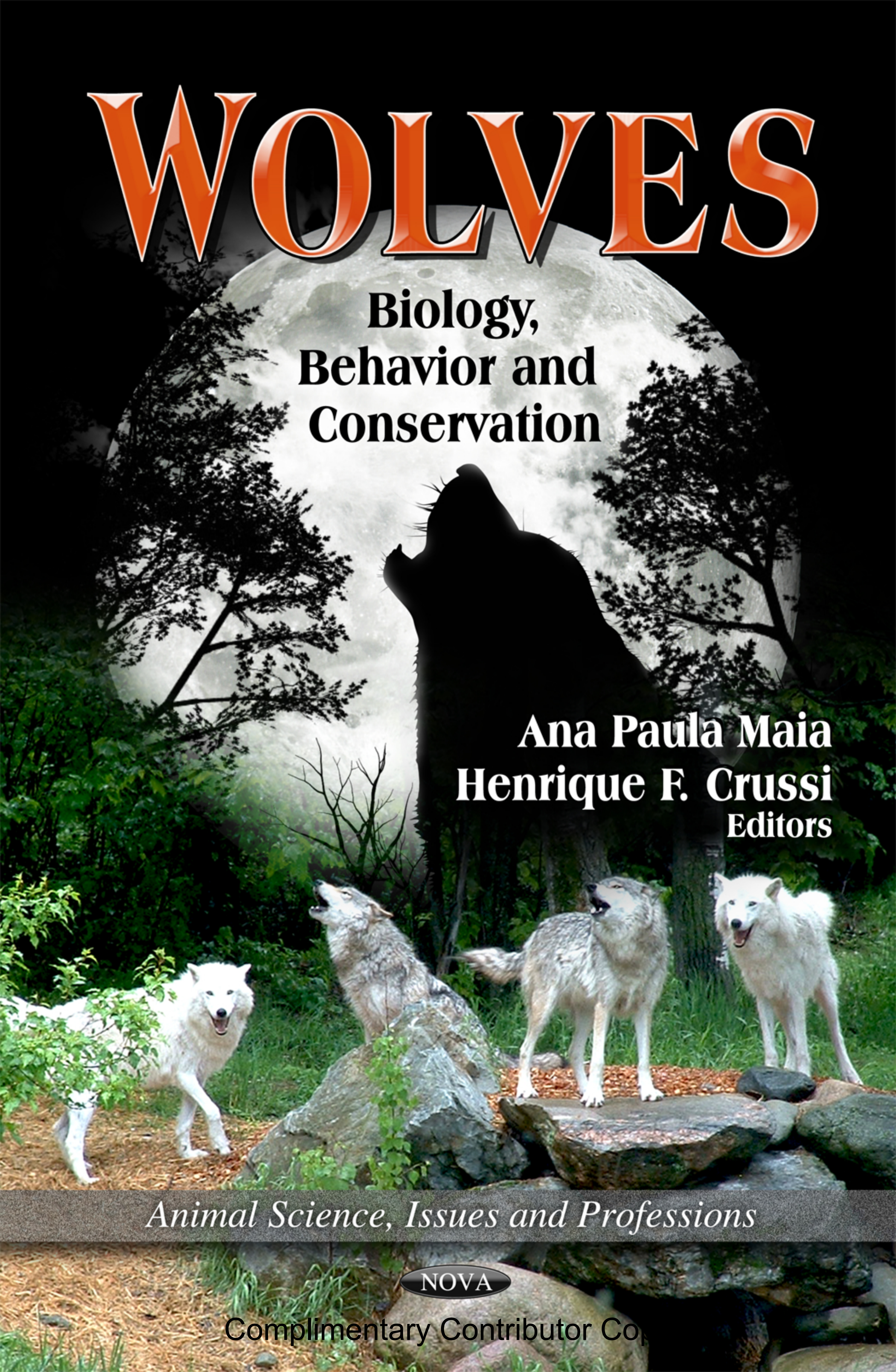

WOLVES

Biology, Behavior and Conservation

Ana Paula Maia
Henrique F. Crussi
Editors

Animal Science, Issues and Professions

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ANIMAL SCIENCE, ISSUES AND PROFESSIONS

WOLVES: BIOLOGY, BEHAVIOR AND CONSERVATION

ANA PAULA MAIA
AND
HENRIQUE F. CRUSSI
EDITORS

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CONTENTS

PREFACE

By whatever measures scientists choose for social intelligence, behavioral resilience of wolves illustrates their adaptations to changing aspects of their environments in the wild and captivity. Intriguing questions about wolves have emerged from studies of life history traits in social carnivores, such as large body size, delayed reproduction, and variable dispersal patterns. In this social context, the rapidly accumulating evidence for behavioral flexibility of wolves is reviewed in terms of learning, communication, problem-solving, and awareness. In this book, the authors present research on the biology, behavior and conservation of wolves.

Chapter 1 - By whatever measures scientists choose for social intelligence, behavioral resilience of wolves illustrates their adaptations to changing aspects of their environments in the wild and captivity. Intriguing questions about wolves have emerged from studies of life history traits in social carnivores, such as large body size, delayed reproduction, and variable dispersal patterns. In this social context, the rapidly accumulating evidence for behavioral flexibility of wolves is reviewed in terms of learning, communication, problem-solving, and awareness. Changing aspects of the social environment include interactions with littermates, care-givers, mates, rivals for mates, hostile neighboring groups and permeability of group barriers to immigration. Hypotheses about the adaptive significance of behavioral resilience are examined for each of the major stages in the lifetime trajectory of individual wolves: dependent pups, pre-reproductive adults, reproductive adults and post-reproductive adults. The emerging answers point toward moving beyond simplistic notions that wolves are social due to the benefits of group hunting, to examine the more complex, and fascinating, intersection of evolutionary processes at nested levels of individuals, kin-groups, dynamic isolation of populations, and inter-species competition. Shifting proximate benefits and costs of apparent monogamy may have far reaching implications for designing effective conservation strategies based on a biological understanding of behavioral mechanisms in wolves.

Chapter 2 - Many canid species (Order Carnivora: Family Canidae) across the globe are under threat, often from human disturbances, which include habitat destruction, expansion of agriculture and road networks, and hunting. This in turn can amplify the impact of infectious diseases, which on occasion have led some species to the brink of extinction such as the rare and endangered Ethiopian wolf (Canis simensis). Such populations are susceptible to infectious diseases including rabies virus (RABV), canine distemper virus (CDV) and canine parvovirus (CPV), all of which can cause high mortality levels. Conversely, canids have been responsible for the global spread of diseases affecting both human populations and their livestock.

With a focus on RABV and CDV, we discuss how transmission both to, and within, rare canid populations can have profound effects on population size and dynamics. The development of novel methodologies to study the interaction of such viruses within widely dispersed, often elusive wild canid populations remains challenging. Serosurveys have proven very useful in this field and retrospective seroanalysis of canid populations has revealed immunological responses to some of these pathogens demonstrating the circulation of important viral diseases within wild canids. Where data are available, we comment on the ability of infectious viral diseases to persist within often fragmented populations and spread between them. Importantly, we discuss the role of surveillance and the methods conservationists use in attempts to protect and maintain endangered canids, such as through vaccination of wild canids and monitoring of both domestic and wild canid populations.

Chapter 3 - The need to conserve terrestrial apex predators is internationally recognized because most of these predators are relatively rare. Derived from the grey wolf (*Canis lupus*), dingoes (*C. l. dingo*) are the largest terrestrial predator in Australia, but they are not threatened by decreasing numbers per se. Rather, hybridization with domestic dogs is changing the genetic integrity of dingo populations despite their widespread and common occurrence. Additionally, maintaining the role of dingoes in suppressing mesopredators and indirectly protecting faunal biodiversity is promoted as a key dingo conservation goal. By extension, lethal dingo control programs aimed at mitigating livestock losses have come under increased scrutiny for their perceived negative effects on biodiversity conservation. This study discusses the effects of lethal control on these two conservation values of dingoes using historical and contemporary datasets from arid Australia as an example. From historical data, it is shown that baiting typically occurred infrequently, though periods of spatially and temporally intensive control has the ability to reduce dingo abundance when conducted repeatedly over many years. From contemporary data, it is shown that sporadic and spatially restricted dingo control practices have little effect on the persistence of dingoes. It is concluded that contemporary dingo control practices may provide a catalyst for localized hybridization, but the ecosystem function of dingoes is unlikely to be altered by current control practices in any significant way. Ongoing lethal dingo control may still be practiced in an ecologically conservative manner while continuing to protect livestock production values.

Chapter 4 - There are different views to the social structure of wolf groups. They all have their history. At first, a simple linear hierarchy in wolf groups was described, then the conception of two parallel hierarchies of males and females was born. But sociograms in different researches showed us a much more complex structure of wolf group organization. The most interesting developing of these points of views was Mech's supposition about labor division of individuals in wolf groups during the one year-season cycle. This conception is close to the conception of social roles suggested in primatology which was applied for other species.We look at wolf social groups under review of this conception. It has features of functional system analysis. That conception describes each individual in the group as a structure element of a system and in that system, every element has its own role for group stabilizing. If the group hasn't been stabilized yet – each individual has his own social position with a direction to the future role. Questions we are interested in are about the development of these roles through their positions from zero, from individuals' childhood. One of the instrumental aspects of our research is using the "Theme" program (NOLDUS). It is for hidden patterns (non-random non-linear sequences) of behavior detecting. We can see animals' behavior real-time complex structure (the projection of the behavioral system they live in) and changes in it with time. It is real to analyze any special parts of behavior structures changing. One of such parts, picture dynamics of meaningful and behavioral events of some category, that significantly interconnect to each other. We observed round-the-clock activity of 2 wolf pups groups within the age of 37-230 days every 7-10 days. Observations were made in 2007 and 2008 in the Tver region (Russia), on the base of the biological research station "Chisty Les". These groups both were made from pups that had been taken from zoos, these pups grew up without parents, so we can detect only those categories of behavior that are in them by nature, genetically. The object of supervision both years: 2 wolf males and 2 wolf females (*Canis lupus*). As far as territory, we used big enclosures – parts of a natural forest. This analysis was focused ecpesially on the age period from 75 to 115 days, it is an important period in wolf ontogenesis. As a partial result of this work, it is two cascade-type schemes of significantly connected events with agonistic types of activity in the wolf pups group. Schemes have been made on the base of hidden patterns which have been detected and decoded. These schemes pictured how agonistic activity types take part in the system-organized process of juvenile hierarchy stabilizing, and how individuals in a simple group connect to each other through this type of behavior in a period which is so important in their life.

Chapter 5 - Cooperation is a series of coordinated interactions in which participants take turns in giving and receiving benefits. Nevertheless, competition is the other side of the coin and it may generate aggression among conspecifics loosing social cohesion. Many social species have developed behavioral strategies to cope with social damage caused by competition. We investigated the occurrence and dynamics of these behavioral strategies in wolves (*Canis lupus lupus*), a species characterized by high sociality and cooperation levels, by carrying out a long-term observational study on the grey wolf colony hosted at the Pistoia Zoo (Italy). We highlighted the occurrence of post-conflict affiliation both between opponents (reconciliation) and between victims and bystanders (solicited and unsolicited contacts). Reconciliation was uniformly distributed across the different sex-class combinations and seemed to be not affected by the hierarchical relationships. Moreover, coalitionary support given to victim and/or to aggressor during a conflict may be a good predictor for high level of reconciliation. Concerning unsolicited triadic contacts (named "consolation" in human and non-human primates), we found that this affilation was more frequent between individuals sharing good relationships and was reciprocated between partners (victims and third-parties), thus suggesting the reciprocal nature of this mechanism (mutualistic behavior). As it occurs in human and non-human primates, unsolicited contacts provide immediate benefits to the victim by breaking-off aggression and restoring victim' social cohesiveness. To investigate other affinitive behaviors used by wolves to promote cohesiveness and cooperation, we evaluated the presence of social play, an activity used by animals for self- and social-assessment purposes. We showed the occurrence of adult play in wolves. Play distribution is not affected by relationship quality and aggression level, thus suggesting that other strategies are employed for strengthening inter-individual relationships and reducing aggressiveness. Rank distance between conspecifics negatively correlate with play distribution: by playing wolves with closest ranking positions tested each other for acquiring information on motor and psychological skills of possible competitors and for gaining hierarchical advantage over it. The overall findings on wolves strongly match with those coming from behavioral studies on human and non-human primates. Even though further comparative-cognitive studies are needed in canids, the similarities between primate and wolf social cohesion strategies suggest an evolutionary convergence in certain traits of cognitive skills at the basis of natural conflict resolution and adult social play.

Chapter 6 - In wild wolf packs social relationships constitute the most important factor influencing the stress levels and welfare. In this review, we summarize factors influencing social stress of wolves, considering different wolf profiles and their relationships with humans. Wolf social relationships are influenced not only by rank order, but also by the affective behaviors individuals display towards other pack members. Cortisol, an important component of the mammalian stress response is found generally in higher levels in dominant wolves than in subordinates in the wild, but cortisol levels are not predictive of rates of agonistic interactions. Social stress in wolves seems thus not to be a consequence of subordination, but a cost of dominance. Higher levels of aggressive interactions are reported from enclosure-kept animals in comparison with wild wolves. Little is known, however, about the behavioral factors mediating the connection between glucocorticoids levels and stress loads in captivity. Some of the data reviewed here indicate higher levels of glucocorticoid in dominants, but similar levels in both dominants and subordinates have also been reported. Stress hormone data from wolves in captivity may be confounded by unnatural group composition, restricted living areas (fences making temporary avoidance impossible), and by the different levels of socialization with humans. As wolves' behavior is flexible, varying according to environmental and social context, data from captivity may be viewed as indicating the potential range of behaviors wolves can perform in the wild. Hand-raised wolves have been recently used as a model for the study of wolf cognition and the origins of dog behavior. This study has brought insights into the role human partners may have in modulating wolves' stress levels. A wide field for further research opens, which may shed light on the adaptive flexibility of wolves, and may contribute to improve wolf welfare in captivity and in the wild.

Chapter 7 - The grey wolf (Canis lupus), sole top-predator of the Japanese forest ecosystem, had been eradicated from the Japanese archipelago by the early 20th century. The absence of wolves, combined with the dwindling number and aging of human hunters, have resulted in overabundance of their prey ungulates such as sika deer (Cervus nippon) and wild boar (Sus scrofa). Aside from ecosystem engineers which have a critical impact on indigenous forest ecosystem processes, in recent years these animals have been recognized as pest mammals that damage agricultural land. Countermeasures against such damage have been quite limited, depending only on human stewardship such as constructing guard fences and culling the population of pest mammals by local hunters. However, depopulation and aging in rural communities, which started in the 1960s, have accelerated and led to demographic changes nationwide since 2005. Further depopulation, tight national finances, abandonment of mountain communities, and loss of small settlements are expected to continue. This social background will inevitably lead to further shortages of manpower and budget for regional wildlife management, and inadequate sustainable conventional countermeasures based on human stewardship. One solution might consider an alternative to human stewardship, i.e., restoring the natural ecosystem function into forest ecosystem by reintroduction top-predator. Here, we review and discuss the need, effectiveness and feasibility of reintroducing wolves in Japan.

In recent years, the reintroduction of wolves has been planned or already implemented in some former ranges of the species across North America and Western Europe. In Yellowstone National Park (YNP) in the U.S., where wolves were reintroduced in 1995–1996, the decline of overbrowsing by elk (C. canadensis), regeneration of native plant communities and restoration of the original landscape have been confirmed since 1995. Although the ecosystem changes have resulted from predation risk by reintroduced wolves, wolf predation has had less impact on the elk population than human hunting. Therefore, not only reintroduction of wolves but culling of pest mammals by human hunters is required for wildlife management in Japan.

A policy that depends only on natural regulation, such as in YNP, would not be appropriate in rural Japan because of the highly mosaic landscape with forests and human settlements, as typified by Satoyama landscape. In this chapter, we suggest that the future policy should include both natural regulation by reintroducing wolves in mountainous forests and artificial population control by professional hunters in lowland Satoyama areas. Given that social attitude to the reintroduction of wolves in Japan is not yet accepted, further feasibility studies related to wolf reintroduction are required for education and consensus-building in Japanese society. Moreover, alternative population control systems (e.g. professional culling or sharpshooting) should also be developed to counter the decline of human hunters.

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Chapter 1

WOLF SOCIAL INTELLIGENCE

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ABSTRACT

By whatever measures scientists choose for social intelligence, behavioral resilience of wolves illustrates their adaptations to changing aspects of their environments in the wild and captivity. Intriguing questions about wolves have emerged from studies of life history traits in social carnivores, such as large body size, delayed reproduction, and variable dispersal patterns. In this social context, the rapidly accumulating evidence for behavioral flexibility of wolves is reviewed in terms of learning, communication, problem-solving, and awareness. Changing aspects of the social environment include interactions with littermates, care-givers, mates, rivals for mates, hostile neighboring groups and permeability of group barriers to immigration. Hypotheses about the adaptive significance of behavioral resilience are examined for each of the major stages in the lifetime trajectory of individual wolves: dependent pups, pre-reproductive adults, reproductive adults and post-reproductive adults. The emerging answers point toward moving beyond simplistic notions that wolves are social due to the benefits of group hunting, to examine the more complex, and fascinating, intersection of evolutionary processes at nested levels of individuals, kin-groups, dynamic isolation of populations, and inter-species competition. Shifting proximate benefits and costs of apparent monogamy may have far reaching implications for designing effective conservation strategies based on a biological understanding of behavioral mechanisms in wolves.

INTRODUCTION

How has the complex social environment of wolves (*Canis lupus*) shaped their capacity to adapt to such a wide range of physical environments? Answers to this, and other related questions about social intelligence in wolves, will emerge from a rapidly expanding body of knowledge integrating the canid genome [1], dog social cognition [2] and dynamic ecology of wolf populations [3-6]. In comparative studies of carnivores, social intelligence has been defined as "those processes by which animals obtain and retain information about their social environments, and use that information to make behavioral decisions" [7] pg 523. Within this analysis of the recent peer-reviewed scientific literature, I will draw on personal experiences observing wolves in the wild [8-10] and captivity [11-13]. My focus will be on the recent literature, referring readers to previous reviews for a historical perspective on wolf social behavior {[14-16] and communication [17]. While assisting Dave Mech in his long-term field studies of arctic wolves on Ellesmere Island [18-20], I was privileged to observe a pack of eight wolves during one summer denning season. The following anecdote from my fieldnotes illustrates why researchers, who have had similar rare opportunities to observe wolves in the wild, are fascinated by how canids solve social problems. In this case, the social problem was that one pup was separated from her brothers, while left alone at the den. Their mother, Nipples (NI), returned to the den to find only one of a litter of four pups.

> "0400 -- NI sits with lone pup and howls-- no response. She checks the crevice [where the 4 pups frequently slept] then the den. [NI crossed the gulley, stared at me and I couldn't resist tossing her a part of my lunch.] NI eats food from me, takes a piece back to the lone pup, regurgitates what she swallowed. They both chew on it….NI lies near the den and the [pup] goes to her. She gently nibbles it, as it lies on her paws, rolls and tumbles away. When NI looks away, the pup moves away and chews on bones. NI takes food from me back to the pup again and regurgitates. (She seemed unusually solicitous--does it imply concern over absence of pups?)
>
> 0557 -- 3 pups return from the W along the stream. NI goes over to the pups and slowly wags her tail as they lick up to her. The pups suckle as NI stands. 2 break off and one touches noses with NI. She startles and jumps away as 2 pups persist. She muzzles one pup who finally sits (do they hurt her as they suckle?)" (J.M. Packard. 12 July 1988; words in brackets added to explain context)

In this review, I first briefly summarize the theoretical framework within which social intelligence has been studied in social carnivores [21], drawing on comparisons with primates [22-24] and birds [25-27]. Second, I synthesize the literature on canids, to clarify how research on wolves fits into a larger picture of comparative social cognition [28, 29] and carnivore life history traits associated with large body size [30, 31]. Third, I evaluate information about wolf social intelligence, using four "yardsticks" widely accepted for comparing intelligence across species: learning, communication, problem-solving, and awareness. Finally, I comment on the implications of an integrated approach to adaptive management of wolves, grounded in an understanding of evolutionary, physiological and ecological processes.

SOCIAL INTELLIGENCE: CONCEPTUAL PERSPECTIVES

Simply stated, the "Social Intelligence Hypothesis" refers to the idea that the genetic basis for "executive brains" has been selected in several taxonomic lineages due to the complexity of social rather than physical environments [7, 21]. As applied to evolution of the bigger brains of social carnivores, Holekamp (2006) critiqued the idea that the effects of social and physical environments could be separated.

She also recommended integrating information about constraints on brain complexity, considering both ontogeny and phylogeny (Figure 1). If the more social primates and hyenas have larger forebrains, Sakai et al (2010) proposed this might be evidence for convergent evolution of two genetically very different taxonomic lineages, which diverged about 90 to 100 MYA [7].

In comparison, divergence of the genus *Canis* has been more recent than divergence of the great apes, e.g. chimps and humans [1]. Comparative psychologists are beginning to better understand how "executive brains" may not only be bigger, but also more complex [28, 29]. Behavioral measures for social intelligence can be compared across species, with careful attention to what is similar and what is unique to each species (Table 1). Many of the traits of social cognition have already been examined for domestic dogs and wolves [2].

The wolf-like canids provide a rich opportunity to tease out the influences of genes and environment, since diverse genotypes have been studied across a wide range of socio-ecological environments (Table 2). Now that the dog genome has been mapped, we are coming closer to understanding the genetic basis of behaviors in the wolf-like canids [1, 32, 33].

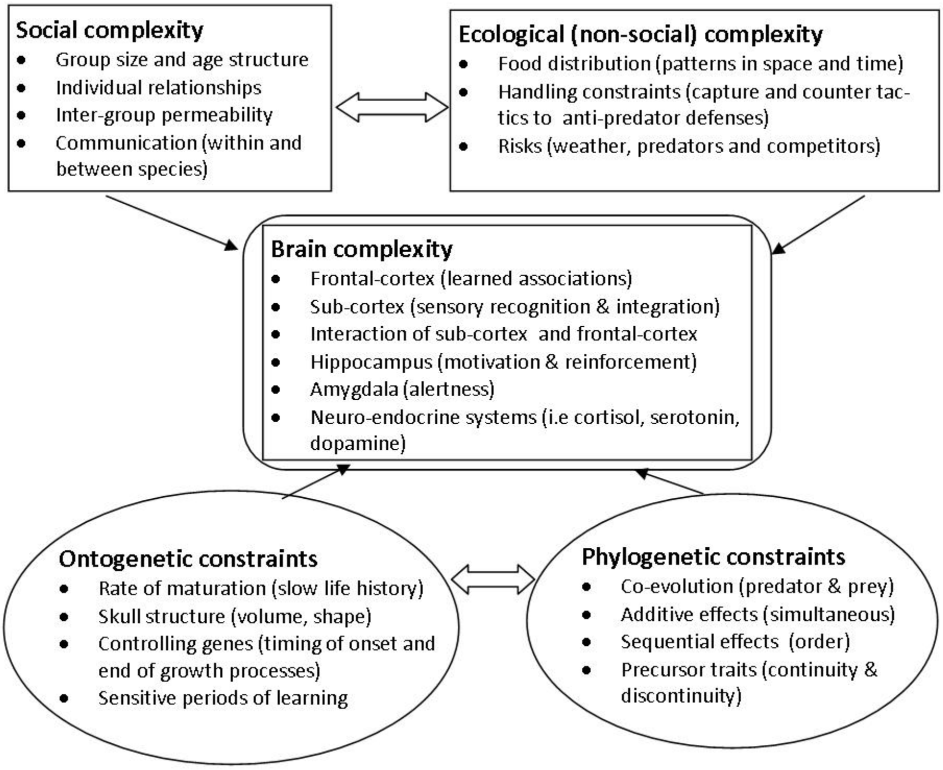

Figure 1. Larger theoretical framework for evolution of intelligence, integrating (a) environmental complexity (social and non-social) and (b) constraints (ontogenetic and phylogentic, adapted from Holekamp 2006).

Table 1. Categories of behavioral measures used to test the social intelligence hypothesis

Category of behavioral measures[1]	Taxonomic groups in which this measure has been tested[2]
1. Individual recognition; respond differently to sounds and/or smells that carry information about individual identity; distinguish "self" from "other"	*carnivores*: spotted hyenas [21], wolves [15,17,18], domesdogs [148] *primates*[21]: cercopithecine monkeys (baboons, vervets) great apes
2. Kin recognition; direct behavior differently toward kin and non-kin; helping at the den, permeability of groups to immigration	*carnivores*: spotted hyenas [21], coyotes [180], wolves [109]148] *primates*[21]: cercopithecine monkeys (baboons, vervets), great apes
3. Rank acquisition and social memory; predictable social relations within a large group with mixed age-classes; modify behavior according to social context; affiliative and agonisticrelationships	*carnivores:* spotted hyenas [21], gray wolves [106,142], domestic dogs [182-185] *primates*[21]: baboons, macaques, chimpanzee
4. Application of knowledge about social_rank; feeding at clumped sources; choice of mates; social competence; social expedience; solve social problems in diverse ways	*carnivores:* Spotted hyenas [21,186], gray wolves [142], coyotes [50], domestic dogs [2] *primates*[21]: great apes, monkeys
5. Partner choice and relationship value (independent of kinship); mate preferences influenced by rank, seniority, familiarity	*carnivores:* Spotted hyenas 21,186], gray wolves [142] *primates*[21]:: great apes, monkeys
6. Repair of damaged relationships; reconciliation; affiliation after conflict	*carnivores:* Spotted hyenas 21,186], gray wolves [142] *primates*[21]:: great apes, monkeys
7. Recognition of 3rd-party relationships; alliances, respond to mother when infant cries	*carnivores:* spotted hyenas [21,35], gray wolves [143,186] *primates:* great apes, vervet monkeys
8. Learning in a social context; changes in behavior associated with observing other's actions/outcomes; social learning; social influence; cooperative problem solving; play; imitation; coordination; culture	*carnivores:* spotted hyenas [21,187], gray wolves [19], domestic dogs [2,58,126,188,189] *primates* [21]: great apes, cercopithecine monkeys
9. Communication; transfer of information between actor and recipient; integration of information from sight, sound and smell; referential gaze or pointing	*carnivores*: spotted hyenas [21], gray wolves [66,96,190], domestic dogs [2,55,117,119,191] *primates*[21]**:** great apes, cercopithecine monkeys

[1] Categories are a synthesis of subheadings from two sources on social carnivores [2, 21].

[2] For scientific names, see Table 2 for wolf-like canids, otherwise see feferences cited.

PHYLOGENY: APPLICATIONS TO SOCIAL MAMMALIAN CARNIVORES

Holekamp et al (2007) set the stage for investigating the social intelligence hypothesis in mammalian carnivores, starting with the Hyenidae. Comparing hyena species, the solitary, semi-social and social species do not vary in the size of the brain relative to the body; however, as predicted for the "most social" species, the spotted hyena (*Crocuta crocuta*) has a relatively larger forebrain [34]. In the forebrain (anterior cortex) are neuronal mechanisms for processing memories of complex patterns of stimuli as would be needed in flexible social problem-solving. In the cortex of dogs and hyenas, the association area (frontal and motor cortex) is not as distinctively separated from the sensory area (somatosensory cortex) as in primates [7].

The next logical step would be to test the social intelligence hypothesis in other species of mammalian carnivores (Order: Carnivora), such as the wolf-like canids (Table 2). Spotted hyenas are behaviorally and morphologically similar to canids (Table 3); however, their genome is more similar to cats (Suborder: Feliformia) than dogs (Suborder: Caniformia) [35, 36]. Both spotted hyenas and wolves show convergent adaptations for chasing swift prey (cursorial), shearing meat, and for crunching bones (durophagy), apparently resulting from parallel processes of evolution over 50 MYA [35, 37, 38]. Although skulls of hyenas and coyotes have been compared in terms of developmental changes with age [39-42], implications for brain mechanisms underlying social cognition have yet to be determined [43]. The genetic basis for variation in skull shape expressed in dog breeds, appears to have existed in the wolf prior to selective breeding [44]. Little is known about comparative brain morphology in the wolf-like canids, although computed tomography (CT) imaging of carnivore brains appears to be a promising technique [7].

How did body size evolve in the wolf-like canids? The first canids emerged on the order of 6 MYA; however, the most closely related wolf-like canids (Table 2) diverged from a jackal-like ancestral species (presumably in what is now North America) on the order of 3-4 MYA [1]. The ancestral form of the gray wolf (*C. lupus*) is thought to be small-bodied, more like the eastern wolf (*C. lycaon*) or red wolf (*C. rufus*). Current fossil evidence suggests that wolves radiated from North America to Eurasia when the land bridge opened during the mid-Pleistocene (<0.5 MYA). Eurasian wolves show distinctive geographic genetic signatures [32], possibly related to geologic barriers such as glaciers during the ice ages. When the land bridge opened again, the wolves that radiated back to North America were large-bodied, possibly more similar to the Northern Rocky Mountain subspecies (*C.l. irremotus*). Compared to wolves, the small semi-social coyotes of North America (*C. latrans*), as well as golden jackals of Eurasia (*C. aureus*), would have been genetically closer to the ancestral species of *Canis*. Although the first stage of domestication of dogs (<100,000 to 18,000 tbp) showed little change in body size, smaller dogs appeared in the Mideastern region during the second stage of domestication [1]. Did evolution of body size in hyenas trace the same historical storyline? Hyenas diverged from arboreal cat-like species in the jungles of what is now Eurasia on the order of 22 MYA.

The fossil record suggests the ancestral hyenas were more dog-like [34], possibly similar to the solitary aardwolf (*Proteles cristata*). The sociality of brown hyenas (*Hyaena brunnea*) appears most similar to the family group structure typical of wolves.

The largest and most social species, the spotted hyena, originated in the African forests on the order of 10 MYA; apparently before *Canis* evolved. Spotted hyenas spread south and north into Eurasia during the mid-Pleistocene [45]; a period when the wolves showed rapid differentiation of subspecies.

Table 2. Examples of variation in the social environment of wolf-like canids, on two dimensions: genetic and socio-ecological (after Miklosi 2007:87)

Socio-ecological Variation[1]	Genetic Variation			
	Wolf genus (*Canis spp*)[2]	Wolf subspecies (*Canis lupus*)[3]	Domestic dogs (*Canis familiaris*)[4]	
	Diverged: 3-4 MYA	Diverged: <1 MYA	Ancient: 0.1-0.015 MYA	Pure bred : <0.002 MYA
Free-ranging (self-sufficient; human-avoidance and independence; human-hunted)	Gray (*Canis lupus*) Eastern *(C. lycaon)* Red (*C. rufus*) Dingo dog (*C. familiaris*) Ethiopian (*C. simensis*) Coyote (*C. latrans*) Golden jackal (*C. aureus*)	Arctic *(C.l. arctos)* Mexican *(C.l. baileyi)* N. Rocky Mountain *(C.l. irremotus)* Eurasian *(C l. lupus)* Gray *(C.l. lycaon)*	Dingo- Australia	unlikely
Feral (subsidized by humans directly or indirectly)	Red Wolf- Great Smokey Mountain National Park (NP)	Eurasian- Abruzzo, Iberian Arctic- Ellesmere Mexican- Arizona, New Mexico	Village dogs- India Village dogs-Ethiopia	Urban/rural (mixed breed)
Enclosed (human- controlled dispersal and access to resources)	Red Wolf- captive breeding program (minimal human contact)	N. Rocky Mountain- Soft release pens at Yellowstone NP Mexican- accommodation pens at La Sevilleta, Ladder-Ranch	Dingo- research	Some no-kill shelter dogs (not adoptable; mostly mixed-breed)
Tamed (human- habituated after 3 months; or unspecified)	Gray- Carlos Avery, Lincoln Park Zoo, Burger's Zoo, Pistoia Zoo, Sawtooth Coyote- USDA-Logan, UT	Mexican- San Juan Lineage Mexican- Ghost Ranch lineage Mexican- McBride lineage	Un-determined	Some shelter dogs (poor adoptability scores; mostly mixed-breed)

Socio-ecological Variation[1]	Genetic Variation			
	Wolf genus (*Canis spp*)[2]	Wolf subspecies (*Canis lupus*)[3]	Domestic dogs (*Canis familiaris*)[4]	
	Diverged: 3-4 MYA	Diverged: <1 MYA	Ancient: 0.1-0.015 MYA	Pure bred : <0.002 MYA
Socialized (human-handled before 3 months; varying degrees of enculturation)	Gray- Wolf Science Center, Wolf Park, Carlos Avery, Univ. Connecticut, Bayerische Wald, Shubenacadie Pack, Godollo Pack	A few orphaned and/or abandoned individuals hand-reared in captive breeding programs for threatened subspecies	Mideast: Basenji, Afghan, Saluki, etc. Asian: Chow chow, Shar-pei, Akita, Dingo, etc. Arctic: malamute, husky, etc.	Toy, terrier, retrievers, scent hounds, sight hounds, mountain breeds, herding breeds, spaniels, working dogs, mastiffs, etc.

[1] The socio-ecological environment of wolves varies (non-independently) with the degree of isolation from other wolves and interaction with humans. Some categories are not mutually exclusive (i.e. enclosed and/or tamed).

[2] Sources (*Canis spp.):* genetics [1,33] free ranging [3,49,192-195], feral [112,196,197], enclosed [205]; tamed/socialized [15]

[3] Sources (*C.l. subspecies*): free ranging [199-202], feral [20,76,203,204], enclosed [205]; tamed [13]

[4] Sources (*C. familiaris*): dingos [206]; shelter dogs [207]; dogs in general [2]; dog breeds [34]

Table 3. Variation in life history traits among social carnivores, comparing gray wolves with larger hyenas (convergent) and smaller coyotes (divergent)

Trait	Spotted hyena (Suborder: Feliformia)	Gray Wolf (Suborder: Caniformia)	Coyote (Suborder: Caniformia)
Peak body size	Small males: 40-52 kg (Serengeti) Females: 44-64 kg	Large males: average 41 kg (Superior NF) Females: average 31 kg Age at peak: 5-6 years	Males and females: 7-21 kg
Birthing synchrony	Year round; synchronized by feast/famine	Late spring: April to May	Late spring: March to May
Litter size	1-2 cubs; 10% less cub production where prey migrate (Serengeti)	1-11 (varies with nutrition, parity) Mean: 3.1 (Ellesmere), 5.6 (Superior NF)	1-19 Mean (Yellowstone): 5.0 (low food), 7.8 (high food)
Socialization period	Peers: 1-6 months; non-peers: 1-9 months	Peers: 0-3 months Caregivers: 1-3 months	Cross-fostering successful <1.5 months
Weaning age	7-24 months; mean is 13.5 months; not capable of killing prey at weaning	3-4 months; at weaning capable of tearing apart small carcasses, not killing large prey	1-2 months; capable of killing small mammals by 6 months; omnivorous
Physiological maturity-age	Males and females: 2 yrs	Usually 2 years; range 10-34 months (variation related to nutrition and social relations)	1 year (full body size 9-12 months)

Table 3. (Continued)

Trait	Spotted hyena (Suborder: Feliformia)	Gray Wolf (Suborder: Caniformia)	Coyote (Suborder: Caniformia)
Dispersal	Males: disperse between 2-6 years Females: philopatric (remain in natal clan)	Males and females disperse at .5-3 years Distances may be 100 to 1,000 kilometers	6-9 months up to 2-3 yr; varies with nutritional and social factors
First breeding- age	Usually 3-4 years	Females: usually 3-4 years	Usually 2 years (varies from 1-3)
Hunting	Cursorial; meat-shearing; bone crunching Scavenge, solitary, clan groups, group defense of carcass against competitors	Cursorial/pounce; meat-shearing; bone crunching Scavenge, solitary, pairs, family groups	Cursorial/pounce; meat-shearing; bone crunching (small mammals, calves) Scavenge (may aggregate), solitary, pairs
Life span	Wild: 18 years; captive: 41 years	Wild: 9-11 years; captive: 20 years	Wild: 10 years; captive: 18 years
Group size- maximum	Up to 90 individuals; varies by location from 3 (desert) to 67 (savannah)	2-29 individuals; average varies by location: 5.6 (Superior NF), 8.9 (Denali NP)	10 individuals (Yellowstone NP); 4.6 (low food); 6.6 (good food)
Group size- variation	Varies with prey migration and prey productivity	Varies with seasonal pup dispersal, latitude, mortality, prey productivity and migration	Varies with pup dispersal and access to large carcasses (i.e. winter-kill elk)
Group composition	Clans are female/offspring lineages with male immigrants (subordinate); inherit rank of mother	Usually parents with pre-reproductive offspring; variations include disrupted and extended families	Pairs in fall/winter (some aggregations); nuclear families in spring/summer include pups and a few yearlings
Cohesiveness	Fission/fusion within clans; female lineage is the core	Winter: breeding pair is core Spring/summer: litter of pups is core	Winter: breeding pair is core Spring/summer: litter of pups is core
Conflict- inside groups	Conflict primarily at carcasses; mothers support youngest offspring;	Subtle signs; learned during interactions; related to context (food, space and mates)	Dominant pups get more food, disperse later, survive better
Conflict- outsiders	Lethal attacks between clans; group attacks on competitors	Lethal attacks toward loners, trespassing packs and smaller canids; compete with bears	Ritualized displays toward loners, trespassers; attacked by wolves

Gray wolves and spotted hyenas both lived in Eurasia until the grasslands and lowlands were replaced by woodlands on the order of 11-14,000 ybp, when the range of the spotted hyena retracted to Africa. According to one hypothesis [45], spotted hyenas were displaced by wolves and humans (possibly better competitors) when the lowlands favored by hyenas dried up in the process of a warming trend and glacial retraction.

This would have been after the first stage of domestication of dogs (*C. familiaris*), estimated at >100,000 to 15,000 ybp [1]. Thus, evolution of large body size did not appear at the same time in the history of hyenas and wolf-like canids. During the evolution of the genus *Canis*, carnivore communities would have been quite different from today [35, 36]. Mammoths and very large dire wolves (*C. dirus*) became extinct on both the American and Eurasian continents [46], about the same time (12-13,000 ybp) as the range retraction of spotted hyenas.

At least seven larger-bodied carnivores also went extinct, suggesting *Canis* evolved in an environment with intense competition among a diverse guild of predators no longer visible to us in the current environment of wolves [35]. Interactions between wolves and coyotes in Yellowstone may give us glimpses into the prehistoric past; large wolves can displace small coyotes at carcasses, but interactions are mediated by group size of both coyotes and wolves [47, 48] as well as the stage of carcass consumption [49].

Large body size is currently an adaptive advantage for spotted hyenas defending large carcasses from large competitors. Large skulls are more effective at crunching large bones. The same line of investigation could be applied to past evolution of large body size in wolves. Such insights reinforce the importance of better understanding the interaction of social and environmental factors in the evolution of brain complexity, as emphasized by Holekamp (2007). She also emphasized the importance of better understanding the constraints imposed by processes of development (ontogeny), as they interact with natural selection (phylogeny). According to the "Large Body Hypothesis", group hunting in wolves may be a "by-product of slowly-growing large bodies", rather than a "driver of sociality".

ONTOGENY: SOCIALITY AND DELAYED REPRODUCTION

Intriguing questions about wolves have emerged from studies of life history traits in social carnivores, such as the correlation of large body size, delayed reproduction (also called reproductive suppression), and variable age of dispersal [30, 31]. In this chapter, I will review the evidence that an alternative to the "Social Intelligence Hypothesis" is the "Large Body Hypothesis". Rather than referring to absolute size alone, this viewpoint focuses more on learning within a social network, which presumably provides a rich environment for learning during delayed maturity and dispersal.

In general, smaller-bodied carnivore species produce smaller pups that mature more quickly and disperse at a younger age, as illustrated by comparison of spotted hyena, gray wolves and coyotes (Table 3). Size of neonates appears constrained by female body size, not driven by adaptive benefits of sociality, such as group hunting [30, 31]. Group size appears more related to the distribution of "resources and risks" rather than genetics. This raises the question of whether pre-reproductive offspring that stay with their natal group are "helpers" or "social parasites" benefitting from extended parental care while they grow larger. For example, Mech noted that when the Ellesmere Pack did not produce pups one year, they cared for the yearlings in a manner similar to pups (Mech 1997:130).

In comparison, pre-reproductive hyenas are not capable of killing large prey on their own, eating as fast as adults, or defending carcasses from lions; thus they benefit greatly by staying home with their mothers until their jaws are fully formed [42]. Males disperse at about 3-4 years, coincidental with maximum brain development and sex-specific enlargement of the frontal cortex, presumably related to the social complexity experienced by males entering into a non-natal group of strangers [50]. Clearly skull size alone is not a determinant of social intelligence in canids, again reinforcing the recommendation by Holekamp (2007) to examine the modular design of the brain in testing the social intelligence hypothesis. Great Danes and Chihuahuas illustrate that body size of dogs can vary on the order of 40% [33]. However, no one has claimed that the social intelligence of Great Danes is greater than Chihuahuas.

Now that the "complete" genome of the dog has been sequenced, new windows will open to a better understanding of the interactions of ontogeny and phylogeny in the wolf-like canids [1, 32]. This information will expand rapidly as the genomes of more species are sequenced [51]. Of special interest is the question of how much of the "raw genetic material", which has become apparent due to modern artificial selection of dog breeds, can be attributed to (1) underlying variation in the basic canid genome and (2) mutations arising (and persisting) since dogs diverged from wolves [52]. For example, only about half of the microsatellite primers identified in the dog genome, are cross-reactive in the analysis of the genomes of wild canids [1].

Techniques for complex trait analysis in dogs [53] will result in rapid advances to our understanding of variation in the developmental timing of behavioral traits [54, 55]. For example, better understanding of changes in the timing of modular development, specific to each part of the skull, promises to unravel the diversification of head shapes in domestic dog breeds [44], possibly leading to similar future analysis of brain complexity [41]. However, skull development in canids suggests dogs are not "paedomorphic wolves"[56], meaning that the skull structures of dogs differ from both juvenile and adult wolves due to tipping of the muzzle (rostrum). Skulls of some dog breeds also vary with the degree of placement of the eyes near the front of the face (brachycephalic) rather than the side, like wolves [57].

Combined, a better understanding of the timing of morphological and behavioral processes will be needed to test the "Domestication Hypothesis" about the evolution of social cognition in dogs [58, 59]. Initially proposed, the predisposition of some dogs to attend to human gestures was thought to be a mutation not existing in wolves. As revised, the "Two Stage Hypothesis" states that socialization to human companions predisposes individual dogs to learn the meaning of referential pointing and gaze by humans [55, 60]. This line of research is driven by the advantages of better approaches to (1) understand social development in dog pups [61, 62], and (2) fill the modern demand for service guide dogs capable of effective problem-solving in complex social and physical environments shaped by humans [63].

The debate surrounding the Domestication Hypothesis illustrates how careful researchers need to be in clearly defining testable hypotheses about the complex set of behavioral traits referred to collectively as social cognition [64]. Strictly defined, social cognition refers to the processing of information used in social problem-solving, which is only part of the behavioral systems engaged in effective lifelong navigation of access to resources and avoidance of risks. Research on social cognition in wolves has been challenged by their diverse emotional responses to testing procedures [65]. For example, hand-reared wolf pups struggled more with their handlers and took longer to establish the eye contact required for the cognitive test.

The emotional (affective) state of individuals may influence the learning performance of wolf-like canids (see references in Miklosi 2007). Researchers are exploring behavioral changes associated with changes in neuro-endocrine systems in dogs, such as those influenced by dopamine, serotonin, and cortisol [66-68], as well as systems controlling blood chemistry and peptides [69, 70]. Undoubtedly, brain structures underlying the mechanisms of learning, recall and emotion, such as the hippocampus [71] and amygdala [70], will need to be added to the list of structures underlying cognitive mechanisms (Figure 1). Genetic patterns associated with the hippocampus varied much more than those associated with the amygdala and frontal cortex in wolf-like canids [1]. Thus, we might predict more variation in emotions (hippocampus) than alertness (amygdala) and memory (cortex).

Until we have better techniques for measuring the interaction between emotion (affect) and cognition (neural processes), I am cautious about using such keyword concepts as "social cognition" and "social learning" when reviewing the emerging literature on wolf social intelligence. "Social learning" is used in referring to dogs [72] as well as "social cognition" [73]. I prefer to use the phrase "social context of learning" when referring to behavior of wolf-like canids, due to some of the paradoxes apparent in comparisons across taxonomic groups [74]. For free-ranging wolves, much of the initial learning about the physical environment takes place in a social context [15, 16]. Obviously, orphaned wolf pups do not survive; learning in a social context starts at birth and shapes the initial interactions of pups with their physical environment.

I agree with the viewpoint that non-human "animals make excellent ethologists but poor psychologists" [28]. The practical difficulty of separating social and physical aspects of the environment reinforces the recommendation by Holekamp (2007) to consider "social" and "physical" factors to be interactive as well as independent effects (Figure 1). To achieve this goal, the emerging broader theoretical framework for examining social intelligence will need to include aspects of life history traits, such as body size, litter size, age at maturity and dispersal.

BEHAVIORAL RESILIENCE IN A DYNAMIC SOCIAL ENVIRONMENT

What would it take to examine implications of the "Large Body Hypothesis" for social intelligence in wolf-like canids? It would imply that there is something different about the selective pressures of growing up in the social environment of families where some offspring do not disperse until their second or third winter. About half of wolf pups do not survive their first winter [14], similar to feral dogs [75]. High juvenile mortality is also typical of coyotes, although actual measures of pup mortality vary among geographic locations, as well as within one site across years [76]. Young coyotes are more likely to disperse when they are successful at independently hunting small mammals [77].

Compared to coyotes, pre-reproductive wolves are more likely to remain longer with the natal group. Coyotes are more likely to mature in their first winter [78], and wolves in their second winter [15], with implications for both the size and age composition of natal groups.

However, about one-third of wolves disperse by the first winter, one-third by the second winter and relatively few adults remain with their natal pack through the third winter [5, 79, 80]. Large packs are likely to split where alternative sources of food are available and multiple females produce litters [14]. Occasionally, post-reproductive females remain associated with a reproductive daughter; older individuals are less successful hunters of large prey [81, 82].

The social environment of wolves is dynamic in the sense that it changes with predictable cycles (e.g. seasonal, prey abundance, wolf territory density) and unpredictable disturbances (e.g. disease outbreaks, severe winters, fire, competitors, prey distribution, imbalances in the age distribution) [4, 14, 83]. Each year, wolf packs expand with the birth of pups in late spring and contract with dispersal and mortality before the next litter. Each lifetime, individuals are “on an elastic tether” to their natal group, until they lose contact, find a mate or are accepted into a family with an opening in the breeding role [15]. Throughout each lifetime, individuals risk encounters with hostile neighbors, challenging their skills of avoiding detection, advertising their presence and escalating to potential lethal combat or escaping when encountered. They assess the willingness of potential mates to join up in producing a litter, of potential rivals to escalate in protecting a mate, of group members in sharing a carcass, regurgitating, or stealing. They decide whether to join others in hunting or to initiate a search for food; whether to keep the food they find, cache it or carry it to preferred companions. On top of all this, are the variations induced by (1) latitude [84] (2) ecosystem productivity [85] and (3) the impacts of human activities [80].

Is the social environment of wolves any more or less complex than the social environment of hyenas or primates? It is different. Puzzling over questions like this while writing this review, I decided that what we really mean by wolf social intelligence, has more to do with the concepts of “flexibility” and “resiliency” than the typical measures of social cognition (Table 1). Flexibility implies variation in response to new situations, resiliency implies "bouncing back" when threatened with a serious problem. Wolves are flexible in learning the specifics of interacting with particular individuals: same age siblings, older siblings, parents and occasionally a grandmother or stranger. They are resilient in coping with stressors that challenge stability of emotional and physiological systems. The stressors that are really challenging, at the cutting edge of natural selection, are usually a combination of social and physical factors.

With the concepts of flexibility and resilience in mind, I went back to the literature on social intelligence to see if I could find some simple way of organizing the diverse set of keyword concepts investigated for social carnivores. Subheadings from two major reviews could be matched up (Table 4), admittedly in a rather forced manner. I was struck with the differences in cognitive maps used by researchers who have studied social cognition in the dog-like canids [2] compared to those who have studied hyenas and primates [7, 21, 86].

Neither of these two cognitive maps was entirely satisfying to me from the perspective of how wolves make decisions in their social environment. I remain puzzled about how we are going to meet the challenges of understanding the complex relations between underlying genetic mechanisms and environmental factors, both social and physical (Figure 1).

