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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 gully, 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].

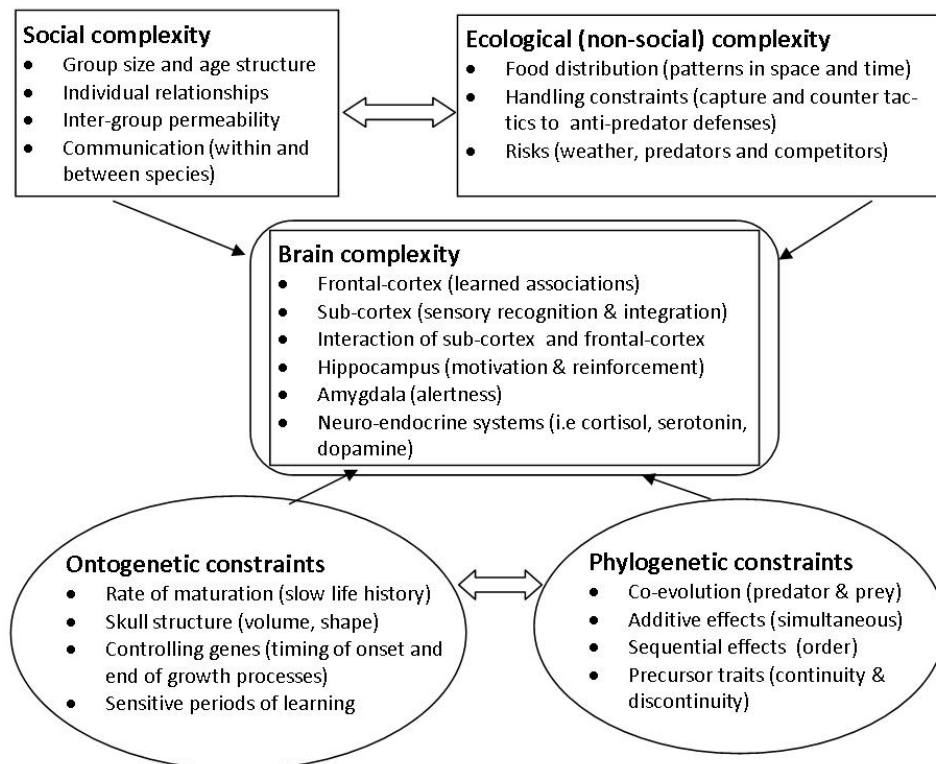


Figure 1. Larger theoretical framework for evolution of intelligence, integrating (a) environmental complexity (social and non-social) and (b) constraints (ontogenetic and phylogenetic, adapted from Holekamp 2006).

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. <i>Individual recognition</i> ; respond differently to sounds and/or smells that carry information about individual identity; distinguish "self" from "other"	<i>carnivores</i> : spotted hyenas [21], wolves [15,17,18], domestic dogs [148] <i>primates</i> [21]: cercopithecine monkeys (baboons, vervets) great apes
2. <i>Kin recognition</i> ; direct behavior differently toward kin and non-kin; helping at the den, permeability of groups to immigration	<i>carnivores</i> : spotted hyenas [21], coyotes [180], wolves [109]148] <i>primates</i> [21]: cercopithecine monkeys (baboons, vervets), great apes
3. <i>Rank acquisition and social memory</i> ; predictable social relations within a large group with mixed age-classes; modify behavior according to social context; affiliative and agonistic relationships	<i>carnivores</i> : spotted hyenas [21], gray wolves [106,142], domestic dogs [182-185] <i>primates</i> [21]: baboons, macaques, chimpanzee
4. <i>Application of knowledge about social rank</i> ; feeding at clumped sources; choice of mates; social competence; social expedience; solve social problems in diverse ways	<i>carnivores</i> : Spotted hyenas [21,186], gray wolves [142], coyotes [50], domestic dogs [2] <i>primates</i> [21]: great apes, monkeys
5. <i>Partner choice and relationship value (independent of kinship)</i> ; mate preferences influenced by rank, seniority, familiarity	<i>carnivores</i> : Spotted hyenas 21,186], gray wolves [142] <i>primates</i> [21]: great apes, monkeys
6. <i>Repair of damaged relationships</i> ; reconciliation; affiliation after conflict	<i>carnivores</i> : Spotted hyenas 21,186], gray wolves [142] <i>primates</i> [21]: great apes, monkeys
7. <i>Recognition of 3rd-party relationships</i> ; alliances, respond to mother when infant cries	<i>carnivores</i> : spotted hyenas [21,35], gray wolves [143,186] <i>primates</i> : great apes, vervet monkeys
8. <i>Learning in a social context</i> ; changes in behavior associated with observing other's actions/outcomes; social learning; social influence; cooperative problem solving; play; imitation; coordination; culture	<i>carnivores</i> : spotted hyenas [21,187], gray wolves [19], domestic dogs [2,58,126,188,189] <i>primates</i> [21]: great apes, cercopithecine monkeys
9. <i>Communication</i> ; transfer of information between actor and recipient; integration of information from sight, sound and smell; referential gaze or pointing	<i>carnivores</i> : spotted hyenas [21], gray wolves [66,96,190], domestic dogs [2,55,117,119,191] <i>primates</i> [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 references 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 bp) 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 (*Hyena 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 (<i>Canis spp</i>) ²	Wolf subspecies (<i>Canis lupus</i>) ³	Domestic dogs (<i>Canis familiaris</i>) 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 (<i>Canis lupus</i>) Eastern (<i>C. lycaon</i>) Red (<i>C. rufus</i>) Dingo dog (<i>C. familiaris</i>) Ethiopian (<i>C. simensis</i>) Coyote (<i>C. latrans</i>) Golden jackal (<i>C. aureus</i>)	Arctic (<i>C.l. arctos</i>) Mexican (<i>C.l. baileyi</i>) N. Rocky Mountain (<i>C.l. irremotus</i>) Eurasian (<i>C.l. lupus</i>) Gray (<i>C.l. lycaon</i>)	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 (<i>Canis spp</i>) ²	Wolf subspecies (<i>Canis lupus</i>) ³	Domestic dogs (<i>Canis familiaris</i>) 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, Sharpei, Akita, Dingo, etc. Arctic: malamute, husky, etc.	Toy, terrier, retrievers, scent hounds, sight hounds, mountain breeds, herding breeds, spaniels, working dogs, mastiffs, etc.

