 1999.
- Snow leopard Conservation Project. A comprehensive management plan. King Mahendra Trust for Nature Conservation, Nepal, pp 20. 1999.
- Some observation on conservation of snow leopard in Hemis National Park, India. International Snow Leopard Trust, Seattle, USA, pp 7. 1998.
- Land-use practices in Nar village, Manang: A need assessment for the Annapurna Conservation Area project, Nepal. USAID, pp 32. 1993.
- Land-use patterns and livestock depredation in several villages of east Kaski district. A Rapid Appraisal report. Biosystem Analysis, California, pp 79. 1993.

POPULAR ARTICLES

- Ale, S. B. and Boesi, R. 2005. Snow leopard sightings on the top of the world. CAT News 43: 19-20.
- Ale, S. B. The Snow Leopard. Nepali Times (weekly): Issue #108: 23 August 02 - 29 August 2002 (http://www.nepalitimes.com/issue/108/Nature/6046)
- Ale, S. B. 2000. Conservation of the snow leopard of Nepal. CAT News 32: 8-9.
- Ale, S. B. 2000. Religion protects Himalayan goral in the Annapurna region. Caprinae. December 2000.
- Ale, S. B. 1994. Snow leopards in remote districts of Nepal. Snowline XII: 2: 3-6.

THESES

- Ecology of the snow leopard and the Himalayan tahr in Sagarmatha (Mt. Everest) National Park, Nepal. PhD thesis, University of Illinois-Chicago, Illinois. USA. 2007.
- The rutting behavior of blue sheep in the Manang valley, Nepal. MS thesis, University of Tromso. Norway. 1999.
- Effects of grazing in Khangsar valley of the Manang region of Annapurna Conservation Area. MSc thesis, Tribhuvan University. Nepal. 1993.
- An Ecological Approach in mixed farming system of Nawrung village, thesis (village profile), Tribhuvan University. Nepal. 1993.

AWARDS

- 2007: Snow leopard Conservancy/Felidae Conservation Fund, California, $14,600.
- 2007: Dean's Scholar Award, University of Illinois-Chicago, $20,000.
- 2006: University Fellowship Award, University of Illinois-Chicago, $20,000
- 2006: Brookfield Zoo, Chicago, $4,000
- 2006. Individuals (private donors): Z. McDonald, Vickers family and others, California $4,000
- 2005: Rufford Small Grant, UK, $8,000.
- 2005: World Wildlife Fund-USA, $8,400.
- 2005. The Institute for Wildlife Studies, California, $ 4,000
- 2005: Ev-K2-CNR (Italy), $450.
- 2004: International Snow Leopard Trust (USA), small grant program, $5,000.
- 2004: Wildlife Conservation Society (USA), Field Conservation Grant, $8,990.
- 2004: Provost Award, University of Illinois-Chicago, $2,000.
- 2004: World Wildlife Fund-Nepal, $1,000.
- 2004-2005: Ev-K2-CNR (Italy), $450.
- 2004: IDEA WILD (USA), $400 (camera support).
- 1999-2001: Earthwatch Institute, $12,000-19,000, contingent on number of volunteers signed.
- 1992: Bio-system Analysis/California (Project No R. D. 424/084/049 Disp. No. 698), 2,000.

PROFESSIONAL MEMBERSHIP

- 2006/07. Member, (Grant) Review committee. International Snow Leopard Trust, Seattle, USA.
- 2006-2008: MEMBER. IUCN Species Survival Committee (SSC) Cat Specialist Group, the largest of the six volunteer commissions of the IUCN.
- 2002: FOUNDER MEMBER. Snow Leopard Network, the special commission of the International Snow Leopard Trust (Seattle).
- 1991: FOUNDER MEMBER. Natural History Society of Nepal, a special research body of the only national natural history museum of Nepal.