Table 4. Comparison and description of categories used to describe social intelligence in mammalian carnivores

Dogs and wolves (Miklosi 2007)		Hyenas (Holekamp et al. 2007)	
Category	Description	Category	Description
(1) affiliative aspects of social relationships	Actor maintains proximity to an attachment figure	b) Recognition of kin	Actor directs affiliative behavior more often toward kin than non-kin
		f) partner choice and recognition of relationship value	Actor directs affiliative behavior toward high-ranking non-kin
		g) repair of damaged relationships	Reconciliation; actor directs friendly action toward opponent after aggressive conflict
(2) agonistic aspects of social relationships	Actor escalates or de-escalates conflict, in the context of a resource or threatening figure Classification (i.e. offensive, defensive) Ethological description of units Decreased aggression in dogs (vs. wolves) Organization of aggressive behavior (learning) Reaction to human agonistic signals	d) Rank acquisition and social memory	Actor learns to associate other cubs with counterattacks by their mothers; lifelong memory even after separation
		e) application of knowledge about social rank	Actor attacks lower, not higher rank individuals in the context of a carcass or mate
		i) recognition of third-party relationships	Alliances; actor waits to attack until joined by another of higher rank than the opponent
(3) communication in a mixed species group	Actor sends information (*unit*) received by another (*meaning*) in a context (*causal aspects*)	a) individual recognition	Whoop call; actor consistently emits an individual distinctive signal that varies between individuals

Table 4. (Continued)

Dogs and wolves (Miklosi 2007)		Hyenas (Holekamp et al. 2007)	
Description	Category	Description	
(6) social influence	Actor adjusts own behavior relative to another (i.e. speed up or slow down while running)	j) tactical deception, gaze following, and theory of mind	Subordinate inhibits direct action until dominants are not present; gain access to food by emitting alarm call
(7) cooperation	Actor pays attention to others while achieving a joint goal (i.e. solo success is not as likely)	c) imitation and coordination of behavior among multiple animals	Actor learns by social facilitation and observation, i.e. simple "rules of thumb" during group hunting
(8) social competence	Actor shows many ways of navigating the social network toward a goal (i.e. expedience)	h) Quotidian experience	Actor uses one behavior to solve multiple problems or solves one problem in multiple ways
(4) play	Actors mutually (1) indicate preferred projects and (2) respect indications of the other for changing projects	*Not specified (appears to include elements of c,h,f,j,k)*	
(5) social learning in dogs	Actor learns from the experience of another in a situation where the actor has no direct experience	k) cultural traditions	Behavioral innovations shared between generations

Bernd Heinrich's recent review of social intelligence in ravens provides a theoretical framework more satisfying to me, perhaps due to its familiar grounding in ethological perspectives and its extension of the social environment to include multiple species, including wolves [27]. He focuses our attention on how individuals interact with "new things" in their environments, including (1) pre-programmed actions effective in response to a narrow range of stimuli (instinct), (2) subsequent broadening of initial behaviors generalizing to changes in contingencies (trial and error learning), (3) indirect learning from others without direct experience (observational learning), and (4) unprogrammed exploration permitting response to shifting scenarios (innovation in problem-solving).

Heinrich also reassures us that there are no clear divisions among the cognitive processes that, as a whole, result in what we identify as flexible and resilient qualities of adaptive behavior: instinct, trial and error learning (associative and operant), culture, problem-solving, theory of mind (internal representations). Inspired by this approach, we can map out how the keyword concepts used in the investigation of social intelligence of carnivores (Table 4) map onto four basic components of intelligence: communication, learning, problem-solving and awareness (Figure 2).

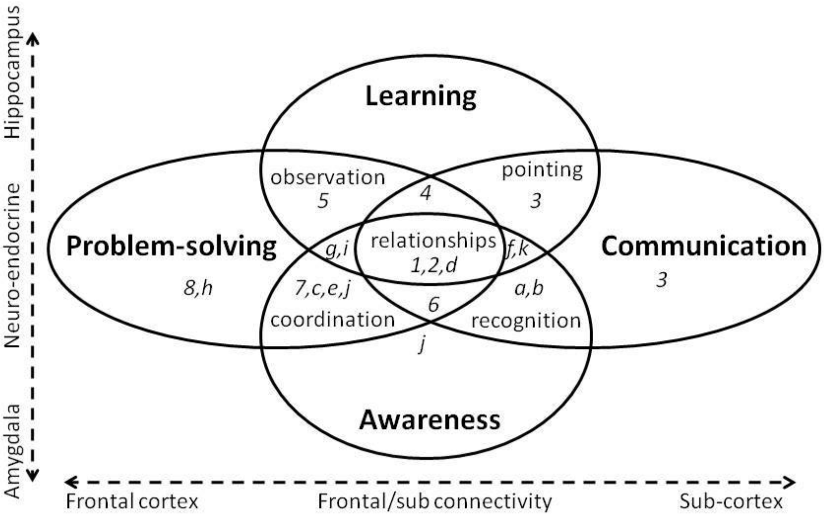

Figure 2. Conceptual map of social intelligence (see codes in Table 4) relative to two theoretical dimensions of brain complexity.

Most of the keyword concepts are in the fuzzy areas of overlap between two or more of the broader components. For example, investigation of canid responses to finger pointing (referential association) combines elements of both communication and learning. Coordinated hunting contains elements of both problem-solving and awareness of the actions of companions. The resulting map was satisfying to me because it also suggested approaches to understanding the underlying brain mechanisms. For example, the instinctive components of communication appear relatively more influenced by sub-cortical processes compared to the flexible qualities of problem-solving, which appear relatively more influenced by associative processes in the frontal cortex (horizontal axis in Figure 2).

Learning (reward contingencies) is dependent relatively more on processes underlying emotion (affect) in the hippocampus, compared to processes affecting alertness (amygdala) that is essential for awareness (vertical axis in Figure 2). The cognitive map illustrated in Figure 2 provides a basic framework for the topics covered below: communication, learning, problem-solving and awareness. These topics are not mutually exclusive, indeed some of the most fascinating aspects of social relationships lie at the intersection of all four.

COMMUNICATION

Wolf communication includes both elements of pre-programmed signals conveying information between strangers, and subtle signs learned during interactions with companions [17]. Experimental approaches to testing predictions about dog/human communication have been summarized elsewhere [64]. First, I will start with recent studies of the signals used in individual and kin recognition, evaluating the degree to which information is integrated across multiple senses (sound, sight, smell). Second, evidence for recognition of the value of relationships and cultural traditions will be evaluated. Finally, the evidence for communication through pointing and gaze will illustrate that there is no clear line between learning and communication, both overlap in social intelligence.

Individual and Kin Recognition. Information about individual identity is carried in howling and scent marking behavior of wolves. Howling provides information about immediate presence without revealing location. Direct scent marking and indirect traces of a scent trail provide information about location, potentially lasting weeks depending on humidity, temperature and wind. Recipients use this information in decisions about whether to join or avoid another wolf, whether to greet or escalate conflict, and whether to remain or leave a location. Distinctive vocalizations conveying information about individual identity has also been documented in hyena [87] and dogs [88]. The howls of gray wolves recorded in Iberia and North America are remarkably similar, varying primarily in modulation of pitch (discontinuities in frequency) [89]. Individuals could be identified by the pitch (fundamental frequency) and patterns of changing pitch (coefficient of fundamental modulation), with 85% accuracy. This illustrates both the pre-programmed consistency ("I am a wolf") and the broadening of distinctive variation during maturation of individuals ("I am me").

In Polish populations, 98% of spontaneous howls were in the context of communication within a family group [90]. Spontaneous howls occurred in core rather than peripheral areas of territories, associated with several scenarios: (1) solo howls by individuals temporarily separated from the family group (43%), (2) chorus howls before group hunting (22%) and (3) chorus howls after separated individuals rejoined the group (18%). Spontaneous howls and response to simulated howls peaked in August when pups would have been travelling with adults and likely to become separated. Duration of responsive chorus howls increased with group size (including pups). Overall, response to playback was infrequent (15%; 24 response-days within 163 days of effort). Howling responses to "strangers" have been tested using playback techniques. Howling in response to playback also was infrequent (13%) in the Italian Apennine mountains [91]. Similar to the Polish wolves, Italian wolves were more likely to respond to playbacks during the period when litters had abandoned the den and moved between rendezvous sites in the late summer or early fall. This pattern is consistent with the idea that wolves are more likely to howl when they have a resource to defend, such as pups or a carcass [17]. Since familiar wolves within a family are closely-related, differential response to strangers implies kin recognition. However, the kin-recognition hypothesis remains difficult to test for wolves due to the low howling response-rate to playbacks.

Wolves direct scent marks to visually distinctive upright objects as well as distinctive odors such as the urine of their mates [17]. In the Polish population, wolves travelling singly or in pairs were more likely to mark than those travelling in a family group [92]. Rates of urine-marking and ground-scratching (1) peaked during the winter mating season and (2) differed between peripheral and core areas of the territory. Ground-scratching is a visual display in which wolves kick backwards with the hind legs, disturbing soil and vegetation.

Reproductive pairs tend to deposit urine on each other's scent marks, a behavior referred to as "double marking" in wolves [93] and "countermarking" in dogs [94]. Double marking and testosterone peaks during the winter breeding season in male wolves [11], but not in dogs [95]. Both males and females initiated double marking sequences in the Ellesmere Pack during the summer pup-rearing season, and ground-scratching was more likely at the end than the beginning of double-marking sequences [96]. Incidence of urine-marking and ground-scratching was higher in the context of unfamiliar wolves that were not part of the familiar family group [93].

Behavioral experiments with dogs have documented effects of familiarity, reproductive condition and individual boldness associated with variation in urine-marking [94, 97]. Only males overmarked urine presented experimentally, and bold individuals (high tail-base posture) preferentially directed marks to intact female urine, independent of familiarity [94]. In response to mixed urine (male and female), bolder males and females (high tail-base posture) were equally likely to investigate and countermark. Intact males and females were equally interested in sniffing urine from unfamiliar intact males and females [97]. In contrast, neutered males preferentially investigated urine of intact males more than females and this response was more pronounced in timid males (low tail-base posture). These studies with dogs may suggest experimental procedures for testing individual and kin recognition in free-ranging wolves.

Information about individual identity and reproductive condition is also communicated when wolves investigate feces deposited at visually conspicuous locations [98]. Iberian wolves were more likely to deposit scat at crossroads (60%) and on conspicuous substrates (72%), suggesting local enhancement of an odor signal by visual cues [98, 99]. Choice of conspicuous locations to deposit feces was more likely outside the den area [100]. Conspicuous marks were high in metabolites of both sex hormones (testosterone, estrogen and progesterone) and adrenal hormones (glucocorticoids), implying that conspicuous marks were deposited by breeding wolves exposed to an environmental stressor [101]. In Yellowstone, breeding wolves also showed higher fecal glucocorticoids [102], validating similar observations that non-breeding wolves in captive groups were not physiologically suppressed due to a social stressor [11].

Therefore, the preceding evidence of howling and scent marking suggests information from several sensory modalities (sound, scent and sight) is integrated in the responses of wolves outside the core areas of their territory, where they are more likely to encounter hostile neighbors. Likewise, both sight and sound cues are used by dogs in recognizing familiar companions [103, 104]. Furthermore, within each modality, information from complex combinations of cues may be integrated. For example, during wolf social interactions, ambivalence may be expressed by apparently "contradictory" positions of the eyes, ears, nose, tail and torso [105]. The social communication system of wolves includes a complex combination of sensory modalities, potentially conveying subtle information about individual and kin recognition. Cross-fertilization of ideas about mechanisms (as tested in dogs) and function (as tested in wolves) promises productive future investigation of individual and kin recognition in wolves.

Recognition of Relationship Value. Although there are multiple dimensions to what might be considered the value of a relationship in social carnivores [86], this topic is only beginning to be investigated for wolves. Potential examples include: (1) affilliative actions (greeting and play) directed more to higher than lower ranking individuals, (2) acceptance of an immigrant from a neighboring group, and (3) leadership during travelling.

Theoretically, individuals should prefer to associate with those individuals (non-kin) that can reciprocate the benefits of positive interactions, often interpreted as individuals with higher social status. Affiliation and play were more likely directed to high status wolves in the captive Sawtooth Pack [106]. However, this pack was formed by placing together hand-raised wolves from three litters into a large enclosure (2 females and 5 males). A group of similar composition would be unlikely to form or to persist under free ranging conditions. In the Pistoia Zoo, play was not influenced by relationship quality, measured in terms of agonistic support or close proximity [107]. Usually the only un-related wolves in a group are the older breeding pair; although they are likely to show close proximity and to receive affilliative behavior from their offspring, they are less likely to engage in the social play typical of pre-reproductive individuals within the family group.

In intact nuclear families, the breeding pair is hostile to both males and females from neighboring groups [15]. However, if one member of the breeding pair disappears as in a hunted population, immigration of non-related wolves is more likely [108]. For example, the process by which a male wolf was accepted into an adjacent pack has been documented in Yellowstone [109]. Both stereotyped threat behaviors and flexible social play were involved in the process. Immigration of an outsider in the context of a loss of a breeder could be interpreted as a change in the value of a relationship. From the perspective of the widowed female, the relationship with the young male was of low value as long as the breeding male was present, but increased in value once the group was without a breeding male.

The tendency to be a leader or a follower could be interpreted as an indication of social value, if we assume that leaders are more likely to go to successful hunting locations. Breeders in Yellowstone were the leaders in 64% of travelling bouts [110]. Usually breeders are wolves older, and more experienced, than the non-breeders in the group. Non-breeders initiated only 25% of the changes in group travel. However, prior to dispersal from the natal pack, subordinate breeding females were more likely to attract followers. Patterns of attendance at carcasses varied seasonally among Yellowstone wolves, suggesting that relationship value may shift with variation in the physical environment [3].

The act of following an older experienced wolf also contains implications for transmitting information across generations, one criteria for behavioral traditions considered to be a precursor to culture in non-human animals. In wolves, the locations of dens and rendezvous sites may persist for many generations. For example, evidence from a carbon-dated bone suggested the den used by the Ellesmere Pack had been used by wolves for hundreds of years [8]. Consistency of den-site characteristics across diverse environments suggests some element of pre-programming influences choice of den-sites; variation suggests flexibility in response to specific cues and risks associated with each site [111, 112]. Both direct trial and error learning and observational learning may be involved.

Social influences on choice of prey may develop when younger wolves follow experienced older family members [15]. For example, wolves translocated to Yellowstone from an area where they primarily hunted elk, subsequently hunted elk for two years even though bison were present [113]. However, the Yellowstone wolves learned to kill bison when availability of elk declined [113], and wolves in northeastern Minnesota switched from deer to moose when deer were locally extirpated [114]. Evidence for prey-switching as a form of behavioral tradition is still ambiguous for wolves, due to the difficulty of separating the effects of the social environment in which individuals learn to hunt and the physical environment where availability of prey changes within a decade (a wolf lifetime). Answers to questions about traditions may emerge with increased understanding of the interaction of learning and communication, such as gestures that draw the attention of inexperienced individuals to the contingencies of the actions of experienced individuals.

Pointing Gestures (Referential Communication). Whether dogs are smarter than wolves, in using information provided by their social companions, has been debated in the literature on pointing gestures (referential social influence) [115]. Variation in canine response to cues from a human companion is associated with both genetic variation [116] and variation in the social environment [117]. Based on these standardized tests, performance of dingos appears to be intermediate between wolves and dogs [118]. However, the variation among dog breeds is not associated with presumed genetic distance from wolves [119].

Although wolves cannot point with a finger, they do point with their noses and eyes. The action of regurgitation results in pointing the nose to meat on the ground (food reward), and wolf pups orient spontaneously to noses during the “lick-up” behavior variously interpreted as “food begging” or “active submission” [9, 15]. The nose may serve as a target cue in other contexts as well. For example, when NI poked her nose in a bumblebee nest and subsequently ate the grubs, her pups oriented to the spot where her nose had pointed (Fieldnotes, 29 July 1988; page 2.10). Pointing with the eyes (gaze) is associated with nose-pointing, and if individuals that monitor gaze are subsequently rewarded, the social cue of gaze predicts where to search for physical cues associated with food [120]. Gaze following “into distant space” developed in socialized wolves by 3 to 4 months and gaze following “around a physical barrier” developed by 6 months [120].

Debate about technical procedures for studying social influences on learning by canids, has revealed important complexities associated with investigating the concept of social influence [121-124]. Emerging from this debate are several ideas that need to be included in future studies of social influence in wolves. First, both emotional (affective) and thinking (cognitive) processes need to be considered, since the initial socialization of individuals appears central to how well subjects will learn to “be aware of” and to “be rewarded by” paying attention to the gestures of their companions. Second, the learning processes include both the basics of learning “which set of cues” predicts reward (associative learning) and “how specific actions” will result in the reward (instrumental learning). Third, in the social environment of wolves, it is very difficult to separate out learning that occurs by watching the actions of companions (observational learning). Although some dogs can learn “imitation-like” behaviors [125-127], and the contagious effects of yawning come close to imitation [128], contextual imitation has not yet been documented in canids [129-131].

LEARNING

Basic mechanisms of learning remain consistent, whether the cues are social or non-social [115]. This subsection focuses more on how social interactions indirectly expose individuals to direct trial and error learning about their physical environment. First, I will examine the evidence that social play has a function of “learning to learn” through repetition of action sequences with variable outcomes (contingent on diverse responses of play partners). Second, I will address the more controversial question about whether wolves learn from each other in situations where they do not directly experience the outcomes of an action (observation). Social play is relatively closer to communication; social learning by observation is closer to problem solving (Figure 2).

Social Play as “Learning to Learn”. Although social play in canids may have multiple functions [2, 107], I choose to focus here more on the developmental mechanisms [132]. My reasoning is related to better understanding how linkages between the frontal cortex and sub-cortex might be strengthened (referring to Figures 1 and 2). Theoretically, behavioral flexibility would have been enhanced in brains that integrate elements of instinctive and learned behaviors in novel situations [27].

The logic is that pre-programmed decision rules and actions (motor coordination) bring each individual into contact with specific stimuli in its environment. This permits each individual to learn specific results of its actions (contingencies) based on direct personal experience (trial and error). This perspective was popularized by Konrad Lorenz as the “innate school marm”.

Miklosi (2007:191) reminds us of a promising model of play as a set of (1) behavioral routines (projects) and (2) switching points between routines [133], which I will refer to as the “Changing Scenarios Hypothesis”. Social play in wolves starts at 2-4 weeks of age, with a limited set of actions such as pawing, mouthing, riding, rolling, and standing-over. Although these basic components initially appear randomly, the associations between movements become more coordinated (structured) with age and experience of each individual [134]. Subsequently, the sequence of interactions between individuals becomes more predictable from 4 to 7 weeks, when pups are better able to learn the contingencies of their specific actions [135]. After 7 weeks, pups were less attentive to the specific actions of the play partner and behaved as if they had formed expectations, suggesting they had gained "control over expressive displays" [135].

According to the "Changing Scenarios Hypothesis", simple actions become organized into action routines through repetition. Although the play bouts of Ellesmere pups were too rapid and distant to record, I watched individuals learn the contingencies of their own actions. They switched roles in games such as "chase and be chased", "straddle and roll", "climb-up and push-down", "mouth and be mouthed". Through direct experience, pups learned what enticed partners to continue rewarding interactions and what caused partners to cut-off interaction. They learned to respond to novel situations. One anecdote comes to mind to illustrate my point about novelty. It was the first time the pups explored a melting snow patch, while interacting with their yearling uncle, Grayback (GB).

> "0534-0553 – GB plays with pups. [The pups] are both scared and excited by his pounces. When he mouths them, his whole mouth encloses a whole head or midsection of a pup. They roll over with paws up when he pounces, then run around crazy with belly low when he starts to lose interest, inviting him to pounce again. First signs of ears down on pups during interaction with GB. Pups add the pounce routine to their play. One pup went exploring on its own. Two follow. They climb on [a]snow patch, stabbing little noses into the snow, [sliding with] awkward footing. One tumbles down the slope when GB pounces on it. Finally a pup snaps at GB's nose when he comes over. Two pups rush over to [the yearling female, Whitey] WH as if they have had enough of GB. He leaves." (fieldnotes, 3 July 1988, page 48)

According to the "Changing Scenarios Hypothesis" the preceding anecdote illustrates how elements of instinct (pre-programmed actions) and learning (operant conditioning) are integrated in novel situations. For example, the "pounce" action in this scenario is pre-programmed, appearing with little practice in the asocial canids (foxes) and semi-social (coyotes and jackals) in the context of hunting small rodents. I even observed it once in a Weimeraner pup in response to rustling sounds in a clump of plants. However, in the case of the Weimeraner, this recognizable fixed-action pattern was not rewarded with a mouthful of mouse and was not repeated. In the case of the Ellesmere pups, the pounce was repeated by both the yearling and the pups. The context and consequences varied slightly each time. Several reactions were effective "cut-off" gestures: "roll over with paws up" and "snap at nose". The pups' action of "run around crazy" enticed GB to repeat the pounce routine. On the slick surface of the snow, pounces by GB resulted in pups sliding and tumbling in a different manner than they had experienced on the soft surface of the tundra.

The point I wish to reinforce here is that learning about the environment happens in a social context for wolf pups. During social play, they also learn about maneuvering on different surfaces, about the advantages of a higher position, and the mechanics of rising from being knocked down. In the context of chase play, they learn to "cut-the-corner" to catch a play partner, a routine that they later may repeat when chasing prey [15]. They learn there are several consequences to the same action, and diverse actions may lead to the same consequence. They learn to learn. However, we still do not have a definitive test of the "Changing Scenarios Hypothesis" of social play in wolves.

Social Learning by "Observation". Among the many nuances associated with the concept of social learning, demonstration has emerged as one aspect that lends itself well to experimental tests in canids [72]. For example, after "demonstration training" dogs were more likely to interact with a novel object [136]. Dogs solved a puzzle-box problem more readily after passively watching a demonstrator (dog or human) push a lever that opened a lid on top of the box [137]. In contrast to social play, the concept of observational learning specifies that the individual does not learn by its own direct trial and error experience, rather by watching the consequences of another's actions.

Since wolves do not respond well in the context of an experimental apparatus, we do not yet have a test of the "Observational Learning Hypothesis" for wolves. However, several anecdotes lend plausibility to the hypothesis in the context of hunting by free-ranging wolves. The general sequence of behavioral routines associated with wolf hunting includes: search, approach, watch, attack-group, attack-individual, and capture [138]. Opportunities for social learning from the contingencies of others' behavior may occur at each stage, as apparent from the following observations of the Ellesmere Pack [18].

Mech described one occasion when the Ellesmere wolves encountered a novel stimulus, his tent. In this case the observers did not mimic the action of the demonstrator, but they joined him in manipulating a strange object.

> "For a few seconds the whole group waited with much suspense when the animal's head disappeared into the tent. Then, after a moment of great anticipation, the back of the wolf's head showed up again tugging and yanking, while his associates watched intently. Suddenly my red sleeping bag appeared, and the pack grew excited. They were eviscerating our tent, just the way they pull the guts out of a musk ox!" (Mech 1997:60).

On another occasion, the actions of a demonstrator were effective in initiating approach to a group of muskoxen (*Ovibos moschatus*). After this interaction, the wolves approached and stalked but were not successful at capturing the muskoxen.

> "1628 hours – Male subordinate Wolf A, while on a ridge just east of the den, stared intently toward the muskoxen for one to two minutes. He then headed to another subadult wolf (Wolf B) of unknown identity, which was lying about 20 m away below the ridge chewing on an object, and "nosed" that wolf…Wolf B immediately abandoned the object, went to where Wolf A had stared toward the muskoxen, and also stared toward them. It appeared that Wolf A had communicated with Wolf B, motivating Wolf B to look toward the muskoxen." (Mech 2006:147)

While hunting arctic hares (*Lepus arcticus*), several times the inexperienced wolves chased the prey while the experienced parents watched. When the skilled hunters caught and killed the hares, the chasers watched, then were rewarded with a meal. I would not claim the parents were intentionally teaching their offspring, but certainly the youngsters had the opportunity to learn from the consequences of the parents' actions.

> "The pack would settle for a few hours in a hare-filled area and some of the wolves would run the bunnies back and forth in front of other pack members. Usually the adult wolves, especially the alpha male, would lie near the end of a raised ridge and wait while the younger wolves chased half-grown hares by them. The adults would then pounce and intercept the hares. A quick shake and a hare was history; the adult would then drop it to one of its offspring, usually the one that chased it." (Mech 1997:127).

A group of muskoxen in a defensive circle are much more formidable prey than hares. Mech's description of seven wolves hunting fourteen muskoxen is well worth reading in its entirety, but here are some choice excerpts.

> "As the casual confrontation continued, however, wolves prowling around behind the herd seemed to unnerve the musk oxen. Gradually the situation changed into one in which the oxen were more scattered and the wolves walked about between subgroups. Every now and then a skirmish developed when an ox charged a wolf, even though other wolves and musk oxen just stood around nearby…It's hard to say how long the skirmishing went on…it probably lasted an hour or more, and the pace kept increasing…The herd panicked….Thirty seconds later, Alpha Male and Mom closed in on a calf, and Mom grabbed it by the right side of its head. Alpha Male latched onto its nose. The rest of the pack quickly gravitated to the pair and their quarry, while the calf's mother joined the stampeding herd. As the calf struggled, it gradually dragged the six wolves stuck to its head and shoulders down a slope. Then suddenly, Left Shoulder who had the posterior grasp on the calf's right side, let up and rushed off after the herd…Mid-Back, who had the last hold on the calf's other side, soon left to join him. They hit the second calf crossing the creek." (Mech 1997:89).

I found the preceding account of wolves capturing muskoxen to be of great interest because it illustrates the possibility that young wolves learn the consequences of their own actions in the context of actions taken by others. The first two wolves to grab a calf were the experienced breeders. Their offspring joined them in holding the struggling calf. The second calf was grabbed by two offspring. I would not claim this illustrates the concept of imitation, because the two offspring had plenty of previous direct experience grabbing each other and other prey. However, it is plausible that the offspring learned to focus on calves separated from the adult herd, rather than skirmishing with defensive adults.

In the broader context of social intelligence, both social play and social learning contribute to behavioral flexibility of individuals. For wolves, flexibility is more a matter of branching, generalizing from actions in one context, to actions in another context. What worked in a social context might work in a prey-catching context; how to catch your sibling generalizes to how to catch a calf. From the individual perspective, whether you are born into a habitat with moose, deer, beaver, mice, caribou, elk, red deer, roe deer, swine, the specifics do not matter; however, those who would have been able to generalize would have been more flexible at invading a variety of habitats.

PROBLEM-SOLVING

The essence of problem-solving is the invention of spontaneous new behaviors in the context of a novel situation [27]. When the situation involves potentially losing access to contested resources, such as food, mates, or safety, then behavioral flexibility attains a quality of resilience in the face of adversity. In this section, I will first address coordinated hunting behavior, a social solution to the problem of overcoming defenses of formidable prey, like the musk oxen. Second, I will examine questions associated with social competence, meaning that individuals show many ways of navigating a social network in the process of attaining contested resources. Finally, the concepts of reconciliation and consolation will illustrate the overlap between problem-solving and awareness, as illustrated in Figure 2.

Coordinated Hunting Behavior. From the preceding accounts of hunting by the Ellesmere Pack, the actions of each individual wolf appear more haphazard than coordinated by a general plan. However, in the context of social intelligence, behavior is considered coordinated if the actions of multiple individuals achieve a goal otherwise not possible for a solo individual. Group hunting may be considered coordinated even if each individual follows certain simple "rules of thumb" augmented by social facilitation and observation.

One major challenge here is to determine which prey a solo wolf can and cannot successfully capture. The answer often depends on circumstances. Experienced solo wolves can kill large prey that are young, injured or in poor health (pg 121)[139]. However, mortality of loners generally is greater than that of group-living wolves, at least in saturated populations [15]. Anti-predator defenses of large ungulates are very effective [19, 83]. Young wolves and senescent wolves are less successful at capturing healthy elk in Yellowstone [82, 140].

Although many wolf biologists may believe wolves hunt cooperatively, little evidence is available to document the claim [19]. After carefully evaluating 19 hunts that he observed on Ellesmere, Mech decided only two met the criteria of showing higher order thinking (mental processing of information).

> "All seven wolves headed north, jumped two hares but did not chase them (which was unusual), and continued on to the northeast where a herd of seven adult muskoxen and three calves was located upwind…We saw two wolves about 200 m from the muskoxen heading toward them up a shallow valley, slowly stalking. At least four other wolves were watching intently from a ridge of rock piles approximately 400 m from the muskoxen. Suddenly the muskoxen ran to each other, two to three muskoxen that were lying down arose, and all grouped up. Then all the wolves, both waiters and stalkers, rushed to the herd, their movement apparently triggered by the running of the muskoxen. The wolves milled around the herd for about one minute, then left and continued north." (Mech 2007:146)

In my opinion, even the preceding anecdote is ambiguous; although the wolves separated into two groups (waiters and stalkers) it is not clear that they were responding to their partners actions more than the actions of the prey. In this case, the wolves did not successfully penetrate the defensive formation of the muskoxen.

Clearly wolves hunt in groups, and in the confusion of a group hunt one or more of them is likely to seize an opportunity not likely to arise if hunting alone. Once one wolf has grabbed a calf, others also grab it. However, the youngsters also appear equally likely to be distracted before a calf is captured, as in the following anecdote.

> "In this case, the musk oxen detected the wolves when they were about one hundred yards (90m) away. However, they remained nonchalant about it. The wolves lay down, while the oxen grazed twenty-five to fifty feet (7.5-15m) apart. Perhaps these particular animals had confronted the others before, for neither group seemed that interested in the other….some of the wolves seemed to go to sleep and it looked like they were just going to keep the group on edge until someone got tired of the whole situation and decided to move. In this case, the strategy worked to the musk oxen's advantage. One of the wolves soon spied a hare on the horizon and headed after it. A couple of others followed… when their hare hunt was unsuccessful, one of the other wolves drifted off while the other remained sleeping around the musk oxen. About twenty minutes later, she too gave up, and the musk oxen eventually resumed grazing." (Mech 1997:105)

The apparent coordination of wolves in hunting groups could be a matter of simple decision rules such as "if it is far away and inattentive, stalk it", "if there is cover, ambush it", "if it behaves differently, focus on it", "if it is not running, wait", "if it runs, chase it", "if it is close, grab it", "if it struggles, hold on". To the extent that all individuals apply the same rules to the same stimulus, their actions will appear coordinated. These decision rules are very similar to the decision rules involved in social play. To convince me that individuals are responding to each other in coordinated hunting, I would need to see evidence that a simple decision rule was "broken", meaning that a wolf inhibited an action that I would have expected given the circumstances. As described below, we do see evidence of inhibited action based on previous experience, as wolves negotiate their social network in solving problems related sharing food and mates.

Social Competence. Much has been written about the social inhibition of sexual behavior in captive wolf packs [15], and the apparent lack of inhibition of male dogs pursuing a female in estrus. However, in Indian village dogs, only 41% of males copulated and there was a negative correlation between the size of the courting group and the number of copulations [141]. Here, I will emphasize that waiting is a learned behavior that may appear at an early age in wolf pups, subsequently generalizing to interactions between rivals over mates.

Waiting is a form of inhibited response that wolves show in several social contexts. In this sense it fits the category of "Quotidian experience", meaning that an individual uses one behavior to solve multiple problems. To meet the criteria of solving a problem, there needs to be some evidence that the behavior is "expedient", that it is part of a goal-directed series of actions. The interactions of pups feeding on a hare carcass illustrate this point (Figure 3).

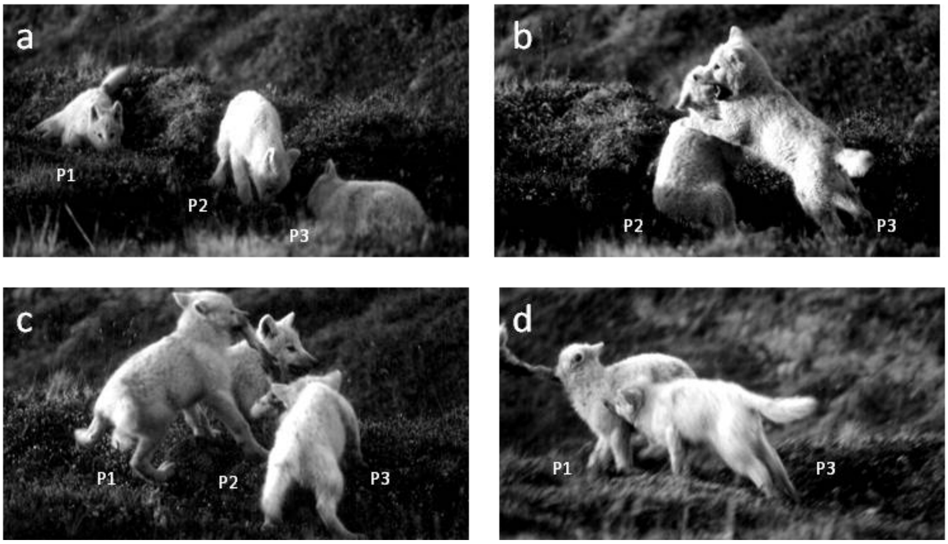

Figure 3. Sequence of interactions among wolf pups illustrate the social context in which pups learn the consequences of their actions.

One pup (P1) laid to the side and waited while two siblings (P2, P3) chewed on opposite ends of the carcass. When a squabble broke out between P2 and P3, P1 dashed in, grabbed the carcass and successfully stole it. The problem for P1 was gaining access to the carcass. By waiting, the situation changed and P1 was in a position to achieve the goal of obtaining a piece. This interaction illustrates one of many similar tactics observed in the developmental stage of weaning (10-11 weeks).

> "Pups were capable of persistence and elaborate countertactics at the developmental stage during which weaning occurred. Such maneuvers occurred in the contexts of playing with sibs and adults, begging for regurgitation, and sharing carcasses. In the context of playing, begging and sharing, pups did not leave when another wolf muzzled, snapped, or lunged. In contrast, the muzzling by the nurser in the context of suckling terminated the pups' attempts to gain access to nipples. The nurser seemed to use subtle tactics to divert the pups' attention when they attempted to suckle. For example, she regurgitated or trotted over to a carcass and manipulated it in a way that attracted their interest. Her tactics worked; the pups did not counter or attempt to resume suckling." (Packard, Mech and Ream 1992:1274)

Waiting and watching were also tactics shaping the interactions of pups with the yearling, Grayback (GB) in the Ellesmere Pack. In this case, the problem was related to stealing cached food. Grayback waited and watched until the pup was not paying attention. Although Grayback stole the cache, the pup was successful at retrieving it from him.

> "One pup carried legbones…across a heather patch, looking in one hollow after another between heather hummocks. It kept going, apparently randomly with a stilted walk until it reached a talus bank. It dug a hole in the loose sand, pushed the mouthful in, paused…The pup returned to sniff around where the carcass had been consumed.

> Meanwhile, GB had been lying in view of the pup's cache. He went up to the general area, sniffed around a bit, sniffed the air, went directly over to the carcass and pulled it out with one motion…As GB headed across the slope back to the stream, the pup that had made the cache rushed down to him and attempted to grab the legs out of GB's mouth. GB dodged, but the pup succeeded in getting the legs from GB. As the pup went down to the stream (presumably to cache again), GB merely stood and watched (he did not press the point – yielded ownership to the pup although he was much larger than the pup and certainly could have taken the meat)." (Fieldnotes, 29 July 1988, page 2.08)

Later in life, waiting and watching were also effective tactics for gaining access to attractive females. In the captive South Pack at Carlos Avery, a yearling male courted a yearling female in the woods while his father attended the estrus female. The father rushed over to the courting pair. Before he reached them, the son rolled over with his ears pulled back (see Figure 2 in Packard 2010). After the son lay motionless in response to a hard stare, the father returned to guard his mate. Later, the son mounted again when his father was not watching. Only the father's mate produced pups. In the North Pack, a younger son waited immobile while his sister courted him from one side and his older brother stared down at him over the other shoulder (see Figure 2.9 in Packard 2003). The younger brother copulated late at night when his older brother was not watching, and pups were produced. This was in the context of a disrupted family, where the father had died after fights with the older brother. These anecdotes are only two of many that could be interpreted as illustrating that a simple rule such as "wait until the situation changes" may be used in several contexts where wolves act as if they have a goal in mind, yet are inhibited by current social circumstances and previous experience.

Reconciliation and Consolation. Inhibition of a behavior has been interpreted as indicating that an individual has learned to expect certain consequences after an action. It implies that an emotional impulsive action is suppressed, presumably due to the inhibitory influence of the frontal cortex. Reconciliation, consolation and appeasement (awareness of third-party relationships) are examples of ways that individuals respond to social tension while gaining access to resources.

Reconciliation has been documented in the wolf pack at the Pistoia Zoo [142]. Conciliatory actions were measured by watching the victim of each aggressive action for ten minutes after the event. The number of friendly (affinitive) actions were counted and compared to a control period for the same animal at the same time the next day. Friendly actions included: body contact, inspecting, play, social lick and social sniff. The wolves were observed for 6 hours a day including feeding, when meat was scattered across a floor. The group was a disrupted family (5 males, 4 females), consisting of the father (age 20), and siblings from four litters (ages 4, 7, 9, 11). Reconciliation was most likely during the first minute after the conflict. Although the wolves showed a linear dominance hierarchy, it was not correlated with the probability of reconciliation. This study illustrates how resilient wolves can be when kept under conditions quite different from free ranging groups.

When a third individual shows unsolicited friendly behavior to a victim after a conflict, this is interpreted as consolation [143]. Any sign of empathy is of great interest to those who believe it is a unique characteristic of humans. Consolation was recorded when the third party approached the victim prior to reconciliation. Theoretically, consolation is risky because the victim may redirect aggression to the third party. In the Pistoia Pack, victims did redirect aggression toward consolers. Redirected aggression was negatively correlated with consolation. Individuals with close relationships were more likely to engage in consolation. When reconciliation did not occur, consolation was more likely.

Both reconciliation and consolation imply that individuals have learned to expect consequences of their actions within the social environment. Documentation of these behaviors in one captive pack of wolves, provides a basis for future comparisons of social cognition in other social carnivores and primates. I am uncertain how this paradigm could be applied to field studies of free ranging wolves; however, it does open a window to speculation about the interaction of emotional mental states and cognitive processing of social information.

AWARENESS

The concept of awareness includes many nuances, yet it gets at an essence of intelligence that is not captured in the concept of flexible problem solving. Pre-programmed decision rules of a robot may solve problems, but awareness implies an individual reflects on some level about his own actions and projects those expectations onto another individual. Self-awareness includes nuances of self-recognition, self-cognizance, self-knowledge, self-referencing, and self-consciousness, thought to be an important aspect of recognizing other's emotional states [144, 145]. If an individual inhibits her own actions in a context where negative consequences of action would be expected, that comes pretty close to what is described in the popular press as "emotional intelligence" in humans. As with humans, we might expect individuals to fade in and out of states of awareness, and some individuals to be in a state of awareness more often than others. Whether species vary in awareness is a topic of ongoing debate.

Bekoff has encouraged us to open our minds to what might be considered empathy and self-awareness in wolves [144]. Humans readily attribute mental or emotional states to canids, and the tendency to describe dog behavior in terms of feelings varies with experience of the observer [146]. Bekoff argues persuasively that the emotions we see in canids are not only a reflection of our own minds, rather self-cognizance is on a theoretical continuum between conscious involvement and social complexity [145]. The sense of "I-ness" is not quite the same as what we interpret as a sense of "body-ness" or "mine-ness" [147]. For example, one dog sniffed the urine of other dogs longer than his own, potentially indicating he detected a difference between "my urine" and "other urine" [148].

Researchers also use the term "awareness" in a context related more to the physical than social environment. For example, caribou in areas without wolves respond as if they are not as aware of the odors of potential predators [149]. Vigilance in Yellowstone elk varies not only with characteristics of the packs of wolves that hunt them, but also the structure of the elk herd and environmental conditions [150]. Although elk tended to be more vigilant during the times of day that wolves hunt, their location was not as predictive as a “risk allocation model” based on more specific brief pulses of risk associated with wolves [151].

In the absence of definitive literature on awareness of wolves, I will offer one last anecdote that seemed relevant from observations of the Ellesmere Pack. If researchers are to look for elements of awareness and empathy in wolves, I would encourage them to examine the interactions between pups and their care-givers. This event occurred in the context of travel from the rendezvous site to the natal den, by Nipples (NI), the breeding male (GN), the yearling female (WH) and the yearling male (GB).

> “0825 – NI started across the slope and the movement of the other 3 adults compelled the pups to follow, walking amongst them. However, a couple pups balked at climbing a small drop and started to wander back the way they came. First, one adult then another turned back to watch the pups and the flow was broken. NI continued without looking back, on a line to the natal den, but the pups trickled back to an open slope. GN laid down [on the ridge], WH and GB sniffed around and the pups disappeared from view. WH and GB headed after NI without looking back and GN joined them. A minute later, WH returned, sniffed the ground, stood near where GN had laid and howled. Puppy voices answer from a pile [of pups lying together,] that looked like a nearby rock. GB returned to WH and GN stood and howled. GB laid near the pups and WH trotted toward GN, followed by GB.
>
> 0831 – NI returns across the skyline with WH nose-touching eagerly (did WH get NI?). As WH and NI return to the pups, GB lies at the ridgeline watching the outcome. NI walks right past the pups who start to follow, pause, then follow as they are joined by the 3 adults.” (Fieldnotes, 1 July 1988, page 1.44)

In this episode from my experience, I see elements of communication, learning, problem-solving and awareness. Although the mother, Nipples, was unaware that the pups stopped following her, all the other adults were very aware and adjusted their travel to the change in behavior of the pups. The problem was that a couple pups could not climb up the steep slope. The other pups were aware of their difficulty, and rather than following the adults, returned to their siblings. Both adult males responded to the problem by lying and waiting, at different times in the sequence of events. The yearling female sniffed and howled in the process of relocating the pups. The pups responded, but they laid and waited until their mother returned. The howl by the breeding male was unanswered when the two yearlings returned to the pups. When Grayback laid near the pups, my impression was that the behavior of the pups was the deciding factor coordinating the travel of the adults. Was his action a gesture of empathy? I don’t know. Did Whitey show foresight in fetching Nipples to come back and care for the pups? Who knows. Somehow it all worked out, and that is the essence of wolf social intelligence.

ADAPTIVE SIGNIFICANCE OF BEHAVIORAL RESILIENCE

Wolves rarely encounter the exact same problem more than once. The flexibility and resilience that we see reflected in their behavior is thought to be an adaptation to a changing environment. My problem is that the social environment of pups is very different from that of non-breeding and breeding adults. Before we can answer questions about adaptive significance of wolf social intelligence, we need to sort out which hypotheses are relevant for each of the major stages in the lifetime trajectory of individual wolves. Then we need to think not only about individual reproductive success, but also how the fate of each individual is nested within kin groups, populations and ecosystems. Ultimately, we need to keep our sights focused on the time when we will have reliable genetic markers for functional traits, which we will strive to measure in free ranging wolves to test our hypotheses.

Variation with Stages of Lifetime Trajectory

To facilitate future comparison with other social carnivores, I used the set of life history traits listed in Table 3 as guidelines to identify key transition times in the lifetime trajectory of wolves. The exact age of each transition is likely to vary across populations and ecosystems, so these are general categories: dependent pups, pre-reproductive adults, reproductive adults and post-reproductive adults.

Dependent Pups. During their first 5-6 months of life, wolf pups are dependent on adults. Until they leave the den, all wolf pups experience a very similar physical environment, whether they are born into a desert, forest or tundra ecosystem. One hypothesis would be that natural selection due to the social environment peaks during this stage, because pups do not survive the challenges of their physical environment without social support. During this stage, the social environment of pups varies with litter size and the number of adults that provide care.

Initially, other members of the litter help regulate temperature stress by huddling. Cohesiveness of the litter is likely to influence survival during movements of the group, as well as escape from avian and terrestrial predators. As they develop, pups learn the consequences of their actions during interactions with both their siblings and adults. Later, such learned behavior patterns generalize to their first experiences catching prey.

Interaction of pups with the mother helps (1) moderate nutritional stress first by providing milk, then regurgitated meat and later pieces of carcasses; (2) regulate temperature stress by the mother lying with the pups, and later choosing sites that are sheltered; (3) reduce mortality risk (i.e. bears, hostile neighbors) by the pups' passive response when carried from the natal den to other locations, and subsequent active following response to interruption of nursing by their mother; (4) reduce infection and disease risks initially by pups holding elimination until stimulated by the mother's licking and subsequently eliminating outside the den when they are physically able to walk to the entrance. Interactions with the mother later generalize to interaction with adult family members.

Several hypotheses have been proposed regarding selective factors salient during the dependent stage of pups. First, pack size is predicted to be positively correlated with pup survival, due to the benefits of additional pup care by helpers. In Algonquin Provincial Park, there was no influence of litter size or pack size on either pup survival or dispersal [152]. Second, pup survival is predicted to be negatively correlated with disease antibody prevalence, such as canine parvovirus. In northeastern Minnesota, annual pup survival was reduced by 40-60% with the spread of parvovirus [153]. In Isle Royale National

Park, a peak in parvovirus occurred during a period of poor pup recruitment [83]. Third, loss of a parent is predicted to decrease the probability of pup survival. Pooling data across several populations, in 84% of the packs that lost a breeder, at least one pup survived independent of whether it was the mother or father that was removed [154]. Probability of pup survival was higher (92%) in groups with auxiliary non-breeders compared to groups without auxiliaries (64%).

Pre-Reproductive Adults. Until they reach physical maturity (2 years) the skulls of young wolves do not function as well in subduing struggling prey, compared to adults of peak body size (5-6 years). During this stage of delayed maturation, the interaction of physical and social factors would appear important especially in the dispersal characteristic of this age class. Physical factors include the range of small to large-bodied prey, as well as the vulnerability and abundance of prey. Social factors include both the interactions within the family and the density of territories in a region.

Several hypotheses about survival and dispersal of pre-reproductive adults have been tested. First, dispersal is predicted to be higher for wolves of 1-2 years than for older age classes. On the Central Brooks Range, dispersal was higher for yearlings (47%) than 2-yr-olds (27%), compared to the dispersal rate for the population as a whole (≥19%) [80]. Second, dispersal is predicted to be longer distance in low density wolf populations. In Scandinavia, where the recovering wolf populations are low-density, one female dispersed over 1,000 km from southeast Northway to northeast Finland [155], much further than records from North America [156]. Third, successful dispersal is predicted to be reduced in areas of high human impact. In the Polish Carpathian Mountains, radio tracking and genetic data did not support this hypothesis [157]. However, dispersal from Finland has been limited by distance, geographic barriers and human exploitation [79]. Fourth, relatively isolated populations are predicted to be more inbred than populations with a high degree of geographic connectivity. On the Scandinavian Peninsula, the slow recruitment rate in the highly isolated population is associated with inbreeding [79]. However, the wolf reintroduction to Yellowstone shows no evidence of inbreeding [158]. Inbreeding effects associated with small numbers of founders in three captive lineages of Mexican wolves, have been reversed by "genetic rescue" in the process of mixing lineages during reintroduction [159].

Reproductive Adults. At the life stage where wolves have paired with a mate, direct mortality appears to be a less important factor than pup production influencing lifetime reproductive success. However, this varies in historic times with human-related causes of mortality and probably in pre-historic times with the prevalence of competitors. It also varies with the degree of conflict between neighboring packs in high density wolf populations, particularly at times of declining prey.

Within the last decade, several hypotheses have been tested regarding the selective factors affecting reproductive adults. First, loss of adults from a hunted population is predicted to be more related to mortality than dispersal. On the Brooks Range, the annual loss of adult wolves (26%) was due to harvest by humans (12%) and natural causes (11%), primarily intraspecific strife [80]. In Southeast Alaska, 87% of mortality was due to legal and illegal harvest [160]. Second, tolerance of auxiliaries by breeders is associated with lower energy expenditure during the nursing period. In Poland, the breeding male in one pack was less active during the breeding season with a pack size of seven compared to a pack size of two [161]. Third, disturbance of the physical environment is associated with movement of pups between dens by adults. In the Deccan Plateau of India, a zone of high human impact, den-shifting was more influenced by age of the pups and water than disturbance [112]. Fourth, adult over-winter survival is related to nutrition. On Ellesmere, adult counts were more highly correlated with variation in hare abundance than muskoxen [20]. Fifth, nutritional stress results in smaller litter size. In northern Spain, decline in litter size was more associated with the local loss of ungulate prey than persecution by humans [162].

Post-Reproductive Adults. When adults are no longer reproductively active, their role in caring for previous offspring and their kin becomes more salient than survival, at least from the perspective of understanding processes of natural selection. Previously, we have had little information to test hypotheses about this “Grandparent Effect”. One hypothesis is that more experienced older wolves are more effective hunters. In the Yellowstone population, this hypothesis was not supported due to the evidence that older wolves are not as effective at taking down large prey [82].

EVOLUTIONARY PROCESSES

The simplistic notion that wolves are social due to the direct benefits of group hunting, has been seriously challenged by the evidence that food per wolf declines as group size increases [14, 139]. At the beginning of this chapter (see Figure 1), I suggested that there might be merit in considering the recommendation by Holekamp et al. (2007) that the theoretical framework for understanding evolution of social intelligence in carnivores be expanded to consider the interaction of social and non-social forms of environmental complexity. To achieve this goal, we would need to examine the more complex, and fascinating, intersection of evolutionary processes at nested levels of individuals, kin-groups, and dynamic isolation of populations. The key question becomes less a matter of whether evolution of a given trait better fits a model of direct individual selection, or indirect kinship selection, as illustrated by the theoretical framework for studying coalitions in hyenas [163].

The key theoretical issue is whether selection “pressure” was in the same direction at the nested levels of individuals, kin-groups, and populations. Directional selection for large body size would have been more rapid if it was consistent at all three levels than if there was counter-selection at one or more level. The “Large Body Hypothesis” suggests that social intelligence in wolves is more a by-product of a slowly maturing large body, rather than a driving factor in evolution of the wolf-like canids. Thus, it is an alternative to the “Dynamic Ratchet Hypothesis" regarding evolution of sociality in primates [164].