¹The 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).

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

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

⁴Sources (*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 (<i>unit</i>) received by another (<i>meaning</i>) in a context (<i>causal aspects</i>)	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	<i>Not specified (appears to include elements of c,h,f,j,k)</i>	
(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).

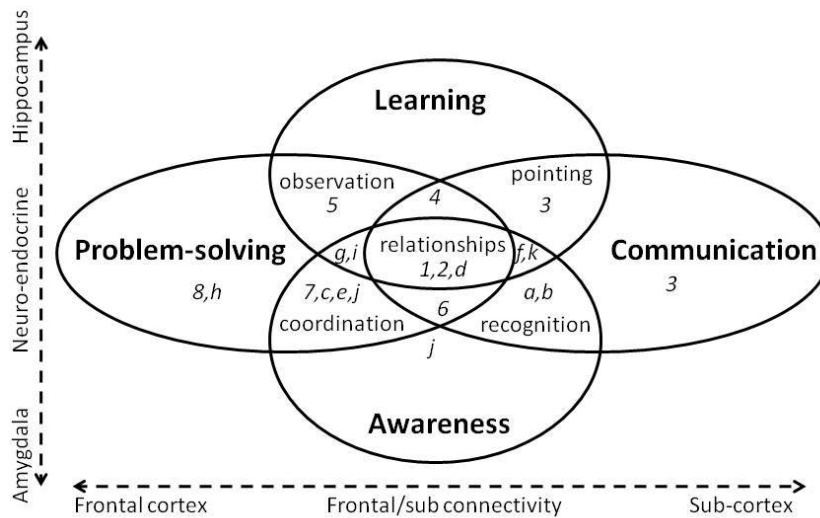


Figure 2. Conceptual map of social intelligence (see codes in Table 4) relative to two theoretical dimensions of brain complexity.

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) affiliative 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 unrelated wolves in a group are the older breeding pair; although they are likely to show close proximity and to receive affiliative 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 dingoes 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).

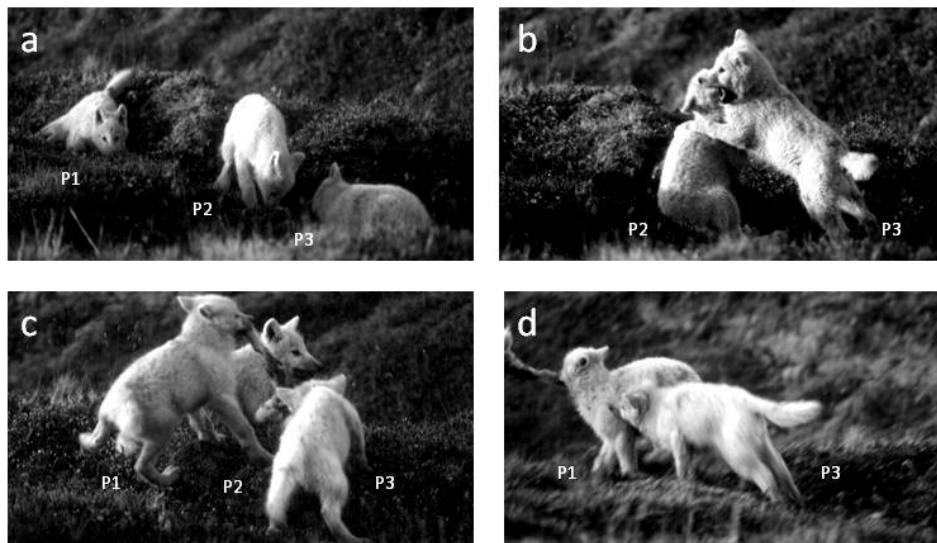


Figure 3. Sequence of interactions among wolf pups illustrate the social context in which pups learn the consequences of their actions.

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 consolars. 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 ($\geq 19\%$) [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 dilemmas 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, caregivers, 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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