Individuals. From the perspective of individual wolves, the advantages of large skulls would include (1) better bone crunching skills when scavenging from carcasses during dispersal in the pre-reproductive life stage, (2) faster chase speed during the pre-reproductive stage, (3) better grabbing strength effective at capturing large ungulates during the period of peak body condition during the reproductive life stage, and (4) better bone crunching skills when scavenging later in life. The disadvantages of large body size would include (1) age at first reproduction delayed by 1-2 years and (2) higher nutritional demands.

Kin-Groups. Where wolves live in family groups, there is little opportunity to test hypotheses about the advantages of differential behavior directed toward kin and non-kin, resulting from inclusive fitness. The social environment of most wolves is quite different than spotted hyenas in clans as large as 90 individuals. In the northeastern Minnesota population, 90% of the packs fluctuated between a low of 2 and a high of 9 wolves over the lifetime of the pack [5]. However, we now have more evidence for the variations on the theme of monogamy in wolves. The Yellowstone reintroduction provided a glimpse into how rapidly group size expands with multiple reproductive females following replacement of a breeder. From the perspective of kin-groups, the advantages of large body size would include (1) more auxiliaries delivering food to breeders and pups, (2) a large group size advantage in conflict with neighboring groups, (3) a longer period of social learning during group hunting, and (4) a group size advantage in overcoming anti-predator defenses of large ungulates. Disadvantages of large body size would include (1) less per capita food intake in groups expanded by pre-reproductive adults remaining with the natal group, and (2) competition of older siblings with younger siblings. The implications include rapid expansion of kin-groups under favorable conditions and contraction during periods of ecological constraints.

Dynamic Isolation of Populations. In isolated populations, inbreeding is a potential disadvantage of pre-reproductive wolves remaining with the natal group. However, the perspective emerging from population level analysis is one of changing connectivity between populations. When the barriers to dispersal are more permeable, dispersers from source populations colonize regions of low wolf density. When conditions change and few dispersers survive, genetic structure of populations becomes more distinctive. In isolated populations where small prey is abundant, there would be no advantage to large body size. However, where small prey are absent, pre-reproductive dispersers would seem to be at a disadvantage compared to those that delayed age of first reproduction and remained in the natal group. Where family groups are decimated due to disease outbreaks or other extreme disturbances, delayed dispersal may have been an advantage under bottleneck conditions.

Interspecific Competition. In ecosystems with a more diverse guild of large carnivores, large body size would appear to be an advantage if large groups are better able to defend carcasses. In historic times, bears are the primary competitors of wolves, both indirectly in reducing numbers of caribou and moose calves available to wolves and directly in terms of chasing wolves off their carcasses. In pre-historic times, when the large bodied wolves diverged from the small bodied subspecies, hyenas and dire wolves would have been competitors as well as other large predatory species now extinct.

In summary, the research results published during the last decade will challenge us to rethink previous explanations of the adaptive significance of sociality in wolf-like canids. The prevailing previous model asserted that wolves are social due to the benefits of cooperative hunting and therefore need mechanisms such as a dominance hierarchy for reducing conflict within the pack. This simplistic model seems naïve given what we now know about the complexity and dynamic nature of both behavioral and ecological systems that have shaped the genome of wolves. Drawing from broader studies of the evolution of social intelligence, a modern synthesis is likely to emerge in the future that will better address the flexible and resilient nature of wolf behavior within the backdrop of environmental fluctuation.

IMPLICATIONS FOR ADAPTIVE MANAGEMENT

Flexibility and resilience may have far reaching implications for designing effective conservation strategies based on a biological understanding of behavioral mechanisms in wolves. Three topics of active research in the previous decade include: (1) population structure, (2) ecological restoration providing for predator recovery, and (3) adaptive management of livestock predation by wolves.

As wildlife managers learn more about the genetic structure of wolf populations, they are better able to make scientifically sound decisions about how to apply available tools to achieve management goals. For example, genetic structure of the wolf populations in southeast Alaska revealed distinctive coastal and inland signatures suggesting relatively little historic gene flow between the regions [165]. A genetic marker for dark coat color has clarified questions about gene flow between domestic and wild canid populations [166]. In the western Great Lakes region, hybridization between the eastern and gray wolves has been verified, and issues of hybridization between coyotes and wolves have been clarified [167].

Reviews of conservation genetics of wolves in the North American and European continents sketch a better understanding of the dynamics of recurrent cycles of expansion and contraction of populations [168, 169]. These dynamic cycles have been accelerated by management decisions to limit wolf populations in some locations and to encourage expansion in others. Where populations have been relatively stable demographically, genetic structure suggests relatively limited gene flow.

A large part of this resilience is thought to be related to the interaction of social and ecological factors influencing dispersal. For example, in the Yellowstone population, males have been more likely to disperse and multiple females more likely to reproduce during the same season within the natal group [158]. Emerging lessons for management decisions include the value of maximizing connectivity between populations and encouraging natural dispersal dynamics [170].

Models of large scale ecological restoration involving wolves are now taking into account the dynamics of land-use change [171, 172]. Resulting scenarios are oriented more to providing managers with information about the upper and lower limits to the consequences of management options, rather than attempting to predict the future of specific populations. Models of dynamic interactions between multiple predator and prey are becoming more effective at integrating the effects of territoriality on demographic (numerical) and prey-switching (functional) responses [173]. Management goals directed toward reducing conflict over livestock depredation are benefitting from improved understanding of the interaction of social and ecological factors influencing dispersal. The implications are relevant to (1) translocation of wolves for control of livestock depredation [174-176], (2) balancing conflicting goals of recovery of wolf populations while minimizing risk to livestock [177], as well as (3) clarifying some of the ethical and practical dilemas associated with removal of entire groups of wolf-like canids [178, 179].

CONCLUSIONS

Cross-fertilization of ideas from several lines of research, which have expanded rapidly during the previous decade, may hold promise for an emerging framework to integrate social and ecological influences in our understanding of the evolution of wolf social intelligence. These areas of research include: (1) functional aspects of the canid genome, (2) implications of large body size for flexible and resilient behavior, and (3) dynamic fluctuations in ecosystems with multiple predators and multiple prey.

The popular notion that sociality evolved in wolves due to the benefits of cooperative hunting now appears overly simplistic. Wolf sociality implies adaptations to a wider range of social environments, not simply more individuals within a social network. Changing aspects of the social environment include interactions with littermates, care-givers, mates, rivals for mates, hostile neighboring groups and permeability of group barriers to immigration.

Future research directions should include critical evaluation of wide range of working hypotheses about the adaptive significance and management implications of wolf social intelligence. Examples of hypotheses addressed in this chapter include the: (1) “Social Intelligence Hypothesis”, (2) “Large Body Hypothesis”, and (3) “Changing Scenarios Hypothesis”.

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Chapter 2

CONSERVATION OF CANIDS: THE IMPACT OF INFECTIOUS VIRAL DISEASE

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ABSTRACT

Many canid species (Order Carnivora: Family Canidae) across the globe are under threat, often from human disturbances, which include habitat destruction, expansion of agriculture and road networks, and hunting. This in turn can amplify the impact of infectious diseases, which on occasion have led some species to the brink of extinction such as the rare and endangered Ethiopian wolf (*Canis simensis*). Such populations are susceptible to infectious diseases including rabies virus (RABV), canine distemper virus (CDV) and canine parvovirus (CPV), all of which can cause high mortality levels. Conversely, canids have been responsible for the global spread of diseases affecting both human populations and their livestock.

With a focus on RABV and CDV, we discuss how transmission both to, and within, rare canid populations can have profound effects on population size and dynamics. The development of novel methodologies to study the interaction of such viruses within widely dispersed, often elusive wild canid populations remains challenging. Serosurveys have proven very useful in this field and retrospective seroanalysis of canid populations has revealed immunological responses to some of

these pathogens demonstrating the circulation of important viral diseases within wild canids. Where data are available, we comment on the ability of infectious viral diseases to persist within often fragmented populations and spread between them. Importantly, we discuss the role of surveillance and the methods conservationists use in attempts to protect and maintain endangered canids, such as through vaccination of wild canids and monitoring of both domestic and wild canid populations.

1. INTRODUCTION

1.1. Canids and Human Interactions

Carnivores are the focus of many conflict-related issues, some dating back to the early days of humankind, where carnivores posed a real threat both as competitors and as predators of our ancestors (Sillero-Zubiri *et al.*, 2006; Woodroffe *et al.* 2005). Subsequently, with the emergence of domestication of livestock, wild carnivores presented both a perceived and real threat to this newly valuable commodity, both as predators of livestock and as a potential vector of infectious disease (Clutton-Brock, 1999). Being predominantly group living and often diurnal, the larger members of the Canidae family (which includes 35 species of wolves, jackals, dogs and foxes) are more visible and thus more likely to attract human attention than most other carnivores. Medium-sized canids, such as coyotes (*Canis latrans*), jackals (e.g., *C. aureus*) and South American foxes (*Pseudalopex* spp.) tend to be widespread and occur at higher densities, often causing substantial economic damage through depredation of livestock (Sillero-Zubiri and Switzer, 2004). Whether the guilty party or not, retaliatory and pre-emptive killings of canids are not uncommon. This direct persecution, however, is by no means the only impact that man has on these wild species.

Growing human populations have also increased the potential for contact between wild canids and domestic dogs (*C. familiaris*), which are often kept to protect livestock, aid hunting efforts, clean waste or as companions (Sillero-Zubiri and Switzer, 2004). This contact often leads to aggressive competition between the two. Occasionally, hybridisation can occur, potentially affecting the genetic diversity of wild canids if the offspring are fertile (Gottelli *et al.,* 1994; Vilà and Wayne, 1999). However, the most immediate threat to wild canids resulting from sympatric domestic dogs is their shared receptivity of numerous pathogens, with both wild and domestic canids often acting as the reservoir for viruses (Woodroffe *et al.*, 2004). Few of these canid infections affect human health with one exception, RABV. This virus is of huge significance to human populations as it remains one of the few viral pathogens that invariably results in human fatality following infection.

1.2. Viral Infections in Wild Canids

A number of viruses have been shown to infect wild canid populations (Table 1) and several of these threaten canine populations across the globe.

Two viruses dominate in terms of their impact on canid populations. These are RABV and CDV. Importantly, recent outbreaks of RABV and CDV have pushed certain endangered canids to the brink of extinction. Both of these viruses are classified, by virtue of their non-segmented negative strand RNA genomes, into the Order *Mononegavirales*. This Order includes some of the most important viruses known in both the medical and veterinary fields.

RABV is classified within the Rhabdoviridae family within the Order Mononegavirales and further within the Lyssavirus genus. The Rhabdovirus family is one of the most diverse virus families and includes viral agents that infect plants, invertebrates, animals and humans. The Lyssavirus genus is undoubtedly the most notable from both a veterinary and human disease perspective with RABV being feared as one of the most significant pathogens known to man. The virus is transmitted by a bite, transferring from the saliva of the infected aggressor into the wound of the naïve individual. Due to their social structures and ability to deliver a damaging bite wound, this type of transmission makes canid species an ideal reservoir host for RABV. Widespread species such as coyotes, red foxes (*Vulpes vulpes*) and crab-eating foxes (*Cerdocyon thous*) may carry infections such as RABV that can be transmitted to people and livestock (Woodroffe *et al*., 2004).

Table 1. Viral diseases of wild canids

Disease	Virus and Classification [Abbreviation] (Family, Genus)	Description of disease
Rabies	Rabies virus [RABV] (Rhabdoviridae, Lyssavirus)	Fatal encephalitis characterised by behavioural changes, aggression and excessive salivation.
Canine distemper	Canine distemper virus [CDV] (Paramyxoviridae, Paramyxovirinae, Morbillivirus)	Acute febrile disease with high mortality rates. Infected animals show signs of jaundice, ulceration, anorexia and neurological abnormalities.
Canine parvovirus	Canine parvovirus [CPV] (Parvoviridae, Parvovirus)	Infection is characterised by severe diarrhoea and vomiting leading to death by dehydration.
Infectious canine hepatitis	Canine adenovirus 1 [CAV] (Adenoviridae, Matodenovirus)	Disease signs vary from coughing, bloody stools and fever to neurological signs including ataxia and convulsions.
Oral papillomatosis	Papilloma virus (Papillomaviridae, Various*)	Small oral papillomas have been observed in grey wolves in Canada.
Canine coronavirus	Canine coronavirus (Coronaviridae, Coronavirus)	Infected animals show signs of diarrhoea, vomiting and anorexia.

* Canine papillomaviruses have been grouped into three different genera, the Lambdapapillomavirus, Chipapillomavirus and Taupapillomavirus (Bernard *et al*., 2010).

Alongside the threat to human and domestic species, infectious diseases are a significant cause of population declines in wildlife (Dobson and Foufopoulos, 2001). Rabies is recognized as the most common cause of disease outbreaks in wild canids

(Funk *et al.*, 2003; Woodroffe *et al.*, 2004), having caused local extirpation of African wild dog populations and dramatic population declines in a number of species such as African wild dogs (Gascoyne *et al.*, 1993; Hofmeyr *et al.*, 2004), Blanford's fox (*V. cana*) (Macdonald, 1993) and Ethiopian wolves (*Canis simensis*) (Sillero-Zubiri *et al.*, 1996a). In Africa in particular, there is growing evidence that the domestic dog has been responsible for the transmission of rabies across the continent following its introduction by European settlers (Talbi *et al.*, 2009) and that this process continues (Hayman *et al.*, 2011).

Only through an understanding of the spread of RABV by dogs will there be any prospect of controlling this disease in many regions of the world (Hampson *et al.*, 2009).

Within the Order mononegavirales, CDV is further classified into the family Paramyxoviridae, sub-family Paramyxovirinae, genus Morbillivirus. This genus includes numerous important viral pathogens including measles virus, rinderpest virus and peste des petits ruminants virus. Despite being named canine distemper virus, studies with CDV have shown that it has possibly the widest host range of all morbilliviruses. Initially, CDV was thought to be restricted to infection of members of the Canidae, Ursidae, Mustelidae and Viverridae families but is now known to infect a wide range of hosts including the Felidae, Hyaenidae and the Artiodactyla (Harder *et al.*, 1997; Barrett *et al.*, 1999). Over the past 20 years, CDV has been responsible for extensive mortalities in a range of wild carnivores including both terrestrial and aquatic species. Members of the Felidae and Hyaenidae have been affected by CDV with reports of infection of large cat species in American zoos, presumably as a result of interaction of CDV-infected native wildlife, such as raccoons with these species (Appel *et al.*, 1994; Appel *et al.*, 1995). CDV has also been shown to cause substantial mortalities in aquatic carnivores, having caused extensive mortalities in Lake Baikal seals (*Phoca sibirica*) in 1987-88 and Caspian seals (*Phoca caspica*) in 1997 and again in 2000 (Mamaev *et al.*, 1995; Kuiken *et al.*, 2006). Such epizootics, along with adverse environmental factors, have pushed seal populations to critically endangered levels. Importantly, CDV is known to be lymphotropic and as such infection, as with other morbilliviruses, may induce a profound immunosuppression that often leads to secondary opportunistic infections that in turn lead to death of the host (von Messling *et al.*, 2004).

Within wild carnivores, high mortality rates caused by CDV have been reported in black-backed jackals (*Canis mesomelas*) in the Serengeti-Mara (Tanzania – Kenya) ecosystem in 1978 and in African wild dogs in 2000. In 1994, CDV struck African wild dog populations, completely eliminating a pack of wild dogs from the Chobe National Park, Botswana (Alexander *et al.*, 1994). In the same year CDV was detected in lions (*Panthera leo*) in the Serengeti National Park, Tanzania. In this instance the affected animals were found suffering fatal neurological signs characterized by grand mal seizures. Positive cases were confirmed in several locations including the Serengeti and Masawa Game reserve in Tanzania (Roelke-Parker *et al.*, 1996) as well as in the Maasai Mara National Reserve, Kenya (Kock *et al.*, 1998). Within the Serengeti, the closely monitored lion population suffered a 30% loss in numbers through death or disappearance. Initially it was thought that these outbreaks were caused by a new virus or that co-infection of animals with feline immunodeficiency virus and CDV served to exacerbate disease within lion populations. However, it was later found that local strains of CDV were the cause and no link could be found to any other viral agents (Roelke-

Parker *et al.*, 1996). At this time, CDV was also confirmed as being present in bat eared foxes (*Otocoyon megalotis*) (Roelke-Parker *et al.*, 1996) and spotted hyaenas (*Crocuta crocuta*) (Haas *et al.*, 1996) as well as domestic dog populations surrounding the Ngorongoro Crater. Virus isolates from these species were serologically indistinguishable from the monoclonal antibody reaction patterns observed with virulent canine distemper virus isolates from domestic dogs. Further molecular testing of separate virus isolates showed genetic clustering within geographic areas rather than host species suggesting that a single virus strain caused mortality in a range of species and that presumably the virus was freely transmissible between domestic dogs and the wild carnivore populations (Cleaveland *et al.*, 2000).

In the following sections specific examples of the impact of viral infections on particular species are given. Each section includes details of the ecology of the species under discussion, the impact of particular viruses and where applied, the conservation activities associated with mitigating the impact of virus infection.

2. THE ETHIOPIAN WOLF

2.1. Ecology of the Ethiopian Wolf

The Ethiopian wolf (*Canis simensis*) has been rare since it was first recorded by science (Marino 2003). Confined to the Afroalpine ecosystem of Ethiopia, where it specializes as a predator of the abundant rodent community, the species is a relatively recent addition to the fauna of the Horn of Africa, where it first appeared during the last glacial period, circa 100,000 years ago (Gottelli *et al.*, 2004) and subsequently colonised the then widespread Afroalpine environment. During this period, Ethiopian wolves may have been relatively widespread across the Ethiopian highlands. However, with the onset of the present interglacial period, approximately 18,000 years ago, Afroalpine habitats started to shrink, replaced by montane forests at lower altitudes. As a result, Ethiopian wolves were stranded in mountain refuges, a process that has left its mark on the current genetic structure of extant populations (Gottelli *et al.*, 1994; Kennedy *et al.*, 2011).

Ethiopian wolves are a specialist predator of rodents, with a slim body, long slender legs, and an extended muzzle. They are smaller than their close lupine relatives, with a mean mass of 16.2 kg (14.2-19.3 kg) for adult males and 12.8 kg (11.2-14.2 kg) for adult females. The wolves feed almost exclusively upon diurnal small mammals of the high altitude Afroalpine grassland community, mainly grass rats (*e.g., Arvicanthis spp, Lophuromys spp, Otomys spp*), and mole rats (*Tachyoryctes macrocephalus* and *T. splendens*) (Sillero-Zubiri and Gottelli 1995a; Marino *et al.* 2010). Wolves are most active during the day, with peaks of foraging activity synchronized with the activity of rodents above the ground (Sillero-Zubiri *et al.*, 1995a, 1995b).

In the Bale Mountains (Figure 1), Ethiopian wolves are present at unusually high densities for a social carnivore of its size, reaching 1.0–1.2 adults and sub-adults/km^2 in prime areas (Sillero-Zubiri and Gottelli, 1995b). Local wolf densities correlate closely with the distribution and abundance of the main rodent prey, which is in turn highest in open areas with short vegetation and relatively deep soils (Sillero-Zubiri *et al.*, 1995a, 1995b). Such high productivity and concentration of rodents has not been found elsewhere in Ethiopia, with wolves consequently found at lower densities (Marino, 2003).

Ethiopian wolves combine solitary foraging with intense sociality. They live in close-knit, territorial, cooperatively-breeding packs but they forage and feed alone, contradicting the general trend in carnivores for grouping and cooperative hunting. Family groups can contain up to 20 adult wolves, with the typical pack consisting of around six adults living on a territory of some 6km². A dominant pair produces one litter of up to six pups each year during a breeding season that runs from October to December (Sillero-Zubiri *et al.*, 2004). All pack members guard the den, chase potential predators, and regurgitate or carry rodent prey to feed the pups. Subordinate females may even assist the dominant female in allo-suckling for the pups (Sillero-Zubiri *et al*, 1996b). By ten weeks of age, the pups subsist almost entirely on solid foods supplied by helpers, and are essentially independent by six months. The independent period for juveniles, from six months to one year, is one of the hardest as they attempt to hone their hunting skills while maintaining their body condition. On average, mortality is seen to be approximately 50%. Full adult appearance is attained at two years and both sexes become sexually mature during their second year.

Today, Ethiopian wolves are confined to several small and isolated populations, perched on islands of suitable habitat at altitudes higher than 3000m above sea level (Marino, 2003). The Bale Mountains, in southeast Ethiopia, contain the largest population of wolves with over half of a global total of some 400 adult wolves found in this extensive mountain range.

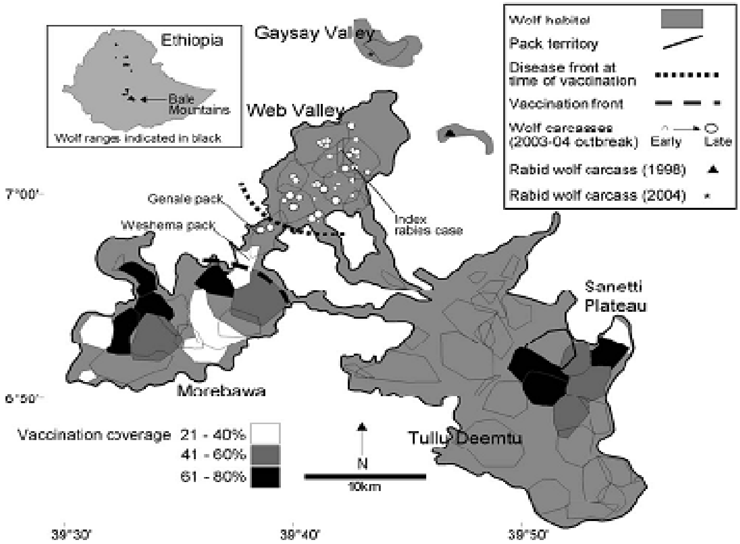

Figure 1. Ethiopian wolf habitat in the Bale Mountains with study areas in the Web Valley, Sanetti Plateau, and Morebawa. Known pack territories are designated by polygons. Carcasses collected during the 2003–2004 rabies epizootic are indicated by white circles, with the size of the circle denoting the relative timing of death. Within pack vaccination coverage during the 2003–2004 emergency vaccination campaign is shown in the lower legend. Unvaccinated packs are designated by unfilled polygons. Single cases of confirmed wolf rabies in 1998 and 2004 are also shown (from Randall *et al.*, 2006).

2.2. Viral Infection in the Ethiopian Wolf

These rare animals are threatened by habitat loss and fragmentation, exacerbated by the expansion of humans into the fertile Ethiopian highlands, and further aggravated by the rate of climate change due to human activities across the globe. However, a more urgent and present threat to the Ethiopian wolves comes from sympatric domestic dogs living within and utilising wolf ranges, which compete, hybridise, and most seriously, transmit viral diseases, particularly RABV and CDV. RABV has killed many Ethiopian wolves in the Bale Mountains over the last two decades. Well-documented outbreaks of rabies occurred in 1991, 2003 and again in 2008/09 (Table 2). On each occasion, mortality was high and concentrated over a short period of time with up to 75% of the known animals dead or unaccounted for in the affected populations. Genetic analysis of the virus provided strong support that the source of each outbreak were domestic dogs. Rabies can enter the highlands and into the wolf population through dogs living in close proximity to wolves. Seasonal movement of people, cattle and dogs into wolf habitat increased the risk of infection further (Laurenson *et al.,* 1998). There is no evidence of major disease outbreaks among wolves outside Bale Mountains, but it is possible that outbreaks may have gone undetected elsewhere as these populations are small and were monitored less intensely.

Table 2. Rabies outbreaks in Ethiopian wolves in the Bale Mountains

Year	Comment	Representative RABV genomic sequence	Reference
1991/1992	41/53 known adults died or disappeared.	AY502132	Sillero-Zubiri *et al*., 1996a
2003/2004	Significant increase in wolves found dead or disappeared. In 2004 13/15 carcasses were tested positive for rabies. 74/95 known adults died or disappeared from Web Valley.	AY500827	Randall *et al*., 2004
2008/2009	5/6 samples confirmed rabies positive. Previous vaccination may have reduced the impact of this outbreak. 52/83 known adults died or disappeared from Web Valley	GU062189	Johnson *et al*., 2010; Stewart *et al*., 2010

2.3. Management of RABV in Ethiopian Wolf Populations

Attempts to manage disease in Ethiopian wolf populations during the past two decades have been multi-disciplinary, involving research, monitoring, planning and action (Laurenson *et al*., 1998). This strategy has been adapted to incorporate lessons learnt, knowledge of potential viruses, and advances in disease management practices, drawing on the knowledge of an advisory panel as well as long-term strategic plans (Sillero-Zubiri and Macdonald, 1997; Sillero-Zubiri *et al*. 2000, 2004; IUCN/SSC Canid Specialist Group, 2011). An ideal solution to the disease threat would be to remove all dog-to-wolf contact, but this is not possible within the current political context in Ethiopia. During 1998-2002, a domestic dog sterilisation campaign was implemented in the Bale Mountains to try and reduce future numbers of domestic dogs. Nearly 500 dogs in the target areas were sterilized (Williams, 2004), but this fell short of 95% of the male dog population that would have to be sterilised, as well as a significant percentage of the females, to have a demographic impact. This approach gave way to the vaccination of dogs against rabies, carried out with the aim of creating a boundary of vaccinated dogs within and around wolf ranges. Since 1996, more than 62,000 domestic dogs in and around the Bale Mountains National Park have been vaccinated against RABV (Stewart *et al.*, 2010). The ongoing vaccination of domestic dogs not only mitigates the threat posed by rabies to the wolves, but also delivers a socio-economic benefit to the local communities who lose not only their valuable livestock to the disease, but also face the risk of rabies transmission to humans.

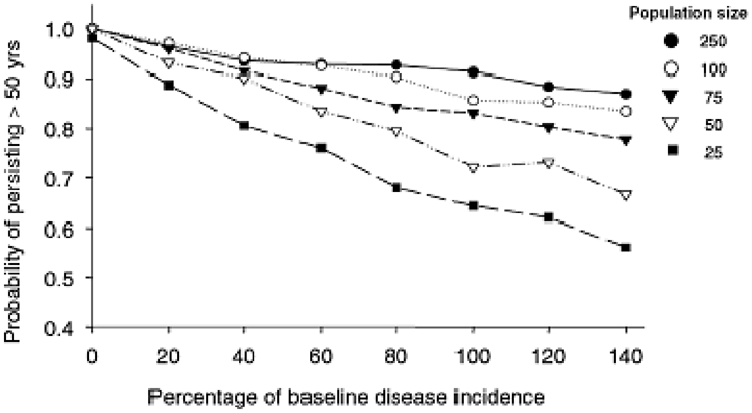

Figure 2. Proportion of 1000 simulations in which populations remained extant after 50 years using baseline demographic parameters for wolf populations of different sizes exposed to different levels of disease incidence in the domestic dog reservoir population (adapted from Haydon *et al.*, 2002).

The extent and long-term risk to Ethiopian wolves imposed by disease has been assessed from the intensive monitoring of wolves in the Bale Mountains (Marino *et al.*, 2006) and from predictive models derived from Bale's long-term demographic data, based on Population Viability Analyses (Fig. 2, Haydon *et al.*, 2002). The empirical data show a series of population crashes and recoveries, suggesting that the large size of the wolf population in the Bale Mountains lends a certain degree of robustness against disease outbreaks. Additionally it can be argued that the vaccination of domestic dogs and the re-active vaccination of wolves in response to epizootics, may have contributed to these recoveries. Models of larger wolf populations (>100 animals) appeared to be relatively persistent in the presence of a significant level of disease in the sympatric dog population (Haydon *et al.*, 2002). However, for the smaller populations the models indicated that disease is a significant threat and could be a critical factor in determining their persistence.

The long-term monitoring of wolves in Bale has been critically important to the disease management strategy, ensuring the rapid detection of outbreaks through the observation of clinical signs and/or the discovery of carcasses, and the diagnosis of putative disease agents by post-mortem analysis. When RABV outbreaks do occur, permission has in the past been granted by the federal authorities to directly vaccinate the wolves to try to prevent the disease from spreading and affecting more of the population. Reactive vaccination of Ethiopian wolf packs were conducted in 2003 (Figure 1; Randall *et al.*, 2006) and again in 2008/09 to control the spread of the disease.

Analysis of the 2003 rabies outbreak provides unequivocal evidence of the effectiveness of reactive vaccination in curtailing rabies outbreaks in Ethiopian wolves (Haydon *et al.*, 2006; Randall *et al.*, 2006). The trials were rigorously conducted to test the effectiveness of injectable rabies vaccines on this species. In total, 84 wolves were vaccinated, of which 25 individuals were re-trapped for a booster dose. Serological analysis showed multiple vaccinations to be most effective, although single doses still returned elevated antibody levels, and the longevity of the vaccine still needs to be assessed (Knobel *et al.*, 2008). The intervention allowed the team to model the most effective strategies to control the spread of an outbreak, in addition to the minimum vaccination target to achieve persistence in each targeted breeding unit (Haydon *et al.*, 2006). Demographic analyses suggested that any vaccination program in wolves should aim to preserve more breeding units to minimise social disruption and facilitate recruitment and recovery of the population (Marino *et al.*, 2006). In even the smallest modelled population (n=25), vaccination coverage of 60% of wolves increased the probability of persistence to over 90% (Haydon *et al.*, 2002).

The resources required to vaccinate the entire reservoir of domestic dogs living in and around the wolf range make this option an unfeasible long-term solution. In addition, the losses incurred in the wolf population when a disease epizootic breaks through the '*cordon sanitaire*' of vaccinated dogs, calls for a more proactive solution to the disease issue. The option of direct vaccination of wolves, prior to an outbreak, appears a favourable and realistic option. With advances in vaccine research and development, vaccines can now be administered orally. These vaccines have the advantage of not requiring animal handling or anaesthesia, which had been a major concern of the Ethiopian authorities and a reason for them prohibiting the vaccination of wolves previously. Oral vaccinations have been used successfully to eliminate rabies in Western Europe and much of North America (Brochier *et al.*, 1996; Fearneyhough *et al.*, 1998; Masson *et al.*, 1999). Oral vaccination might be the most effective means of pre-empting epizootics among Ethiopian wolves as modelling suggests that as little as 20-40% vaccination coverage in the wolf population would be needed to enhance overall population persistence (Haydon *et al.*, 2002, Williams *et al.*, 2004).

2.4. Canine Distemper in Ethiopian Wolf Populations

CDV is not necessary fatal to Ethiopian wolves, as CDV-specific seropositivity detected in wolf samples indicates that individuals can survive infection with this virus (Laurenson *et al.*, 1998). However, with high CDV transmissibility, mortality cannot be precluded. Epizootics of CDV have often been shown to cause considerable mortality in dogs as well as population crashes in wild carnivores, such as lions (Roelke-Parker *et al.*, 1996). Anecdotal and serological evidence suggested that an epidemic of CDV occurred in the dog population of the Bale Mountains in 1992–93, but it was not possible to assess whether the disease spilled over into wolves and whether it accounted for the post-1992 decline in wolf numbers or the lack of immediate recovery from the 1991 rabies outbreak (Laurenson *et al.*, 1998). Simulations of the effect of CDV on long-term persistence of Ethiopian wolf populations have suggested that it may not be significant (Haydon *et al.* 2002), but the disease may be more important than previously thought, or increasing among dogs and/or wolves in Bale. CDV outbreaks affecting wolves were confirmed in the Bale Mountains in 2005/06, and in 2010 (Gordon *et al.,* 2011). In the most recent outbreak 24 carcasses were discovered, and five of seven carcasses that were tested returned positive CDV results (Unpublished data). During 2010, many wolves disappeared in Bale during the period of the outbreak, in addition to the 24 carcasses that were discovered. From the focal monitoring areas, packs lost 51.3% of adults and sub-adults during the epidemic, while recruitment from juveniles to sub-adults was severely affected with only 12% survival rates in focal packs compared to expected levels of 50%.

Even when large populations face consecutive outbreaks, models predict that the chance for extinction is greatly increased (Haydon *et al*., 2002) with population persistence rapidly decreasing when a rabies epidemic occurred every seven years in models with or without CDV–related mortality. It would seem that the larger Ethiopian wolf populations can cope with outbreaks of RABV or CDV but that it is a major concern if the outbreaks occur simultaneously or concurrently. This seems to be the case now in the Bale Mountains, where the rabies epizootic of 2008/09 was followed by the canine distemper outbreak of 2010. In the Web Valley, the population most seriously affected by rabies in 2008, few adults remain from the original six focal packs (eight adults compared to 43 before the epizootics).

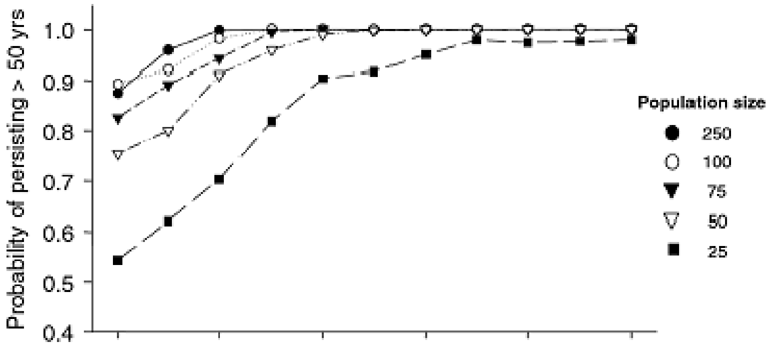

Figure 3. Effect of vaccination on a 50-year persistence of Ethiopian wolf populations of different sizes based on simulations using baseline demographic and epidemiological parameters for wolf populations (adapted from Haydon et al., 2002).

Management to prevent further disease outbreaks might be advisable after such population crashes. In model predictions over 50 years, the relationship between wolf population persistence and disease reduction in dogs appears approximately linear. Thus, even if incomplete rabies and CDV control in dogs were achievable, any reduction in disease incidence should have a beneficial effect on wolf persistence. Rabies must be almost completely eradicated, however, before these smaller populations are almost certain to persist, which might require vaccination of at least 70% of the dog population (Coleman and Dye, 1996) in a band of up to 15km around wolf habitat. On the other hand, the population viability models indicated that disease-induced population fluctuations and extinction risks can be markedly reduced with the vaccination against rabies of a relatively small proportion of wolves (Haydon *et al.*, 2002) (Figure 3).

2.5. Disease Management of the Ethiopian Wolf

The disease management strategy has been recently reviewed on the back of the extensive CDV outbreak during 2010 (IUCN/SSC Canid Specialist Group, 2011). Vaccinations of both host and target populations will continue to be important strategies for disease management in Ethiopian wolves, continuing under the premise that every dog vaccinated, reduces the risk to the Ethiopian wolf. Vaccination of domestic dogs against CDV has re-commenced during 2011, following a ten year absence due to the high costs of such a project. The vaccination of Ethiopian wolves against CDV will most likely follow a similar pattern to the past vaccinations against rabies. Injectable CDV vaccines should be proved safe in this species as a matter of urgency, with later investigations into the safety and efficacy of oral CDV vaccines. Ongoing oral rabies vaccine trials are testing the preferred methodology and oral rabies vaccine for effectively protecting Ethiopian wolves. Modelling these results will enable the development of a nationwide plan for delivering oral rabies vaccines to all populations of wolves.

3. THE GREY WOLF

3.1. Ecology of the Grey Wolf

The grey wolf is the largest extant member of the family Canidae. The species *Canis lupus*, which includes a number of subspecies, is found throughout the northern hemisphere. The domestic dog is thought to have been derived from one of these (Vila *et al.*, 1997) and feral wolf/dog hybrids are commonly observed. Although historically one of the most widely distributed mammals, the relentless increase in the human population has seen a dramatic change in the grey wolf's range. This has been most profound in Europe where the species has been almost eliminated from Western Europe and is restricted to populations in Scandinavia, Northern Spain, the Balkans and Eastern Europe. Conflict with humans can manifest itself in a number of ways from: direct persecution of the wolf with the intention of eliminating local populations; human encroachment on wolf territories sometimes resulting in wolf predation on livestock; and the transmission of diseases from wolves to livestock and humans. The most dramatic of these being transmission of rabies following a wolf attack, which in some circumstances can result in life-threatening injures that if survived could then develop into infection with rabies in the absence of post-exposure prophylaxis (Gremliza, 1953; Baltazard and Ghodssi, 1954; Shah and Jaswal, 1976).

Despite the encroachment of humans, the grey wolf remains widely distributed around the world and its populations are sufficiently high to mean that they are not considered endangered. Grey wolves are found across North America, the Middle East and Eurasia. In the absence of human impact, the main restriction on wolf distribution is the availability of prey species. Their diet is very varied but mainly consists of large ungulates such as deer, moose, caribou and elk, populations of which can be highly mobile. Individual animals will also prey on smaller mammals or when prey is scarce, eat carrion or human refuse. Adult wolves can weigh between 45 and 55 kgs with males being larger than females and are typically between 100-160 cm in length and 80-85 cm at the shoulder. The head of a grey wolf is large with a wide forehead and strong jaws capable of exerting great crushing pressure (1,500 lbs/inch^2). Pack sizes can vary but usually consist of five to 10 animals dominated by an alpha male and female, who are the only adults that breed within the family group. Depending on prey availability, packs may form a territory or migrate to follow particular prey species. Juveniles may remain within the pack until reaching maturity at two years before dispersing to mate and establish territories of their own. Within the hierarchical structure of the pack, communication between pack members can be varied often involving physical contact such as facial licking. Although mortality is high in newborns, adults can live on average about seven years, with captive animals surviving over 15 years (Mech and Boitani, 2006).

Study of wolf behaviour and biology present a number of challenges to researchers. Wolves are by their nature elusive creatures, relying on stealth to approach and kill prey and thus can be difficult to observe in the natural environment. Furthermore, wolves are highly mobile and can travel large distances in a short period of time. The natural habitat of wolves is often found in remote, inaccessible areas, with packs occupying large ranges. It has also been noted that the behaviour of captive populations can be different from those in the natural environment with captive animals often being more aggressive and having higher reproductive rates.

3.2. The Impact of Rabies Virus Infection on the Grey Wolf

Despite difficulties in studying wolves in the natural environment, a number of studies, particularly in North America, have observed the impact of RABV on packs. Thorough descriptions of the disease in the grey wolf are rare and this species of canid is not considered an important wildlife reservoir for this disease (Niezgoda *et al.*, 2003). One of the best descriptions of rabies in an individual wolf was reported by Richard Chapman in the journal *Science* (Chapman, 1978). Whilst conducting field surveys of a single pack over two summers, the author described an encounter with a wolf that approached his campsite. This was unusual behaviour in itself. The wolf, an adult male weighing almost 30 kg, repeatedly approached the author, walking with a staggering gait and with excessive saliva on its muzzle. This animal had been observed fighting with other pack members on previous days. The author was forced to shoot the animal, which was subsequently confirmed rabid by laboratory tests. The post-mortem analysis of its stomach contents was also unusual, including wolf hair, moss, wood chips and sand. A follow-up study of the pack showed that the remaining pack members died, some confirmed from rabies, or disappeared. From these observations it is clear that rabies in the wolf shows identical manifestations to that in dogs with clinical signs of aggressive behaviour, salivation and incoordination being common features. A further repeated observation in rabid North American wolves that are rabid has been the presence of porcupine quills in the muzzle of the animal (Weiler *et al.*, 1995). Wolves tend to avoid porcupines (*Erethizan dorsatum*), although rabid animals lose inhibitions leading to such attacks. The source of such RABV outbreaks varies depending on the location. In Arctic regions, rabies epizootics within the Arctic fox (*Alopex lagopus*) are thought to cause spillover into the wolf population. The Arctic fox has long been known to be the main reservoir of rabies in Arctic regions (Mork and Prestrud, 2004). Phylogenetic analysis of rabies isolates suggests that this vector has been responsible for transmission of rabies throughout the Arctic Circle, often causing movement of rabies between continents (Mansfield *et al.*, 2006) and to isolated islands (Johnson *et al.*, 2007). In temperate regions, particularly in the Middle East, the source of rabies infections in wolves may be from wildlife reservoirs such as the red fox (*Vulpes vulpes*) and the golden jackal or the domestic dog.

In all the studies of rabies of North American wolves, the local impact appears to be devastating, often eliminating whole packs (Chapman, 1978; Theberge *et al.*, 1994; Weiler *et al.*, 1995) and can change den usage as alpha pairings are removed from the population (Weiler *et al.*, 1995). However, the overall impact on wolf population and density is minimal with dispersing animals rapidly reoccupying empty territories. When comparisons have been made on the causes of wolf mortality during particular outbreaks the main cause of death is always human activities such as hunting or trapping over those caused by rabies infection.

Few seroprevalence studies have been reported in grey wolf populations and where data is available a very low level of seropositivity to rabies virus, consisting of around 1% of surveyed individuals (Zarnke and Ballard, 1987; Ballard and Krausman, 1997). This likely reflects the high mortality of animals infected with rabies, thus removing those individuals who develop the disease, leaving a small number who were exposed to virus, perhaps through a bite, but did not develop disease.

3.3. The Impact of Canine Distemper Virus Infection on the Grey Wolf

The impact CDV has on populations of wolves within grey wolf packs is largely unknown. Serosurveillance initiatives have attempted to detect antibodies specific to this viral agent from historical samples but have only found relatively low levels of seropositivity within the assessed population. One example of this is from a study of sera taken from 116 wolves captured in south central Alaska. In this instance, 12% (10/83 samples tested) were positive for CDV specific antibodies with a single sample out of 88 being positive for rabies virus antibodies. These findings led to the conclusion that these viruses had little impact on the wolf populations. In reality, these data are poor indicators of the impact. For CDV, circulation of the virus may have a negative impact on populations or the individuals within, without high levels of mortality and morbidity (Zarnke and Ballard, 1987).

Canada and the USA have had some of the largest grey wolf studies in the world and as such, a number of studies have been conducted on the presence and effect of infectious diseases. Between 1984 and 2000, grey wolves were captured in several geographic areas of Alaska (USA) and the Yukon Territory (Canada) so that antibody prevalence could be investigated for several infectious diseases. Area-specific CDV seroprevalence ranged from 0% to 41% and was reported to be age-specific, with higher values seen in the adult cohort compared than the pup cohort (Zarnke *et al.*, 2004). Another smaller scale Canadian study at the Riding Mountain National Park found that 44% (n=18) of blood samples taken from grey wolves indicated CDV exposure with one wolf dying from CDV (Stronen *et al.,* 2011) whilst Philippa *et al.,* (2004) found 67% seropositivity in a small group of wolves sampled (n=9) from different locations across Canada.

Pup mortalities have occasionally been used as indicators of infectious disease within populations. For example, both CDV and canine parvovirus antibody titres were shown to be high in packs that had experienced pup deaths or disappearances across northwest Montana (USA) and south eastern British Colombia. A further study in the Yellowstone National Park correlated peaks in CDV seroprevalence with high wolf-pup mortality and suggested that CDV contributed to the observed mortality (Almberg *et al.*, 2009). Studies with both grey wolves and coyotes (*C. latrans*) within the Greater Yellowstone ecosystem have also been carried out to attempt to determine how CDV is able to persist among terrestrial carnivores that have small, fragmented population structures (Almberg *et al.*, 2009). Early studies reported a continuing CDV seropositivity in wolf populations and it was suggested that CDV was enzootic in free-ranging canid populations (Choquette and Kuyt, 1974). Others studies speculated that the virus was being introduced into wolf populations sporadically from domestic dogs (Stephenson *et al.*, 1982). Certainly, the latter suggestion appears to be the most likely as CDV seropositivity within packs is often reported occasionally over long periods (Almberg *et al.*, 2009) suggesting as hypothesised that that exposure of wolves to CDV is uncommon (Zarnke and Ballard, 1987).

However, more recent studies have suggested that CDV requires either large spatial scales or multi-host transmission for persistence and have postulated that reintroduction into wolf populations may occur through coyotes although even then, the presence of a further carnivore reservoir cannot be discounted as population sizes of coyotes and wolves are assumed to be too low to maintain the virus. Additional information on how and where CDV is maintained and the frequency with which future epizootics might be useful for management of large protected canid populations across the USA and Canada.

Across Europe a similar trend is seen with sporadic fluctuations in CDV serostatus of animals. In Spain, 18.7% (n=37) of grey wolf samples tested were positive for CDV specific antibodies although a geographical isolation was reported with CDV seropositivity being much greater in certain areas (Sobrino *et al.*, 2008). A similar serosurveillance initiative was also carried out in Portugal. In this study CDV specific antibodies were detected in a small number of grey wolves (3/27) and red foxes (2/22). Unfortunately, as with all serosurveillance initiatives involving free roaming wildlife, sample sizes are low but at least they serve to confirm that wolf populations had come into contact with the virus at some point (Santos *et al.*, 2009). A further recent study has demonstrated endemnicity of CDV in grey wolves within free ranging Scandinavian canids in the Swedish-Norwegian population. Assessment of serological positivity in both red foxes and arctic foxes has suggested that these species may act as maintenance reservoirs for the virus, as suggested for rabies virus (Mansfield *et al.*, 2006), spreading it intermittently into wolf populations (Akerstedt *et al.*, 2010).

Vaccination of grey wolves with different CDV vaccine formulations has been attempted but as with trials with CDV vaccines in other wildlife populations, vaccine associated deaths have occurred restricting the use of vaccination to protect this species (Halbrooks *et al.*, 1981).

3.4. The Impact of Canine Parvovirus Infection on the Grey Wolf

Canine parvovirus (CPV) emerged relatively recently as a disease within the domestic dog population. The first descriptions of the disease, a severe haemorrhagic enteritis with associated leucopoenia, were reported in the USA in 1978 (Appel *et al.*, 1978). Retrospective serology suggests that the virus was present in Europe between 1974 and 1976, becoming global by 1978. Its origins remain unknown but could have resulted from a spillover of the closely related feline panleucopoenia virus infecting wild canids (Hoelzer and Parrish, 2010). Evidence rapidly accumulated for its presence in wild canid populations between 1979 and 1983. The first evidence for its presence in the grey wolf came from serology studies on wild populations in Minnesota (Mech *et al.*, 1986). Of 77 wolves sampled between 1980 and 1983, 57% were seropositive for CPV. A more dramatic demonstration of the impact of CPV on wolves was the report of the death of nine pups and two yearlings from captive wolf packs (Mech *et al.*, 1986). The first documented description of CPV infection in a free roaming wolf did not come until 1997. The animal was a nine month old female that had been fitted with a radio-collar enabling recovery of it carcass. Microscopic investigation of sections of the ileal mucosa showed loss of villi and dilation of the intestinal crypts (Mech *et al.*, 1997). CPV was confirmed as the cause of death when parvovirus particles were detected by electron microscopy in faecal samples obtained from the wolf.

The impact of CPV on wild wolf population survival has remained unclear. Long-term studies on wild populations in the USA, mainly using serosurveys, suggest that when endemic, CPV-induced mortality occurred among pups, but did not lead to an overall population decrease (Mech and Goyal, 1995). However, CPV may limit the ability of a wolf population to increase and have a greater impact on small isolated populations where immigration cannot compensate for increases in mortality.

4. THE AFRICAN WILD DOG

4.1. Ecology of African Wild Dogs

The African wild dog (*Lycaon pictus*) is one of several endangered canine species present in sub-Saharan Africa. Although this species was once found throughout the non-forested areas of sub-Saharan Africa, today only small pockets remain and their numbers have declined significantly over the last 15 years. The species has been virtually eradicated from West Africa, and population numbers have reduced in central Africa and north-east Africa. Southern Africa retains the largest population although significant populations of wild dogs are also thought to exist in the southern part of East Africa, especially within Tanzania and northern Mozambique. Surveys have suggested that between 3,000 and 5,500 free-ranging wild dogs remain in Africa. Where they do remain, wild dogs inhabit a diverse range of environments ranging from dense forest to woodland to open plains. This ability to cover diverse habitats ensures that prey species are constantly available. Its Latin name translates as “painted wolf” and reflects the brown, black and yellow coat that is unique to each animal and serves as a useful unique identifier. The species is a top predator and as such plays a significant role in the maintenance of the predator-prey dynamic, often predating weak or sick animals, in turn ensuring a natural balance within the ecosystem. Its primary food source is considered to be relatively small to medium-sized mammals, including various antelope, wildebeest calves, and warthogs although when larger prey items are scarce, they have also been known to hunt rats and birds. Occasionally, they may also take domestic livestock, a consequence of which is their persecution by humans.

Due to their high hunting success rates, and the large quantities of prey required to maintain the pack, farmers often shoot or poison wild dogs, often driving numbers low enough to threaten pack viability.

An adult African wild dog can weigh between 18 to 34 kg. They are tall, lean animals with characteristically long legs reaching 76cm at the shoulder in adulthood. They have long lean bodies averaging 1 metre in length and a long tail that is often 30-45 cm in length. The tail has a distinctive white tip that is thought to be used as a visual signal to maintain pack structure during a hunt. Other characteristic features include very large, strong jaws. The bite force quotient, a measure of bite strength relative to body mass, for these dogs is the highest of any extant mammal within the Order Carnivora. They also have very large, erect ‘bat-like’ ears that hint at the species’ excellent hearing.

As with many canid species, the African wild dogs form highly organised cooperatively-breeding packs. Packs have been reported to range from six to 20 animals, although it is widely thought that the lower limit of pack size dictates the sustainability of the pack to maintain hunting efficiency. These animals are highly sociable and pack hunts are well organised and targeted. The prey species rarely escapes a wild dog pack as the individuals support each other to ensure a successful hunt.

The ability of these dogs to cover vast areas due to their high levels of stamina, often moving at speeds of over 45 kilometers an hour to ensure that prey species do not escape.

Following a successful hunt, pack members will return to the den and regurgitate meat for nursing females and pups. Despite the fact that litters can be large, few survive often dying from exposure, predation by larger carnivores or disease. Where pups do grow to adulthood, it is the shared responsibility of the entire pack to sustain the younger animals with all members providing food and support.

4.2. Impact of RABV and CDV on African Wild Dog Populations

Reasons for the decline seen in wild dog populations are not completely understood although interaction with man, either through loss of habitat or conflict is thought to play a significant role. Furthermore, with the advent of molecular characterisation of infectious disease agents, more and more deaths are being attributed to infection with viruses such as CDV and RABV. Population decline has long been attributed to infection with these viruses, and these diseases have been diagnosed in wild dogs in the Serengeti National Park, Tanzania (Gascoyne *et al.*, 1993), the Maasai Mara National Reserve, Kenya (Kat *et al.*, 1996) and Madikwe Game Reserve, South Africa (Hofmyer, *et al.*, 2004), where wild dog populations have been driven to the brink of extinction (Hofmeyer *et al.*, 2000).

For CDV, serological evidence within African wild dog populations has been described in numerous reports (Alexander *et al.*, 2010) although few clinical cases have been reported. However, three confirmed outbreaks have been reported in free ranging African wild dogs. The first outbreak reported was in Chobe National Park, Botswana during 1994 where a pack of 12 animals were reduced to two surviving females (Alexander *et al.*, 1994). Then in Mkozami Game Reserve, Tanzania, 49 members of a 52 animal pack died during a CDV epidemic during 2000, some of which had been previously vaccinated. This remains the most extensive mortality reported in this species that has been characterized to date. Most recently, a further outbreak was characterized in Tanzania, close to the boundary of the Serengeti National park where 23 members of a pack of approximately 38 animals died following CDV infection. In this outbreak genetic characterization confirmed CDV as the causative agent although secondary bacterial infection was evident through histopathological examination of tissue samples (Goller *et al.*, 2010).

In the interests of conservation, numerous attempts have been made to assess the appropriateness of vaccination of wild dog populations against CDV. However, several reports have detailed vaccine associated mortalities in vaccinated animals where standard live attenuated vaccines, safe for domestic canids, have been used. Despite a reduced immune response following vaccination, the alternative, inactivated vaccine preparations, may be of use in vaccinating these animals where necessary (Cirone *et al.*, 2004). Likewise, there have been a number of attempts to develop oral vaccination strategies against RABV for African wild dog populations (Knobel *et al.*, 2002).

5. OTHER ENDANGERED CANIDS

5.1. The Maned Wolf

Genetically and morphologically, the maned (*Chryscyon brachyurus*) wolf is quite distinct from the grey wolf. However, it is one of the largest carnivores in South America. The maned wolf weighs approximately 25 kg with a reddish-brown coat, thickened around the neck to give the species its name. Its' long stilt-like legs allow the wolf to move quickly across dense vegetation. The maned wolf has an omnivorous diet consisting of small mammals, reptiles, birds and fruit. The range of the maned wolf is extensive covering southern Brazil, south of the Amazon forest, Argentina and eastern Bolivia, favouring habitats of open forest and savannah grasslands. Males and females form monogamous partnerships that defend territories of approximately 30km^2 in size.

Litter sizes can vary between one and five cubs although little is known of how cubs are raised or what triggers the young to disperse and at what age.

The maned wolf is not considered endangered although it is absent from much of its potential range and the wild population may consist of as few as 1,500 individuals. Habitat destruction, road mortality and hunting are commonly cited as reasons for this apparently low population level. In response, captive breeding programs have been initiated with some success. Captive maned wolves have been reported to be susceptible to many infectious diseases including the giant kidney worm (*Dioctophyme renale*), one of the largest helminthic parasites (Bevilaqu *et al.*, 1993) and CPV (Fletcher *et al.*, 1979). A single study has reported on the seroprevalence in maned wolves to a range of viral diseases affecting the maned wolf (Deem and Emmons, 2005). The study measured seropositivity in four individuals sampled in the Noël Kempff Mercado National Park in Bolivia and demonstrated that these animals had been exposed to canine adenovirus (CAV), CDV, CPV and coronavirus. One animal was also weakly positive for rabies virus but none were positive for canine herpesvirus. In a similar study, 40 domestic dogs from areas adjoining the national park were tested and shown to have high seropositivity to CDV (93%), CPV (85%) and RABV (56%) (Bronson *et al.*, 2008). Rabies is present throughout South America in both domestic dog and both insectivorous and haematophagous bat populations (Favi *et al.*, 2003) and the danger of spillover of this and other viral diseases presents a constant challenge to the survival of the maned wolf.

5.2. The Red Wolf

The precise taxonomic status of the red wolf (*Canis rufus*) is unclear with some advocates suggesting that it is a subspecies of the grey wolf (Wilson *et al.*, 2000), whereas others argue that based on morphological grounds the red wolf is a distinct species (Nowak, 2002). The red wolf is smaller than the grey wolf weighing between 18 kgs and 36 kgs. Its coat, from which it derives its name, is often red but can also be grey and black. The species is also highly susceptible to hybridization with coyotes (*C. latrans*). However, most of what is known about wild-living red wolves has been derived from pre-1960s literature as the species is now thought to be extinct in the wild. The original geographic range of the red wolf extended over southeast and south central USA, but by the 1960s, this species was considered endangered to the extent that in 1973 a captive breeding program was instigated to save the species. Over 400 canids resembling the red wolf were captured of which only 43 were positively identified as being of the correct species. Following initial breeding trials only 14 were considered pure red wolves and not coyote hybrids (Philips *et al.*, 2006). From this meagre start there is now a captive population of over 150 individuals. Four pairs of red wolves were released in 1987 into the Alligator River National Wildlife Refuge in North Carolina where there are now approximately 100 red wolves.

To date there have been no reports of infectious diseases affecting the re-introduced population compared to numerous reports in other wild canids across the United States (Krebs *et al.*, 2003). However, the small size of this wild population suggests that the effect, should a pathogen be introduced, would be devastating. This is a real threat as the incidence of rabies in the wildlife of North Carolina is high in comparison to other American states, particularly within the raccoon population (Blanton *et al.*, 2010).

5.3. African Jackals

There are three jackal species found in Africa although the most common, the golden jackal (*Canis aureus*) is also found in Europe and Asia (see Table 3). The other two species, the side-striped (*C. adustus*) and the black-backed (*C. mesomelas*) jackals are found only in Africa but with distinct geographical distributions. The black-backed jackal is further separated into two sub-species and located in two separate regions of Africa.

Table 3. An overview of three African jackal species

	Golden Jackal	Side-striped Jackal	Black-backed Jackal
Geographical distribution	Widespread across northern Africa, southeastern Europe, Middle East and Southern Asia	West, central and southern Africa	Two separate subspecies: *Canis m. schmidti* located in east Africa *Canis m. mesomelas* located in southern Africa
Physical description	Yellow to pale golden fur across the whole pelt.	Buff-grey pelt with a single white strip running along both flanks bordered by black areas.	Reddish brown fur on flanks and legs with the back being covered with black and silver fur.
Weight	8-10 kg	7-12 kg	7-14 kg (East African jackal) 5-10 kg (Cape jackal)
Length	70-80 cm	65-80 cm	65-75 cm

Each of the African jackal species shares a number of common features including adaptability to a wide range of habitats, an omnivorous diet and all form monogamous pairs that will defend a territory. Critically, none of these species is considered endangered and estimates of population numbers for each are cited in the millions suggesting that they will be minimally affected by an infectious disease. Seroprevalence surveys of all three species in Kenya, where all three species are present, detected a relatively high prevalence for CPV-2 (34%) but much lower levels for CDV (9%) and rabies virus (1%) (Alexander *et al.*, 1994). Certainly, evidence suggests that a distemper-like disease has affected jackal populations, reducing population numbers significantly between 1978 and 1979. Interestingly, it appears that sympatric golden jackals and African wild dogs were not affected during this outbreak. Factors such as habitat loss, human encroachment and persecution will all have a greater impact on jackal populations. However, after livestock depredation, one of the main reasons for persecution is the jackal's role as a reservoir for rabies. Retrospective studies of rabies cases in South Africa indicated that over 25% of animals tested were either the side-striped or black-backed jackal (Bingham *et al.*, 1999). Mapping of these cases demonstrated regional separation of cases based on the dominant jackal species with temporal analysis of particular outbreaks suggesting that although the origin of infection was likely to be the domestic dog, there was strong evidence that the black-backed jackal could maintain independent transmission cycles of the virus. In parts of South Africa, regular incidences of rabies in the black-backed jackal are reported (Zulu *et al.*, 2009). In Zimbabwe, the majority of rabies cases occurred in side-striped jackals rather than black-backed jackals (Rhodes *et al.*, 1998). Rabies cases in jackals do occur but independent transmission cycles are rare and may be related to changes in population density.

The adaptability of jackals enables them to be more resilient to human persecution. In South Africa, persecution of carnivores in general removed the larger species that compete with jackals enabling the jackal population density to rise, particularly in rural areas (McKenzie, 1993). In addition, persecution encourages dispersal of young adults into areas where the population of resident jackals have been reduced, encouraging mixing of populations and increasing the chance of disease transmission. Oral vaccination has been demonstrated to be effective in both the black-backed and side-striped jackals (Bingham *et al.*, 1995) and this offers the most effective means of protecting the species from infection and limiting the public health risk of rabies transmission to humans.

CONCLUSIONS

Populations of wild canids are declining globally due to a variety of factors. The expansion of humans into most available environments has brought humans and wild canids into direct contact. And with humans, come domestic dogs. The close genetic relationship between domestic dogs and wild canids readily allows the transmission of infectious diseases between the two, due to their shared receptivity of numerous pathogens. While wild canids can transmit diseases to domestic dogs, humans and their livestock, the major flow of diseases has been shown to move from domestic dogs into wild canid species, often with detrimental effects on the population sizes of the wild canids. Indeed, several species have experienced local extirpation due to diseases such as rabies and canine distemper, while some species are left finely balanced on the brink of extinction.

While preventing contact between domestic dogs and wild canids remains a potential method for reducing disease transmission between the two, such measures are often unrealistic, especially considering that many wild canids roam outside formally protected areas. In fact, contact is likely to increase in the future as human populations, and the number of their domestic dogs, continue to grow. With this in mind, it is crucial to immediately implement methods to reduce or even eliminate infectious disease as a threat to wild canids.

Our knowledge of canid-associated diseases, particularly common viruses such as rabies and canine distemper, has increased substantially over the past three decades. While there is yet more to learn, especially for relatively recent discoveries such as canine parvovirus, the increased efficiency of laboratory analysis should allow for more effective diagnosis of disease epidemics, helping to guide subsequent conservation actions. Furthermore, the development of vaccines for these canid-related diseases has been rapid and impressive. Ideally, conservationists should move away from reactive vaccinations in response to disease outbreaks, an exercise in damage limitation, performed once individuals have already been lost. Diseases brought by humans and their domestic dogs into the habitats of wild canids should be treated as an unnatural anthropogenic threat, rather than as a natural regulator of wild canid populations. In these situations, conservationists should consider proactive vaccinations as a means of immunizing endangered species against such threats. Any form of vaccination is expensive and requires commitment over a number of years in order to achieve disease elimination. However, the successful eradication of rabies through oral vaccinations in western Europe and parts of the United States offers hope to many of these highly endangered species.

As a general observation, there is strong evidence that wild canid populations are repeatedly exposed to viral infectious diseases that can in some instances have dramatic effects. Seroprevalence studies in a range of species repeatedly provide evidence for exposure but also indicate that such exposure lead to seroconversion and survival. However, particular properties of certain viruses suggest that they can have serious negative effects on canid species. Two viruses in particular are noteworthy. Firstly RABV, where infection inevitably leads to death, and secondly, CDV, which following infection leads to immunosuppression of the host rendering it more susceptible to other infections. Thus the impact of these two viruses on wolf species and other rare canids can, depending on a number of factors, be incredibly significant with respect to population sustainability. A critical factor here is the initial size of the population at either the local or global level. For the Ethiopian wolf, the impact of viral disease can be devastating and human intervention, in the form of vaccination campaigns and local dog management, is needed to ensure the survival of the species. A similar situation exists for the African wild dog where the fragmentation of the population into discrete areas makes any one population of the species susceptible to viral outbreaks and elimination. For the grey wolf, the impact on global numbers of any one infectious disease is minimal. However, the impact locally can be equally devastating such as the effects of introduction of rabies into a wolf pack described by Chapman (1978). The communal nature of many canid species compounds the impact following introduction of a new virus at the local level. A further factor indicated by seroprevalence studies is the possibility of multiple infections, that when occurring simultaneously could increase the impact on the species.

Finally, human activities, both positive and negative should be considered. The creation and protection of habitats suitable for wolves and wild canids is probably the most important action that can be taken to ensure that natural drivers on populations, including viral infections, are minimised. Likewise, vaccination programmes, such as those initiated for the Ethiopian wolf are of great importance in protecting endangered species from incursions of viral pathogens from domestic dog populations.

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Chapter 3

THE EFFECTS OF LETHAL CONTROL ON THE CONSERVATION VALUES OF *CANIS LUPUS DINGO*

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ABSTRACT

The need to conserve terrestrial apex predators is internationally recognized because most of these predators are relatively rare. Derived from the grey wolf (*Canis lupus*), dingoes (*C. l. dingo*) are the largest terrestrial predator in Australia, but they are not threatened by decreasing numbers per se. Rather, hybridization with domestic dogs is changing the genetic integrity of dingo populations despite their widespread and common occurrence. Additionally, maintaining the role of dingoes in suppressing mesopredators and indirectly protecting faunal biodiversity is promoted as a key dingo conservation goal. By extension, lethal dingo control programs aimed at mitigating livestock losses have come under increased scrutiny for their perceived negative effects on biodiversity conservation. This study discusses the effects of lethal control on these two conservation values of dingoes using historical and contemporary datasets from arid Australia as an example. From historical data, it is shown that baiting typically occurred infrequently, though periods of spatially and temporally intensive control has the ability to reduce dingo abundance when conducted repeatedly over many years. From contemporary data, it is shown that sporadic and spatially restricted dingo control practices have little effect on the persistence of dingoes. It is concluded that contemporary dingo control practices may provide a catalyst for localized hybridization, but the ecosystem function of dingoes is unlikely to be altered by current control practices in any significant way. Ongoing lethal dingo control may still be practiced in an ecologically conservative manner while continuing to protect livestock production values.

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Keywords: apex predator, *Canis lupus dingo*, hybridization, lethal control, mesopredator release, sodium monofluoroacetate (1080)

INTRODUCTION

Terrestrial apex predators have been in conflict with humans for millennia, which led to the widespread declines of predators in many parts of the world (Estes *et al.* 2011). Grey wolves (*Canis lupus*) have fared particularly poorly, having been locally eradicated from many parts of their former range across Europe and the Middle East, Asia, and North America (Chapron *et al.* 2003; Trouwborst 2010). Recent concern over the plight of apex predators generally has led to the restoration and recovery of wolves in many countries (Hayward and Somers 2009; Randi 2011).

Dingoes (*Canis lupus dingo* and hybrids) have an average weight of ~15 kg (Corbett 2001b), and are the largest terrestrial predator in Australia. Dingoes are classic mesopredators (see definitions in Roemer *et al.* 2009), as are most canids, but in Australia they act as apex predators when the role of humans is disregarded (Fleming *et al.* 2011b). Like all dogs, dingoes were derived from wolves by human selection pressure (Corbett 2001b; Saetre *et al.* 2004; von Holdt *et al.* 2010). Hence, they are not ‘Australian wolves’ as such, but rather, they are the feral descendants of the most primitive domesticated wolf. Their accepted taxonomic name has undergone multiple changes since being first described (Corbett 2001b), but they are presently classed as a sub-species of grey wolves (Savolainen *et al.* 2004; Pang *et al.* 2009) and are referred to by a range of commonly used names (Allen *et al.* 2011a). In other words, dingoes are not wolves but may be the most closely related canid to them. After over 10,000 years of domestication pressure, just a handful of domesticated dingoes were brought to Australia through southeast Asia about 4,000 years ago and literally ‘let loose’ (Corbett 2001b; Savolainen *et al.* 2004; Oskarsson *et al.* 2011). Despite the many phenotypic, morphological, and behavioral differences between them, dingoes are often considered to occupy a similar ecological niche to wolves, and are assumed to fulfill similar ecological functions.

One aspect of dingo ecology that has transcended the domestication process is their ability to cause conflicts with humans. Dingoes are controlled in many areas because they are a well-known threat to viable livestock production (Fleming *et al.* 2001; Rural Management Partners 2004; Gong *et al.* 2009; Hewitt 2009; Fleming *et al.* 2011a). However, dingoes also have iconic wildlife status with many Australian people (Hytten 2009; Smith and Litchfield 2009). In line with international studies on wolves, there is growing concern over the conservation of dingoes in Australian ecosystems. Two primary conservation values appear particularly significant; these are the loss of pure dingo populations through hybridization with domestic dogs and their perceived ability to structure ecosystems by suppressing mesopredators. Other conservation values are also very important, such as dingoes’ ability to suppress some herbivore populations, such as macropods (e.g. Wallach *et al.* 2010). Some studies support the hypothesis that intensive and persistent dingo control can free kangaroos (*Macropus* spp.) from dingo suppression (e.g. Caughley *et al.* 1980; Allen 2010b), but this issue is addressed more comprehensively elsewhere, and is not discussed here.

Although there are more dingoes in Australia now than at any other time in their ecological history (Corbett 2001b; Davies *et al.* 2010), dingoes were recently identified on the IUCN Red List as a 'vulnerable' species owing to the alteration of their genetic identity through hybridization (Corbett 2008). Genetic change appears to effect dingoes through two processes. First, pure dingoes might mate directly with domestic dogs to create hybrids, and second, hybrids may back-cross with pure dingoes. Behavioral differences are likely to limit opportunities for the former to occur, with the latter process appearing much more insidious (Daniels and Corbett 2003). Lethal dingo control is expected to facilitate encounters between pure dingoes and hybrids, creating opportunities for hybrids to successfully raise offspring (Corbett 2001b; Fleming *et al.* 2001).

Dingoes might also exclude, limit, suppress, or regulate mesopredators (Johnson 2006). Their effects on fox (*Vulpes vulpes*) and feral cat (*Felis catus*) populations are of greatest interest because these two smaller mesopredators have been implicated in the declines and extinctions of dozens of threatened vertebrates (DEWHA 2008b, 2008a). In accord with the mesopredator release hypothesis and trophic cascade theory (Hairston *et al.* 1960; Crooks and Soulé 1999), dingoes are believed to reduce the impacts of these mesopredators on threatened fauna, thereby providing biodiversity benefits to threatened species at lower trophic levels. The generally accepted formula for the positive role of dingoes is: more dingoes = less foxes and cats = more threatened species and greater biodiversity. Importantly however, dingoes are only expected to provide *net* benefits to biodiversity because dingoes have also been implicated in the historical declines of many fauna (e.g. Archer 1974; Kerle *et al.* 1992; Moseby *et al.* 1998; Corbett 2001b; Allen 2011) and presently pose significant direct risks to many other threatened species (e.g. Palmer *et al.* 2003; Coutts-Smith *et al.* 2007; Major 2009; Read and Ward 2011). The strength of interactions between dingoes and mesopredators is therefore assumed to be greater than the strength of interactions between dingoes and prey in most cases, although there is little information quantifying these processes in Australia (Robley *et al.* 2004).

Much discussion has centered on these two conservation values of dingoes in recent years (Robley *et al.* 2004; Glen and Dickman 2005; Glen *et al.* 2007a; Visser *et al.* 2009). However, the majority of the literature supporting the positive ecological roles of dingoes is still weak and unreliable (Allen 2011; Allen *et al.* 2011b, but see also Letnic *et al.* 2011a and Allen *et al.* 2011a), while debate continues over the ecological or functional importance of retaining *pure* dingo populations (Claridge and Hunt 2008; Jones 2009; Purcell 2010). Regardless, recent studies have culminated in calls to prohibit the lethal control of dingoes (e.g. Wallach *et al.* 2010; Carwardine *et al.* 2011) or to actively reintroduce them back into livestock production areas where they have been locally eradicated (e.g. Dickman *et al.* 2009) – collectively referred to hereafter as 'positive dingo management'. The areas where dingoes were locally eradicated are restricted to sheep (*Ovis aries*) production areas in southeastern Australia and amount to <25% of the continent, with dingoes being widespread, common, or abundant elsewhere (West 2008).

Such proposals for positive dingo management are based most commonly on the implicit assumption that lethal dingo control somehow compromises the two conservation values described; though alternative interest groups sometimes encourage positive dingo management on other grounds, such as animal welfare or their intrinsic value as a wildlife species. The basic premise is that lethal dingo control increases hybridization and indirectly harms threatened species populations by releasing mesopredators (Johnson *et al.* 2007; Wallach *et al.* 2010). Thus, as an expected extension to the formula described above: contemporary dingo control = less dingoes = more foxes and cats = less threatened species and reduced biodiversity. Such mechanisms are unlikely to be so simple in reality (Holmes 1995; Fleming *et al.* 2011b), but many recent reports nevertheless tend to view the role of lethal dingo control in this way. For lethal control to exacerbate hybridization, contemporary control practices would need to increase the rate of hybridization by facilitating breeding between dingoes and genetically undesirable individuals. Or alternatively, lethal control would need to selectively remove pure dingoes and not hybrids. To harm threatened species populations through the release of mesopredators, lethal dingo control would first need to reduce or remove dingoes, then release mesopredators, and then have mesopredators harm threatened species further. While quantifying interactions between predators and prey may be difficult, the implicit assumption (i.e. the applied science question) becomes conceptually easy to test through dingo control experiments – comparing areas where dingoes are and are not controlled while monitoring species and variables suitable to make reliable inferences about the effects of control on dingo conservation values.

This study uses contemporary data from such an experiment to report the short- and medium-term effects of lethal control on dingo populations in the arid zone of far northern South Australia (NSA). This was supplemented with historical data on dingo control effort, which was used to investigate longer-term effects. Unless explicitly discussed, the term ‘lethal control’ refers to ground-placed sodium fluoroacetate (referred to hereafter as 1080) poison baiting campaigns and opportunistic shooting, which have been the only noteworthy dingo control methods used in NSA since the early 1970s (Allen 2010b). The approach used here aims to highlight the effects of lethal control on dingoes, thereby providing insight into the likely effects on their conservation values.

METHODS

Two primary data sets were used for analysis. One comprised of historical 1080 bait usage records across the whole of NSA, while the other was derived from recent manipulative experiments on four large cattle properties (Allen 2009b). Historical bait usage records provided the longer-term context for the shorter-term responses of dingoes to lethal control, together allowing an evaluation of the short-, medium-, and longer-term effects of lethal control on dingoes. These data were supplemented with anecdotal information on contemporary levels of opportunistic shooting.

Study System

The beef cattle production regions of NSA are predominantly sandy deserts or stony gibber plains systems interspersed with alluvial drainage lines and flood plains. Mean annual rainfall is <180 mm and is highly variable (Bureau of Meteorology, available at www.bom.gov.au). The soils of NSA are typically old and of low fertility, and the landscape is generally flat with small rises, although some low altitude (<200 m) rocky ranges and mesas are present in selected areas (further details can be found in Kutsche and Lay 2003). For management purposes, NSA is divided into the northeast (NE) and northwest (NW) pastoral regions (~122,000 km^2 and ~126,000 km^2 respectively), each comprising ~20 properties (Figure 2), of which most are used for beef cattle production. The two regions are broadly separated by Lake Eyre and the Simpson Desert.

The NE region is generally dominated by sandy environments, and is the hottest and driest region in Australia. It incorporates large portions of the sandy Strzelecki Desert and the Sturt Stony Desert. Flowing into this region are three large river systems (the Diamantina and Georgina Rivers, and the Cooper Creek) fed by interstate rainfall events that occur outside NSA several hundred kilometers away in northeastern Australia. Flows into the NE region are not constant and the rivers are often dry, but significant flows can occur 2–3 times each decade. The NW region is generally dominated by stony environments (and contains most of the rocky ranges) and has vast areas of gibber plains (Smyth *et al.* 2009). It incorporates the sandy Pedirka Desert and the aptly named ‘Moon Plain’. River systems occurring in this region are fed only by local rainfall events and are usually dry.

Despite the aridity of NSA, the many permanent and semi-permanent water holes present along the river systems in both regions are a valuable water resource for pastoralism (James *et al.* 1999; Box *et al.* 2008; Smyth *et al.* 2009). Nevertheless, surface water alone is too unreliable to maintain significant cattle herds, and economically viable beef production is made possible only through a network of artificial waterpoints sourcing artesian and sub-artesian water resources (James *et al.* 1999). Creation of artificial waterpoints (e.g. bores, wells, dams, and tanks) in NSA began with the arrival of European pastoralists in the late 19th century and continues today on properties not yet fully developed. Waterpoint density therefore varies between properties, but there are few pastoral areas in NSA >10 km from an artificial water source and none >50 km (Landsberg *et al.* 1997; Fensham and Fairfax 2008; Smyth *et al.* 2009).

Long-Term Bait Usage

Official 1080 bait supply records for each property within NSA were obtained from the state government department responsible for administration of 1080 usage in South Australia. Units of measure were ‘kilograms of meat’, which was converted to ‘number of baits’ by dividing each value by seven – the approximate number of ‘dingo size’ baits cut from each kilogram of meat. This was necessary to incorporate data on commercially manufactured 1080 baits (e.g. Doggone®, manufactured by Animal Control Technologies, Melbourne), which have been widely used in recent years. From 1972 to 1986, meat baits were prepared by tumbling them in 1080 solution, whereas from 1987 until the present, baits were injected with 1080 concentrate. Both methods produce baits lethal to dingoes (Korn and Livanos 1986). Records were property-specific, facilitating easy spatial representation in GIS software (ArcGIS 9.3, ESRI Inc.). Information on opportunistic shooting was obtained informally through discussions with approximately half of the beef producers in NSA during public workshops and phone interviews conducted between 2008 and 2010.

The use of historical 1080 baiting records assumes that bait usage (as reported) was the primary dingo control tool applied in NSA throughout the period. It is further assumed that other forms of lethal control (such as unreported baiting or landholder-manufactured strychnine baits) were substantially less important at a regional scale during this time. Interviews with long-time cattle producers and senior government staff assert that besides opportunistic shooting, other forms of dingo control were seldom used, and none were near as common as 1080 baiting. It was also assumed that baits were used soon after their supply. While baits may have been dried or frozen for some time before distribution, it would be unusual for baits to be stored longer than a few months before use.

Because of these assumptions, the use of 1080 supply records as the primary descriptor of dingo control may be better viewed as an indicative measure or index of dingo control effort, rather than the unequivocal descriptor of it. In any case, these assumptions are likely to apply equally to both regions, and no other significant forms of dingo control have been assessed in this study.

Manipulative Experiments

A large-scale manipulative experiment was conducted between 2008 and 2010 on four large cattle properties in NSA (Figure 2). Quinyambie is located in the sandy Strzelecki Desert about 200 km northwest of Broken Hill. The only two habitat types present in the study area there were parallel sand dunes and the clay swales that separate them. Cordillo Downs is located in the extreme northeast corner of South Australia, where gently undulating stony gibber plains and high irregular sand dunes are present. Significant proportions of the study area there were also located in large, flat floodplain habitats with almost no vegetation higher than 50 cm at any time, besides an occasional tree. Todmorden and Lambina adjoin each other, contain both sandy and stony gibber habitats, and are situated between Oodnadatta and Marla in the central north of South Australia, ~400 km south of Alice Springs. Habitats at the latter three sites were interspersed with timbered drainage lines that form key refuge areas in hot weather conditions. Additional and more detailed information on the study sites is provided in Allen *et al.* (2011c).

According to the recommended experimental design presented in Allen et al. (2011b), and in accord with similar experiments previously conducted elsewhere (e.g. Eldridge *et al.* 2002; Allen 2005), each property was divided into two treatment areas; one where dingoes were subjected to 1080 baiting twice annually and another non-baited 'experimental control' where dingoes were not exposed to lethal control of any kind during the study. At each site, each treatment area contained a similar mixture of habitats found in the adjacent treatment area, with both matched treatments being representative of the surrounding regions. The size of the baited treatment areas ranged between 1,300 km^2 and 2,500 km^2. Matched non-baited areas on each property were approximately equal or of greater size in most cases. Poison baits were distributed from the ground around livestock waterpoints and along the vehicle tracks that interconnect them, according to common practice and in line with legislative requirements. Baiting intensity in each baited area varied between properties, though no fewer than 600 baits were distributed in <48 hours during each baiting session. In this way, the experiment was able to monitor the response of dingo populations to contemporary baiting practices. The baited area on Quinyambie was surrounded by areas infrequently subjected to lethal control while the baited area on Cordillo Downs was located within a wider mosaic of baited and non-baited areas. The baited areas on Todmorden and Lambina were within the most intensively baited region in NSA (Figure 2).

Dingo population responses to baiting were monitored using the passive activity index of Allen et al. (1996) according to the principles described in Engeman (2005). Activity surveys were conducted three or more times each year (beginning in March 2008 and continuing for up to 3 years) and repeated at similar times each subsequent year. A transect was established in each treatment, each containing 50 sandplot tracking stations spaced 1 km apart along vehicle tracks. Each tracking station was ~120 cm wide, spanned the width of the road, and was typically smoothed and read daily for 2–3 consecutive days at each survey. Each set of tracks/footprints identified on the tracking stations was recorded. Results are expressed as the number of dingo tracks/tracking station/night, after excluding any stations rendered unreadable by wind, rain, or other factors.

RESULTS AND DISCUSSION

Opportunistic Shooting Intensity

Opportunistic shooting has been a common practice in livestock production areas since the advent of pastoralism in the 19th century, but it has an unknown influence on dingo social structure and behavior. In principle, shooting has the ability to be more selective than baiting because specific individuals can be identified and targeted for control. Thus, dingoes of hybrid appearance or those responsible for attacking livestock can be selectively removed. In practice however, the genetic identity of dingoes is not reliably discernable from visual characteristics (Elledge *et al.* 2006; Elledge *et al.* 2008; Jones 2009), and unless an individual dingo is witnessed attacking livestock firsthand, there is no reliable way of determining whether or not a particular individual poses a risk to cattle. Hence, most dingoes seen are shot or shot at, rendering the technique as similarly unselective as baiting (discussed below).

The numbers of dingoes shot in any given year in NSA is unknown, but will be a function of the number of dingoes seen, the ability of the shooter, and the ability of the dingo to avoid being shot. Unless beef producers are especially motivated and proficient, the number of dingoes shot in most years is likely to be negligible. There are less than 40 properties in NSA, and conversations with beef producers indicate that few dingoes (i.e. <20) are shot on most properties in any given year, if any at all. The average property size within NSA is over 5,000 km^2, the largest being over 16,000 km^2 (Figure 2). Moreover, in most cases, beef cattle management practices in the arid zone also mean that tracts of land away from sparsely distributed vehicle tracks are only visited by humans once or maybe twice a year during cattle mustering times. This restricts opportunities to shoot dingoes to the immediate vicinity of the vehicle tracks most of the time. Areas requiring the frequent maintenance of water infrastructure are visited more often, usually weekly, though this naturally occurs less frequently on properties with a greater proportion of large dams and waterholes, which retain water longer than small bores and troughs. Coarse calculations therefore suggest that approximately 200–400 individuals are shot in most years in an area of ~248,000 km^2. Additionally, dingoes are rarely if ever exposed to lethal control in adjacent nature conservation zones of approximately 255,000 km^2. Similar sized areas largely free of dingo control also exist in Western Australia and the Northern Territory (Fleming *et al.* 2001), meaning that dingo populations in much of inland Australia remain largely unmanaged, even in some pastoral regions.

Besides opportunistic shooting, the active hunting and shooting of dingoes sometimes occurs in response to extraordinarily high dingo numbers in localized areas and a perceived high risk to calves. Some extreme cases report several hundred dingoes being shot on some NSA properties in years when introduced rabbit (*Oryctolagus cuniculus*) numbers have supported high dingo densities. However, such hunting efforts probably only remove a modest proportion of the dingoes present at these times (B. Allen, unpublished data). Properties hunted in this way still retain similarly high-density dingo populations whenever prey is in abundance.

Long-Term Bait Usage

Official 1080 bait supply records indicate that baiting occurred infrequently across most of NSA between 1972 and 1990 (Figure 1). Thereafter, the NE region continued to receive baits only occasionally, while supply to the NW region noticeably increased in 1990 and remained comparatively high until 2005. Provision of 1080 baits to the whole of NSA fell dramatically after 2005 to the point where no baits at all were supplied in 2009 and only six properties (three each in the NE and NW) received baits in 2010. Prior to 1990, the mean number of properties receiving baits annually was 14% and 7% in the NE and NW regions respectively. After 1990, this increased to 23% and 55% respectively.

These historically low levels of baiting were likely to have been influenced by government policy subsequent to the withdrawal of sheep from the region (Allen 2011), which then recognized dingoes as a legitimate wildlife species worthy of preservation in NSA (Animal and Plant Control Commission 1993; DWLBC 2005). Explanations for the increase in baiting in the NW region in 1990 are not fully known, but the increase had its genesis at a time of reportedly very high dingo abundance and livestock losses. The increase might also be related to greater promotion of baiting (for calf protection) by government staff or motivated local champions, perhaps facilitated by the advent of telephone communications to this remote region in the late 1980s. Additional information can be found in Allen (2010b).

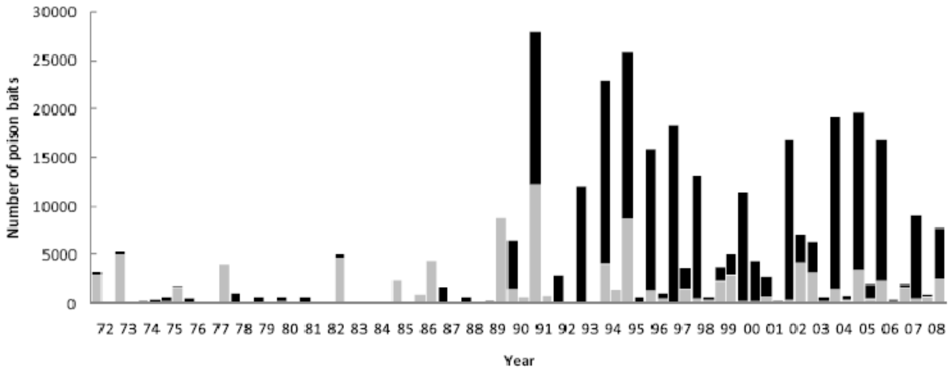


Figure 1. The total number of poison 1080 baits supplied to the northeast (light) and northwest (dark) pastoral regions for each six-monthly period between 1972 and 2008 (results stacked).

The 1080 ‘Directions for Use’ permit a baiting intensity of up to 10 baits/km^2 (APVMA 2008). However, the greatest annual supply of baits to the NE region (8,810 baits) occurred in 1989, equating to a regional baiting intensity of only 0.07 baits/km^2. The greatest supply of baits to the NW region (20,360 baits) occurred in 1997 when baiting intensity reached only 0.16 baits/km^2, demonstrating that actual levels of dingo control in NSA are far lower than what is permissible. However, baiting intensity would never be expected to reach such permissible levels because of the way baits are distributed in NSA (discussed below).

As expected, spatial comparison revealed that baiting intensity was not consistent between properties in space or over time (Figure 2). In other words, some areas received baits more frequently than others, which changed from year to year, creating a spatiotemporally fluctuating mosaic of baited and non-baited areas. Sheep grazing in NSA persisted longer in the NW than in the NE (Allen 2011), and between 1972 and 1989, the most intensive baiting occurred on the last remaining sheep-grazing property in the NW region (Figure 2a). Between 1990 and 2008, baiting most frequently occurred in the NW region and on those properties adjoining the dog fence (Figure 2b). Baits were also supplied (and presumably used) predominantly in the first six months of the year (Figure 1), which may reflect the popular approach to target mature dingo populations before their annual breeding season (Fleming *et al.* 2001).

At a finer scale, the distribution of many post-1990 baits on properties abutting the dog fence were most likely concentrated in areas immediately north of the fence as part of a ‘buffer baiting’ strategy designed to remove dingoes ‘in the vicinity of the fence’ and reduce dingo incursions into protected sheep grazing lands to the south (Bird 1994; DWLBC 2005). Part of the reported increase in baiting effort was therefore likely associated with the expansion of the baited buffer zone from a simple line of baits laid immediately along the fence prior to 1993 to a strategy which permitted all artificial waterpoints in a buffer zone extending 35 km out from the fence to be baited thereafter.

For this reason, the spatial representation of baiting intensity for properties that adjoin the dog fence in Figure 2b may be overstated, whereas the reported baiting intensities for properties not adjoining the dog fence are likely to be represented more accurately. Disregarding properties along the dog fence, only a few properties in the entire NE pastoral region received baits more than five times in the last 20 years (Figure 2b).

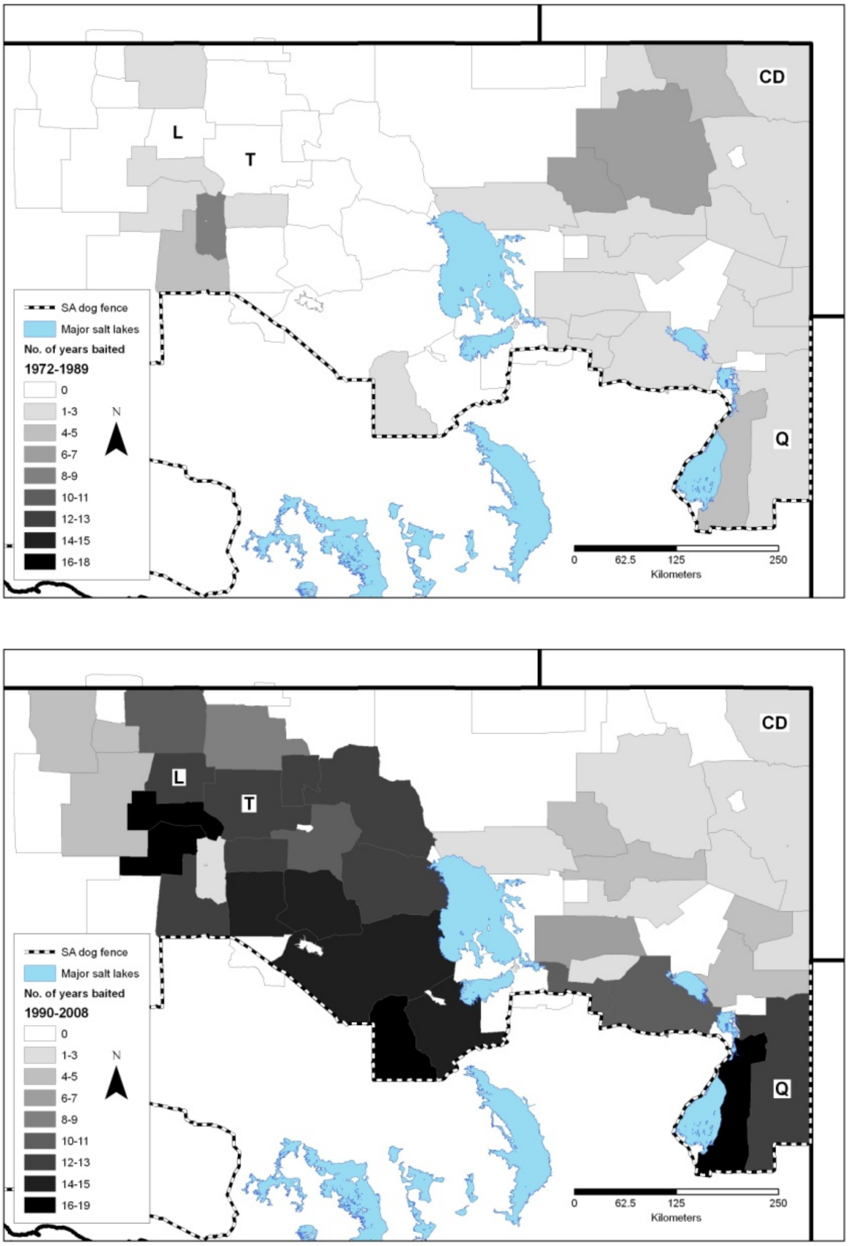


Figure 2. Location of study sites (Q = Quinyambie, CD = Cordillo Downs, T = Todmorden, and L = Lambina), and the frequency and distribution of poison 1080 bait supply to pastoral properties in northern South Australia, 1972–1989 (top) and 1990–2008 (bottom). Baiting intensity in areas south of the SA dog fence are not represented.

The relatively infrequent use of 1080 baiting in the NE suggests that present-day dingo abundance is not the product of lethal control, but is instead primarily determined by the carrying capacity of the area, or other bottom-up factors such as drought, prey shortage, or social constraints (Allen 2010a; Scherber *et al.* 2010). Bait usage records further indicate a generally conservative attitude towards dingo control by beef producers, suggesting that dingo populations have remained relatively unaltered by lethal control across ~122,000 km^2 of northeastern NSA for at least 40 years (the NW region is discussed in more detail below). This is supported by information from Quinyambie and Cordillo Downs demonstrating that baiting has limited short-medium term effects on the activity or relative abundance of dingoes in the NE region.

Short-Medium Term Effects of Baiting

The experimental data demonstrates that dingo activity fluctuated independently of 1080 baiting at Quinyambie and Lambina and was highly variable at Cordillo Downs and Todmorden (Figure 3). There was, therefore, no clear evidence for sustained, baiting-induced reductions of dingo activity at each of the four sites during the study period. Although baiting undoubtedly killed some dingoes (multiple individuals were witnessed eating poisoned baits), baiting had no lasting effects on activity trends beyond the initial reductions expected. Moreover, initial reductions (or a ‘knock down’ effect) were not apparent each time baits were distributed (Figure 3). This suggests that baiting can have short-term effects on dingo abundance (as intended) on some occasions, but these are only temporary.

Besides Quinyambie, it could be argued that the relative abundance of dingoes in each treatment at the other three sites was similar at the beginning of the experiment and that populations were subsequently tempered by baiting (Figure 3).

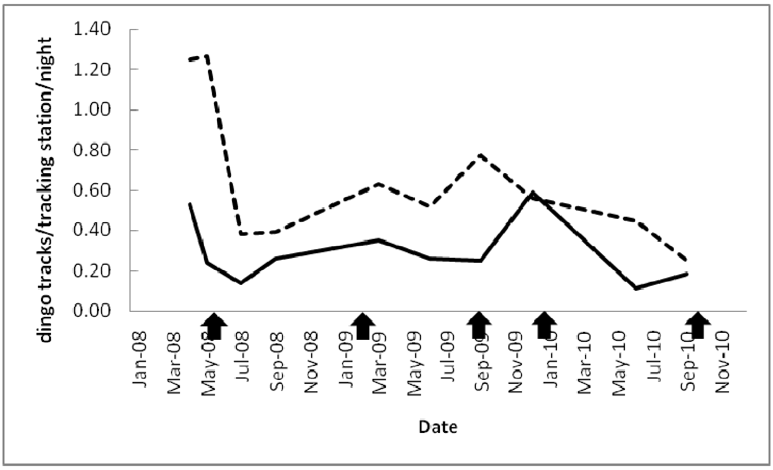
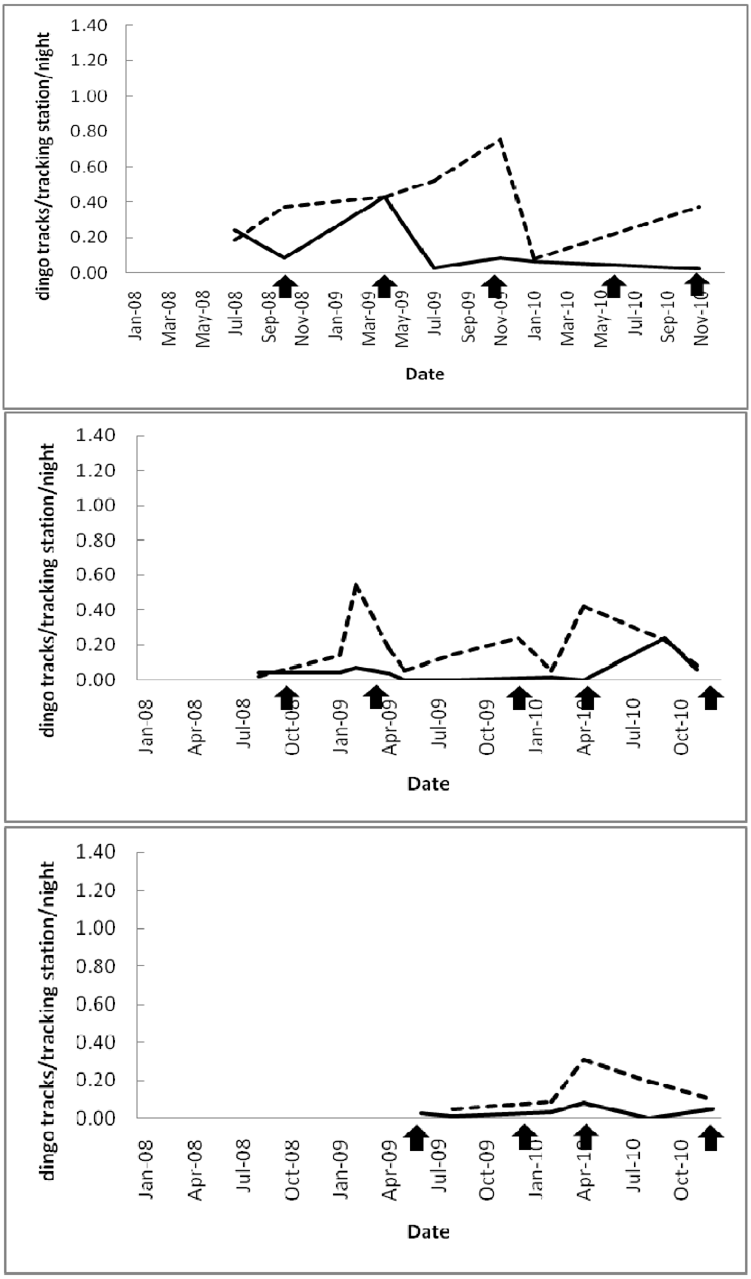


Figure 3. (Continued).



Note: Three of the horizontal axis in Figure 3 (i.e. the dates) may be removed and condensed into one provided the graphs are stacked on top of each other. When formatting Figure 3, it is critical that the black arrows stay in their correct place, properly identifying the correct dates. The correct dates are provided with Figure 3 should there be any uncertainty about placement of black arrows.

Figure 3. The activity trends of dingoes in baited (solid lines) and non-baited (dashed lines) treatment areas on Quinyambie (top), Cordillo Downs (middle top), Todmorden (middle bottom), and Lambina (bottom). Baiting times are indicated by black arrows.

Alternatively, these lower levels of activity in baited areas may also reflect local variation in dingo densities given their identical population trends, and the results cannot therefore be confidently viewed as localized baiting-induced abundance differences (Engeman 2005). Prior to the study, Quinyambie rarely baited outside the buffer zone and baiting was historically applied to both treatments on Todmorden and Lambina for many years (Figure 2b). Non-baited populations also exhibited greater variation in activity, often resulting in similar relative abundance estimates for both treatments during a given survey (Figure 3). This further suggests that the similar population levels recorded at the onset of the experiment could simply be an artifact of naturally fluctuating activity levels (i.e. not baiting-induced).

While the increased activity of surviving dingoes might have contributed to the immediate post-baiting observations (a behavioral response), rapid immigration from nearby tracts of land (including non-baited areas within the overall ‘baited’ treatment) over subsequent weeks and months probably negated any baiting-induced population reductions. This result was expected, because contemporary dingo control practices rarely reduce dingo activity by even 50% (Twigg *et al.* 2000; Eldridge *et al.* 2002; Allen 2005; Allen 2006; Kennedy *et al.* 2011), and immigrant dingoes typically reinvade baited areas within a few months, usually returning to pre-baiting levels by the following year or two (Fleming 1996; Allen 2006).

Hence, experimental results from Quinyambie and Lambina are consistent with other studies (those referenced in the previous sentence) demonstrating that the relative abundance of dingoes is not negatively affected by baiting for very long when baited areas are located within a wider spatiotemporal mosaic of landscapes inclusive of non-baited areas.

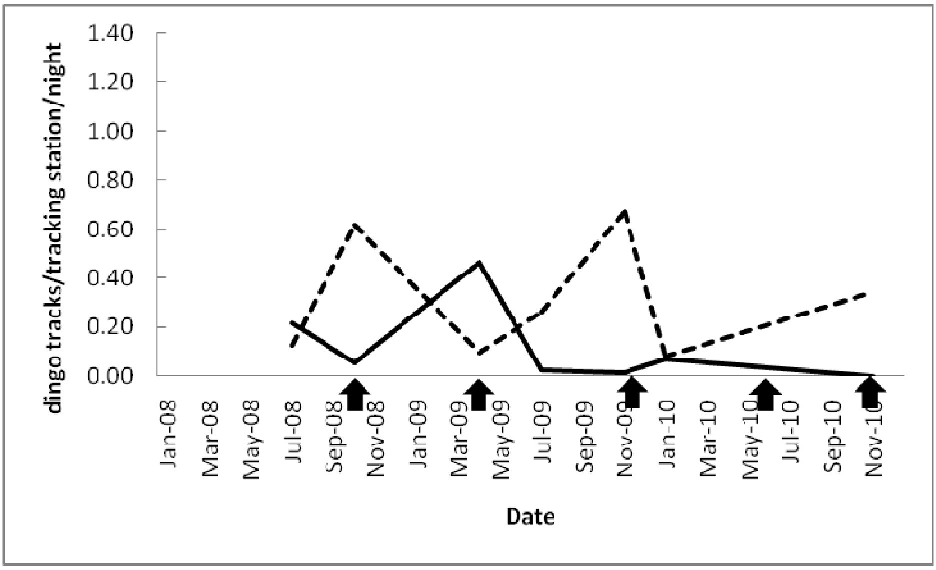
The activity of dingoes on Todmorden and Cordillo Downs was different to the other two sites, and the immediate responses of dingoes to baiting varied between baiting sessions (Figure 3).

On Cordillo Downs for example, dingo activity increased sharply between October 2008 and April 2009 following the baiting program that occurred immediately after the October 2008 survey. Dingo activity also increased over the same period in the non-baited area. Conversely, dingo activity was dramatically reduced to very low levels after baiting in April 2009, and remained at low levels until the end of 2010 (Figure 3). Inconsistent dingo population responses to baiting in different seasons are not uncommon because seasonal effects often influence bait-efficacy assessments (Allen 2000). Hence, the results for Cordillo Downs are not unusual and were also expected. The summertime increase in dingo activity coincides with normal activity increases over this period, as dingo populations transition from ‘whelping season’ to ‘breeding season’ (Purcell 2010; Allen *et al.* 2011b). Allen (2006) found that baiting at this time of year can facilitate an increase in dingo activity by up to 219%, thought to be caused primarily by immigrating individuals (Allen 2005). By comparison, dingo activity in the baited area on Cordillo Downs increased by >400% over the summer of 2008/09.

Conversely, dingo activity markedly declined in the baited area following baiting in April 2009 (Figure 3). Although activity reductions at this time can be an artifact of cyclical behavioral changes as dingoes transition back from ‘breeding season’ to ‘whelping season’ (Purcell 2010; Allen *et al.* 2011b), comparison with the non-baited treatment area (where dingo activity continued to increase) revealed that this reduction was baiting-induced. That dingo populations in the baited area remained at low levels for the next 18 months (not recovering through immigration as would be expected) can be explained by the simultaneous and dramatic decrease in dingo activity in the non-baited area (Figure 3). Additional data (B. Allen, unpublished data) indicates that important prey populations also declined rapidly over the last few months of 2009 as a result of drought, suggesting that the carrying capacity of dingoes was much lower in early 2010 when dingoes may have been attempting to re-establish.

The results from Todmorden indicate that dingo activity in non-baited areas fluctuated from time to time, while activity in baited areas remained low for much of the study (Figure 3). It is tempting to presume that baiting was solely responsible for this lack of dingo activity in the baited area. Baiting may be at least partly responsible for this result, considering the baiting history of this region (Figure 2). In consideration of this history, the results from Todmorden (and possibly Lambina) may be showing the reinvasion of dingoes back into the now non-baited areas at these two sites. However, dingo activity at both Todmorden and Lambina was very low, perhaps too low to interpret the results in this way with any confidence. Alternatively, Todmorden, Lambina, and especially Cordillo Downs are characterized by a variety of habitat types, which may also have a significant influence on dingo activity at finer scales within each treatment. This may also influence the results from these sites.

For example, the two primary habitat types sampled in each treatment at Cordillo Downs were stony gibber plains (36% of tracking plots were in the non-baited area, and 32% in the baited area) and flat, treeless floodplains (42% and 58% of tracking plots in non-baited and baited areas respectively). Analysis of dingo activity trends in these two habitat types shows that dingo activity fluctuated independently of baiting in stony gibber habitats (Figure 4).



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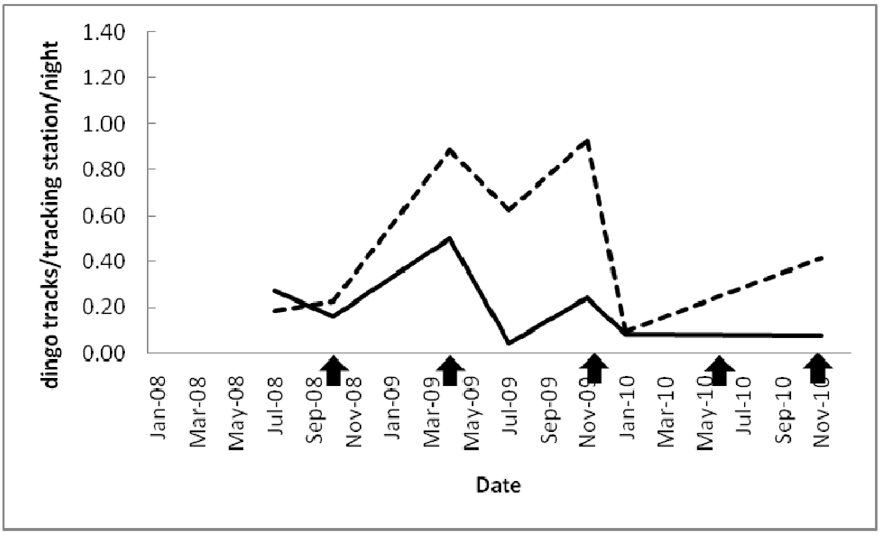

Note: See comment for Figure 3, and make sure that the black arrows in Figure 4 are likewise represented accurately.

Figure 4. The activity trends of dingoes in flat floodplains (top) and stony gibber plains (bottom) in the baited (solid lines) and non-baited (dashed lines) treatment areas on Cordillo Downs. Baiting times are indicated by black arrows.

In contrast, dingo activity in baited and non-baited floodplain areas was almost the opposite of each other. Comparison between Figure 3 and Figure 4 suggests that the dingo activity observed in the 'baited area' of Cordillo Downs is predominately dependent on dingo activity recorded in floodplain habitats only. These contrasting observations provide insight into the underlying reasons why baiting can measurably reduce dingo activity in the short-term, only to be negated by immigration from nearby populations in adjacent habitats apparently unaffected. In other words, baiting may disrupt dingo populations in some habitats temporarily, but it does not appear to have lasting effects on dingo activity or relative abundance at larger scales (Figure 3 and Figure 4).

The results from these experiments help illustrate why bottom-up factors are probably more important than top-down lethal control in influencing the abundance and persistence of dingoes in arid environments. While these experiments were conducted at relatively small scales, they are representative of larger areas given that they reflect contemporary baiting practices across Australia. The finding that dingo populations are affected little by contemporary dingo control is supported by similar experimental results from other areas (Fleming 1996; Eldridge *et al.* 2002; Allen 2005; Allen 2006). Few places in Australia achieve spatially and temporally intensive baiting programs (Fleming *et al.* 2001), and contemporary dingo control could be described as the sporadic application of lethal control to restricted areas on an irregular basis. Justifiable explanations for these experimental observations may be attributed to this dingo management approach. Such is unlikely to reduce or remove large proportions of extant dingo populations given rapid reinvasion, with apex predator removal being a critical prerequisite for mesopredator release to occur (Crooks and Soulé 1999; Terborgh and

Estes 2010). This further suggests that contemporary dingo control practices may not be as ‘effective’ or targeted as intuitively expected.

Target Specificity of Baiting

Prohibition of aerial baiting in NSA means that baits can only be distributed from the ground around livestock waterpoints and along the vehicle tracks that interconnect them. Evaluation of aerial baiting programs interstate have shown that the effect of baiting on dingo activity diminishes with increasing distance from aerial flight lines (Allen 2006, and additional unpublished data from that study). In that study, the activity of dingo populations >5 km away fluctuated independently of aerial baiting. In other words, the further away dingoes are from the baits, the less effect baiting has on the dingoes. If this effect is similar for ground baiting in NSA, then dingo populations occupying the vast tracts of habitat not bisected by vehicle tracks may not encounter baits or be subject to the direct effects of lethal dingo control (Allen In press). These tracts of land can contain source populations of immigrating dingoes (B. Allen, unpublished GPS tracking data).

Livestock waterpoints in NSA are targeted for baiting operations for logistical convenience and because it is assumed that all dingoes visit waterpoints often to drink (e.g. Wallach and O'Neill 2009). If this assumption holds true, it is conceivable that all dingoes on a property might be targeted by laying baits only around waterpoints. That arid zone dingo populations can persist away from available water, returning only infrequently to drink, has oft been reported (e.g. Marsack and Campbell 1990; Corbett 2001b). For example, Allen (In press) showed that individual dingoes on Quinyambie did not visit livestock waterpoints for up to 22 days in both summer and winter, although they likely accessed surface water (away from livestock waterpoints) during the summer when rain provided temporary sources. Dingoes also occupied territories removed from direct access to water, and individuals commonly did not visit waterpoints for several days at a time (Allen In press). This suggests that dingo distribution in the arid zone is geographically limited by water at larger scales (Davies *et al.* 2010), though at finer scales, dingo populations can persist some distance away from water. Just how far away and for how long appears dependant on their ability to obtain (and then conserve) other sources of water, such as that found in the prey they eat (Corbett 2001b; Allen In press).

In addition to dingoes’ ability to persist away from water, the few individuals that encounter baits at a waterpoint first are likely to consume the majority of the baits within the first couple of days, if not hours (Bird 1994; Fleming *et al.* 2001). This is why permissible bait rates allow for a greater distribution of baits than what is used in some places, but this gluttonous behavior also means that dingoes visiting waterpoints less frequently may not encounter baits laid there (Allen In press). Bait-replacement programs, which typically overcome this problem (Fleming 1996), are uncommonly conducted by beef producers in NSA (except in the buffer zone adjoining the dog fence) where once-off baiting usually occurs annually at its most frequent rate (Figure 1). Moreover, extant foxes also readily consume baits laid for dingoes (Fleming 1996; Letnic *et al.* 2011b), further reducing their availability. Anecdotal reports and unpublished data (B. Allen) suggests that fox densities are low, however West (2008) reports that foxes are common and widespread in NSA. Dead foxes have been observed following 1080 baiting exercises undertaken in the presence of extremely high density (300–400 dingoes per waterpoint) dingo populations on Quinyambie in the past (Bird 1994), and foxes have been captured in dingo trapping programs conducted at the same site as late as May 2011 (B. Allen, unpublished data). This further indicates that not all dingoes in NSA are targeted by contemporary dingo control practices, which may help explain why dingoes remain widespread, common, or abundant across NSA and many other areas of Australia (West 2008) despite a long history of dingo control in selected places.

In parts of southeastern Australia where dingoes were largely eradicated by the early 1900s, baiting and shooting occurred in a place, and during a period when intensive netting fences and increased human persecution (i.e. reduced migration and increased mortality) limited opportunities for immigration and increased dingo natality. Tens of thousands of kilometers of netting fences historically bisected livestock production areas in many parts of Australia (Payne *et al.* 1930; Breckwoldt 1988; Crawford 2001; Yelland 2001). In other words, historical lethal control practices in these areas were able to reduce dingo populations because fencing inhibited reinvasion. In contrast, present-day dingo populations in NSA (and other areas not delimited by netting fences) are unlikely to be influenced by baiting to the same extent given that there are no geographic barriers to dingo migrations there. A similar situation exists for foxes, which also rapidly recolonize baited areas provided source populations are available (Saunders and McLeod 2007; Wheeler and Priddel 2009). The historical control of dingoes in southeastern Australia also occurred at a time when domestic dogs often accompanied Europeans as pastoralism expanded across the continent (Corbett 2001b, 2001a). Because of the way baiting encourages dingo migration, baiting has the potential to increase opportunities for pure dingoes to encounter wandering domestic dogs or already hybridized individuals.

Effects on Hybridization

The genetic integrity of dingo populations in NSA is largely unknown, although preliminary results from the NE region suggest that >75% of dingoes are ≥75% ‘pure’ (Allen 2009a). This indicates that some NSA dingo populations are among the purest known populations in Australia (Fleming *et al.* 2011a, but see www.wilddogdna.animals.uwa.edu.au for updated information). The maintenance of the national dingo barrier fence, which separates the most hybridized individuals found in southeastern Australia (Jones 2009; Glen 2010) from the purer individuals found in central and northern Australia (Corbett 2001a), helps to reduce the introgression of domestic dog genes from one side of the fence to the other. Even though dingoes have been found to disperse over 500km in less than a month, or over 1,300km in four months (Allen 2009c), netting fences appear a particularly useful barrier to dingo movements (Newsome *et al.* 2001; Yelland 2001). Hence, the limited and sporadic baiting that occurs throughout NSA is unlikely to facilitate a major immigration of genetically undesirable individuals into the area, while 1080 baits are lethal to dingoes and domestic dogs alike (McIlroy 1981; APVMA 2008).

Perhaps of greater concern is the localized dispersal of unrestrained and non-desexed town dogs from human settlements into surrounding areas. Anecdotal reports of dingo sightings suggest that hybridization is greater in the NW (i.e. there is reportedly a greater frequency on ‘non-yellow’ coat colors there), perhaps attributable to the higher number of human settlements in and adjacent to that region. Hence, introgression of domestic dog genes into the NW dingo population might be promoted by dingo control through sink effects. Under normal circumstances, the “behavioural differences between wild living dingoes and feral domestic dogs seem great enough to make it difficult for cross breeding to occur in remote areas [such as NSA] where there are more dingoes” than feral domestic dogs (Daniels and Corbett 2003, pg. 215). However, if dingo control removes the breeding individuals within a pack, it may facilitate mating between wandering domestic dogs and surviving pack members at the next annual breeding season. Alternatively, the disruption of packs through baiting may encourage wild living dingoes to seek mates from promiscuous town dogs, the hybrid progeny of which might find their way back into the wild population (Thomson 1992b; Daniels and Corbett 2003). Genetic change is likely to accelerate with the increasing proportion of hybrids in the population, while backcrossing hybrids with purebreds provides a catalyst for this process (Daniels and Corbett 2003; Purcell 2010). Importantly however, it must also be kept in mind that genetic change is probably inevitable, irrespective of lethal dingo control practices.

A way to investigate these processes in more detail would be to evaluate the genetic relatedness between town dog populations and nearby dingo populations in areas with and without a history of baiting. This could be further explored by comparing baited and non-baited areas, using tracking collars and DNA sampling to measure movements and introgression. Although unlikely to be significant en mass, at least in the short term, the potential for baiting-induced hybridization at finer scales requires further investigation, because such a process may contribute to the alteration of the genetic status of dingoes in the long term. Arguably more important than their genetic identity is their ecosystem function (Corbett 2001b; Purcell 2010; Fleming *et al.* 2011b). Hybridization is not currently thought to alter the ecosystem function of dingoes, though this remains a poorly studied aspect of dingo ecology (Claridge and Hunt 2008).

Effects on Ecosystem Function

The level of dingo control in the NE suggests that human-induced dingo mortality is unlikely to be influencing the ecosystem function of dingo populations there in any substantial way. This is essentially because contemporary dingo control does not reduce or remove dingo abundance for very long (discussed above), so a baiting-induced increase of mesopredators would be unexpected. It might be argued that the disruption of packs through baiting could reduce the ability of dingo populations to effectively suppress or repel mesopredators (Wallach *et al.* 2009, but see also Allen 2010a). However, this presumes that a non-baited pack is required to repel mesopredators, while knowledge of the behavior and demography of post-control dingo populations suggests that foxes and cats are unlikely to suffer less persecution and competition from dingo populations subject to baiting (Thomson 1986, 1992a, 1992b; Allen and Gonzalez 1998; Allen 2005). This is because baited populations are comprised predominantly of surviving adults and the largest immigrating individuals, which are unencumbered by pup-rearing, and which exhibit heightened activity, territorial behavior, and preference for smaller, more vulnerable prey species. Each of these characteristics would likely increase pressure from dingoes on foxes and cats in baited areas.

Additionally, the provision of artificial waterpoints and supplementary food resources may presently be sustaining dingoes at levels greater than those in pre-pastoral times (James *et al.* 1999; Corbett 2001b), and it might be argued that contemporary baiting merely reduces dingo populations to something like their pre-European levels. Hence, whatever the ecosystem function of dingoes is, contemporary dingo control in the NE region is unlikely to be influencing it there one way or the other.

In contrast, information from the NW region does suggest that dingo populations there have been significantly influenced by historical dingo control practices. Although activity indices cannot be reliably compared between habitats (Wilson and Delahay 2001; Engeman 2005), the experimental data presented here suggests that dingo populations in the NW region are at very low levels when compared with other NSA sites (Figure 3). This is corroborated by scat collection data (B. Allen, unpublished data) that also suggests that the NW is only sparsely populated with dingoes. Although activity data from Todmorden and Lambina suggest that contemporary baiting practices have little short-medium term effects on dingoes (Figure 3), the long-term effects of coordinated baiting over extensive areas (Figure 2b) may have reduced dingo abundance in this region by curtailing immigration (potentially reflecting pre-European densities). This has been reported to occur in other places where coordinated, routine baiting programs cover large, contiguous areas (Allen and Gonzalez 1998). This effect might also have been aided by the longer persistence of sheep, and sheep netting fences in this region (Allen 2011). An alternative explanation may be that the NW region is less productive than the NE – dingoes being less common due to bottom-up factors, such as the fewer rabbits that occur there.

While dingo control in the NW may have reduced dingo abundance, the increase of some mesopredators does not appear to have occurred there as a result. This is probably because foxes are also susceptible to dingo baiting practices (McIlroy 1981; Korn and Livanos 1986; Saunders and McLeod 2007; Claridge *et al.* 2010), often moreso (e.g. Fleming 1996), while cat populations typically fluctuate independent of dingoes or dingo control (Allen 2005; Letnic *et al.* 2009; Letnic and Koch 2010; Kennedy *et al.* 2011), being more greatly influenced by habitat factors (e.g. Edwards *et al.* 2002). Foxes (like dingoes) are also monoestrous with similar finite rates of increase to dingoes, and hence are unlikely to repopulate a baited area through natality any faster than dingoes (Fleming *et al.* 2011b). Furthermore, some threatened small mammal populations (e.g. plains mice, *Pseudomys australis*) highly vulnerable to foxes and cats declined from the NE region where baiting has rarely occurred, yet persist in the NW region where dingo control has been most intensive (compare Figure 2 with Moseby In prep). However, caution should be exercised here because assessments of species distribution patterns allow only weak inferences, and such an approach should be used only for hypothesis generation (MacKenzie *et al.* 2006). As such, alternative factors besides dingo control may very well be responsible for the status of threatened small mammals in NSA. It is also important to remember that 'threatened species' are not a single entity, and variable responses to predation by apparently similar prey species should be expected (Sinclair *et al.* 1998; Gese and Knowlton 2001; Moseby *et al.* 2009; Read and Cunningham 2010). That said, a positive relationship between the distribution of intensive dingo control and the persistence of plains mice does not conform to the simple formula that dingo control = less threatened species through trophic cascade effects, but it does support alternative findings in temperate regions (e.g. Fenner *et al.* 2009) which indicate that small mammal populations function independently of contemporary dingo control.

This is further supported by the results of other manipulative experiments (e.g. Fleming 1996; Eldridge *et al.* 2002; Allen 2005; Claridge *et al.* 2010; Kennedy *et al.* 2011) which have likewise found no evidence for mesopredator release of foxes or cats following contemporary dingo control programs in arid, semi-arid, temperate, or tropical areas. Moreover, and most importantly, "no studies published to date have found significant reductions in populations of non-target animals following 1080 baiting" (Glen *et al.* 2007b, pg. 195; but see also APVMA 2008). Such experiments have the ability to provide 'conclusive proof' for the impacts of baiting on non-target species (Glen *et al.* 2007b). Hence, these studies strongly and clearly indicate that calls to suspend lethal dingo control, on the grounds that it may release mesopredators and reduce threatened species, remain unjustified.

An important caveat relating to the inability of lethal dingo control to influence the ecosystem function of dingoes relates to the scale and frequency at which control programs are conducted, or the effectiveness of the program at actually removing sufficient dingoes for a sufficient length of time. Contemporary dingo control, or the spatiotemporally sporadic application of control effort, is unlikely to result in the release of foxes and cats because of rapid dingo reinvasion back into controlled areas from other areas not subjected to lethal control (in addition to the simultaneous control of foxes), while the behavioral attributes of surviving dingo populations are unlikely to favor positive and temporary behavioral responses by mesopredators as well. However, if coordinated control programs were to cover large, contiguous areas and achieve a sustained numerical reduction of dingoes only, then a release of other mesopredators might occur as theoretically predicted (though this does not presently appear to be the case for the NW). Whether or not this translates into negative affects for threatened species would then require investigation. The disparity between expected and realized dingo activity following contemporary dingo control programs has been often overlooked in studies that promote cessation of 1080 baiting and assume that infrequent property-level dingo control somehow benefits foxes or cats.

It is also important to remember that although dingoes are a relatively well-studied species, there is still much uncertainty about the primary mechanisms responsible for the observed outcomes of predator-prey interactions in Australia (Robley *et al.* 2004; Glen and Dickman 2005). The outcomes of positive apex predator management are also highly context specific (Soule *et al.* 2005; Sergio *et al.* 2008; Terborgh and Estes 2010), and the results of a given study may not be widely applicable to other situations. The familiar 'Yellowstone model' based on wolves may be the exception rather than the rule, and support for the notion of widespread trophic cascades in terrestrial systems relies heavily on just a handful of 'classic' studies that do not represent the anthropogenically altered landscapes that dominate the earth's surface (Linnell 2011), such as Australian rangeland systems. We would not expect the management of wolves in North America to be decided by a limited number of spatiotemporally restricted studies on dingoes in Australia, nor should we allow the management of dingoes to be decided by such studies of wolves overseas. Dingoes are not wolves and Australia is not America (Fleming *et al.*

2011b). That is not to say that the positive management of dingoes would not have some biodiversity benefits in some circumstances, but that such an action would likely produce unexpected and inconsistent results with international studies on other apex predators. International studies on the biodiversity benefits of wolves or the occurrence of trophic cascades generally (e.g. Estes *et al.* 2011) are therefore unlikely to be synonymous with dingoes or contemporary dingo control.

In the quest to illuminate the biodiversity benefits of positive dingo management at lower trophic levels, researchers attempting to find support from international studies on wolves or any other apex predator species have a unique obligation to demonstrate that dingoes are comparable in function to them. This would be necessary before the findings of wolf-studies could be applied to dingoes in Australia, but doing so would first require an understanding of the ecological functions of dingoes. Moreover, caution should be exercised when attempting to fit "pieces of empirical evidence to the prevailing framework of theories [because it] opens the door to dogmatism [and is] hardly attractive" (Oksanen 2001, pg. 35). Likewise, those promoting the prohibition of dingo control on biodiversity conservation grounds have an obligation to demonstrate that dingo control harms threatened species. Moreover, given the known ability of dingoes to exploit many of the same threatened species they are also assumed to protect, researchers also have an obligation to provide objective assessments of the net benefit of promoting dingoes in a given landscape. This "may help avoid the potentially disastrous consequences of encouraging a predator that might have been largely, or at least partly responsible for their destruction" in the first place (Allen 2011, pg. 29).

These assessments would require the consideration of several economical, social, and environmental factors, and should not be limited to a narrow focus on only biodiversity issues (Fleming *et al.* 2011b). When considering policy and practice changes, the precautionary approach would be to maintain current practice until more robust information is available (Cooney 2004) or until "the evidence warrants it" (Soule *et al.* 2005, pg. 175), which is presently not the case (Visser *et al.* 2009; Allen *et al.* 2011a). Such an approach dictates that contemporary dingo control practices could continue until more reliable information suggests otherwise.

CONCLUSIONS

In summary, the results presented here demonstrate that dingo control historically occurred infrequently in the arid beef cattle zone of far northern South Australia, though the NW region was subjected to higher levels of control in the 1990s and early 2000s. Information from the NW during this time suggests that dingo populations can be suppressed by baiting provided lethal control occurs frequently and intensively over large areas, though dingo control does not appear to have led to an increase in mesopredators or the decline of some threatened species in that area. Contemporary dingo control practices in NSA and elsewhere in Australia are unlikely to have a major influence on the genetic integrity of the dingo populations in the short term, though baiting may increase interactions between pure dingoes and genetically undesirable individuals, contributing to the alteration of their genetic identity in the long term. Contemporary dingo control practices are also unlikely to facilitate a release of foxes or cats (or result in reductions of threatened species populations) so long as control practices fail to remove dingoes for any great length of time. However, there is still much to learn and these processes should continue to be an important research priority. Accepting inevitable changes to their genetic identity and assuming the ecosystem function of purebreds and hybrids is similar, contemporary dingo control practices are unlikely to compromise the primary conservation values of dingoes into the future.

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Chapter 4

AGONISTIC BEHAVIOR INTER-CONNECTIONS IN HIDDEN PATTERNS IN WOLF PUPS GROUP DURING THE JUVENILE HIERARCHY STABILIZING PERIOD

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ABSTRACT

There are different views to the social structure of wolf groups. They all have their history. At first, a simple linear hierarchy in wolf groups was described (Schenkel, 1947; Zimen, 1975; Fox, 1980), then the conception of two parallel hierarchies of males and females was born (Schenkel, 1947; Zimen, 1982). But sociograms in different researches showed us a much more complex structure of wolf group organization. The most interesting developing of these points of views was Mech's supposition about labor division of individuals in wolf groups during the one year-season cycle (Mech, 1999, Mech, 2000). This conception is close to the conception of social roles suggested in primatology (Gartlan, 1968; Bramblett, 1973) which was applied for other species (Gol'tsman, 1976; Poyarkov, 1986).We look at wolf social groups under review of this conception. It has features of functional system analysis (Croock, 1970; Anokhin, 1971). That conception describes each individual in the group as a structure element of a system and in that system, every element has its own role for group stabilizing. If the group hasn't been stabilized yet – each individual has his own social position with a direction to the future role. Questions we are interested in are about the development of these roles through their positions from zero, from individuals' childhood. One of the instrumental aspects of our research is using the "Theme" program (NOLDUS). It is for hidden patterns (non-random non-linear sequences) of behavior detecting. We can see animals' behavior real-time complex structure (the projection of the behavioral system they live in) and changes in it with time. It is real to analyze any special parts of behavior structures changing. One of such parts, picture dynamics of meaningful and

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behavioral events of some category, that significantly interconnect to each other. We observed round-the-clock activity of 2 wolf pups groups within the age of 37-230 days every 7-10 days. Observations were made in 2007 and 2008 in the Tver region (Russia), on the base of the biological research station "Chisty Les". These groups both were made from pups that had been taken from zoos, these pups grew up without parents, so we can detect only those categories of behavior that are in them by nature, genetically. The object of supervision both years: 2 wolf males and 2 wolf females (*Canis lupus*). As far as territory, we used big enclosures – parts of a natural forest. This analysis was focused ecpesially on the age period from 75 to 115 days, it is an important period in wolf ontogenesis (Yachmennikova et al., 2009, Yachmennikova, Poyarkov, 2011). As a partial result of this work, it is two cascade-type schemes of significantly connected events with agonistic types of activity in the wolf pups group. Schemes have been made on the base of hidden patterns which have been detected and decoded. These schemes pictured how agonistic activity types take part in the system-organized process of juvenile hierarchy stabilizing, and how individuals in a simple group connect to each other through this type of behavior in a period which is so important in their life.

Keywords: wolf pup, behavior ontogeny, hidden patterns, juvenile hierarchy

INTRODUCTION

Agonistic Interactions as a Part of Dominance-Subordination Relations

All works concerned with hierarchy system establishments in any social group in any species contain, in different views, the information on agonistic interactions intensity, or information on domination-submission ritualized relations that are consequences of them. The result of the interaction providing an establishment of domination-submission relations is difficult to sign as communications with a ”+”. But each interaction is a source of both positive and negative stimulation. Thus, domination of one individual over the others, that is based on agonistic contacts though doesn't provide positive communications of individuals among themselves, however, is the "rallying" group factor as a whole (Goltsman, 1983). As such, connection between domination and orderliness of relations in a group is, for example, a fact that the most active role in domination-submission relations play in individuals are in the subordinated position maintenance (Goltsman, 1983). Here, frequency of submission displays is meant as ”an subdominants active role” – poses of passive submission, the actions designating active submission that is normal for some species of primacies, canids. In nature, the higher rank of the individual that is revealed on the basis of agonistic interactions research doesn't mean that this individual is dominant in all parts of group social life (Pojarkov 1986, Croock, 1970). Thus, the hierarchy of dominant ranging isn't a basis of social systems. But the hierarchy of domination-submission is one of the major descriptive concepts nevertheless. And it reflects one of many characteristics of a society (Goltsman, 1983). The description of hierarchical systems becomes from the basis of the serial analysis of each individual's interaction with another in the group. After that, all possible combinations, are tested. In such research, interrelation of events considering method is impossible. Thus, it is worth to note that it is impossible to see a full real picture of all individuals' mutual relations structure in the group and rules formed on their basis without the events interrelations analysis. Besides, there are different factors that cause hierarchical systems unlinearity and interactions of individuals net in group complexity.

Wolves' Social Structure Description

First, the classical concept describing wolf social structure as a hierarchy of domination was developed on the basis of supervision over wolves in captivity (Schenkel, 1947). *The linear hierarchy of domination* is an elementary scheme which explained an aggression orientation in wolf groups for a long time. It was based on such calculations as body weight, agonistic interactions percent, where the individual x is the initiator; quantities of the poses that are personally addressed and certificates of "submission"; frequencies of smell labels; results of the test of a food competition. All of these factors were markers of domination-submission relations in group establishment. According to the linear hierarchy theory, it is the prepotent wolf on the top of hierarchy, who called alpha-male. It wins all agonistic situations with any other individual. All other individuals of the group occupy the subordinated position in relation to the alpha male, and they carry indexes beta males (- females) etc. Individuals in the beta status (in the subordinated position) lose the fight with an animal of the alpha status only. The pair from which the pack takes in the beginning is named the alpha pair, it has a predominating position in the pack and reproduces. In this pair, the alpha female occupies the subordinated position concerning the alpha male. The wolf on the last hierarchy position, which loses his fights to all – the omega-wolf; its status depends little on its sex. All of these terms (an alpha, a beta, an omega) were used in the description of interactions between wolf puppies growing in groups observed in captivity (Zimen, 1975; Fox, 1980). Small puppies were not ranged under statuses in the beginning, and their social structure also has been described as a linear hierarchy still forming.

Two parallel hierarchies system, of males and females. It is also absolutely legal the point of view about two parallel systems of domination hierarchy of males and females that exist in wolves packs simultaneously (Schenkel, 1947; Zimen, 1982). As well as the previous, this concept has been developed on the long-term supervision of wolf groups in captivity. It is structured wider and considers individuals age in the group ("age-graded dominance hierarchy" (Zimen, 1982)). However, the described structure is real for wolf groups in captivity only – that is artificial, which never consisted of a breeding pair and its descendants of different ages and puppies of this year. According to this theory, the reproduction is allowed for the dominating alpha pair only (Schenkel, 1947) despite other receptive females in the group (age of pair). The alpha female's aggressive behavior directed to them during the estrous period excludes the subordinated females from participation in reproduction because of feromonal suppression. In nature, the strongest tendencies to leave the pack are observed in females (adults and one-two year wolves) which do not participate in reproduction (Pulliainen, 1965; Messier, 1985). Because of it, one of the group size regulation mechanisms works. It promotes emigration of the individuals which can't maintain social pressure and reduces the birth rate level to optimum (Packard, Mech in Cohen, Malpass, Klein, 1980). It is the dominating male in the pack who keeps a distance between the possible applicants of the breeding female and the breeding male roles, and he is aggressive to such applicants. The concept was true until new data appeared. Data contained information that the temperaments types allocated in wolf-pups in captivity and an alpha - a beta - scale ranging of individuals because of these types, don't correlate with their prospective participation in reproduction in a consequence; mood and character (defined initially as temperament) are very changeable characteristics depending on the individual's physiological condition, age (its individual experience), conditions of environment. Thus, the two parallel hierarchies system is only an enlarged variant of the linear hierarchy concept. In reality, an absolute domination linear hierarchy establishment is probable in wolves, if individuals come to group one by one; conditions allows the new wolf and wolves of earlier domination-submission relations to be stabilized; there is an accurate distinction in aggressive struggle abilities between individuals of each dyad (Packard in Mech, Boitani 2003). Actually, if any animal doesn't mark much or doesn't achieve success in competitive struggle for a forage, it doesn't mean that the individual is at the lowest hierarchy position; "… each wolf it is a bright individual, and should be considered in a full spectrum of his behavioral interactions …" (on Goltsman, 1984).

Besides the actual linear hierarchy in a group there is also another social structure which is regulated by social communications and the psychological condition of each individual and their intra-group relations. The social organization is not just a groups size and simple structure characteristics, or its hierarchical or role structure (distribution of dominant ranks and roles), but also a composition of societies in which there is a structure of personal relations, besides the others (Ovsjanikov, 1993; Poyarkov, 1986). Such relations are defined as a set of group members' social positions. The social position includes a wider spectrum of relations, rather than the domination-submission underlying the hierarchical ranks concept. A.D.Poyarkov (1986) defines a social position as set of different possibilities which are available for each group member. Thus, the social position is the adaptation-in-advance characteristic, and it comprises of potential metamorphosis (Ovsjanikov, 1993).

The "labor division" concept. The "labor division" concept has appeared as a result of the long supervision over wild wolves in the nature system works, and has been offered by Mech (1999). The concept takes into account the difference of wolf pack individuals' social interactions with their intensity and quality in comparing the similarity in any other group or common working and living command. It can be called the hierarchy of dominant ranging in subgroups, where sex, age, and reproductive status of each animal are dynamically coordinated among them, in the rough form. The typical wolf pack is structured as a family group. The breeding pair (the male and a female), two adults wolves are the group basis; they regulate activity of all pack and sometimes have positions of both leadership and dominance. The breeding male always dominates over all other members of the pack, although exception cases (depending on personal relations in the breeding pair) are known. During the period when the female raises the puppies, she can dominate over her the partner. Besides, the pack includes the breeding pair's offspring at the ages of 1 to 3 years. Here the domination hierarchy is built on seniority – subadults of the third year dominate over subadults of the second, etc. Inside "age layers" mutual relations are established on the basis of individuals' temperaments and characteristics from their childhood (from birth to physiological puberty), mainly these relations are warm and friendly. Positions of last year puppies in hierarchies system is regulated by the parents – wolves of the breeding pair. Notorious "labor divisions " contain in it the knowledge that in the period when puppies appears, the female and the male of the breeding pair are changed in their status; and the female can dominate over the male because of their specialization in different spheres of activity. The female should take care of the puppies and should protect the den; the male is responsible for hunting and delivering food for feeding the female and storing food for her (Mech, 1999). All members of the pack can take part in bringing up the newborn puppies. Parents have the power to change the sequence of approaching the food. Despite age order puppies can eat first, during the period when it is first allowed for them to go to carcasses after the parents.

The concept of social roles (Goltsman, 1977; Poyarkov, 1986; Ovsyanikov, 1993) is close to the concept of labor division offered by Mech. However, it considers labor division between all other members of the pack, not just the breeding pair, but is similar to Mech's described theory as a whole. The concept of social roles assumes that in a stable pack, each individual's social status (a social niche) is defined by its social role. Here, the role is understood as individual functions concentration or specialization (domination) of the individual in a separate sphere. Thus, stable group existence becomes possible in a case of unique social composition of those individuals which make up this group only. It is similar to a puzzle where the required picture can be realized only with a correct combination of unequal elements. Every animal in the group is characterized by a certain social position that there is an adaptation-in-advance characteristic (it was mentioned above). It considers individual potential which is defined by personal qualities of character and has abilities to variability, which is shown in unusual daily occurrence situations. At such an approach to the wolf group structure analysis, the simple linear hierarchy, seemingly at first, will be transformed into a unique self-organizing system; it has an adaptation property in situations of environmental conditions changing, capable to change its structure when the system interacts with environment, but it always keeps properties of integrity; and it is capable to form a great number of various variants of behavior and able to choose from them the best. Thus, gradually, during the system's daily functioning (that is the cyclic process, incorporating activity of each individual and by that activity of whole group), the structure of individuals' inter-relations is optimum for group survival is established and stabilized.

Patterns as System Analyses Method

Are there mechanisms of the social groups' behavior analysis from the interdependence of all events occurring in them? In Magnusson's (2000) paper which concerns information about the Theme (NOLDUS), there are words: "… Dynamics of interactions between individuals represents itself the complex system in which tens of events can occur simultaneously, where each of them is effective and functional, and all streams of these events in behavior is characterized by time and spatial changes …"[1]

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[1] L. Anolli, S. Duncan Jr., M.S. Magnusson and G. Riva (Eds.),The Hidden Structure of Interaction: From Neurons to Culture Patterns Amsterdam: IOS Press, 2005.

What gives these patterns detection? It follows, from the literature devoted to this question, that patterns allow to understand more precisely, firstly, how the file of events you are interested in is structured if it consists of the consecutive repeating of elements of the limited variety. Secondly, similarly ”bird’s eye” – the magnifying glass, patterns allow seeing essentially important significant structures in the general file. As an explanation, we consider a behavior stream. In this stream all actions occur consistently one behind the other for each animal accordingly. Each animal behavior organization various surrounding factors the contribution has brought. Which of them defines animal action at the present time? It is not possible to always understand precisely. However, these factors themselves are organized in systems. We assume what behavior of animals to analyze possibly proceeding from different systems of factors. The basic question here is whether the simultaneous behavior analysis from the point of view of different categories systems is possible. For example, we can take social behavior and activity systems. It is obvious that they exist together, but are integrated one into another. *System of activities:* the daily activity of individuals entered in a round-the-clock cycle, providing the ability to live. This cycle is determined with physiological processes, processes of growth and development and also power exchange processes – for example, game activity, comfort, moving, foraging, excretion, manipulating activity, researching activity, rest and so on; another is the *system of mutual relations* of individuals and dynamics of these mutual relations. This system implies the picture of attachments changing (the degree of changing of psychological dependence of individuals from each other), individuals’ orientations against each other in different situations, and individuals’ relations of domination-submission and so on. The system of social inter-relations in wolf pups growing up exists and develops in time. The basic questions here are the continuity and intermittence cohesion of a behavior stream in time; and a categorization of elements of behavior also. As well as time, behavior of an animal is continuous during life. In this connection there is a question on divisibility of behavior; what a behavior unit in research is. It is obvious that it all depends on an empirical characteristic which is allocated by the observer. It is possible to notice that to each hierarchical behavioral category a time step of various durations corresponds. And it is logical to choose the size of a step depending on the investigated level of categories. And when we choose a step in time we choose a research category on the contrary. Suppose we choose a level of sequences of poses or expressive movements, i.e. some Elementary Moving Acts, which it is possible to unite an activity-type category. It can be added that element separateness in a category is a necessary condition for defined function implementation by it as a part of the whole. The unity of intermittence and continuity of parts and whole provides the possibility of existence and whole object development. Influences of one event on another in a behavior stream is the elementary form of a causal relationship, as though it is the phenomenon unit. Recurrence, or rhythm, is peculiar to any development. Any daily existence of the individual is entered in cycles which are normalized and repeated regularly. All changes occurring in the developing process organically keep within these cycles, supplementing them, but having basis at them. And in that case, each subsequent cycle is similar to the previous, however, it has its own individual characteristics. As if each new coil of a spiral – is precisely similar to the previous, but extensive and dispose on a level above. Biological cycles are the basis for understanding all of the rhythmically organized forms of behavior which play the major role in behavior formation in general (Kruchenkova, 2002).

So, the initial data flow from which patterns are formed consists of a sequence of events. One unique event contains the information about the individual; if it begins or ends the activity; the type of its activity, and combination of other individual (s) this activity is interconnected with. As a result, we have the list of patterns illustrating the behavioral stream organization. What is called a pattern in the given context? As a concept, a pattern in modern ethology has some different interpretations so the explanation here is required. In our case, it is rigidly determined, ordered, non-linear repeating sequence of behavior elements. In this aspect, patterns are calculated by the Theme (NOLDUS). The settlement algorithm means the first step position in comparison with each event afterwards. Roughly speaking, at first it searches for everyone *b* after everyone *a* on a time scale. Furthermore, the step of check automatically changes and every third position after each *a* is tested, then every fourth etc. It works as such until the rules won't cease to be allocated. On the position *n,* the higher border of a critical interval is formed and all further data is tested in limits of it. It is obvious that the settled pair combinations is found out at first, after their allocation, all of them are added as a new file in an initial database. And each steady pair combination is accepted as one complex event further algorithm searches for steady threefold combinations and so on. For us, the "Theme" is important as the special mechanism which allows estimating rules of elementary social group formation and development from the social roles concept point of view in such animals as wolves in their most intensive growth, developments and behavior formations period.

RESEARCH

Methods

The behavioral material of two experimental groups of 4 wolves each was used. It was collected during round-the-clock supervisions in 2007 and 2008 in the Tver region (Russia), on a biological research station "Chisty Les" territory. The complex of enclosures consists of three open-air cages with the area 150 m^2, 5 000 m^2, and 10 000 m^2. Open-air cages represent the sites of natural wood with a complex structure fenced with metal grid. The area of enclosure, a relief there and environment's saturation is similar to rendezvous sites, where wolf pups first ontogeny stages in nature take place (Joslin 1967; Mech, 1970; Hernandes-Blanko, etc. 2005). During the summer period, wolf-pups are constantly on rendezvous sites, expecting their parents. They spend time in games, moving and searches of small extraction (Badridze, 2003). By analogy to how mother-wolf replaces rendezvous sites 1-2 times for the summer period, we moved wolf-pups from one enclosure to another with much bigger area during the season they grow. Every time it was territory unfamiliar to them. Thus, we believe the behavior development of our wolf-pups is the simplified model of their natural behavior ontogenye. ***Object of supervision:*** two groups consisted of 2 wolf males and 2 wolf females(*Canis lupus*). Males and females of 2007 were born in two different zoos in different Russian towns. Males were born on April 18th and females on April 25th. They are named: Gai and Rem (males), Tais and the Lika (for females). Males are from a brood, where it was 6 pups. Their family structure included a breeding female (mother), the male (father) and one more wolf that was one-year-old. In a zoo, the family lived in an open-air cage with the area of 150 m^2. Puppies have been separated from their mother at 28 days of age. Females are from a brood where there was only pair of puppies. Besides them, there was the female (mother) and the male (father) in their family. They lived in a zoo, in a cage with 24 m^2 area. They were separated from mother at the age of 16 days. Individuals of 2008 were born in a third zoo. They have one father and two mothers. Three pups had one, and fourth pup had another. Pups were named Nika and Rada (for females), Amur and Dunai (for males). The animals were united in a group before the beginning of collecting data. Furthermore, all pups were fed artificially. *Maintenance and feeding conditions:* Until wolf-pup age: ~52 days-old (the middle of June) puppies received dried milk ("Esbilac") for large breeds of dog and a special dry feed for puppies daily. Small slices of meat were soaked in gastric juice with complex vitamins and have been entered into a diet from 25 days old (wolf-pup age 48-55 days). Wolf-pups have used only meat as a diet after the period 45-52 days old, while periodically receiving small sea fish as the food addition. The data for 336 hours (2007) and 281 hours (2008) of behavior registration has been used for the analysis. Each 7-10 days within summer 24-hour registrations were spent. For the summer and autumn beginning period of the puppies growth (their age: 37-137 days) 14 supervisions have been made in 2007, and 11 in 2008 for the second group. The behavioral stream was fixed by the observer during 24 hours with a method of time cuts (Lehner, 1996; Popov, Ilchenko, 2008) each 1 minute (20160 (in 2007); 15840 (in 2008) cuts have been made). An Olympus VN-3100 PC Digital Voice Recorder was used for it. The activity type, and also subjects these activities have been directed was fixed. Every parameter was fixed for each animal. The observer stayed in an enclosure with wolf-pups. The influence on behavior of animals was minimized (researcher did not contact them by hands or face, fixed the information by an equal low voice without emotional differences in his intonations, was above level of sight of an animal constantly, worked constantly in clothes which were not used for other purposes). The day-period consisted from 2–4 equal parts and observation spent serially for 6 hours by 2–4 observers. Each observer knew the full list of activities and behavior-forms. Each observer passed special training with the subsequent testing on video-recordings for observations standardization. "The sequence of behavior elements consisting of the following for other units (1 Unit=the sequence of EMA (Elementary Moving Action)" was registered by observer. Until the data was processed, we united the forms of behavior in big functional categories (activity types), such as "game" or "aggression". One type of activity joined some forms of behavior, which are described in the ethogram (Yachmennikova, Poyarkov, 2011). As a result of observation for us was an simple ethogram, and it has been made an ethogram at a higher level with the use of ethograms of the lowest level, we have after an observation, for the next analysis: if one of several forms of sequences of the behavior, the activity type was registered. Carried to this type of activity and based on behavioral repertoire of a wolf (Schenkel, 1947) was marked. All activities we noted concerned one of 18 activity-types of animals (see lower). The observer fixes behavior or a condition of object at the termination moment of the time interval in advance stipulated, for example, 1 minute (Popov, Ilchenko 2008). The constancy of these intervals during all periods of observations was followed. We observed animals 10 seconds before a signal, and fixed their behavior observed at the last part of minute, i.e. into account "10" seconds (Sackett, 1978). Between fixings we have defined the duration of intervals as 1 minute, because of: 1) speed of an animal condition changes. A cut step satisfied to the requirement we planned to analyze, like activity-type, instead of sequences of actions; 2) numbers of animals. If the number of animals is large, it is hard to describe a condition of all of them correctly; 3) the large duration of the general period of supervision (24 hours=1441 a cut). During the animals activity registration, the observer followed a turn order of individuals: Gai, Rem, Tais, Lika (2007), Amur, Dunai, Nika, Rada (2008). The material registered was reprinted in the text files by each participant of observation. Then, one person coded all of the information. There were: the author of activity (individual); activity type; individuals synchronization – brought in data base. We carried out simple tests for revealing linear hierarchy on the basis of possession of the limited resource (food) for the checking of our data and schemes (Shenkel, 1947; Fox, 1970). *Data processing methods:* The analysis of the hidden patterns. For the detection of prospective appropriateness in consecutive changes of wolf-pups activities in a 24h cycle in their ontogeny period, the process we used was theNOLDUS Theme 5.0, especially developed for revealing hidden time patterns (Magnusson, 2000). A basis of work of the program is the algorithm, that detects dependences between events and their combinations in time series within a critical time interval which is installed by internal parametres of the program at calculation product. "… This ascending algorithm is based on binary dendrogram of mutual relations of events. Simple patterns which can form more difficult ones …" (Magnusson, 1996, Filatova, etc. 2009) . The general principle of a method which is used by the program at the analysis of the big arch of the data consisting of repeating events see below. Program tests a hypothesis- zero according to which, after each event "***A***", at least one event "***B***" within the limits of a distance would follow more often. If such distance is found, its bottom and top borders form a critical interval, and connection between "A" and "B" would become a critical interval connection. For these calculations, it is accepted that "***A***" and "***B***" are distributed independently from each other, and "B" possesses constant probability of display in an interval of time (= N ***(B)****/t*) during supervision, where N (- quantity of displays, and t – duration of supervision). If such connection is found in a critical interval, the set quantity of times the simple pattern (***AB***) is allocated – it is shown everywhere where after "***A***" would follow "***B***" in a critical interval limits. The real data usually contains much more types of events that can be found except a simple pattern (***A-B***), for example, (***C-D***). Furthermore, each display of a simple pattern is considered a separate event, and is added in the primary arch of the data, and used as that at the subsequent level of the analysis. For the described analysis, in our case, as the countable unit (the whole event), the next line was positioned: the author of activity (individual), the beginning or the end of activity, type of activity and the individual with whom activity is connected. The program perceived such a record as a single whole event and allocated patterns of interconnection of these events. *Adjusting parameters were used:* a significance value (p-level) <0.005; the minimum number of the facts of a meeting of a pattern (min. occurrence) 5. For further analysis, all results of the above described processing – patterns and their characteristics- have been organized in a database in program Access (Microsoft Office) which was analyzed by means of program Statistica 8.0.

Patterns in Wolves' Behavior

At first, it is required to characterize quantitatively the patterns containing 2 types of social activity (agonistic and friendly) we are interesting in for all periods of supervision. For the group of 2007, this number is much less than that for the group of 2008. Mann-Whitney U Test: U = 0,00; Z =-16,479; p = 0,00. The quantity of pattern types containing agonistic contacts for group 2007 investigated is 112 patt (97 patt (87 %) – for males, 15 patt (13 %) – for females), containing friendly contacts – 101 patt (9 patt (9 %) – for males; 92 patt (91 %) – for females). The quantity of pattern types containing agonistic contacts for group 2008 investigated is 3720 patt (3084 patt (83 %) – for males; 636 patt (17 %) – for females), containing friendly contacts – 177 patt (28 patt (16 %) – for males; 142 patt (84 %) – for females). The majority of these patterns concerns to a category of the "mixed": containing both "individual" and "social" types of activity (Yachmennikova, Poyarkov 2011). Patterns number which contain agonistic and friendly types of activity only, and do not contain others is 14 patt. for group of 2007 (14 %); and 82 patt. for group of 2008 (2 % from all).

Agonistic Behavior Included in Patterns

Essentially important to us was checking up the interesting period in group formation, as a complete system, from day 75 until day 115 of the wolf pups development, proceeding from its role in development of puppies was shown (Yachmennikova, et al. 2010; Yachmennikova, Poyarkov, 2011). However, to our surprise, during this period, the patterns comprising agonistic activity, practically isn't present, though as a whole. their quantity is huge (Yachmennikova, Poyarkov, 2011; Yachmennikova, Blidchenko, Poyarkov *in print*). See Figures 1a and 1b.

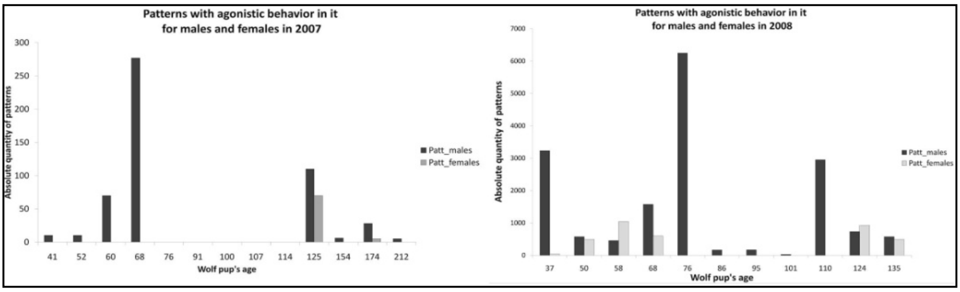


Figure 1. Patterns with agonistic type of behavior in quantity dynamics for 2007 and 2008 seasons; for both males and females.

It is necessary to explain that patterns can be written in the form of schemes and in a line. The scheme represents a type of kluster drawing, in a line it can be written by using of dividing brackets (Yachmennikova, Poyarkov, 2011), see Figure 2. This pattern from 6/25/2008 in linear record looks like:

((rada,b,agon,nr_rada,e,agon,nr)(dunai,b,agon,ad_dunai,e,agon,ad))

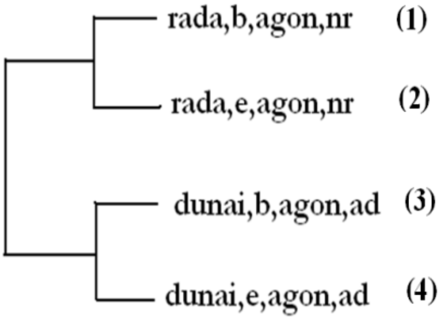


Figure 2. How the pattern looks as a picture.

Events 1,2,3,4 connected in the pattern, occur one after another in time; and events 1 and 2; 3 and 4 are significantly interconnected among themselves stronger than events 1 and 3; 2 and 3 1 and 4, 2 and 4. There can be events which are not entered into a pattern between them. If we have written a communication order "at line", its importance (firstly, secondary), is defined by quantity of brackets in which expression is concluded. Letters "*b*" and "*e*" mean the beginning or the end of activity. Individuals' names in patterns in the end of line designates an individuals' interaction during the activity. Names of individuals are coded by the first letters of their names: letters "*nr*" designate a combination of two females Nika-Rada, a letter "*ad*" – designate a combination of individuals the Amur-Dunai. This pattern is correctly read so: The female Rada begins an agonistic behavior directed on a female Nika, and itself interrupts and stops it, however, right after, the male Dunai attacks (also shows the agonistic behavior directed on) another male, the Amur, and also finishes it itself.

Furthermore, we will analyze patterns' occurrence on an onthogeny scale and will disassemble its sense. Two tables with the most important patterns for groups 2007, 2008 are pictured below. All patterns in tables are written at lines for simplicity of reading and comparison.

The main picture of agonistic behavior participation during the group social formation process will be considered on the patterns having exclusively social maintenance, which are not concerning a "mixed" category ("mixed" patterns have in itself both social and individual types of activity) Some patterns of the mixed type also will be considered and explained below. The analysis occurs in the conditions of time changing.

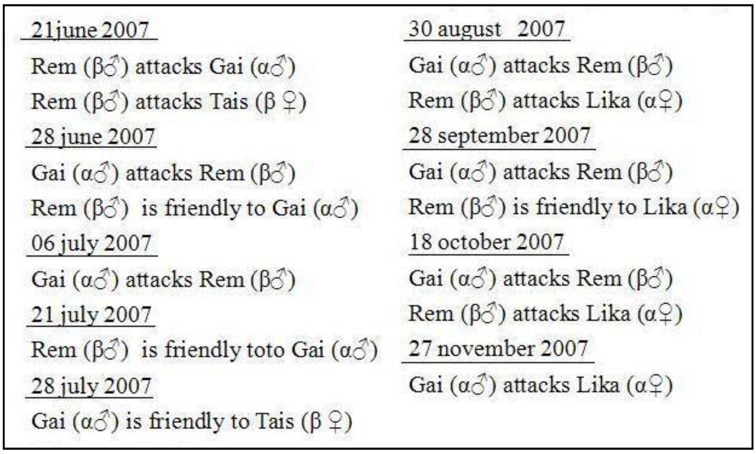
Let us analyze Table 1. Occurring events are deciphered as follows (it is necessary to remind that each of the resulted patterns has repeated not less than 5 times in those days when it is registered). So up until June, 21st, at age 52 days, any pattern comprising only agonistic behavior aren't revealed. At the age of 52 days, 2 simple patterns were registered; they describe attacks of the male Rem on male Gai; and also attacks of the male Rem on the female Tais. Furthermore, at 60 days old, there were 2 simple patterns registered; these patterns are fixing attacks of the male Gai to the male Rem and displaying friendly behavior of the male Rem turned to male Gai. Similar patterns are registered at the age of 68 and 84 days independently from each other. At the age of 91 days, we can note the simple pattern containing friendly activity addressed by male Gai to the female Tais. At the age of 125 days, three simple patterns were registered; in these patterns is the agonistic activity addressed by male Gai to the other male Rem; the displaced activity of the same sort addressed by the Rem to the female Lika, and a pattern containing attacks by a female Lika of male Gai (not repeating in other days). At the age of 154 days, attacks by male Gai of the male Rem were displayed and friendly behavior of the male Rem concerning a female Lika were already registered. Furthermore, at the age of 174 days, the aggression directed from male Gai to the other male Rem; from the male Rem to the female Lika, and its reciprocal readdressed aggression on the weaker female Tais is in patterns. It is necessary to notice that the full picture of social interactions changing for this group can't be fully depicted if the mixed patterns are excluded from the analysis.

Table 1. Agonistic/friend activity in hidden patterns in group 2007

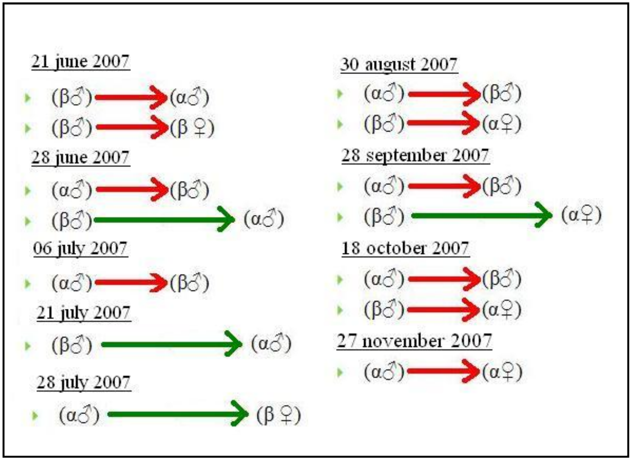
Date	Pups Age	Pattern
21-jun-07	52	(rem,b,agon,gr rem,e,agon,gr)
21- jun-07	52	(rem,b,agon,rt rem,e,agon,rt)
28- jun-07	60	(gai,b,agon,gr gai,e,agon,gr)
28- jun-07	60	(rem,b,friend,gr rem,e,friend,gr)
06- july-07	68	(gai,b,agon,gr gai,e,agon,gr)
21- july-07	84	(rem,b,friend,gr rem,e,friend,gr)
28- july-07	91	(gai,b,friend,gt gai,e,friend,gt)
30-aug-07	125	(gai,b,agon,gr gai,e,agon,gr)
30- aug-07	125	(rem,b,agon,rl rem,e,agon,rl)
30- aug-07	125	(lika,b,agon,gl lika,e,agon,gl)
28-sept-07	154	(gai,b,agon,gr gai,e,agon,gr)
28-sept-07	154	(rem,b,friend,rl rem,e,friend,rl)
18-oct-07	174	(gai,b,agon,gr gai,e,agon,gr)
18-oct-07	174	(rem,b,agon,rl rem,e,agon,rl)
18-oct-07	174	(lika,b,agon,tl lika,e,agon,tl)

For example, at the beginning of supervision, the first pattern which contained an agonistic activity was registered on June 9th when wolf pups were about 40 days old: *(rem, b, manip, r (gai, b, agon, gr gai, e, agon, gr))*, it means a chain of actions: the male Rem starts to manipulate with a subject (maybe he gnaws a stick-toy), and it significantly precisely connects with the male Gai attacking the Rem aggressively. This pattern had been repeated on June 9th not less than 5 times. Furthermore, on June 28th, at the age of 60 days, we can see that one of patterns contains such information: male Rem is fed and this event is significantly connected to the event when the other male Gai attacks him aggressively. This pattern looks like: *((rem, b, feed, r rem, e, feed, r) (gai, b, agon, gr gai, e, agon, gr))*.

Also on this day, the pattern *((rem, b, play, rt tais, b, play, rt) (rem, e, play is registered, rt (gai, b, agon, gr gai, e, agon, gr)))* is registered; it means that the chain of actions are: the male Rem invites the female Tais to play with him, she accepts his game, they are playing, then their game stops and it is significantly connected with the subsequent event that the male Gai attacks the male Rem aggressively. Or next, on July 6th at the age of 68 days, one of the registered patterns contains a complex picture of three individuals' behavior: the Rem, the female Tais, and the male Gai: *(((gai, b, agon, gr gai, e, agon, gr) (gai, b, rest, g rem, b, move, r)) (rem, e, move, r (rem, b, rest, r tais, e, manip, t)))*. It is deciphered as such: Gai initiates agonistic interaction with Rem and itself finishes it then he is so quiet after that and begins independent resting-behavior, whereas the Rem shows moving-behavior, he defuses after-stress tensions with movement and then he has rests also. These interactions ending significantly connects with the event in which the female Tais stops her manipulatory activity (probably displaced) by which she has been occupied during this interaction with the 2 males. The above-stated table and an explanation are here for easier understanding of schemes mentioned below. See Figure 3a and 3b.


21june 2007
Rem (β♂) attacks Gai (α♂)
Rem (β♂) attacks Tais (β ♀)
28 june 2007
Gai (α♂) attacks Rem (β♂)
Rem (β♂) is friendly to Gai (α♂)
06 july 2007
Gai (α♂) attacks Rem (β♂)
21 july 2007
Rem (β♂) is friendly toto Gai (α♂)
28 july 2007
Gai (α♂) is friendly to Tais (β ♀)
30 august 2007
Gai (α♂) attacks Rem (β♂)
Rem (β♂) attacks Lika (α♀)
28 september 2007
Gai (α♂) attacks Rem (β♂)
Rem (β♂) is friendly to Lika (α♀)
18 october 2007
Gai (α♂) attacks Rem (β♂)
Rem (β♂) attacks Lika (α♀)
27 november 2007
Gai (α♂) attacks Lika (α♀)

(a)



(b)

Figure 3. Scheme of interactions described the history of group 2007 social forming: a) with individual names and statuses; b) without names.

From the resulted schemes and the description, and also from from supervision and results of individuals testing on revealing of linear hierarchy (Shenkel, 1947; Fox, 1971), we assumed a following general conclusion about this group. In the beginning of the investigation period when individuals only start to understand each other’s individuality and were not incorporated in a social unit, they get into disputes for any limited resource, whether it be the meal or a toy. So relations of a simple direct competition revealed the stronger, this result defined its access to a resource. Initially in this group of 2007, male Gai applies that role. At the age of 21 days, the α position for male Gai it is not established yet and the male Rem initiates agonistic interactions himself. However, in the next days of supervision, after 60 days of age, the Rem position β concerning male Gai is established; and the Rem turns to Gai his behavior of submission, friendliness. It is necessary to notice that male Gai showed the personal positive relation to the weakest female in the group (Tais) since childhood (it also was shown in patterns with pups 60 days aged). The female Tais appears in patterns rare, as the initiator, but also as the recipient of aggressive behavior of any other individual in the group[2]. Why is that? Maybe it connects her with spontaneity and friendliness in the relations to all other individuals. After 68 days of age, a position of the strongest is distributed for males, and the male Rem doesn't turn either aggressions or behavior of domination towards male Guy, aside from other individuals. However, since the age of 125 days, it is the Rem role allocation period, as frontier guard[3] (Poyarkov, 1986). The Rem renews agonistic interactions directed on the stronger female Lika. In the age of about 100 days, we first registered that the Rem marked the territory with the lifted paw and he made scratches after marking, whereas α – male Gai made his excretions activity with all 4 paws on the ground, sitting down, as small pup. The relations between the female Lika and the male Rem was established in the period of about 120-130 days.

Relations between both females were constantly friendly, on numerical indicators the female Lika is allocated as the lead, only by non-standard behavior in different novelty situations (results of testing). She had the lowest level of neophobia[4]. Neofobia is the normal reaction of fear concerning new subjects in wolves. The female Lika needed several days to overcome fear towards a sheet of plywood or a bucket, whereas other individuals avoided these subjects within a week and more. Later in similar tests, all group individuals overcame this psychological obstacle faster- being guided in their behavior by Lika. In competition tests for a resource (food), Lika was stronger than female Tais in 4 cases out of 5; after that, she was marked by us as a female α at juvenile hierarchy’s formation.

Now we will analyze other group social formations of pups born in 2008, see Table 2.

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[2] Significant difference, Friedman-test ANOVA Chi Sqr. (N = 47, df = 3) = 90,23; p =0,00000; Coeff. of Concordance =0, 64; Aver. rank r = 0,63.

[3] Guard Social role in Canids –term was offered by A.D. Poyarkov firstly in his Stray Dogs Investigation, his PhD work text

[4] Neofobia it is the behavioral trait of the wolf adaptibility. The reaction of panic fear if the animal sees the new subject. It is true for subjects made by humans only. Wolves can make tens and hundreds kilometers through territory unknown with new trees and rivers, new stones, animals it firstly meets, but can’t understand even a small simple subject (like a rope for example). This nature trait is the behavioral base of flagged peoples’ hunt on the wolf.

Table 2.

Date	**Pups' Age**	**Pattern**
12-jun-08	*37*	*(amur,b,agon,ad amur,e,agon,ad)*
12-jun-08	37	(dunai,b,agon,dr dunai,e,agon,dr)
12-jun-08	37	((dunai,b,agon,dn nika,b,agon,dn)(dunai,e,agon,dn nika,e,agon,dn))
12-jun-08	37	((nika,b,agon,dn nika,e,agon,dn) dunai,b,agon,dn)
25-jun-08	*50*	*(amur,b,agon,ad amur,e,agon,ad)*
25-jun-08	50	(amur,b,agon,an amur,e,agon,an)
25-jun-08	50	(amur,b,agon,ar amur,e,agon,ar)
25-jun-08	*50*	*(dunai,b,agon,ad dunai,e,agon,ad)*
25-jun-08	50	(dunai,b,agon,dn dunai,e,agon,dn)
25-jun-08	*50*	*(amur,b,agon,an rada,b,agon,nr)*
25-jun-08	*50*	*((rada,b,agon,nr rada,e,agon,nr)(dunai,b,agon,ad dunai,e,agon,ad))*
03-july-08	58	(dunai,b,agon,dn dunai,e,agon,dn)
13-july-08	*68*	*(amur,b,agon,ad amur,e,agon,ad)*
13-july-08	68	(amur,b,agon,ad dunai,e,agon,ad)
13-july-08	68	(amur,b,agon,an amur,e,agon,an)
13-july-08	68	(amur,b,agon,ar amur,e,agon,ar)
13-july-08	68	(dunai,b,agon,dn dunai,e,agon,dn)
13-july-08	*68*	*((amur,b,agon,ad amur,e,agon,ad)(dunai,b,agon,dn dunai,e,agon,dn))*
13-july-08	*68*	*((rada,b,agon,nr rada,e,agon,nr)(dunai,b,agon,dn dunai,e,agon,dn))*
21-july-08	*76*	*(amur,b,agon,ad amur,e,agon,ad)*
21-july-08	76	(amur,b,agon,an amur,e,agon,an)
21-july-08	76	(amur,b,agon,ar amur,e,agon,ar)
21-july-08	76	(dunai,b,agon,dn dunai,e,agon,dn)
21-july-08	76	(dunai,b,agon,dr dunai,e,agon,dr)
21-july-08	*76*	*(dunai,b,friend,dr dunai,e,friend,dr)*
21-july-08	*76*	*((amur,b,agon,ad amur,e,agon,ad)(dunai,b,agon,dn dunai,e,agon,dn))*
31-july-08	*86*	*(amur,b,agon,ad amur,e,agon,ad)*
31-july-08	86	(amur,b,agon,an amur,e,agon,an)
31-july-08	86	(dunai,b,agon,dn dunai,e,agon,dn)
09-aug-08	*95*	*(amur,b,agon,ad amur,e,agon,ad)*
09-aug-08	95	(amur,b,agon,ar amur,e,agon,ar)
09-aug-08	*95*	*(amur,b,friend,an amur,e,friend,an)*
09-aug-08	*95*	*(amur,b,friend,ar amur,e,friend,ar)*
09-aug-08	95	(dunai,b,agon,dn dunai,e,agon,dn)
15-aug-08	*101*	*(amur,b,agon,ad amur,e,agon,ad)*
15-aug-08	*101*	*(dunai,b,agon,ad dunai,e,agon,ad)*
24-aug-08	*110*	*(amur,b,agon,ad amur,e,agon,ad)*
24-aug-08	110	(dunai,b,agon,ad dunai,e,agon,ad)
24-aug-08	110	(dunai,b,agon,dn dunai,e,agon,dn)
24-aug-08	*110*	*((amur,b,agon,ad amur,e,agon,ad)(dunai,b,agon,dn dunai,e,agon,dn))*
08-sept-08	*124*	*(amur,b,agon,ad amur,e,agon,ad)*
08-sept-08	124	(amur,b,agon,ar amur,e,agon,ar)

Table 2. (Continued)

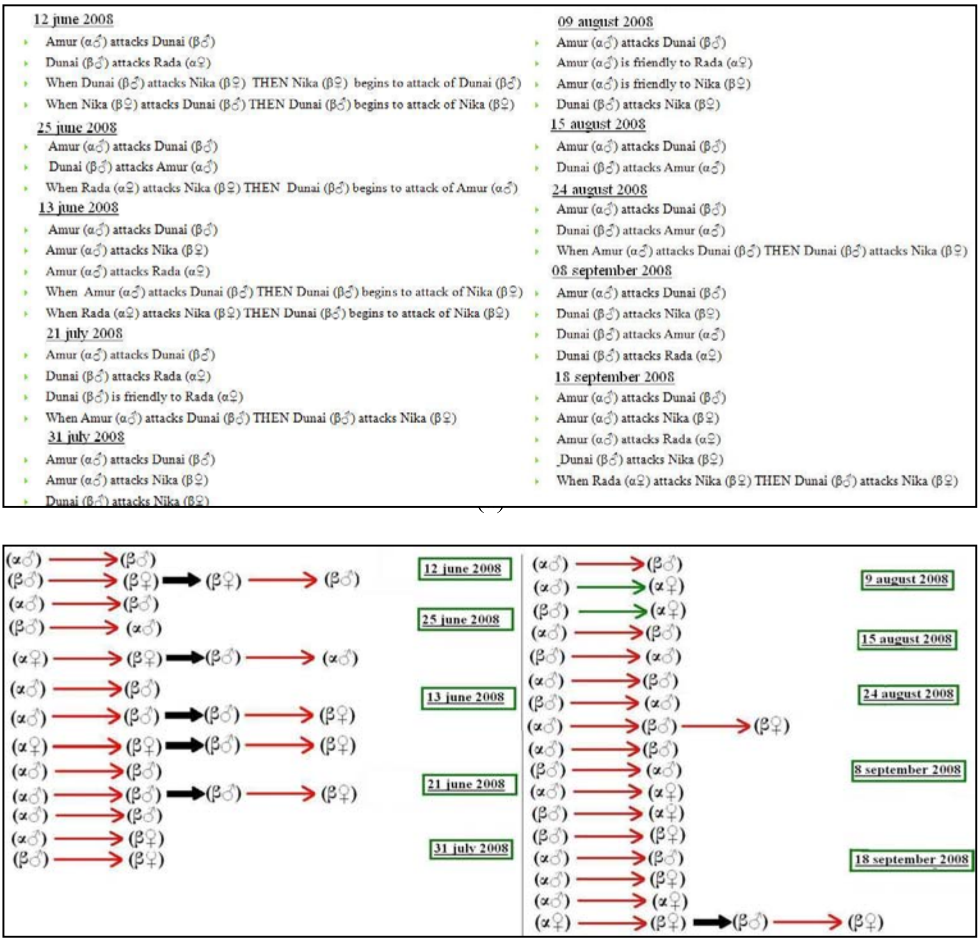
Date	**Pups' Age**	**Pattern**
08-sept-08	124	(dunai,b,agon,ad dunai,e,agon,ad)
08-sept-08	124	(dunai,b,agon,dn dunai,e,agon,dn)
08-sept-08	124	(dunai,b,agon,dr dunai,e,agon,dr)
18-sept-08	*135*	*(amur,b,agon,ad amur,e,agon,ad)*
18-sept-08	135	(amur,b,agon,an amur,e,agon,an)
18-sept-08	135	(amur,b,agon,ar amur,e,agon,ar)
18-sept-08	135	(dunai,b,agon,ad dunai,e,agon,ad)
18-sept-08	135	(dunai,b,agon,dn dunai,e,agon,dn)
18-sept-08	*135*	*((rada,b,agon,nr rada,e,agon,nr)(dunai,b,agon,ad dunai,e,agon,ad))*

Proceeding from Table 2 we can decipher events which occurred as follows: (reminding again that each of the resulted pattern has repeated in days it was registered not less than 5 times). On June 12th at the age of 37 days, 2 simple patterns are registered; it contains information about attacks of the male Amur directed to the male Dunai and also attacks of the male Dunai directed to the female Rada; and also on this day, we have 2 complex patterns in which the meaning of male Dunai with female Nika fight development is concluded: the Dunai attacks the female Nika, and she, in turn, attacks the male Dunai, these inter-connected events attract the similar events one by one, and we have a fight as a result. Furthermore, on June 25th at the age of 50 days, the patterns from the male Amur consisted of attacks directed on the male Dunai and those on females Nika and Rada were registered. Also, we can describe some attacks of the male Dunai to the male Amur which are not registered earlier and once after. At the age of 37 days, the male Dunai attacks the Nika female (it is the same pettern, that repeats in different day). It is worth to note significant inter-relation of attacks of the female Nika by the female Rada and the subsequent attacks of the male Amur by the male Dunai. These were not marked on other days. Probably females' aggressive interactions provoke the subsequent collision of males; also, aggressive attacks of the male Amur to female Nika entail the subsequent attack of the female Rada to the female Nika also. For July 3rd, 2008 at the age of 58 days, only one type of the pattern, which comprises agonistic activity, was registered. It contains attacks by the male Dunai directed on the female Nika (the same as in previous days). Furthermore, for July 13th (age of 68 days) simple patterns that are not inter-connected were registered. It contains attacks of the male Amur directed on all other individuals of the group (the male Dunai, females Rada and Nika). We can also see the male Dunai attacks directed on the female Nika, which were the same registered on ,all previous days. Also, we have two complex patterns in which the inter-relation of events described below is allocated: at first, an attack by the male Amur directed on the male Dunai provokes the subsequent attack by the male Dunai on the female Nika; secondly, such event as an attack by the female Rada on the female Nika also entails the attack on the female Nika by the male Dunai. As a result, we can describe that the female Nika gradually gets a more weakened position in the group. On July 21st, 2008 at the age of 76 days registration of patterns repeated were registered attacks of the male Amur on all other individuals of the group: the male Dunai, females Rada and Nika; attacks of the male Dunai directed on the female Nika; in the pattern where the male

Dunai attacks the other female Rada was registered, but he also showed friendliness to her (necessary to notice that patterns for males with friendly behavior were registered rare as a whole). All pictures are similar to the age of 68 days. Besides, it is an interesting pattern with aggression readdressing by the male Dunai directed on the female Nika, after the conflict with the obvious stronger male Amur (same as at the age of 68 days). 10 days later, at the age of 86 days, there were only the simple patterns concluding all of the same attacks by the Amur on the Dunai, and also attacks by both males directed on the female Nika were registered. At the age of 95 days, the agonistic behavior of the male Amur connects into 2 simple patterns: he attacks the male Dunai again, and he also attacks the stronger female Rada. Patterns with the friendly behavior of the male Amur directed to both females were registered also. The pattern containing attacks of the weaker male Dunai directed on the weaker female Nika was registered again. On August,15th (101 days of age) females weren't joined in patterns; this time, we have 2 simple patterns containing both males mutual agonistic behavior directed to each other. At the 110 days of age, mutual attacks of males Amur and Dunai were in patterns, as well as attacks of the male Dunai to the weaker female Nika, then a fact of aggression readdressing by the Dunai to her after an attack by the male Amur directed on the Dinai were registerd. In the end of the supervision period, at the age of 135 days, we can possibly allocate the complex compound pattern having that attack by the stronger female Rada of the weaker female Nika encouraged attacks directed on the stronger male Amur by the weaker male Dunai. Attacks of the Amur directed on the Dunai are registered on all of the days.

It is interesting to add the described picture with the patterns containing "mixed" behavior. The inter-relation of many occurring events is visible better with their decoding. For example, in the beginning on June 6th at 30 days of age when pups' have been just incorporated in the group, simple patterns were registered: *(amur, b, agon, ad_rada, b, play, nr)* and *(dunai, b, agon, dn_rada, b, rest, r)*. They mean that when the male Amur attacks the other male Dunai, then the female Rada starts to play with the other female Nika (these events are connected significantly); the following pattern is deciphered as behavior of the male Dunai aggressively attacking the female Nika, connects with the event that the other female Rada shows rest behavior; that indicates her psychological condition is comfortable. In a week at the age of 37 days, as an example, we have a pattern *((dunai, b, agon, dr rada, b, play, ar) (nika, b, rest, n (amur, b, play, ar amur, e, play, ar)))*, it is deciphered as such: the male Dunai aggressively attacks the female Rada, however, she evades this contact by beginning the game with the stronger male Amur, and all of these events take place in the female Nika's presence, she has a rest and this is a marker of her stable emotional condition. This is evidently a system functioning of important elements. The male Amur receives the game of the female Rada, he plays with her and finishes this game by himself. Furthermore, at 50 days of age, as an example of a group social condition, we have a pattern*: ((dunai, b, comf, d rada, b, comf, r) ((amur, b, agon, ad amur, e, agon, ad) (amur, b, orient, an amur, e, orient, a)))*. It can be deciphered as such: when the male Dunai is in a stable emotional condition and shows comfortable behavior which is connected with the comfortable behavior shown by the female Rada in significant degree, then rather suddenly, the Dunai is aggressively attacked by the other, stronger male Amur who finishes subsequently that agonistic interaction by himself and distracts after that, with independent orientation behavior showing. Maybe it is very important for Amur to attack the Dunai because he doesn't believe he is powerful enough yet. Further, on July 3rd, when the pups' are at the age of 58 days, a pattern was allocated: *((amur, b, agon, ad amur, b, move, a) (amur, b, manip, a dunai, b, manip, d)).* It illustrates that the male Amur initiates the aggressive interaction with the other male Dunai, however, this interaction consists of very strong emotional excitation for him. In connection with it, after this sort of interactions end, he shows moving behavior for some time, and then secondly realizes the psychological pressure inside of him of a manipulating activity (he gnaws a stick); the second male Dunai in connection with it, also begins manipulating. On July 13th, at 68 days of age, an example-pattern was registered: *((amur, b, agon, ad rada, b, move, r) (dunai, b, rest, ad dunai, e, rest, ad)).* It shows that in spite of the fact that the male Amur initiated aggressive interaction with the male Dunai, the male Dunai doesn't avoid the male Amur, but he also is attracted to have a rest near him. This is an example of the interaction with emotional sign "-" (minus) have a result with a sign "+" (plus). On July 21st, at the age of 76 days, a pattern *((amur, b, orient, a nika, b, orient, n) ((dunai, b, feed, d dunai, e, feed, d) (amur, e, move, a dunai, b, agon, dn)))* was registered and it describes a social condition of the group on this day. The male Amur shows research and rough behavior, and after it, this behavior is also shown by female Nika. The male Dunai in connection with it shows food behavior (he is in safety). However, as soon as the male Amur leaves, the male Dunai attacks the female Nika (he protects his food from her, but he wouldn't have attacked her if the Amur was near). Here, an example of a pattern from August 24th: *((amur, b, play, ad amur, e, play, ad) (dunai, b, agon, ad dunai, e, agon, ad)).* The male Amur initiates the game with the male Dunai, and this game becomes the agonistic interaction then, dishonesty appears in the Dunai behavior, because his game opponent isn't ready to attack. On August 8th we have one pattern with specifying character: *(((rada, b, feed, r rada, e, feed, r) (nika, b, move, n (dunai, b, agon, dn dunai, e, agon, dn))) ((amur, b, move, a rada, b, move, r) (rada, e, move, r (dunai, b, move, d rada, b, rest, r)))).* It is decoded as such: the female Rada shows food behavior, the female Nika can be exited with it, and she moves; the male Dunai become exited too, however he doesn't attack the female Rada (she is not weaker than him), and the Dunai addresses his aggressive with attacks directed to the female Nika. This complex of interactions is connected with another significantly: the male Amur begins moving, the female Rada reacts to it; the male Dunai, is guided by the group and wants to move with them also, but his protest connected with the female Rada foraged and because of that, the Dunai realize his wants of moving behavior occurs only when the Rada stops moving and starts to show the rest behavior. The mixed pattern for August 18th is shown below: *(amur, e, feed, a (rada, e, orient, r ((dunai, b, agon, dn dunai, e, agon, dn) dunai, b, manip, d))).* The male Amur has food behavior, the female Rada sees it and has the roughly-research behavior; the male Dunai, as the most excitable individual, starts to attack the female Nika, and after that, he begins to gnaw a stick (independent manipulating activity) for his normalizing psychological excitation.

All of the above mentioned is shown in the simplified and schematical drawings, and is presented in a scheme more simplified without nicknames of individuals below. See Figure 4a and 4b.



12 june 2008
- Amur (α♂) attacks Dunai (β♂)
- Dunai (β♂) attacks Rada (α♀)
- When Dunai (β♂) attacks Nika (β♀) THEN Nika (β♀) begins to attack of Dunai (β♂)
- When Nika (β♀) attacks Dunai (β♂) THEN Dunai (β♂) begins to attack of Nika (β♀)

25 june 2008
- Amur (α♂) attacks Dunai (β♂)
- Dunai (β♂) attacks Amur (α♂)
- When Rada (α♀) attacks Nika (β♀) THEN Dunai (β♂) begins to attack of Amur (α♂)

13 june 2008
- Amur (α♂) attacks Dunai (β♂)
- Amur (α♂) attacks Nika (β♀)
- Amur (α♂) attacks Rada (α♀)
- When Amur (α♂) attacks Dunai (β♂) THEN Dunai (β♂) begins to attack of Nika (β♀)
- When Rada (α♀) attacks Nika (β♀) THEN Dunai (β♂) begins to attack of Nika (β♀)

21 july 2008
- Amur (α♂) attacks Dunai (β♂)
- Dunai (β♂) attacks Rada (α♀)
- Dunai (β♂) is friendly to Rada (α♀)
- When Amur (α♂) attacks Dunai (β♂) THEN Dunai (β♂) attacks Nika (β♀)

31 july 2008
- Amur (α♂) attacks Dunai (β♂)
- Amur (α♂) attacks Nika (β♀)
- Dunai (β♂) attacks Nika (β♀)

09 august 2008
- Amur (α♂) attacks Dunai (β♂)
- Amur (α♂) is friendly to Rada (α♀)
- Amur (α♂) is friendly to Nika (β♀)
- Dunai (β♂) attacks Nika (β♀)

15 august 2008
- Amur (α♂) attacks Dunai (β♂)
- Dunai (β♂) attacks Amur (α♂)

24 august 2008
- Amur (α♂) attacks Dunai (β♂)
- Dunai (β♂) attacks Amur (α♂)
- When Amur (α♂) attacks Dunai (β♂) THEN Dunai (β♂) attacks Nika (β♀)

08 september 2008
- Amur (α♂) attacks Dunai (β♂)
- Dunai (β♂) attacks Nika (β♀)
- Dunai (β♂) attacks Amur (α♂)
- Dunai (β♂) attacks Rada (α♀)

18 september 2008
- Amur (α♂) attacks Dunai (β♂)
- Amur (α♂) attacks Nika (β♀)
- Amur (α♂) attacks Rada (α♀)
- _Dunai (β♂) attacks Nika (β♀)
- When Rada (α♀) attacks Nika (β♀) THEN Dunai (β♂) attacks Nika (β♀)

(b)

Figure 4. Scheme of interactions described the history of group 2008’s social forming: a) with individual names and statuses; b) without names.

From the resulted schemes and the description above, and also with our observations and individuals’ testing on linear hierarchy revealing results analyzing (Shenkel, 1947; Fox,1971), we assume the following conclusion on this group. In the beginning of the investigation period when individuals were independent from each other, they are independent social units. Until roles between them were defined, males were thought to be ”equalized” in their positions. Thus, the weaker male Dunai applies for a role α, that proves by connection its attacks directed on the male Amur with attacks of the stronger female Rada directed on the weaker female Nika (because their roles are also equalized in the beginning). Attacks by the female Nika initiations are registered in patterns, only at the beginning of the investigation. Then her position of the weakest individual in the group was established and her role becomes the emotional buffer of the group; all other individuals in the group needs her for an emotional emissions equilibration. At 68 days of age in the males dyad, the relation is established. At this age, a resource constantly acquired by the male Amur, and it was possible to allocate it as α, and his role of “power” in the group was established. This is from a result of all tests based on struggle for the limited resource (food). The male Dunai during this period has started to show submissive ritualized behavior concerning the Amur and became marked as β (just β in this level of group forming). However, owing to the Dunai's character, he displaces aggression he accumulated towards the weakest female Nika regularly: both as a result of "losing" in fights with the Amur (α), and as a result of relations between two females. Patterns prove that all of these communications are highly significant. Within a month, there are no agonistic interactions turned by the β male Dunai towards the α male Amur registered in patterns, only toward the β female. As to the following 100 days of age, attacks of males β→α were registered in patterns again. It is connected with the beginning of the independent social role of the Dunai allocation period (role as frontier guard and the security guard of group territory); he partially dominates in this role, it is proved also by its attacks turned towards both females (the weakest and the stronger). During this period, we registered the daily observation that contain information that the male Dunai (β), who conceded to the Amur (α) in all enclosure territory, dominates over him in the region along a limiting enclosure's territory fence. And in this geographical zone, the Amur (α) concedes a resource (food) to him. As a result of supervision, the system is stabilized. The α-male Amur dominates over all members of the group. The inter-relation of α-female Rada's domination over the β-female Nika is strengthened; the β-male Dunai over the β-female Nika domination is also normalized. A social position of the female Rada is slightly separate, she is equalized by forces with the male Dunai. However, by sense, she has the most plastic and adaptive and smart individuality in the group by her behavior (that follows from our observation and pups' group testing with new subjects, new conditions, environment changing), so Rada becomes the leader during those moments when the group faces novelty and the group social system meets a necessity to react to the introduced destabilizing factor correctly.

CONCLUSIONS

Of all of the descriptions resulted above, we can concentrate on the following: The wolf pups' group as a system of unique cooperating elements itself is unique. Therefore, the way it is formed is also unique; although the general rule in existing sequences and rule of forming process as a whole, probably can't be. It is organized and functions using its own ways, abilities and possibilities. In one wolf pups' group, the fullest picture of the group formation process is given by patterns of a "mixed" category - where social and individual types of activity are connected simultaneously, where two categories of the analysis (daily activity and social life of group) are integrated into each other. In such patterns, it is possible to see situations when private types of one individual personal behavior become an occasion or a consequence to social interaction. So, patterns here represent graphic drawings of coherence of situations in time; but all of these situations arise repeatedly. As it is known, the situation as a coincidence of circumstances, is unique in its own way (Pojarkov, 1986); but its repetition (that patterns fix) testifies that it potentially exists and repeats until time won't cease to be claimed and actual. In growing pups, drawing of repeating situations changes with time (in one week for example), therefore the most part of patterns registered for all periods are unique (Yachmennikova, Poyarkov, 2011). When generalizing, it is necessary to notice that the same working structure of a simple group consisting of 4 wolf pups is established inevitably; and it is irrespective of unique psychotypes and characters of individuals as soon as they cease to be their species representatives and formed primary functioning system (social group) through juvenile hierarchy establishment. It is easily reduced to linear hierarchy in daily occurrences of group existence. However, even at these primary stages when puppies are still small, in various non-standard situations which the group faces, in existing conditions and at changes of these conditions, the linear hierarchy is absent. But some difficult structure skeleton, that is plastic in time, exists constantly. And individuals in the existence constantly and variously depend on each other. In some measure, it is possible to see an illustration of this elements interdependence process in a hidden patterns picture. So, what rules of a juvenile social system establishment of 4 puppies of a wolf pack (2 males and 2 females) in their developing initial stage period with the structures (patterns) containing agonistic activity analysis exist? First, we can notice that the establishment of communication and definition of positions between two males is necessary and that occurs at the age of 68 days. After that, their social positions initially (because it is juvenile hierarchy formed and it will collapse after some time period) are fixed. After that, further development of the system and definition of a role of the second male became possible. With the allocation of a second male social role, the social role of the most active and strong (in terms of linear hierarchy) females is rather quickly allocated, also. Social predisposition of the weaker female is defined during the various periods of dependences system in the group establishment, and during the most difficult moments of social reorganizations, this female is the most demanded social partner. For us, in one case, the female was the most cheerful and friendly individual in the group and all contacts of any other individual to it were frictionless. In another case, all unembodied conflicts were realized by other individuals in interaction with such female. Definitively its position becomes clear after an establishment of all other individuals positions. Maybe it would be more correct not to attach to an individuals' sex, but on groups with which we worked,. The question demands further researches.

In summary, it would be desirable to say that any wolves' social group really is a unique system of bright individualities. And even the existing general rules of its formation caused, undoubtedly, specificity of animal ecology, its mental abilities and a way of life, we can understand only by attentively observing each of their steps. Patterns are the unique mathematical mechanism, helping to open these rules and connections. However, without private unique supervision, results of this mathematical mechanism work turns to the mysterious number code which needs a special key.

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Chapter 5

PLAY AND POST-CONFLICT MECHANISMS IN WOLVES: A COMPARISON WITH HUMAN AND NON-HUMAN PRIMATES

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ABSTRACT

Cooperation is a series of coordinated interactions in which participants take turns in giving and receiving benefits. Nevertheless, competition is the other side of the coin and it may generate aggression among conspecifics loosing social cohesion. Many social species have developed behavioral strategies to cope with social damage caused by competition. We investigated the occurrence and dynamics of these behavioral strategies in wolves (*Canis lupus lupus*), a species characterized by high sociality and cooperation levels, by carrying out a long-term observational study on the grey wolf colony hosted at the Pistoia Zoo (Italy). We highlighted the occurrence of post-conflict affiliation both between opponents (reconciliation) and between victims and bystanders (solicited and unsolicited contacts). Reconciliation was uniformly distributed across the different sex-class combinations and seemed to be not affected by the hierarchical relationships. Moreover, coalitionary support given to victim and/or to aggressor during a conflict may be a good predictor for high level of reconciliation. Concerning unsolicited triadic contacts (named “consolation” in human and non-human primates), we found that this affilation was more frequent between individuals sharing good relationships and was reciprocated between partners (victims and third-parties), thus suggesting the reciprocal nature of this mechanism (mutualistic behavior). As it occurs in human and non-human primates, unsolicited contacts provide immediate benefits to the victim by breaking-off aggression and restoring victim’ social cohesiveness. To investigate other affinitive behaviors used by wolves to promote cohesiveness and cooperation, we evaluated the presence of social play, an activity used by animals for self- and social-assessment purposes. We showed the occurrence of adult play in wolves. Play distribution is not affected by relationship quality and aggression level, thus suggesting that other strategies are employed for strengthening inter-individual relationships and reducing aggressiveness. Rank distance between conspecifics negatively correlate with play distribution: by playing wolves with closest ranking positions tested each other for acquiring information on motor and psychological skills of possible competitors and for gaining hierarchical advantage over it. The overall findings on wolves strongly match with those coming from behavioral studies on human and non-human primates. Even though further comparative-cognitive studies are needed in canids, the similarities between primate and wolf social cohesion strategies suggest an evolutionary convergence in certain traits of cognitive skills at the basis of natural conflict resolution and adult social play.

INTRODUCTION

Many animals live in social groups. Sociality has been viewed as an evolutionarily advantageous state, in which members take turns in giving and receiving benefits from cooperation in protection against predators, mate choice, collective rearing of offspring, and territory defense (Parrish and Edelstein-Keshet, 1999; Schuster and Perelberg, 2004; Noë, 2006; Silk, 2007). Cooperation is particularly effective in those species which show a clear division of labour based on different and complementary roles and high tolerance levels (de Waal and Brosnan, 2006; Anderson, 2007; Hare *et al.*, 2007). Like humans, other cooperative animals may learn to fine-tune their actions in order to coordinate and anticipate each other's behaviors (see Schuster and Perelberg, 2004). When individuals cooperate, they may engage in behavior that would be ineffectual if performed alone (e.g. group hunting in lions *Panthera leo*, Scheel and Packer, 1991; Stander, 1992; in chimpanzees *Pan troglodytes*, Boesch and Boesch, 1989; in bottlenose dolphins *Tursiops truncatus*, Connor, 2000; in humans, *Homo sapiens*, Stiner *et al.*, 2009). Nevertheless, competition and conflict of interests represent the other side of the coin of these cooperative systems and may generate aggression among conspecifics loosing social cohesion. Many group-living species have developed non-dispersive modes of coping with conflicts and maintaining cooperative bonds, such as post-conflict behaviors and play activity (de Waal, 1986; van Hooff, 2001).

POST-CONFLICT BEHAVIORS: RECONCILIATION AND THIRD-PARTY INTERACTIONS

To manage aggressions, several primate (including humans) and non-primate species have developed a variety of peace-keeping tactics, such as reconciliation and triadic contacts (solicited and unsolicited) (de Waal and van Roosmalen, 1979; Das, 2000; Call *et al.*, 2002; Kutsukake and Castles, 2004; Palagi *et al.*, 2004, 2006; Cordoni *et al.*, 2006; Koski and Sterck, 2007; Norscia and Palagi, 2011).

de Waal and van Roosmalen (1979) first defined reconciliation as a tendency by former opponents to contact each other relatively shortly after a conflict and to engage in affinitive behavioral patterns.

During the last 25 yrs., much effort centered on the systematic demonstration of reconciliation in several primate species (Aureli *et al*., 2002). However, for other taxa, few systematic data exist (for domestic goats Schino, 1998; for spotted hyenas Wahaj *et al*., 2001; for dolphins Weaver, 2003; for rooks Seed *et al*., 2007; for domestic dogs Cools *et al*., 2008; for grey wolves Cordoni and Palagi, 2008; for red-necked wallaby Cordoni and Norscia, unpublished data), even though anecdotal descriptions of post-conflict affiliation have been reported for several non-primate species before the ‘discovery’ of primate reconciliation (*Ovis ammon* Pfeffer, 1967; *Helogale undulata* Rasa, 1977; *Ovis aries* Rowell and Rowell, 1993). One of the reasons for the rare systematic studies on reconciliation in non-primate species may derive ‘*from the widespread belief that primates (all of them) are in some way special and that the degree of social sophistication they show is unmatched in the animal kingdom*’ (Schino 2000, p. 226). However, any species having individual recognition and good memory of previous social interactions, is potentially able to engage in conciliatory contacts (de Waal and Yoshihara, 1983); this assumption is supported by the occurrence of reconciliation in several animal species with marked difference in their relative brain size (Kappeler and van Schaik, 1992; Kappeler, 1993).

After a conflict both victim and aggressor can also receive affiliation (solicited and/or unsolicited) from a third-party individual not involved in the previous aggression (Palagi *et al*., 2004, 2006, 2008; Fraser *et al*., 2009). Particularly, consolation (a term coined for humans and great apes) has been defined as the first post-conflict affinitive contact directed by a third party to the victim (chimpanzees, *Pan troglodytes*: Wittig and Boesch, 2003; Kutsukake and Castles, 2004; Palagi *et al*., 2006; Koski and Sterck, 2007; Fraser and Aureli, 2008; Fraser *et al*., 2008; gorillas, *Gorilla gorilla*: Cordoni *et al.*, 2006; Mallavarapu *et al*., 2006; bonobos, *Pan paniscus*: Palagi *et al*., 2004; children: Fujisawa *et al*., 2006). There has been some debate in the literature about the use of the word ‘consolation’, since the term includes a hypothesis about the function of this post-conflict mechanism as distress alleviation. Yet, to date, such a function has been demonstrated only in humans (Zahn-Waxler *et al*., 1995) and chimpanzees (Fraser *et al.*, 2008); for this reason, the use of a less value-laden term, ‘unsolicited third-party contacts’, is generally preferred.

de Waal and Aureli (1996) applied the same observational protocol used for apes to demonstrate the occurrence of unsolicited post-conflict affiliation in monkeys (*Macaca fascicularis*, *M. fuscata*, *M. sylvanus*, *M. nemestrina*), but they failed to find any, nor did others (Watts *et al.,* 2000: *Macaca fascicularis*, *M. mulatta*, *M. arctoides*, *M. fuscata*, *M. sylvanus*, *Chlorocebus aethiops*, *Erythrocebus patas*, *Papio anubis*, *Papio hamadryas*). Several researchers have interpreted such difference in the light of the high cognitive ability and empathy levels that characterize great apes and humans (de Waal, 2008; Fraser *et al*., 2008). Nevertheless, the assumption of empathy-based third-party affiliation in apes is still not supported by strong and clear data. In fact, Preston and de Waal (2002) argued that consolation may represent an intermediate level of empathy that corresponds to ‘sympathetic concern’ in developmental psychology (de Waal, 2008; Romero *et al*., 2010). Seed *et al.* (2007) and Cools *et al.* (2008) showed the presence of third-party affiliation in rooks, *Corvus frugilegus* (a large brained bird), and in dogs, *Canis familiaris*, respectively, although these authors did not provide any results on the potential functions of peaceful third-party contacts in their studies.

PLAY BEHAVIOR: FEATURES AND ROLES

Play is an affinitive behavior used by animals to assess and maintain social and cooperative bonds and to face tension situation (Pellis and Pellis, 1991; Pellis and Iwaniuk, 2000; Palagi *et al.,* 2004, 2007; Palagi, 2006, 2008). This activity contains cooperative and competitive elements (Bauer and Smuts, 2007) and it has been thought to be more prevalent and multi-layered in larger-brained species because it requires socially complex skills to be performed so as to maximize benefits and minimize risks (Fagen, 1981; Martin and Caro, 1985; Byers, 1999; Iwaniuk *et al*., 2001).

Many functional hypotheses have been formulated on playful activity: providing physical training (Smith, 1982; Byers and Walker, 1995), developing cognitive skills (Loizos, 1967; Poirier *et al*., 1978; Fagen, 1981; Martin and Caro, 1985; Dolhinow, 1999), improving fighting abilities (Palagi *et al*., 2007; Cordoni, 2009), achieving social assessment (Thompson, 1998; Pellis and Iwaniuk, 1999, 2000), training for the unexpected (Špinka *et al*., 2001), limiting aggression, and increasing tolerance around food (Palagi *et al*., 2004, 2006, 2007).

A widely accepted view is that the function of play is not the same in all species; furthermore, within a given species, play can be influenced by different variables such as dominance relationships, context, habitat, sex, and age (Breuggeman, 1978; Poirier *et al*., 1978; Dolhinow, 1999; Cordoni, 2009). Concerning age, playful activity is most commonly reported during the juvenile phase (Fagen, 1981, 1993; Mendoza-Granados and Sommer, 1995; Dolhinow, 1999; Palagi *et al*., 2004, 2007).

Nevertheless, play can continue into adulthood, thus suggesting that this behavior provides benefits also at a proximate level, such as overcoming the resistance of a potential sexual partner (by promoting the familiarization process), establishing and maintaining social bonds, and probing for strength/weakness in dominance relationships (Pellis and Pellis, 1991; Pellis and Iwaniuk, 2000; Palagi *et al*., 2004, 2007; Palagi, 2006, 2008; Cordoni, 2009).

Adult-adult play has been described in many mammals such as human and non-human primates (see Pellis and Iwaniuk, 2000; Palagi, 2006, 2008; Gray, 2010), social canids (Bekoff, 1974, 1977, 1995; Bernal and Packard, 1997; Cipponeri and Verrell, 2003; Bauer and Smuts, 2007; Cordoni, 2009), domestic horses (Hughes, 2002; McDonnell and Poulin, 2002), meerkats (Sharpe, 2005), and rats (Pellis *et al*., 1993; Smith *et al*., 1999).

THE SPECIES AND THE AIM OF THE STUDY

Wolves live in packs, which are defined as family groups including a breeding pair and their offspring and characterized by male and female dispersal (Mech and Boitani, 2003). Within a pack, each animal has a certain rank in a dominance hierarchy and cooperates with conspecifics as a unit to defend the pack's territory and offspring. It was originally thought that the high level of social organization had more to do with hunting success, and while this still may be true to a certain extent, emerging theories suggest that the pack has less to do with hunting and more to do with the collective rearing of offspring and, consequently, with reproductive success (Mech and Boitani, 2003). The pack activity may be affected by hierarchical relationships that are maintained by elaborate dominance ⁄submission displays. Particularly, the *alpha* male guides movements of the pack and initiates aggressions against intruders (Mech, 1977). However, as the subordinate group members can sometimes oppose their leader's actions, Zimen (1981) defined the leadership in wolf packs as a 'qualified democracy', in which no subject decides alone the carrying out of activities that are vital to the group cohesion.

We had the opportunity to investigate the occurrence and features of post-conflict behaviors and playful activity in a captive reproductive colony of grey wolves (*Canis lupus lupus*) hosted at the Giardino Zoologico of Pistoia (Pistoia, Italy).

The colony was composed by eleven adult wolves, 5 males and 6 females (see Table 1). During the study period the *alpha* female was dead and another female was separated by the rest of the group, thus the observations were carried out on nine individuals. All wolves were captive-bred siblings (range of age 3–10 years) with the exception of the *alpha* parental male; the kin composition was similar to that of wild groups (Mech and Boitani, 2003). The animals were housed in a part of natural hill of about 4000 m^2 enriched with trees, branches and dens (see Figure 1.a and 1.b).

Figure 1.a. Eastern side view of the wolf enclosure of the Pistoia Zoo (Italy) (Photo by Ivan Norscia).

Facility enrichment features vary naturally across the seasons and small animals coming from the surrounding wood (e.g., squirrels, lizards, birds, rats) may enter wolves' enclosure. The wolves received food (meat, which was scattered on the floor) once a day in early afternoon (around 3.00 pm); water was available ad libitum. No stereotypic or aberrant behavior was observed.

We carried out a 3-year-length observational study (2004-2007) during which we recorded all aggressive, affinitive, and playful interactions among individuals (see Table 2) by employing all occurrences sampling method (1,115 hrs. of observation) (Altmann, 1974). Observations took place at least 1 day per week, over one 6-h period that spanned morning and afternoon, including feeding times at 03.00 pm.

Figure 1.b. South side view of the wolf enclosure of the Pistoia Zoo (Italy) (Photo by Ivan Norscia).

Table 1. The colony of grey wolf (*Canis lupus lupus*) hosted at the Giardino Zoologico of Pistoia (Italy)

SUBJECT	SEX	YEAR OF BIRTH
Wolf (Wo) *alpha* male	M	1986
Luna (Lu) *alpha* female	F	1989 †
Flat (Fl)	F	1995
Tala (Ta)	F	2002
Wantolla (Wa)	F	1995
Hateia (Ha)	F	2002
Ookami (Oo)	M	1997
Anouk (An)	M	1999
High Tail (Ht)	M	1999
White (Wh)	F	1999
Ruga (Ru)	M	1995

For studying post-conflict behaviors, we used the conventional measures of reconciliation/third-party-interaction from human and non-human primate conflict research; the employment of the same procedure permitted us to interpret the findings in a comparative perspective. After the last aggressive pattern of any given agonistic event (Figure 2), we followed the victim as the focal individual for a 10-min post-conflict period (PC).

Control observations (matched controls-MC) took place in a next possible day at the same time as the original PC, on the same focal animal, in the absence of agonistic interactions during the 30 min before the beginning of MC and when the opponents had the opportunity to interact (de Waal and Yoshihara, 1983; Kappeler and van Schaik, 1992). Both for PCs and MCs we recorded: (1) starting time (minute), (2) type of first affinitive interaction, (3) the minute of first affinitive behavior, (4) initiator of the affinitive behavior and (5) partner identity. A ‘‘third-party’’ was defined as an individual, other than the victim or the aggressor, not involved in the conflict. In order to estimate reconciliation and third-party interaction (solicited and unsolicited) for each animal we determined the number of attracted (A), dispersed (D) and neutral (N) pairs overall PC–MC pairs. In attracted pairs, affinitive contacts between victim and aggressor and/or between victim and third-party occurred earlier in the PC than in the MC (or in the PC, but not in the MC), whereas in dispersed pairs affinitive contacts occurred earlier in the MC than in the PC (or they did not occur at all in the PC).

Figure 2. Hateya stands over Flat (a typical aggressive pattern) (Photo by Federica Pacini).

Table 2. Aggressive, affinitive, and playful patterns recorded during the observation of the Pistoia wolf colony

AGGRESSIVE PATTERNS	
Aggressive Bite	An animal bites a fellow snapping jaws shut; often it is a head-shake bite
Aggressive Charge	An animal walks towards fellow with piloerect, stiff forelegs and ears back
Aggressive Chase	An animal chases a conspecific, usually with ears back and piloerect
Aggressive Jump	An animal jumps forcefully on a fellow with its forelegs
Aggressive Push	An animal pushes forcefully a conspecific
Aggressive Wrestle	An animal fights with a fellow
Gape	An animal shows open mouth and ears back orienting toward fellow. This pattern often accompanies charge
Growl	An animal growls at fellow and shows the teeth
Knock-down	An animal pushes down another
Standing over	The dominant animal stands over a subordinate one
AFFINITIVE PATTERNS	
Body Contact	Two animals stay for at least 10 sec. with a part of their bodies in contact
Inspecting	An animal sniffs or licks another's ano-genital region
Play	One or more animals engage in motor patterns typical of 'serious' functional contexts but in a different manner. See the following definition
Social Lick	An animal licks part of another's body except the ano-genital area
Social Sniff	An animal sniffs a fellow except its ano-genital area
PLAY PATTERNS	
Solitary Play Patterns	
Chase-own-tail	An animal runs around itself trying to catch own tail
Play jump	An animal jumps alone often on environmental objects
Play manipulation (object play)	An animal tugs, chases, pulls to piece, kicks, shakes and bites an object with mouth or paw
Play roll	An animal turns its body from side to side while supine
Play run	An animal runs alone in a playful manner
Squirm	An animal squirms its body while supine
Social play patterns	
Hide-and-seek	An animal hides and a fellow seeks it
Play ambush	An animal waits in ambush a fellow that is coming and it usually jumps on it
Play bite	An animal gives an inhibited bite to a fellow
Play bow	An animal bows in front of another. It is usually used as play invitation or as play signal. It also has a role in hunting as a good 'all-purpose' position from which the animal may easily break in any direction depending on the movements of the prey
Play fighting	An animal stands up on its hind legs and puts front legs on fellow' shoulders, usually silent and with open mouth, individuals usually bite each other
Play invitation	An animal stamps or bows on forelegs with ears up, facing other animal, or use foreleg to paw at shoulder of another animal
Play jump	An animal jumps on another wolf or leaps away in a non-serious manner
Play paw	An animal paws on another's body part in a non-serious manner
Play run	An animal chases another animal, usually with ears forward and not piloerection

In neutral pairs, affinitive contacts occurred during the same minute in the PC and the MC, or no contact at all occurred in either the PC or MC. Overall, the minimum number of PC–MC pairs per focal animal was 11. To evaluate individual reconciliation, we used Veenema *et al.*'s (1994) measure of conciliatory tendency (CCT), defined as 'A minus D pairs divided by the sum of (A+D+N) pairs'. On the other hand, we followed Call *et al.* (2002) to estimate individual triadic contact tendency (TCT) defined as ''A minus D pairs divided by the sum of (A+D+N) pairs". The CCT and TCT provide a quantitative estimation of reconciliation and third-party interaction levels, respectively.

We also extracted background information on relationship quality among wolves using affinitive interactions (see Table 2) collected via scan animal sampling (510.5 hrs. of observation for a total of 6112 scans. Altmann, 1974).

The collected data were used to achieve the following aims:

- investigating the occurrence of reconciliation and third-party affiliation (solicited and unsolicited) in wolves and determining CCT and TCT at group-level.
- describing the distribution and dynamic of reconciliation and third-party affiliation in relation to sex, hierarchical *status* and relationship quality, highlighting the role of post-conflict interactions in stress alleviation.
- determining the level of solitary and social playful activity and investigating the distribution and function of social play according to sex, hierarchical *status* and relationship quality.
- evaluating the possible roles of social play in managing tension situation (e.g. pre-feeding time, mating period) and scaffolding social network among group-fellows.

DYNAMICS AND ROLES OF RECONCILIATION AND THIRD-PARTY INTERACTIONS

For the first time, we confirm the occurrence of reconciliation in grey wolf (A pairs > D pairs, Wilcoxon exact test: T = 0, ties = 0, N = 8, $p < 0.01$. Figure 3), determining a mean group CCT of 53.2% ± 4.6% SEM (Cordoni and Palagi, 2008). The presence of high reconciliation level in the Pistoia wolves may be related to the high degree of cooperation typical of the species (Mech and Boitani, 2003) and may suggest that daily affinitive interactions and coalitions do not generate sufficient 'social security', which generally prevents the disruption of the social bond among opponents. In this view, reconciliation is probably needed to reaffirm the relationship jeopardized by previous aggression, which was reconciled independently of its intensity level (low intensity conflict mean CCT 59.2% ± 8.5% SEM; high intensity conflict mean CCT 50.1% ± 7.7% SEM; Wilcoxon exact test: T = 12, ties = 0, N = 8, $p>0.05$). The colony under study showed the presence of a linear hierarchy (h' = 0.875, $p < 0.001$, directional consistency index = 0.96). Nevertheless, the hierarchical relationships did not affect the wolf conciliatory tendency (correlation CCTs - rank distances, Partial row-wise matrix permutation test $\tau_{Kr\ xy,\ z} = 0.64$, N = 9, $p>0.05$). A similar finding has been shown for spotted hyenas (*Crocuta crocuta*), a species whose members cooperate to acquire and defend resources (Holekamp *et al.*, 1997; Boydston *et al.*, 2001); despite their highly structured clans (Drea and Frank, 2003), victims and aggressors begin conciliatory contacts with comparable rates (Wahaj *et al.*, 2001). Vehrencamp (1983) argued that when the cooperation of subordinates is essential to dominants, dominance may be relaxed, because subordinates can exert leverage power by withholding cooperation. Like in humans (Stiner et al. 2009), in wolves alliance and strong cohesion between leader and subordinates keep the pack together and improve the cooperation among group members (Fox, 1980); in this species non-dispersive behavioral mechanisms may be favored independently of hierarchical rules (Bekoff, 2002). In the Pistoia wolves, the absence of difference between winners and victims in the initiation of the first post-conflict affinitive contact may support this assumption (Wilcoxon exact test: $T = 4$, ties = 2, $N = 9$, $p > 0.05$). Some authors suggested that after a conflict both aggressor and victim experience stress (Aureli, 1997; Castles and Whiten, 1998; Das *et al.*, 1998; Schino, 1998), which could be related with the uncertainty about the relationship of the opponents (Aureli, 1997; Aureli *et al.*, 2002). Palagi *et al.* (2005) found an asymmetry in the initiator of post-conflict reunion in a captive group of ring-tailed lemurs (*Lemur catta*), with aggressors initiating first post-conflict affinitive contacts more often than victims. The authors suggested that, in a despotic and non-cooperative society as that of ring-tailed lemurs (Pereira and Kappeler, 1997), aggressors are more likely to initiate post-conflict reunions because victims experience fear due to their condition as losers. A striking asymmetry between victims and aggressors with respect to the initiation of reconciliation was also found in spotted hyenas: victims exhibited higher conciliatory contact rates compared to aggressors (Wahaj *et al.*, 2001). The authors argued that, if the function of reconciliation is to yield information about the intentions of the opponents, such information is likely to be more useful for victims (Cords, 1988), because they are more likely than aggressors to be uncertain about whether conflicts will continue. The lack of asymmetry with respect to the initiation of reconciliation found in the Pistoia wolves suggests that both aggressor and victim may gain benefits from restoring the damaged relationship. Moreover, in the studied colony, conciliatory contacts were more common between individuals sharing high levels of coalitionary support. To our knowledge, only one study on primates reported similar evidence: Assamese macaque females showed a higher CCT level with females with whom they exchanged higher rates of agonistic support (Cooper *et al.*, 2005). The wolf finding may be interpreted in view of cooperation as a cause (stronger interest in reconciling of partners with highly cooperative relationships given the greater loss of benefits) and ⁄or as a consequence (greater benefits to be regained by the restoration of the relationship between partners usually involved in highly cooperative actions) (Aureli and Schaffner, 2006).

Anyway, the correlation between reconciliation and coalitionary support highlights the intrinsic cooperative nature of the wolf species. The wolf cooperative social system may affect also the occurrence of post-conflict third-party affiliation. In the Pistoia group, we confirm the presence of both solicited and unsolicited third-party interactions (solicited contact A>D: Wilcoxon exact test $T=0$, ties=0, $N=8$, $P<0.01$; not-solicited contact A>D: Wilcoxon exact test $T=0$, ties=0, $N=8$, $P<0.01$. Figure 4) with the mean group TCT of 78.5% ± 5.7% SEM and 62.1% ± 5.8% SEM, respectively (Palagi and Cordoni, 2009).

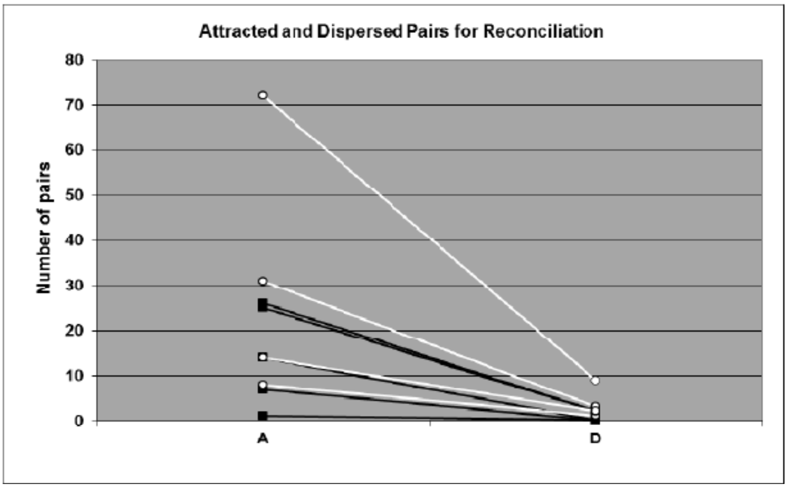

Figure 3. Attracted (A) *vs* Dispersed (D) pairs for reconciliation in wolves. Males: black lines and squares; Females: white lines and circles.

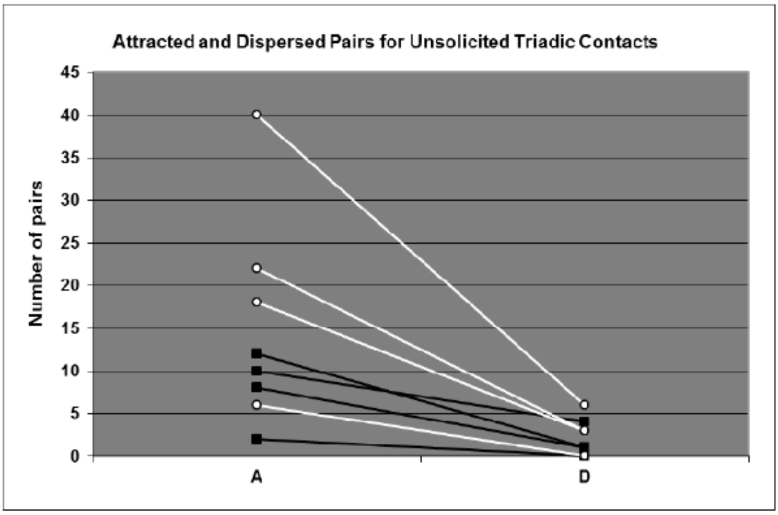

Figure 4. Attracted (A) *vs* Dispersed (D) pairs for unsolicited triadic contacts in wolves (named "consolation" in human and non-human primates). Males: black lines and squares; Females: white lines and circles.

In this chapter, we focused on unsolicited contacts offered by bystanders toward victims of aggressions.

Bystanders face some possible risks in initiating an affinitive contact with a victim (Koski and Sterck, 2007). The wolves seemed to manage the potential risks associated with post-conflict interactions by engaging in unsolicited third-party contacts after aggressions of lower intensity level (Wilcoxon exact test; low intensity conflict: A>D T=0, ties=1, N=9, P<0.01; medium intensity conflict: A>D T=0, ties=2, N=9, P<0.05; high intensity conflict: A=D T=0, ties=5, N=9, P>0.05) and offering affiliation more frequently to the victims showing lower levels of redirection (Correlation unsolicited contact received and redirection performed; Row-wise matrix permutation test: K_r= -35, τ_{rw}= -0.209, N=9, P<0.025; α=0.025 Bonferroni correction). To minimize the threat of being target of redirection, wolves may fine-tune their third-party contacts according to the aggressiveness of the victim and to the quality of relationship shared with it. Indeed, in the Pistoia colony, unsolicited third-party affiliations were directed towards those victims with whom bystanders shared a higher degree of social familiarity (good affinitive relationships measured by body contact rates), thus highlighting the capacity to discriminate specific fellows as more valuable social partners than others. We have to consider that, as in the wild (Mech and Boitani, 2003; Packard, 2003), the study wolves were all highly related and kinship may affect the distribution of affinitive interactions. However, also among related subjects, it was possible to classify dyads on the basis of their social relationship closeness. This evidence is consistent with the friendship hypothesis (de Waal, 1982; de Waal and Yoshihara, 1983), which predicts that affinitive post-conflict interactions are more frequent between those subjects sharing close bonds. A similar result has recently been found by Fraser and colleagues (2008) in unrelated chimpanzees: the value of the relationship (measured by grooming, food sharing and agonistic support rates) between victims and bystanders strongly affected the unsolicited contact rates.

Watts and colleagues (2000) suggested that unsolicited third-party interactions (consolation) may substitute reconciliation in stress reduction and protection. Some studies carried out on hominoid species (bonobos, chimpanzees and gorillas) evidenced higher levels of "consolation" in absence of reconciliation (Wittig and Boesch, 2003; Palagi *et al.*, 2004, 2006; Cordoni *et al.*, 2006; Fraser *et al.*, 2008). When reconciliation fails to occur, consolation may function as a post-conflict alternative mechanism for reducing stress in the victim. In the Pistoia wolves, we found the same result obtained for the great apes: the incidence of unsolicited third-party interactions decreased in presence of previous reconciliation (occurrence of unsolicited contacts in absence *vs* in presence of reconciliation-Wilcoxon exact test: in absence > in presence T=2, ties=1, N=9, P<0.05), thus confirming the hypothesis that "consolation" may function as an alternative post-conflict behavior.

Koski and Sterck (2007) showed that third-party affiliation neither serves to reduce stress nor represents an alternative mechanism to reconciliation in chimpanzees. Recently, in the same species, Fraser *et al.* (2008) found contrasting results. They showed that consolation reduced stress in the victim. Unfortunately we have no quantitative data to investigate whether unsolicited contacts reduce victims' stress in wolves. However, Cools and co-authors (2008) reported an anecdotal observation in *Canis familiaris*, in which those bystanders that had not directly witnessed the conflict were attracted by the whimpering sounds of the victim.

In social canids, the winner effect (an increased willingness to initiate further fights; Chase *et al.*, 1994; Hsu and Wolf, 1999) is a well-known phenomenon. In wolves, high levels of aggressive contests induce chronic stress in both dominant and subordinate subjects (Sands and Creel, 2004). Our results showed that unsolicited third-party contacts significantly reduced the probability of renewed aggression to the victim. From this perspective, this kind of post-conflict affiliation provides positive and immediate benefits to the victim in a sort of break-off aggression service. Moreover, unsolicited third-party contacts may restore the levels of victim social cohesiveness (measured by contact sitting *plus* proximity rates), thus suggesting that this post-conflict behavior may preserve social relationships and buffer the pack's social tension arising from the previous agonistic encounters.

PLAY AND ITS SOCIAL AND POST-CONFLICT ROLES

The occurrence of social play during adulthood suggests that this behavior may provide short-term benefits (Pellis and Iwaniuk, 2000; Palagi *et al*., 2004; Palagi, 2006; Cordoni, 2009). In some primate species adult-adult play may occur in both sexual and non-sexual contexts. Courtship play is found to be especially prevalent in solitary species where males and females are unfamiliar with one another (e.g., *Mirza*, *Daubentonia*, *Perodicticus*, and *Pongo*); on the other hand, non-sexual play is more prevalent in species with a high degree of social cohesion (Pellis and Iwaniuk, 2000). However, the size of social groups does not seem to be sufficient to affect and increase the frequency of adult play (Spijkerman *et al*., 1996). In fact, in many species of cercopithecids, such as *Papio*, characterized by large troops and highly cohesive subgroups with structured relationships (Kummer, 1995), play among adults has not been reported. Conversely, adult-adult play was reported in species such as *Ateles*, *Cacajao*, and *Pan*, whose social organizations are based on a more fluid composition, with many combinations of association which frequently change (Pellis and Iwaniuk, 2000).

In the Pistoia wolves, both social relationship quality (measured by body contact levels and agonistic support) and aggressive interaction rate did not affect the frequency of adult play (correlation between dyadic play frequency and body contact rate - Row-wise matrix permutation test: $K_r = 38$, $\tau_{rw} = 0.158$, $N = 9$, $p>0.05$; correlation between dyadic play frequency and agonistic support rate – Row-wise matrix permutation test: $K_r = 23$, $\tau_{rw} = 0.102$, $N = 9$, $p>0.05$, correlation between dyadic play frequency and aggression rate - Row-wise matrix permutation test $K_r = -11$, $\tau_{rw} = -0.046$, $N = 9$, $p>0.05$) (Cordoni, 2009). In infant spotted hyenas, the increase of play is correlated with the reduction of aggressive interactions between siblings and with the integration of pups into the pack (Drea *et al*., 1996). Conversely, no correlation was found between aggression rates and social play in red-necked wallabies (Watson, 1993). Moreover, some studies on free-ranging primates did not reveal any negative influence of play reduction on social relationship strength (Baldwin and Baldwin, 1974; Lee, 1984). In meerkats (*Suricata suricatta*), another cohesive and cooperative mammal species, play levels were not linked either with aggressive or with affinitive contact rates (Sharpe and Cherry, 2003; Sharpe, 2005). Accordingly, Biben (1983) suggested that inter-specific play is not correlated with the development and maintenance of social bonds between group-members. On the contrary, hunter-gatherer human societies, where play (both with rules and without) is used in social practices (religion, bargaining, children's education, etc.), show a more fluid, democratic structure and are more open to new incomers (Gray, 2010). Probably, in wolf packs other behavioral mechanisms are used for strengthening social cohesiveness and reducing conflicts among fellows. Cordoni and Palagi (2008) previously demonstrated that, in the Pistoia wolves, subjects showing more cooperative relationships (measured by agonistic support during aggressions) exchanged more conciliatory contacts with each other (see the former paragraph). Even if it is not possible to establish a cause-effect relationship, it seems that the more the wolves cooperate during agonistic contests the more they are inclined to preserve peaceful social relationships.

Contact play, in general, and play fighting (rough and tumble play), in particular, seem to have a role in socialization and in developing motor and psychological skills, especially during infancy (Smith and Boulton, 1990; Pellegrini, 1995; Thompson, 1998; Pellis and Iwaniuk, 1999; Power, 2000; Palagi *et al.*, 2004, 2006, 2007; Tanner *et al.*, 2007; Pellis and Pellis, 2009). In juvenile subjects, play fighting begins to include competitive elements that will be used by animals to establish social dominance relationships (Paquette, 1994; Pellegrini, 2002; Pellegrini and Smith, 1998). In humans, Pellegrini (1995) found that adolescent rough and tumble was positively correlated with aggression and negatively correlated with social preference, thus suggesting that play fighting could be a sort of training to acquire information on partner's skills; this information will be useful in the future to gain an advantage on fellow during real fights. In the Pistoia colony, wolves performed contact play with a greater extent respect to non-contact play (Wilcoxon exact test: $T = 0$, ties $= 0$, $N = 9$, $p < 0.01$). A wolf pack can be defined as a division-of-labor-system in which individuals cooperate to maintain the cohesiveness of the group (Mech, 1999; Peterson et al., 2002). In this perspective, social play may be used by wolves as a safe tool for practicing, coordinating, and fine-tuning their behaviors.

Mech (1970) stated that in the wild all young wolves could be potential breeders and could automatically become *alpha* males when breeding. Also in captive packs, individuals may change their dominance *status*, because they do not have a permanent ranking position (Fox, 1971; Fox and Andrews, 1973; Zimen, 1976; Wilson, 2000). For example, without the stabilizing influence of parents (group defined as 'complex family', Zimen, 1975), the siblings fight to compete for the social roles of *alpha* and *beta* (Packard, 2003). In this perspective, by playing wolves may gain information about physical and cognitive abilities of fellows with whom they could compete in the near future for acquiring a higher ranking position. In the study group, a negative correlation between dyadic play frequency and rank distance (measured by the absolute value of the differences of individual David's scores) was found (Row-wise matrix permutation test: $K_r = -105$, $\tau_{rw} = -0.43$, $N = 9$, $p < 0.01$) (Cordoni, 2009). This finding may suggest that wolves with closest ranking positions may need to test each other for social assessment purpose and, certainly, play may serve this function in a safer and fruitful way.

When animals are under environmental (heat, cold, presence of predators), physiological (need for food, drink, sleep, or sexual activity), or social stress, the levels of play are reduced or cease altogether (Loizos, 1967; Rensch, 1973; Baldwin and Baldwin, 1976; Fagen, 1981; Martin and Caro, 1985; Sharpe *et al.*, 2002). For example, both in wild and in food supplemented groups of golden lion tamarins, play usually occurs after foraging (de Oliveira *et al.*, 2003); in highly seasonal Malagasy prosimians, such as *Propithecus verreauxi*, play was mainly or exclusively performed during the wet season when food is much available (Antonacci *et al.*, 2010). Conversely, some studies carried out on captive chimpanzees, bonobos and lowland gorillas, reveal an increase of play behavior during the pre-feeding time, that is the period immediately before the food distribution (Palagi *et al.*, 2004, 2006, 2007) when the conflict of interests between conspecifics is more elevated (Aureli *et al.*, 2002). Also a study carried out on spotted hyenas reveals that social play occurred more frequently during periods of low prey availability than when preys were abundant (Tanner *et al.*, 2007). The Pistoia wolves showed a decrease in social play rate during two periods of high physiological and social stress, that is mating period and pre-feeding time.

Mating Period (MP, from January to March) was defined as the interval between the first and the last day that we witnessed mating within the pack (Sands and Creel, 2004). The frequency of both solitary and social play decreased during MP compared to Non Mating Period (NMP), whereas the level of aggressiveness within the group significantly raised (solitary play MP *vs* NMP: Wilcoxon exact test $T = 0$, ties = 0, $N = 9$, $p < 0.01$; social play MP *vs* NMP: Wilcoxon exact test $T = 2$, ties = 0, $N = 9$, $p < 0.05$; aggressions MP *vs* NMP: Wilcoxon exact test $T = 1$, ties = 0, $N = 9$, $p < 0.01$). The privilege of *alpha* male to access oestrous females as first is not absolute because other group-males may compete with leader for mating with a particular female, thus subordinates may sometimes breed successfully as well (Packard, 1980; Creel and Waser, 1991; Mech, 1999; Wilson, 2000; Creel and Creel, 2002). In captive condition more than one oestrus female is usually present in the group and individuals cannot disperse, therefore multiple breeding and male-male aggressions may be very frequent (Packard, 1980). Accordingly, qualitative observation in the Pistoia colony revealed that the *alpha* male (Wolf) frequently fought with the other high-ranking males (Ruga and High-tail) for mating purposes. Since play mainly occurs in safe and relaxed context (Fagen, 1981; Pellegrini *et al.*, 1998, 2007; Burghardt, 2005), the decrease of such activity during MP, a highly risky period, is not surprising.

Nutritional need is another physiological stress for animals and the period preceding the food provisioning represents a high conflict of interest phase (Aureli *et al.*, 2002). Many studies on primate and non-primate species have demonstrated that during this period play rates are reduced (e.g., vervet monkeys, Lee, 1984; gelada baboons, Barrett *et al.*, 1992; squirrel monkeys, Stone, 2008; ground squirrels, Nunes *et al.*, 1999; meerkats, Sharpe *et al.*, 2002), suggesting that play carries significant energetic costs (Baldwin and Baldwin, 1976; Martin and Caro, 1985).

To investigate whether the presence of food affected play distribution, we distinguished four different periods by preliminary observations: Pre-feeding (PRE, the last 25 min before food provisioning), Feeding (FEED, the 25 min block starting from food provisioning), Post-feeding (POST, the 25 min after FEED), and Control (C, the time block farthest from feeding time, when individuals showed high activity levels). The analysis revealed that social play frequency was significantly different between the four conditions, showing a peak level in POST compared to any other condition (Friedman exact test $\chi^2_r = 18.44$, df = 3, $N = 9$, $p < 0.001$; post-hoc test: POST *vs* PRE: $q = 3.73$, $N = 9$, $p = 0.01$; POST *vs* FEED: $q = 4.50$, $N = 9$, $p = 0.01$; POST *vs* C: $q = 4.70$, $N = 9$, $p = 0.01$. Figure 5). Accordingly, in captive oriental small clawed otters (*Anonyx cinerea*), Pellis (1991) showed a decrease in social play rates as the feeding session got closer and a subsequent increase when animals have fed. The finding on the Pistoia colony suggests that, when the basic physiological needs are not satisfied and the conflict of interests arises, wolves decrease or cease altogether their playful activity by employing other behavioral mechanisms for managing tension situation and aggressive context.

CONCLUSIONS

In this chapter we overviewed the different behavioral mechanisms that are used by wolves to maintain social cohesiveness and to face the negative consequences of conflict of interests. Data on wolves strongly matched with those coming from human and non-human primates. Post-aggression interactions and playful activity are performed in a selective manner in order to preserve social benefits linked to valuable partners (e.g. agonistic support), to restore group cohesiveness by reducing the probability of further attacks and to assess social and dominance relationships by acquiring information on partners' motor and psychological abilities. Even though further comparative-cognitive studies are needed in canids, the similarities between primate and wolf social cohesion strategies suggest an evolutionary convergence in certain traits of cognitive skills at the basis of natural conflict resolution and adult social play. Considering all the data presented in this chapter, it is not surprising that wolves, due to their cooperative nature, had been domesticated by humans for helping and sociable purposes.

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Chapter 6

SOCIAL STRESS IN WOLVES

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ABSTRACT

In wild wolf packs social relationships constitute the most important factor influencing the stress levels and welfare. In this review, we summarize factors influencing social stress of wolves, considering different wolf profiles and their relationships with humans. Wolf social relationships are influenced not only by rank order, but also by the affective behaviors individuals display towards other pack members. Cortisol, an important component of the mammalian stress response is found generally in higher levels in dominant wolves than in subordinates in the wild, but cortisol levels are not predictive of rates of agonistic interactions. Social stress in wolves seems thus not to be a consequence of subordination, but a cost of dominance. Higher levels of aggressive interactions are reported from enclosure-kept animals in comparison with wild wolves. Little is known, however, about the behavioral factors mediating the connection between glucocorticoids levels and stress loads in captivity. Some of the data reviewed here indicate higher levels of glucocorticoid in dominants, but similar levels in both dominants and subordinates have also been reported. Stress hormone data from wolves in captivity may be confounded by unnatural group composition, restricted living areas (fences making temporary avoidance impossible), and by the different levels of socialization with humans. As wolves' behavior is flexible, varying according to environmental and social context, data from captivity may be viewed as indicating the potential range of behaviors wolves can perform in the wild. Hand-raised wolves have been recently used as a model for the study of wolf cognition and the origins of dog behavior. This study has brought insights into the role human partners may have in modulating wolves' stress levels. A wide field for further research opens, which may shed light on the adaptive flexibility of wolves, and may contribute to improve wolf welfare in captivity and in the wild.

INTRODUCTION

A limited number of studies has dealt with stress related to sociality in wolves [McLeod et al. 1996; Moger et al. 1998; Creel 2001; Gadbois 2002; Sands and Creel 2004; Creel 2005; Vasconcellos et al. submitted[1]]. Such knowledge would however be quite relevant to understand the behavior of this highly social species, to promote conservation, and to provide wolves with a better quality of life in the wild and in captivity. In this review, we summarize factors that may influence wolf's social stress and present a few data of our own on that topic. We will consider different levels of socialization and, therefore, distinguish wild wolves, wolves living in enclosures and wolves subjected to intense socialization with humans. We also suggest potentially important future research topics.

To start with, it is important to mention that there is no such an entity as "the wolf". Different populations of wolves were intensively shaped by natural and even anthropogenic selection, including the diffusion of dog and coyote genes into the wolf gene pools [Lehman et al. 1991; Vilà and Wayne 1999]. This has resulted in a wide range of phenotypes, expressing the response to the variety of social and physical environments to which wolves adapted. Compared to other canids, like foxes and coyotes, wolves are the most variable in temperament, within the species [Fox 1975]. Wolves' behavioral phenotypes not only have been found to vary among individuals, but may also change with time and experience in different individuals, mainly as a function of social context [Zimen 1975].

Individual social position in a pack is not constant, but conditional on the behavior of other wolves, at least in packs with another structure than parent-offspring. The old and deterministic view of static wolf packs structure resulted in tests for early signs of leadership in wolf pups [Fox 1971]. In contrast, Mech [1970; 1999] suggested that all young wolves are potential breeders and potential alphas, and that there is no permanent social status in wolves, in contrast to macaques in which social status may also be genetically heritable [Beisner et al. 2011]. This idea is supported by the study of Cipponeri and Verrell [2003], who found that interactions among pack members are significant predictors of rank changes, at least in captive wolves. It is thus important to study the different wolf profiles, taking into account their social past and their social context.

STRESS RESPONSE

Unpredictable components of life cause an emergency state [Wingfield and Ramenofsky 1999], which results in changes in the endocrine and metabolic status of an organism, with increases in glucocorticoids and catecholamines secretion. These increases are the first endocrine mechanisms which defend the organism against challenging situations [first studied by Selye and Cannon, widely reviewed by Moberg 2000]. The hypothalamic-pituitary-adrenal axis is activated by a wide variety of

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environmental and social stressors, in particular, exposure to novelty and lack of predictability or controllability of important events [Sapolsky 1992a; Möstl and Palme 2002; McEwen and Wingfield 2003]. The nature of the stressor is of course relevant, but due to the individuals' subjective evaluation, a certain object/context may be stressful for a certain individual, but not for another one [Beck 2000].

Among the substances involved in the stress-response cascade, glucocorticoids are particularly widely studied, because their effects are more long-lasting than the effects of catecholamines, and potentially more harmful in the longer term [i.e., with permanence or repetition of stressful events]. Glucocorticoids are, in addition, relatively stable and also easily determined as varying metabolites [Möstl and Palme 2002]. The functions of glucocorticoids include increasing blood glucose levels and cardiovascular tone, and inhibiting the gastrointestinal, reproductive and immune systems. Cortisol is also widely known to be associated with aggressiveness, as indicated by studies with wild animals [e.g, Levine et al. 1970], and even in humans [Verona et al. 2009]. There is a direct brain link between stress and aggression.

In order to evaluate the stress levels of captive animals, the concentrations of glucocorticoids may be used as parameters. Measures taken from faeces, in canids, proved to be linked to events occurring 1-2 days before (Schatz & Palme 2001), whilst blood, urine and saliva samples showed to reflect adrenal alterations occurring some minutes before (Kobelt *et al.* 2003). Fecal samples are therefore generally used in studies on the general (average) levels of stress [Sands and Creel 2004; Vasconcellos et al. submitted[1]], while blood, urine and saliva samples are preferred in investigations of the effect of punctual events over the stress levels of the organism [McLoad et al. 1996; Creel et al. 2002].

In dogs, among other species, acute stress is followed by an increase in the activity of the sympathetic-adrenal-medullary axis [Parilla *et al.* 1990; Pagani *et al.* 1991] and the hypothalamic-pituitary-adrenal axis [Knol 1989; Rothuizen *et al.* 1993]. These conditions may result in increased cortisol secretion, the main glucocorticoid in dogs and most mammals, which may be adaptive if brief [McEwen and Wingfield 2003]. However, severe and chronic levels of stress may reduce individual fitness through immunosuppression and tissue atrophy [Munck *et al.* 1984], and through a decrease in reproductive success [Dobson, Smith 1995].

SOURCES OF SOCIAL STRESS IN WILD WOLF PACKS

In wild wolf packs, the social relationships in the group are among the most important factors influencing the wolves' stress levels and welfare. Social environment provides support for the learning and management of physical environment but is also a source of challenges [Packard 2003]. Relationships are influenced not only by dominance and rank order, which determine wolf reproductive success, but also by affective behaviors individuals display towards their pack members. Packard [2003] underlines the emotional aspects of the relationships within the packs, in which stability is maintained through a balance between cohesive and agonistic forces. This suggests that the endeavor for a higher social status is counteracted by the necessity to maintain affiliative bonds with the companions [Miklósi 2007]. Social stability in the pack indeed seems to be one of the most important issues and all members tend to perform pacifying behaviors [Fentress et al. 1987; Packard 2003].

The social structure in wolf packs was formerly seen as a linear hierarchy, with strict and stable hierarchical status [Zimen 1982; Fentress et al. 1987; Derix et al. 1993; Miklósi 2007]. There is still disagreement about the existence of separate hierarchies for males and females [Zimen 1982; Fentress et al. 1987; Derix et al. 1993; Mech 1999], but a mainstream of recent research shows that the pack may be considered as a family-structured group, with the breeding pair and its pups and, possibly, yearlings [Mech and Boitani 2003; Miklósi 2003; Packard 2003]. A great variability in this structure has been observed [one adult male and two adult females, an adult male with yearlings from other mates and a new mate, a mated pair with siblings of one of them; Mech and Nelson 1990]. The dominance hierarchy in the wild seems thus less a result of agonistic interactions, but may rather be due to acceptance of the parents/elders' rules by offspring.

The exclusive reproduction of one pair (usually the parents) in a family-structured pack, at least in the wild, is supposed to be relatively peaceful, partly as a function of inclusive fitness advantages the yearlings or non-breeding family members would achieve from helping raising the pups of the breeding pair. The parents also profit from having extra help in raising their pups, and the expectation to find relatively peaceful packs was confirmed [Mech 1999; Mech and Boitani 2003]. This also matched the findings in studies on other social species in the wild [Creel et al. 1992; 1997].

Even reconciliation, observed formerly by de Waal and van Roosmalen [1979] in primates, was observed in wolves of both sexes, independently of hierarchy: both winners and losers would initiate reconciliation [Cordoni and Palagi 2008]. Unsolicited third-party affiliative intervention [the first post-conflict affinitive contact directed by bystanders to victims], a behavior previously observed in apes [Palagi, Paoli and Borgognini Tarli 2004; Mallavarapu, Stoinski and Bloomsmith 2006; Fraser, Stahl, and Aureli 2008], birds [Seed, Clayton and Emery 2007] and dogs [Cools, van Hout and Nelissen 2008], was also reported for wolves [Palagi and Cordoni 2009].

Although stress loads may be lower than expected in packs due to family-structure, these may increase if the offspring mature and still remain in the pack [Derix et al. 1993]. Tensions may be relieved with their dispersal [Mech and Boitani 2003]. Dispersing may be, on the other hand, highly risky and stressful for the wolves which are leaving their original pack. As most wolf packs are strongly territorial, it may be hard for a newly dispersed wolf to breed successfully, because this presupposes the need to find a mate and a territory with sufficient resources [Rothman and Mech 1979]. In addition, transgressing strangers are often killed by packs [Marhenke 1971; Mech 1993; Mech 1994]. Such difficulties in dispersing may contribute to the permanence of young wolves in the natal pack for up to 54 months [Mech and Boitani 2003]. Remaining home, young wolves are however mostly physically prevented from breeding. This may explain wolves' low inhibition to inbreed [Shields 1983; Theberge 1983; Wayne et al. 1991].

Considering the high level of sociality in wolves, and the importance of the maintenance of close bonds among pack members, some level of social stress related to hierarchy is expected. Based mostly on studies of non-social or social non-cooperative breeders (either in captive or in the wild), it was thought that high glucocorticoids levels were associated with submission, low sexual activity, and even sexual suppression [for reviews, see Creel 2001; 2005]. Thus wolf researchers considered the possibility of hormonal reproductive suppression in wolves [Mech 1970; Zimen 1976; Packard and Mech 1980]. It makes sense to believe that an increase in glucocorticoids would in the long term lead to sexual suppression, or even complete inhibition, once the catecholamines, secreted in the cascade of stress response [sympathetic-adrenal-medullary axis], activate the sympathetic branch of the autonomous nervous system, then inhibiting the parasympathetic branch and, as a consequence, reproduction [Moberg and Mench 2000]. However, other studies on non-reproducing animals have found no such connection with high levels of cortisol [e.g., Abbot 1989].

The results of more recent research show that dominants may have higher concentrations of glucocorticoids, especially if the hierarchy is instable [Sapolsky 1983] or dominants fight more often than subordinates [Creel et al. 1996]. Higher glucocorticoid concentrations in dominants are generally more common in cooperatively-breeding species [Creel 2001]. In addition, no evidence of hormonal sexual suppression in wolves was found [Packard, Mech and Seal 1983; Creel and Waser 1991; Asa 1997; Creel and Creel 2002; Sands and Creel 2004]. The occurrence of packs with multiple breeders [Mech 2003], although exceptional and probably mainly caused by agonistic pressure of neighboring packs, supports this finding. There is more evidence than lack of hormonal suppression: studies have reported that, in general, the alpha pair agonistically prevents subordinates from mating [Seal et al. 1979; Packard, Mech and Seal 1983; Packard et al. 1985; Derix et al. 1993].

Sands and Creel [2004] found significantly higher levels of glucocorticoid in dominant wolves than in subordinates. There was also glucocorticoid concentration increases for wolves of all ranks during the breeding season. However, counter-intuitively, these concentrations could not predict rates of aggression or agonistic interactions: dominant individuals won more fights than subordinates, although did not fight more often. As Sapolsky concluded [1990; Virgin and Sapolsky 1997], there are some aspects of hierarchical dynamics which are not measurable by simply recording frequency and results of interactions among pack members. It seems that social stress in wolves is not simply a consequence of subordination, but rather a cost of dominance. We agree with Sands and Creel [2004] when they suggest that higher levels of stress in dominants could be a consequence of their general behavioral state (i.e., an internal state, like a readiness to fight). We can also add to this idea the effect of being constantly monitored [Virgin and Sapolsky 1997] by subordinates, or even monitoring the situation of the pack in order to be prepared for possible agonistic interactions. Moreover, social stress in wolves may vary with the seasons, as observed in geese [Kotrschal et al. 1998] and baboons [Sapolsky 1983].

Another relevant stress source for wild wolves is territorial defense, a common cause of death in wild wolves [Mech 1994]. Territorial defense tends to peak in the breeding season, in tandem with territorial advertisement [Peters and Mech 1975; Harrington and Mech 1979] and aggression [Zimen 1976]. Behaviors reported to be related to the defense of territory are scent marking, howling and direct attacks [Mech and Boitani 2003]. A recent, unpublished study [Mazzini, personal communication] demonstrated a correlation between parameters of vocal emissions and cortisol levels (see the section “Sources of social stress in captive wolf packs”).

When it comes to stress potentially generated by contact with people in wild-living wolves, opinions are not all convergent. Creel et al. [2002], studying the physiological effects (assessed through fecal analysis) of snowmobile activities in the Yellowstone National Park found that wolves' glucocorticoids levels were higher in areas and times of heavy snowmobile use. Although there was no evidence of acute effects of this increase in the wolves' population dynamics (i.e., no significant increase or decrease in the number of individuals), a long-term decrease in reproduction and survival may be expected based on the well-known deleterious effects of high, chronic glucocorticoids levels. Such data indicate the need of a stricter management of areas where wild wolves are living.

Murray et al. [2010] found that anthropogenic influence accounted for almost 80% of all recorded wolf deaths, in northwestern United States. Humans are considered as the major cause of wolf mortality in much of the wolf's territory [Fritts et al. 2003; Murray et al. 2010]. However, while increasing wolf densities promoted higher anthropogenic risk, these actually reduced natural risks of death, indicating partially-compensatory effects of anthropogenic mortality with increasing population density. Several studies have shown that wolves' behaviors towards humans depend pretty much on their previous experience with people [Parmelee 1964; Grace 1976; Mech 1998]. Wolves may survive in crowded regions [Zimen and Boitani 1979; Boitani 1986; Ciucci et al. 1997; Kumar and Rahmani 2001], and even den next to people's routes [Smith 1998; Thiel et al. 1998]. Additionally, tracked in Yellowstone National Park prior and during the big-game hunting season (when elk, moose, mule deer and bighorn sheep are available for hunters, and discarded at the boundaries of the Park), and differently from grizzly bears and cougars, wolves did not change their movement pattern [Ruth et al. 2003].

Proximity and contact between wolves and humans may (and must) be managed in order to promote wolves with a more positive experience and prevent anthropogenic-generated stress and interference in wild wolves' survival and reproduction.

SOURCES OF SOCIAL STRESS IN CAPTIVE WOLF PACKS

Higher levels of aggression are reported in captive wolves, in comparison to the levels reported in wild ones, probably due to the non-natural composition of the group and restrictions in available movement area (making it impossible for wolves to regulate interindividual distance according to social tension) in the former case [Schenkel 1947; Zimen 1982; Miklósi 2007]. Zimen [1982] reported that adult lower-ranking animals can behave cryptically, or even perform "pup-mimicry", possibly to avoid aggression from higher-ranking animals. Infanticide was only reported, so far, for captive packs [Packard 2003].

A different view about aggressiveness of captive wolves was expressed regarding captive packs with a family-structure, similarly to most wild packs [Packard 2003]. Comparing six packs of captive wolves living in enclosures with different environmental and social structures, Frézard and Le Pape [2003] found that behavioral diversity, one of the parameters normally used to evaluate welfare, was little affected by the size of the enclosure, but was highly related to the social environment. Packs with a "bad atmosphere" were usually composed of unrelated individuals: when one of such unrelated individuals from one of the packs died, the number of socio-positive behaviors increased.

In our own observations of a mixed pack (three pairs of siblings from different origins and three unrelated individuals), aggression was expressed mostly through ritualized behaviors. The few occurrences of overt aggression [which resemble the descriptions by Miklósi 2007] occurred during the reproductive season [2009-2010]. Some of the six newcomers in that pack (11 months old, at that moment) started challenging the reproductive male. As the introduced individuals were not sexually mature, the aggression observed may have been mostly promoted by the general seasonal stress increase, as observed in wild wolves [Sands and Creel 2004].

One hypothesis to explain this low level of aggressiveness even in captive, mixed packs (i.e. non-exclusively family-structured) is the possible stress-reducing effect of such behaviors: the performance of ritualized behaviors instead of overt aggression may be the key to solve most agonistic interactions with low or no harmful consequences. It may indeed reduce tension, promote relief and act, through a physiological process, reducing glucocorticoids concentrations [Moynihan, 1998].

Little is known about the social interactions which mediate the connection between behavior, glucocorticoids levels and stress in captivity. Some data point at higher levels of glucocorticoids in dominants [measured from feces, Vasconcellos et al., submitted[1]], with no correlation between the levels of these hormones and the expression of agonistic or affiliative behaviors. In contrast, similar glucocorticoids concentrations in both dominants and subordinates have also been reported [measured from urine, Mcleod et al. 1996], with some correlation between aggression and glucocorticoids. No differences were found between cortisol concentrations of male and female wolves, and an increase in these concentrations was measured in the mating season [McLeod et al. 1996]. Sapolsky [1992b, 1993] suggested that part of the discrepancy between the results of captive studies may be caused by the way dominance is expressed and whether the social environment is stable or instable. In fact, social stress can even be seasonal, as observed by McLeod et al. [1996, increase in aggression] and Cordoni [2009, reduction of play].

The low level of aggression and the lack of a correlation between ranking and agonistic interactions we found [Vasconcellos et al., submitted[1]], in contrast to the results of McLoad et al. [1996], are striking. The animals they studied lived in a huge area (32.000 m^2) while ours shared an enclosure which measured 3.500 m$^{2.}$ Even thus, the agonistic interactions we observed were less intense than those reported by them, and did not affect glucocorticoids levels. A reasonable explanation for this apparent incongruity could be the high intensity of human contact and activity in our wolves. The wolves we worked with were daily trained on commands, were taken out for leash walking, and participated in several tests on temperament, cognition and communication, at least every third day. This kind of cognitive stimulation may, at least partially replace social hunting and other demanding activities wolves engage in the wild and hence, be responsible for low levels of agonistic interactions, as well as for the lack of correlation between aggressive events and fecal glucocorticoids concentrations.

Is dominance correlated with testosterone levels? Asa et al. [1990] found a correlation between testosterone and scent marking, and Packard et al. [1985] a relationship between testosterone and the initiation of overt aggressive acts. An increase in testosterone concentrations was also observed prior to the reproductive season

[Packard et al. 1983; Asa et al. 2004]. Males have significantly higher levels of testosterone than females (as expected) and, for some individuals, cortisol levels co-vary with testosterone [Gadbois 2002]. This fiding indirectly supports our findings of higher glucocorticoid concentrations in dominants [Vasconcellos et al., submitted[1]], which normally initiate most aggressive interactions, which, in turn, are facilitated by high testosterone concentrations [McLeod et al. 1996].

In a recent, yet unpublished study [Mazzini, personal communication, in preparation] the possible correlation between howling and stress through the measurement of salivary cortisol concentrations was investigated in captive packs. Similarly to what is normally found for humans [Lindblom et al. 2007; Shue et al. 2007; Van Lierde et al. 2009] and other mammals [Watts 2000; Schon 2001; Ikeda and Ishii 2008], some vocal parameters of howling varied with cortisol concentrations: mean maximum frequency, as well as mean range and mean standard deviation. In sum, howling shows higher and shorter pitches and sounds more instable in tone with increasing stress. However, no correlation was found between stress and the mean fundamental frequency or the occurrence of howling bouts.

Negative effects of captivity are generally attributed to a possible increase in the animals' stress load due to: (a) the restricted area captive wolves are housed in, which artificially reduces the distance between individuals and prevents dispersion; (b) the obligatory proximity to human beings [visitors, researchers, keepers]; (c) pack composition, formed, most of times, arbitrarily [Miklósi 2007]. Captivity allows, on the other hand, the assessment and control of parameters in a way not possible in the wild. An example is the study of cortisol responses to acute stressors, which is performed through the training of animals for saliva collection within 15 minutes from a stressor and at short intervals afterwards [Vasconcellos et al., submitted[2]]. Careful choice of pack members, regular assessment of stress indicators and the use of well-established techniques to improve welfare may promote a more naturalistic environment for wolves and favor the maintenance of more adequate stress levels and welfare. Such procedures may also ensure the study of specific aspects of the wolves' behavior, cognition or physiology, with the necessary control over social and physical factors.

Granted that studies in captive wolves demand control of the stress load generated by group composition, restricted area, different levels of socialization, and different, or uncertain origins of the animals, it is crucial to keep in mind that wolves' behavior is flexible, and that they are prepared to adapt to certain environmental and social constraints. As Packard [2003], we think that although data from captivity may not reflect the exact behavior of wolves in the wild, they may be viewed as representative of the *potential* range of wolves' behavior in the wild.

SOURCES OF SOCIAL STRESS IN SOCIALIZED WOLVES

Socialization [socially involved hand-raising, Hemetsberger et al 2010] is increasingly been used in the fields of cognition and communication, in order to allow the

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study of behavioral processes in experimental settings without undue disturbance. In the case of wolves, this approach is often adopted as a way to understand the origins of domestic dog behavior [Fentress 1967; Frank and Frank 1982; Hare et al. 2002]. Socialization is essential in such case once contact with humans during testing is inevitable: appropriate early socialization may reduce fearfulness, promote cooperation and ensure safety for the human partners.

In order to hand-raise (or socialize) animals, they have to be submitted to a constant and intense contact (24 hours a day) with humans in their early age. In wolves, this intense contact, which includes bottle and, later, hand feeding, must start around the 4th-10th day of age and last until they are about 16-20 weeks old. During this period, the animals may have contact with conspecific pups and with suitable dogs and, occasionally, with adult wolves, but most of their time is spent with the human raisers. After this period, animals may be integrated in a pack with older conspecifics [Miklósi 2007], and human interaction can be reduced to one or two days per week [Kubinyi et al. 2007]. This procedure potentially results in socially "normal" animals, which however, are more cooperative and less stress-prone than wolf-raised wolves [Hemetsberger et al. 2010].

This approach has led to interesting results about the role humans perform in the stress levels of captive wolves. Compared to wolf pups, dog pups display more communicative signals when in relatively stressful situations [e.g. vocalizations, tail wagging, and gazing at humans' face; Gácsi et al. 2005]. Wolves seem to be less interested in physical contact with humans [Vasconcellos et al., submitted[3]] and more attentive than dogs to environmental features [Fentress 1967; MacDonald 1980; Zimen 1981; Hiestand 1989]. This can be also observed in novel object tests with hand-raised dogs and wolves: the dogs, after entering the test enclosure, were quicker than the wolves to approach a novel object (conspicuous, plastic or metal-made objects), but showed less interest in these objects [Vasconcellos, unpublished]. These findings suggest that selection under human influence has provided dogs with abilities for a faster habituation to physical features of a human-dominated environment and that dogs are, therefore, less prone to stress due to anthropogenic influence.

Topál *et al.* [2005], in a comparative study of socialized dog and wolf pups, observed that dogs showed more attachment to their owners than to an unknown person, but wolves did not. Continuous contact with human beings during ontogeny may, however, change the degree of attachment of wolves to humans and it should be taken into account that wolves may simply show their attachment to people in a different way than dogs. There are indications that some communicative skills, thought to be absent in wolves, may show up later in development [Virányi et al. 2008].

In human-socialized wolves, social reinforcement (the contact with a familiar dog or with the caretaker) may be more powerful than food in some learning tasks [Frank and Frank 1988; Gácsi et al. 2005]. Additionally, Frank and Frank [1988] observed that, depending on the experimental task, the wolves' performance may be superior to the performance of similarly raised dogs [Frank and Frank 1987].

There are conflicting results in the studies which compare the performance of wolves and dogs in cognitive tasks mediated by humans (the results of which may be confused

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by human interference). Milkósi et al. [2003] report an inferior performance in young wolves in following pointing gestures, compared to dogs. Virányi et al. [2008] and Gácsi et al. [2009] had similar results, but added that wolves' performance improved with intensive training [Virányi et al. 2008] or ontogenetic development [Gácsi et al. 2009]. Range and Virányi [2011] reported that wolves are able to follow humans' and dogs' gaze into distant space while dogs would not [comp. Agnetta et al. 2000]. Moreover, Udell et al. [2008] report a superior performance in wolves, as compared to dogs in following human pointing gestures. Udell et al. [2008] hold that not only the raising environment should be the same for dogs and wolves (hand-raising), but also that the testing environment should be adequate for both.

As to motivational aspects associated with performance, we found that wolves can be trained to obey commands without behavioral evidence of stress [Vasconcellos et al. submitted[2]]. This is supported by the wolves' behavior during training. These hand-raised wolves were trained individually to attend to commands under positive reinforcement. During the sessions, disruptive behaviors (replacement sniffing, retreating and jumping) were very unfrequently observed. Trainers, which observed such behaviors, were generally quick to re-gain the wolves' attention and cooperation. The mean percentage of time spent within one meter of the trainers was more than 90%, and the percentage of time wolves were oriented towards their trainer was approximately 85%. Although the mean percentage of correct commands attended at first request (about 65%) was below the percentage observed from dogs equally raised and trained (about 71%), the mean latency to attend these commands was surprisingly low for both species (1,16 seconds for wolves and 0,72 seconds for dogs). Moreover, the identity of the trainer and the wolf were relevant in determining the animals' behavior, suggesting that the bond built between individual trainers and wolves may significantly affect their performance. The performance and the motivation of the wolves to participate in these sessions suggest that this kind of training does not cause distress. On the contrary, wolves seemed to enjoy this activity.

The differences in performance of wolves and dogs as reported above may develop because human interaction may be a confounding factor: dogs seem more interested in such interactions than wolves. Additionally, wolves seem to be more prone than dogs to suffer the stress of contention [Frank and Frank 1983]. According to Miklósi [2007], dogs' eagerness for social reward can even negatively influence their performance in tests. Differently from dogs, it seems that wolves are less prone to over-motivational stress [Gácsi et al. 2005].

Inter-species or intra-species social contact has been used as a valuable tool to improve welfare of captive animals. It has been shown that social contact may reduce the levels of abnormal behaviors and increase affiliative behaviors [Bayne *et al.* 1993; Doyle et al. 2008], decrease fear and reactivity to stressors [e.g. being handled, Hubrecht 1993], and promote desired behavior patterns [i.e. foraging, exploration, activity and play, Hubrecht 1993].

For many species, contact with humans may even, to a certain degree, substitute for contact with conspecifics [Young 2003]. Bayne *et al.* [1993] demonstrated that only six minutes per week of human contact was sufficient to significantly reduce abnormal behavior in rhesus macaques [*Macaca mulatta*]. It has been also shown that positive human–animal interaction is also associated with reproductive success and a reduction in stress in small exotic felids [Mellen 1991], domestic felids [McCune 1997], and farm animal species [Hemsworth et al. 1986; Hemsworth and Barnett 1987; Pedersen *et al.* 1998; Hemsworth *et al.* 2000].

It has also been reported that training can improve animal welfare, for instance by reducing fearfulness and aggression [Haverbeke *et al.* 2010] and abnormal behavior [Kastelein and Wiepkema 1988], likely because it promotes environmental predictability [Greiveldinger and Boissy 2007], and creates opportunities for positive interactions with humans [Wells, 2004]. Training may give the animal a chance to act upon its environment with predictable outcomes, for instance when attending to commands previously learned. By allowing for predictable interactions and increasing controllability of the environment [Luescher 2008], such activities may improve welfare [Weiss 1972; Veissier, Boissy 2007; Greiveldinger *et al.* 2007]. Hemetsberger et al. [2010] found that hand-raised greylag geese were less stressed during social, handling and predator stress than parent-raised conspecifics. In addition, these animals kept their species-typical life histories and social behaviors, but were less attacked by conspecifics and less vigilant. From the scientific perspective, this is good news, indicating that work with human-socialized animals may result in trustworthy data (i.e. results representative of a certain species/context etc.). From the welfare point of view, such animals may benefit from the hand-raising procedures if they are expected to remain in captivity, in constant contact with humans. These findings may also be true for other species, and deserve further investigation.

CONCLUSIONS

Compared to times when the view of wolves was mostly based on common sense, as well as on anecdotic observations, the body of knowledge on this highly social species has undeniably broadened. Nevertheless, more studies are needed to advance the understanding of the sources of social stress for wolves and, therefore, to ameliorate the life quality of wolves – both in the wild, by taking conservationist measures to protect areas where these animals remain, and in captivity, by improving the relationship between humans and wolves, and providing these animals with appropriate levels of activity and cognitive stimulation. Social and environmental features seem to have shaped wolves' behavior in so many different ways that they developed the potential to express a wide range of behaviors in response to environmental challenges. This kind of flexibility is also reflected in their wide geographical and ecological distribution. It also opens a field for further research on wolf-human relationship, which may shed light in the numerous capabilities of this species, and contribute to the promotion of their welfare via a better understanding of this charismatic and still enigmatic species.

In this chapter, we summarized results of studies run with socialized wolves, from a stress perspective. Some of those results suggest that the constant and positive interaction between wolves and humans, which is mainly scientifically motivating, may also benefit the welfare and balance the social lives of these animals. Therefore, we suggest that socialization and training may be a useful tool to keep captive wolves (and other potentially stress-prone animals) healthy, by promoting activity, predictable interactions and cognitive stimulation, which is known to improve animals' welfare [Wells, 2004; Greiveldinger and Boissy 2007; Haverbeke *et al.* 2010].

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Chapter 7

ECOLOGICAL ROLE AND SOCIAL SIGNIFICANCE OF REINTRODUCING WOLVES IN JAPAN UNDER THE SHRINKING SOCIETY

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ABSTRACT

The grey wolf (*Canis lupus*), sole top-predator of the Japanese forest ecosystem, had been eradicated from the Japanese archipelago by the early 20th century. The absence of wolves, combined with the dwindling number and aging of human hunters, have resulted in overabundance of their prey ungulates such as sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*). Aside from ecosystem engineers which have a critical impact on indigenous forest ecosystem processes, in recent years these animals have been recognized as pest mammals that damage agricultural land. Countermeasures against such damage have been quite limited, depending only on human stewardship such as constructing guard fences and culling the population of pest mammals by local hunters. However, depopulation and aging in rural communities, which started in the 1960s, have accelerated and led to demographic changes nationwide since 2005. Further depopulation, tight national finances, abandonment of mountain communities, and loss of small settlements are expected to continue. This social background will inevitably lead to further shortages of manpower and budget for regional wildlife management, and inadequate sustainable conventional countermeasures based on human stewardship. One solution might consider an alternative to human stewardship, i.e., restoring the natural ecosystem function into forest ecosystem by reintroduction top-predator. Here, we review and discuss the need, effectiveness and feasibility of reintroducing wolves in Japan.

In recent years, the reintroduction of wolves has been planned or already implemented in some former ranges of the species across North America and Western Europe. In Yellowstone National Park (YNP) in the U.S., where wolves were reintroduced in 1995–1996, the decline of overbrowsing by elk (*C. canadensis*), regeneration of native plant communities and restoration of the original landscape have been confirmed since 1995. Although the ecosystem changes have resulted from predation risk by reintroduced wolves, wolf predation has had less impact on the elk population than human hunting. Therefore, not only reintroduction of wolves but culling of pest mammals by human hunters is required for wildlife management in Japan.

A policy that depends only on natural regulation, such as in YNP, would not be appropriate in rural Japan because of the highly mosaic landscape with forests and human settlements, as typified by *Satoyama* landscape. In this chapter, we suggest that the future policy should include both natural regulation by reintroducing wolves in mountainous forests and artificial population control by professional hunters in lowland *Satoyama* areas. Given that social attitude to the reintroduction of wolves in Japan is not yet accepted, further feasibility studies related to wolf reintroduction are required for education and consensus-building in Japanese society. Moreover, alternative population control systems (e.g. professional culling or sharpshooting) should also be developed to counter the decline of human hunters.

INTRODUCTION

Restoring ecosystem altered and degraded by human activity is globally recognized as an important issue (Millennium Ecosystem Assessment, 2005). Reintroduction of organisms, which had been locally or regionally extinct, is a challenging but effective approach to achieve ecosystem restoration (Gogan, 1990; Macdonald et al., 1995). In particular, reintroducing "keystone species", whose impact on the ecological community is large compared to its abundance (Paine, 1969; Power et al., 1996), is important, since it could contribute to restoring ecological community and ecosystem processes broadly via both direct and indirect effects (Soule and Terborgh, 1999; Beschta and Ripple, 2009; 2010).

From a historical perspective, large carnivores have consistently been persecuted by humans; consequently habitat loss, extinction of local populations and species extinction have occurred across the world thus far (Weber and Rabinowitz, 1996; Boitani, 2003; Treves and Karanth, 2003). It has resulted in overabundance of prey ungulates and overbrowsing by them has disturbed ecosystem processes and degraded forest biodiversity (Berger et al. 2001; Fuller and Gill, 2001; Rooney, 2001; Wardle et al., 2004; Beschta and Ripple, 2009; Takatsuki, 2009; Ripple et al., 2009). However, a number of programs on conserving and reintroducing large carnivores have been attempted in recent years: e.g. grey wolf (*Canis lupus*) in North America and Europe (Mech, 1995; 2001; Parsons, 1998; Boitani, 2003; Musiani and Paquet, 2004); red wolf (*C. rufus*) in the southeastern U.S. (Phillips et al., 2003); African wild dog (*Lycaon pictus*) in South Africa (Woodroffe et al., 1997); and Iberian lynx (*Lynx pardinus*) in Spain (Delibes et al., 2000; Vargas et al., 2008). Moreover, some of these programs focused on the importance of natural regulation of large carnivores and were intended to not only establish translocated populations but also to restore ecosystem processes, as in the case of reintroduction projects for the grey wolf in Yellowstone National Park (YNP) and the northern Rocky Mountains in the U.S. (Frits et al., 1997; Smith et al., 2003).

In Japan, the grey wolf as the sole top-predator of the forest ecosystem was eradicated from the Japanese archipelago by the early 20th century (Walker, 2005) and there is no large mammalian predator in Japan's terrestrial ecosystem at the present time. Accordingly, large herbivores such as sika deer (*Cervus nippon*) and wild boar (*Sus scrofa)* have been overabundant and impacted both the forest ecosystem and human agri-communities: degradation of native flora and forest biodiversity (Takatsuki, 2009; Figure 1), soil erosion (Furusawa et al., 2003; Yanagi et al., 2008), landscape alteration (McCullough et al., 2009) and severe damage to agricultural crops and forestry (Knight, 2003; Kaji, 2010). In recent years, the reintroduction of wolves in Japan has been progressively discussed as a means for decreasing the overabundant ungulate populations (Angeli et al., 1998; Knight, 2003; Ishigaki and Nakagawa, 2005; Yoneda, 2006).

This chapter discusses the ecological role and social significance of reintroducing wolves in Japan. First, we review the historical background of the extinction of wolf populations and subsequent ecosystem changes in Japan. Second, we discuss the problems and limitations of the present wildlife management policies in Japan based on future views. Third, we suggest an alternative wildlife management policy that combines both human stewardship and restoring natural regulation, by emphasizing the focus on wolf reintroduction. Lastly, we address the current problems of feasibility and future prospects of wolf reintroduction in Japan.

Figure 1. Understory vegetation inside (above) and outside (below) a deer-proof fence. These photos were taken in Nikko, Tochigi prefecture, eastern Japan.

HISTORICAL BACKGROUND

Two subspecies of grey wolf were present on the Japanese archipelago by the close of the 19th century: the Ezo wolf (*C. l. hattai*) on the isolated Hokkaido Island in northernmost Japan, and the Japanese wolf (*C. l. hodphilax*) on Honshu, Shikoku and Kyusyu islands (Waker, 2005; Ohdachi et al., 2009). Prior to the Meiji era (1868–1912), considering that livestock farming had restrictedly conducted and thus human-wolf conflicts were likely less frequent in Japan compared to in Western Europe and North America (Maruyama et al., 1996). In addition, because gun ownership of common people was severely restricted during this era, hunting pressure on wildlife including wolves would have been relatively low (Kaji, 2010). However, from the Meiji era, wolf habitats had been degraded and the wild prey population had declined resulting from alteration of forested and mountainous areas to settlements or agricultural lands and lifting of the hunting restriction (Kaji, 2010). Moreover, livestock farming, especially cattle, pigs and sheep, was extensively implemented in some parts of Japan (e.g., Hokkaido Island) with introducing Western culture. Wolves began causing serious damage to livestock due to the decrease in wild prey (Waker, 2005). As a result, the Meiji government initiated the financial incentive system for culling wolves across Japan: for example, 630 wolves were killed during 1878 to 1886 on Hokkaido Island (Yamada, 2002; Walker, 2005); 201 and 24 wolves were culled in Miyagi (1875–1880) and Iwate prefecture (1879 and 1880), respectively, both located on the north-eastern mainland of Japan (Nakazawa, 2010). The last hunted wolf was officially recorded in Washikaguchi, Nara prefecture, western Japan in 1905, indicating that wolves in Japan were led to extinction within only about three decades since the Meiji era.

From 1905 to the 1970s, overabundance of prey ungulates, ecosystem degradation, and agricultural damages by those animals were not yet obvious. Since the number of human hunter had rapidly increased from about 100,000 to more than 500,000 during the 1920s to 1970s (Ueda et al., 2010), the populations of most mammalian species had been over-harvested; hence, those populations had kept in low density due to such consecutive high hunting pressure. However, along with the Japan’s dramatic economic growth since the late 1970s, the country’s social structure has also undergone significant changes, including the outflow of rural population and the aging of rural communities across Japan. These changes in rural communities have influenced the impact of human activity on the natural ecosystem, the largest change being the decline in the numbers of human hunters, which decreased from 530,000 in 1975 to 166,000 in 2005 resulting from depopulation and aging in rural communities (Ueda et al., 2010).

Decreasing hunting pressure has resulted in decreasing mortality of wildlife populations. In addition, clear-cut sites in forests had increased during the 1950s to 1970s under the national expansive afforestation policy. Abandoned cultivated-land has also increased from 123,000 (ha) (2.7% of total cultivated land) in the 1990s to about 400,000 (ha) (10.9%) in 2005 with declining agricultural activities (Ministry of Agriculture, Forestry and Fisheries: MAFF, 2007). These human land-use changes resulted in increasing cover and food sources (Agetsuma, 2007) and, consequently, in expanding preferable habitats for most medium- and large-sized mammals such as sika deer, wild boar and Japanese macaque (*Macaca fuscata*). Both the abundance and range of herbivorous animals has drastically expanded resulting from both decline of mortality and increase of population growth. In fact, during the 25 years from 1978 to 2003, the range of sika deer and wild boar expanded by 1.7 and 1.3 times, respectively (Biodiversity Center of Japan, 2004), and has continued to their former range (e.g., Tohoku district, north-eastern mainland of Japan). The population of sika deer has increased across their range: for example, the population index of sika deer increased by an estimated 1.4 times in eastern Hokkaido during fifteen years (1993 to 2008) and by more than three times in western Hokkaido during ten years (1998 to 2008) (Yamamura et al. 2008). High population density of sika deer has also been observed across Japan: for example, 22.1 deer/km^2 in Nikko (Li et al., 1996) and 9.2–57.2 deer/km^2 in Tanzawa (Tamura, 2010) in eastern Japan; and 17.5–30.9 deer/km^2 in Odaigahara in western Japan (Maeji et al., 1999).

Agricultural damage by medium- and large-sized mammals has reached 250,000,000 US$ annually according to the public database derived from MAFF (MAFF, unpublished data). Damage to agriculture and forestry by sika deer is the largest among mammalian species and increased by more than 30 times and 3 times, respectively from 1992 to 2007. Agricultural damage by wild boar also increased by 1.5 times from 1992 to 2007 (MAFF, unpublished data). The impact of sika deer on the forest ecosystem is more serious, and degradation of plant species diversity in the forest understory has resulted from heavy browsing/grazing by deer, similar to that in foreign countries with high deer density, such as Scotland (Fuller and Gill, 2001) and the U.S. (Rooney, 2001). In addition, bark-stripping and foraging of leaf litter by sika deer has resulted in dieback and sparseness of trees (Shibata and Torazawa, 2008), soil erosion (Furusawa et al., 2003; Yanagi et al., 2008; Chu et al. 2010) and landslide. These changes in the forest ecosystem have also impacted small organisms in forest and soil communities via trophic cascades (Miyashita et al., 2004; Niwa et al., 2008; Sato, 2008).

CURRENT MEASURES FOR WILDLIFE DAMAGE CONTROL

The Wildlife Protection and Hunting Law, which is the only fundamental legislation on the management of game and non-game wildlife in Japan, was revised in 1999. According to the revised law, in regulating excessively growing wildlife populations or conserving endangered populations, prefectural governments assume the obligation for developing the “Specified Wildlife Conservation and Management Plan.” The Plan was established to be aimed at ensuring stable conservation and management for a specific mammal or bird species based strictly on a feedback management procedure (similar to adaptive management) by using successive population monitoring. The number of Plans made to date exceeds 100; for example, the Plans for sika deer and wild boar management have been established in 35 and 28 prefectures, respectively, of the 47 prefectures.

One of the main measures for wildlife damage control contained in these Plans is constructing mammal-proof fences or nets to prevent their intrusion. Recently developed such physical countermeasures have beneficial effects on reducing not only agricultural damage (Honda et al., 2009) but also ecological damage (e.g., Tamura, 2010) by mammals, as long as land owners or managers adequately maintain the fences or nets. In many situations, however, such maintenance requires great cost and effort and, therefore, has not been sufficiently continued (Enari and Maruyama, 2005; Figure 2). In another common case, undulating landscape peculiar to rural Japan prevents local residents from constructing fences or nets in the first place. It should also be noted that these physical countermeasures are only stopgap. Thus, excessive population growth of wildlife is not expected to be stopped, given that the causalities of overpopulation (as previously described) cannot be eliminated by these measures.

In this context, as for the problems of overpopulation of sika deer, population regulation under scientific population monitoring has been recently incorporated into the Plans and been actively implemented by intensification of nuisance control as well as the promotion of hunting activities by the general public by loosening the hunting regulations (e.g., extending the hunting season, allowing to hunt female deer). Eastern Hokkaido has been proactively engaged in the deer management, and probatively conducted an intensive harvest of deer in 1998, resulting in a temporary decrease in the deer population (Yamamura et al., 2008). The effect of the intense harvest, however, did not last long and the present deer population size has grown by 140% from the size in 1993. As is the case with this area, most other prefectural and city governments have tried to strengthen the hunting pressure on growing deer populations, but successful cases on deer population control has been locally and temporally limited as yet (Kaji et al., 2006).

The situation of population management of other mammalian species is much more critical than for deer. This is because the scientific knowledge required for feedback management, including techniques for population monitoring and population regulation, is severely deficient for most mammalian species, and there is no falsifiable management policy such as numerical targets for population regulation (Murakami and Oi, 2007; Mano et al., 2008; Hirata et al., 2009; Watanabe et al., 2010). Thus, we must note that most Plans have been poorly functioned to suppress expanding and exacerbating wildlife damage thus far.

Figure 2. Collapsing macaque-proof electric fences (in Aomori prefecture, northernmost mainland of Japan). Although these fences can prevent against macaque intrusion into farmland, the steep terrain surrounding the farmland and inclement weather condition (e.g., typhoon, heavy snowfall) make it more difficult for the owners (i.e., farmers) to maintain the fences in good condition.

HUMAN-WILDLIFE CONFLICTS UNDER THE SHRINKING SOCIETY: LIMITATIONS OF PRESENT COUNTERMEASURES AGAINST WILDLIFE DAMAGE

Along with several European countries (e.g., Germany and Russia), modern Japan has become the depopulating society, which the population growth rate falls into negative territory, having started in 2005. According to the recent official report from Japanese Ministry of Land, Infrastructure, Transport and Tourism (MLIT, 2011), this demographic downward trend will continue in the future; the total population is expected to further decline by more than 30,000,000 in 2050, whereas the proportion of elderly to the total population rapidly increases and will reach 40% by the mid 21st century (Figure 3). This report also points out the serious future prospects that the populations of >60% Japanese settlements decrease by half and 21.6% settlements becomes uninhabited by 2050, because the population distribution in Japan will become more biased along with the trend that the outflow of the rural population to urban areas has remained unchanged (MLIT, 2011). This means that the demographic catastrophe will occur intensively in rural communities, the areas of which are neighboring mountainous forests (i.e., wildlife habitat).

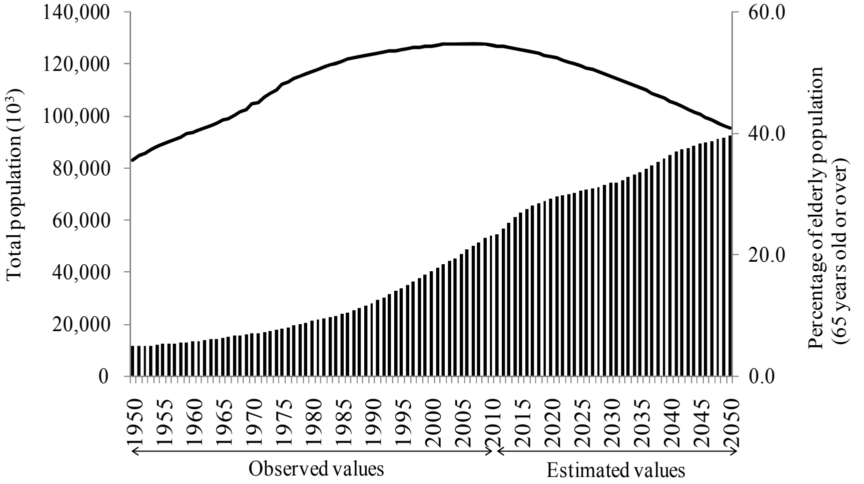

Figure 3. Historical demographic movement and its future prospects in Japan, drawn by public database from MLIT (2011). The black polygonal line shows the total population and the gray bars indicate the percentage of elderly population.

These future prospects suggest that wildlife populations and their habitats will expand and the shortage of wildlife managers in rural areas will worsen (Enari, 2010). In fact, the number of hunters, who play a key role in Japanese wildlife management, has rapidly decreased since the 1970s (as seen above). In addition, more than 60% of hunters are over 60 years old, and most of them are farmers and/or foresters (Figure 4; according to the public database in 2008, derived from Biodiversity Center of Japan). Supposing that the number of agriculture and forestry workers continues to decline with the decimation of rural communities, it is highly likely that the increments of the new candidates for hunting cannot be expected. This indicates that the suppression factor for increasing wildlife populations more weakens than ever before.

In accordance with this weakened population suppression factor, the wildlife damage could become more intensified in remaining agri-communities and the expanding ecological damage to native vegetation by rapidly increasing ungulate species is inevitable. Moreover, the distribution of most wildlife is expected to enlarge and partly overlap flatland on the outskirts of urban regions, causing the urbanite-wildlife conflicts (such as intruding on home, scavenging through garbage, and biting residents by wildlife). In fact, wildlife damage in urban areas by Japanese macaques (e.g. Yamanashi pref., central Honshu; Figure 5) and wild boars (e.g. Hyogo pref., western Honshu; Ozaki and Hirayama, 2003) has already been reported in various regions of the country.

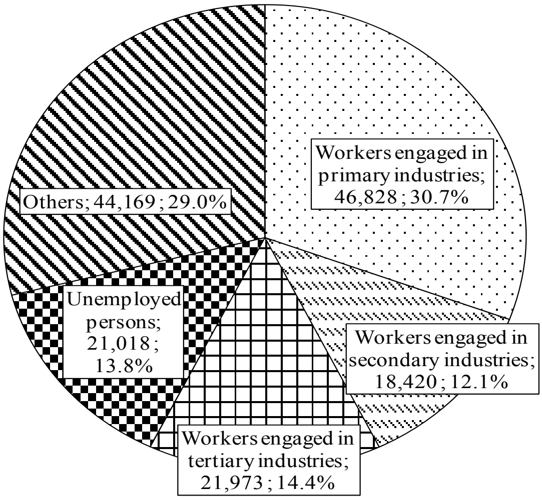

Figure 4. Type of occupation of hunters in Japan, according to the public database derived from Biodiversity Center of Japan for 2008.

Figure 5. Japanese macaques intruding into a garden (left) and grave (right) next to houses to forage horticultural crops and flower offerings, respectively. In recent years, the opportunity to make a close encounter with macaques has gradually increased even in areas surrounding cities. These photos were taken in Yamanashi Prefecture, central Japan.

Thus, the efficacy and sustainability of population management only by human stewardship for species with growing populations are quite limited, assuming that the above future scenario under the shrinking society become a reality. Aged hunters seldom hunt animals in mountainous forests far from settlements due to their limited physical ability. Along with the declination of rural communities, roadway infrastructure, especially located around the outer edge of residential areas, deteriorates—such as abandoned forest roads. This indicates that mountainous forests become less accessible and hunting activity becomes more diminished in the deep mountains than ever before, even if the hunters are young. As a corollary, it should be considered that it is quite difficult to implement and sustainably continue artificial population regulation in the deep mountainous forests.

WILDLIFE MANAGEMENT POLICY AND WOLF REINTRODUCTION IN THE CHANGING JAPANESE SOCIETY

Since depopulation and social shrinkage will be inevitable, it needs to change from the present management policy that completely depends on human stewardship (Figure 6–A). Restoring natural regulation—reintroduction of regionally extinct grey wolf as a potential predator—has been actively discussed as a population regulation measure for overabundant ungulates in some regions of the Holarctic, e.g., the Scottish Highland in the UK (Wilson, 2004; Gorman, 2007; Nilsen et al., 2008; Manning et al., 2009), and is actually practiced in parts of the U.S. such YNP (Fritts et al., 1997; Smith et al., 2003). Since the wolf reintroduction in YNP and the Greater Yellowstone Ecosystem (GYE), the abundance of large ungulates such as elk (*C. canadensis*) has decreased due to the combination of snow fall, human harvesting (outer YNP) and wolf predation (Vucetich et al., 2005; Evans et al., 2006). In addition, the presence of wolves has increased the vigilance of large ungulates, which have changed their habitat use (Creel et al., 2005; Fortin et al., 2005; Mao et al., 2005). Accordingly, regeneration of vegetation (especially riparian tree species such as cottonwoods (*Populus* spp.) and willows (*Salix* sp.)) and restoring landscape has observed resulted from a trophic cascade through both the decreased ungulates population and their avoidance of habitats with high predation risk (referred to as “predation risk effect”: see Ripple et al., 2001; Ripple and Beschta, 2004; 2007; Beschta and Ripple, 2010).

The trophic cascade due to wolf reintroduction has also extensively influenced the forest ecosystem: e.g., reconstruction of songbird assemblage (Berger et al., 2001; Hollenbeck and Ripple, 2008); changes in soil nutrition (Frank, 2008); and food supply to scavenger assemblages (Stahler et al., 2002; Wilmers et al., 2003a). Given that the function of food supply by wolves to scavenger assemblages is not alternated by carcasses providing from human hunters (Wilmers et al., 2003b; Wilmers and Getz, 2005), the wolf reintroduction would be more effective for restoring ecosystem processes than regulating ungulate populations. Thus, we stress that wolf reintroduction should be considered and discussed actively in Japan, especially on the purpose of restoring forest ecosystem processes that have degraded due to overbrowsing by sika deer.

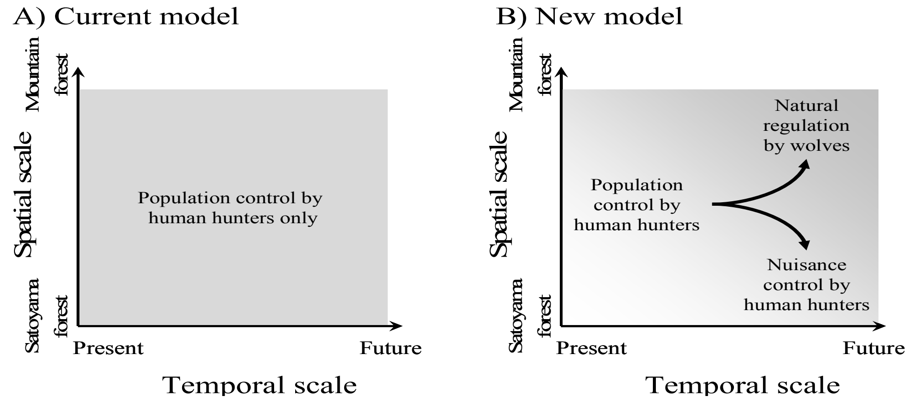

Figure 6. Conceptual model of wildlife management in Japan. A) Current policy completely depends on the human stewardship. However, Japan's shrinking society will inevitably lead to further shortages of manpower and budget for regional wildlife management, and inadequate sustainable conventional countermeasures based on human stewardship. B) Hence, we propose a future wildlife management model constructed of both natural regulation by translocated wolves and human stewardship by nuisance control. In this model, policy of the wildlife management policy changes spatio-temporally.

We should mention here the limitation of predation risk effect. The predation risk effects by reintroduced wolves would be more limited in human-modified areas than in mountainous forested areas due to the sensitivity of wolves and their avoidance to human-dominated environments such as settlements, agricultural land, highways and primary roads (Thurber et al., 1994; Ciucci et al., 2003; Theuerkauf et al., 2003; 2007; Kaartinen et al., 2005; Kusak et al., 2005; Theuerkauf, 2009). In Banff National Park, Canada, it was observed that a high level of human activities affected the predatory impact of wolves on prey ungulates, resulting in interrupting the restoration of potential ecosystem processes (i.e., trophic cascade effect on vegetation) and forest biodiversity (such as avian fauna and abundance of beaver, *Castor canadensis*) (Hebblewhite et al., 2005). In addition, deer tend to avoid habitats with high wolf density (i.e., high predation risk) and move to areas with lower predation risk (Mech, 1977; Laundre et al., 2001; Creel et al., 2005; Fortin et al., 2005; Mao et al., 2005). In Japan, it is found that highly mosaic landscape composed with forests, agricultural lands and human settlements, and there are many secondary forests adjacent to suburban areas with relatively high human population density. Moreover, the national parks of Japan are generally small (average: 7.2 km^2, range: 0.7–22.7 km^2) and some are urbanized and/or developed as leisure venues, because the purpose of the national parks is to preserve the scenery and promote its utilization in Japan. Hence, supposing that proposed area for wolf reintroduction in Japan covers both mountainous and suburban areas, it is highly likely that sika deer, as well as other herbivores, would escape to habitats surrounding suburban areas such as secondary forests and abandoned cultivated-lands in lowland after wolf reintroduction. Secondary forests in suburban areas are the part of the "*Satoyama*" ecosystem with relatively high biodiversity (Kato, 2001; Nakamura et al., 2006; Katoh et al., 2009) and some mammalian species such as sika deer have already negatively affected the biota and altered the ecosystem processes of *Satoyama* ecosystems (Takada et al., 2002; Suzuki, et al. 2008). The impacts of sika deer on *Satoyama* ecosystems might then become even more serious as their habitat shift from mountainous to suburban areas to avoid predation risk. Thus, population regulation of deer by human hunters would be required even after the reintroduction of wolves, especially in the suburban areas, because of less effectiveness of predation risk effects.

We must also pay attention to the fact that overabundant deer populations could not be regulated by wolf predation alone. The decrease in elk population in the Northern Range of YNP mainly resulted from both the severe winter during 1995–2004 and human harvest outside the park: the impact of wolf predation was a secondary effect (White and Garrot, 2005a; 2005b; Vucetich et al., 2005). Gorman (2007) also showed that translocated wolf predation is unlikely to have any significant impact on overabundant populations of red deer (*C. elaphus*) in Scotland and so would fail to decrease the deer population to the target density (5 deer/km^2). Those findings also support our proposal that both natural regulation and population control by human hunters is required for controlling the overabundant sika deer population in Japan.

In Japan, it would be insufficient to adopt a management policy similar to that used in YNP, which relies only on natural regulation by reintroduced wolves and completely excludes human stewardship (see Huff and Varley, 1999; Wagner, 2006). Hence, we propose here that a future wildlife management policy that changes in a spatio-temporal manner from reliance on human stewardship to a combination of both natural regulation by translocated wolves and human stewardship by nuisance control (Figure. 6–B). Whereas the role of population control is mainly suppression of prey populations, the reintroduction of wolves has three ecological functions: 1) both direct (i.e., predation) and indirect (i.e., predation risk) effects on prey populations; 2) maintenance of prey population at lower density by continuous predation pressure; and 3) restoration of various ecosystem functions and processes such as trophic cascading for native plant communities and food supply for scavenging assemblages. The management goal is to decrease the impact of overabundant mammalian species (mainly sika deer, wild boar, and Japanese macaque) on both natural ecosystem and human society; therefore, it needs primarily to control and maintain the population level of those animals at a lower density. For example, a suitable density level for the sika deer population which minimize the destructive impact on forest ecosystems, is generally 1–5 deer/km^2 in Japan (Uno et al., 2007). To achieve this goal, differences in effects between wolf predation and human harvest on prey populations and the planning of strategic nuisance control in temporal, spatial and age-specific should be considered.

1) Temporal strategy (Figure 7–A): In the first step, intensive harvest (or aggressive culling) should be conducted before reintroducing wolves for the following reasons: first, human harvest is likely to have a greater impact on the overabundant ungulate population than predation by wolves (e.g., White and Garrot, 2005a; 2005b; Vucetich et al., 2005; Evans et al., 2006); second, the intensive harvest was the only successful case, albeit briefly, means of decreasing an overabundant sika deer population (Yamamura et al., 2008); third, since suppression on mammalian populations by human harvest would decrease due to the depopulation and the aging of hunters in the near future (Figure 7–A), there is uncertainty and difficulty associated with maintaining intensive harvest over the long term. During this period, it is necessary to plan and prepare for the

reintroduction of wolves including consensus-building (see the next section). After intensive harvesting, wolf predation is an alternative to human harvest and the main suppression factor on prey populations, while human harvest should be consecutively maintained in human-modified landscapes (see below).

2) Spatial strategy (Figure 7–B): The predatory impact of translocated wolves would be weaker on prey populations inhabiting the regions adjacent to suburban areas such as secondary forests of *Satoyama*, similarly to the case of Banff National Park (Hebblewhite et al., 2005), since wolves generally avoid human-altered habitats, as mentioned above. Thus, human harvesting should be maintained (or enforced) in those regions after wolf reintroduction, and the purpose of human stewardship is mainly to decrease the damage to secondary forests or agricultural crops by wildlife.
3) Strategic targeting of age-specific class: Since wolves mainly prey on calves and aging individuals of prey ungulates in general (Mech and Peterson, 2003) and also in YNP (Smith et al., 2004; White and Garrot, 2005a; 2005b; Evans et al., 2006), culling of adults, especially on prime females, should be conducted. These age-different impacts between wolf predation and human harvests have drastically decreased elk population in YNP (White and Garrot, 2005a; 2005b; Vucetich et al., 2005).

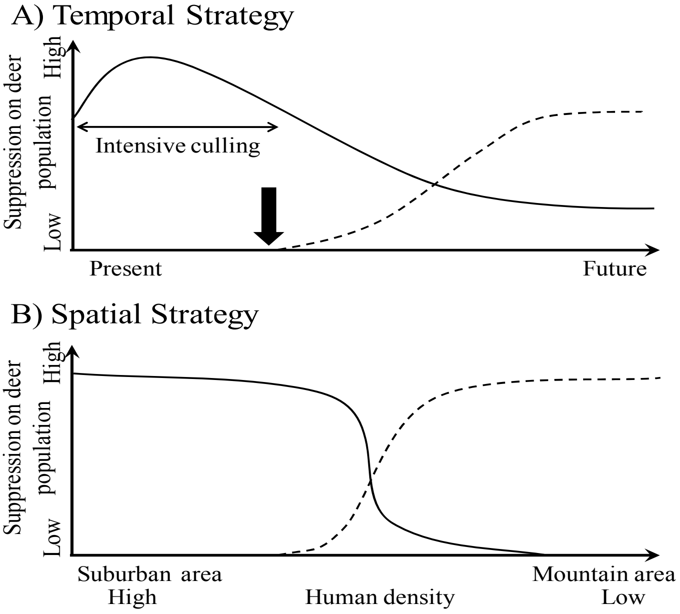

Figure 7. Conceptual model of strategic population control of sika deer. A) Temporal strategy: At first, intensive culling is necessary for decreasing the overabundant deer population, whereas wolf reintroduction is planned and prepared. After wolf reintroduction, wolf predation is an alternative to human harvests and the main suppression factor for prey populations, while human harvest should also be consecutively maintained. Solid arrow indicates the start of translocation of wolves. B) The predatory impact of wolves on prey populations would be weaker in suburban areas because wolves generally avoid human-altered habitats. Thus, human harvesting should be conducted mainly in regions adjacent to suburban areas for resolving urbanite-wildlife conflicts. The solid line is pressure from human harvesting and dotted line is pressure from wolf predation.

In this model, not only wolf reintroduction but also the maintaining a level of human harvest should be planed, including: increasing the hunter population, recruiting of young hunters and establishing a system for professional culling or sharpshooting (DeNicola et al., 1997; DeNicola and Williams, 2008). Human hunters/cullers also play an important role in controlling pest individuals of translocated wolves that rely on human garbage, prey on livestock or attack humans.

SOCIAL ISSUES OF WOLF REINTRODUCTION: ATTITUDES AND CONSENSUS-BUILDING

The subject of wolf reintroduction has not yet been discussed in Japan as a national issue; therefore, the consensus-building is required to achieve the reintroduction project. Two steps are involved in consensus-building: the first step is gaining national consensus on wolf reintroduction in Japan and the second step is obtaining the agreement of local residents and stakeholders in the proposed regions for the reintroduction project. Some reintroduction projects for large carnivore species had been eventually failed due to the lack of consensus-building among stakeholders (e.g., reintroduction of wolves in Minnesota, the U.S.; Decker et al., 2001). However, because people in Japan are generally negative toward wolf reintroduction, as are some ecologists, conservationists and administrators showed disapproval (e.g., Yoneda, 2006), consensus-building would be crucial in implementing the practice of the reintroduction project. One of Japan’s NGOs that advocates wolf reintroduction has conducted questionnaire surveys on the subject every five years since 1993. It reported that 12% to 28% of the respondents approved of wolf reintroduction (Angeli et al., 1998; Nambu, 2007). On the other hand, it also reported that 27% to 44% of the respondents disapproved (i.e., about twice the number of approvals) for the following reasons: negative impact on Japanese native species and/or ecosystems (confusing reintroducing wolves as an exotic species); absence of viable wolf habitats in Japan; and fear of wolf attacks on livestock or humans (Angeli et al., 1998; Knight, 2003).

Some of these views are related to Japanese citizens’ lack of accurate knowledge on wolf biology and misinterpretation of wolves as a pest mammal (as mentioned by Angeli et al., 1998). For example, the species of *Canis lupus* is native to Japan (Ohdachi et al., 2009) and its natural range included the Japanese archipelago (Nowak, 2003): the image of wolves as an exotic species is an apparent error. According to the “IUCN/SSC Guidelines For Re-Introductions” (IUCN, 1998) that suggests the reintroduction of subspecies, reintroduction of the species of “*Canis lupus*” in Japan becomes legal. In addition, Takahashi and Maruyama (1999) compared land cover and human density in the national parks of Japan to those of Poland, where large populations of wolves exist, and showed that ten of the 29 national parks in Japan are viable habitats for wolves.

Although wolf attacks on humans are usually rare (Linnell et al., 2002; 2003; Fritts et al., 2003), many of Japanese people are unduly afraid of wolf attacks. In general, such attacks occur under anomalous situations, such as in a habitat where prey is scarce (Jhala and Sharma, 1997) or where there are rabid wolves (Linnell et al., 2002; Fritts et al., 2003). Since prey ungulates are overabundant in Japan, the habitat situation is different from, for example, India where a child lifting by wolves were observed due to scarcity of prey (Jhala and Sharma, 1997). In addition, although rabies is one of the causes of a wolf attack (Linnell et al., 2002; Fritts et al., 2003), no case of rabies has been observed in Japan since 1957 (Tojinbara, 2003). Thus, it is expected that the risk of the wolf attack on humans is relatively low in Japan, compared to other countries.

Wolf depredation on livestock is another concern of respondents who disapprove of the wolf reintroduction. Since wolf depredation on livestock has been observed in every country where wolves and livestock are both present (Fritts et al., 2003) and has also observed in the GYE after the reintroduction project (Musiani et al., 2003), it could certainly occur in Japan as well. Both lethal (e.g., shooting or trapping) and nonlethal techniques (e.g., guard dog and "fladry[*]") have successful prevented wolf depredation (Fritts et al., 2003; Musiani et al., 2003). It is necessary to provide information about these techniques to the stakeholders such as ranchers, wildlife managers and administrators of local government in Japan. In addition, a compensation program for livestock loss by wolf depredation is indispensable for public acceptance (Van Tassell et al., 1999).

To solve the social issues related to consensus-building on wolf reintroduction, it is important to plan several effective approaches: education and enlightenment programs to provide accurate information on wolf biology for Japanese citizens and stakeholders; risk communication on wolf attacks on humans; introduction of prevention techniques for depredation on livestock; and design and preparation of a compensation system for depredation on livestock and attack on humans. Jacobson (2009) noted that enlightenment programs for opposition stakeholders resulted in the successful achievement of the YNP wolf reintroduction project.

CONCLUSIONS

Conservation and reintroduction of large carnivores for the purpose of restoring native ecosystem processes have become a paradigm in conservation biology, and wolf reintroduction has been discussed actively in Europe and the U.S. (Mech, 1995; 2001; Mladenloff and Sickley, 1998; Boitani, 2003; Musiani and Paquet, 2004; Wilson, 2004; Carol et al., 2006; Nilsen et al., 2007; Manning et al., 2009; Licht et al., 2010). In Japan, however, the results of the YNP wolf reintroduction project are not yet fully recognized and therefore many ecologists, conservationists, administrators and citizens are negative towards wolf reintroduction. As mentioned above, the potential effectiveness of wolf reintroduction could greatly help restore forest ecosystem processes and biodiversity in the shrinking society of future Japan. Thus, discussion on wolf reintroduction in Japan should be started as soon as possible, since we would face the "extinction" of Japanese hunters in the near future and the wolf reintroduction is a lengthy process.

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[*] Fladry: Flags are hung from ropes stretched a short distance above the ground. This technique has been traditionally used to hunt wolves in Eastern Europe (Okarma, 1993).

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